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## REVIEW

How many genera of vascular plants are endemic to New Caledonia? A critical review based  
on phylogenetic evidence

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Running title: New Caledonian endemic genera

New Caledonia is a biodiversity hotspot located in the south-western Pacific, well known for its rich, unique and endangered flora. The island flora has a high level of endemism at the species level (75%), but also at the generic and family (three endemic) levels. We review here the taxonomic validity of the *c.* 100 endemic New Caledonian genera of vascular plants (13%) by using the monophyly criterion based on available phylogenetic data. As observed for other island floras, some of these genera were recovered nested in larger genera and are consequently likely to lose their rank. After a critical review, we concluded that the New Caledonian plant vascular flora contains between 62 and 91 endemic genera. This large variation in the number of endemic genera is mainly caused by a lack of DNA sequences (eight genera) and limited phylogenetic evidence. This work highlights gaps of knowledge that will have to be addressed to stabilize the taxonomy of the New Caledonian flora. Although this study shows that several genera are not monophyletic, New Caledonia still harbours more endemic genera than any other islands in the Pacific Ocean. Preliminary results indicate that the high level of endemism at higher taxonomic levels could be explained by an accumulation of relictual lineages, rather than adaptive radiations. Hypotheses explaining this phenomenon are provided in this study.

Keywords: adaptive radiation, biodiversity hotspots, biogeography, extinction, Pacific islands, relicts, ultramafic rocks.

*Endemics can be either relicts—“left behind,” or they can be autochthonous—evolving their distinguishing characteristics, which place them in distinct genera or families, after arrival on islands. The two processes are not always different. Relicts may change after they have become island residents.*

Sherwin Carlquist (1965: 305)

## INTRODUCTION

New Caledonia is well known for its rich and unique flora and is the smallest biodiversity hotspot listed by Myers *et al.* (2000). This archipelago, located in the southwestern Pacific, has an unusual geological history and does not have a volcanic origin like most Pacific islands. New Caledonia detached from Australia during the late Cretaceous (*c.* 80 million years ago; Pelletier, 2006). During its drift eastward, New Caledonia was submerged under deep water as suggested by sediments (Cluzel, Chiron & Courme, 1998; Picard, 1999). Geological evidence strongly supports the emergence of New Caledonia at the Eocene (*c.* 37 million years ago) when a portion of oceanic crust was deposited over the island (Cluzel *et al.*, 1998; Pelletier, 2006). Weathering subsequently produced the ultramafic substrates, which are home to a peculiar flora (Virost, 1956; Jaffré, 1980; Isnard *et al.*, 2016). Thus in spite of its continental origin, the submergence of New Caledonia implies that the island was entirely re-colonized by terrestrial life after its Eocene emergence and it therefore fits the ‘Darwinian’ island hypothesis (Grandcolas *et al.*, 2008) comparable to most Pacific islands.

New Caledonia is not only unique because of its species diversity and rate of endemism, but also because of its unique diversity of gymnosperms and early diverging angiosperms (Morat *et al.*, 2012), many of which qualify as relicts (Grandcolas, Nattier &

Trewick, 2014). The island harbours three endemic families and 98 endemic genera of vascular plants, a number much greater than most other Pacific islands (Morat *et al.*, 2012). Recent reviews have suggested that the number of endemic genera on islands may be over-estimated for many reasons (Garnock-Jones, 2014), but a common pattern is that an endemic genus may be nested in a more widespread genus (Buerki *et al.*, 2013; Stuessy, König & Sepulveda, 2014). There is no clear universal definition of what a genus is; however, there are a number of criteria that can be applied to circumscribe them (see, e.g., Garnock-Jones, 2014, for a review), including monophyly, ease of recognition (morphologically), minimizing redundancy and time of divergence. Although some of these criteria cannot be applied objectively and the delimitation of a genus may be considered as arbitrary, they may actually be in many cases higher evolutionary significant units (Barraclough & Humphreys, 2015).

In this review, we aimed to evaluate the status of all of the endemic New Caledonian genera of vascular plants based on available phylogenetic evidence. We mostly investigated whether each genus fulfils the most objective criterion to define genera: monophyly. We do not discuss here morphological distinctiveness for each genus except in a few cases where phylogenetic evidence is ambiguous. This synthesis should allow a more objective comparison of the flora of New Caledonia with that of other Pacific islands, for which this work has already been done (e.g. New Zealand; Garnock-Jones, 2014). Identifying the most distinctive endemic genera is also paramount for the conservation of phylogenetic diversity (Mace, Gittleman & Purvis, 2003; Buerki *et al.*, 2015). It has long been accepted that the flora of New Caledonia is composed of ancient elements and the offspring of recent migrants (Virot, 1956: 373; Carlquist, 1965: 42), but their classification requires more scrutiny because supposedly ancient groups such as New Caledonian *Araucaria* Juss. may be more recent than previously thought (Kranitz *et al.*, 2014). Thus, we hoped to gain evidence on the prevailing patterns of endemism in New Caledonia: an ancient species repository or a hot-bed of recent

radiation (*sensu* Verboom *et al.*, 2009). We also hope that this review will trigger further taxonomic work on the flora of New Caledonia by raising potential issues on generic delimitations and also encourage the inference of a generic level phylogeny for this unique flora.

## REVIEWING THE PHYLOGENETIC STATUS OF THE NEW CALEDONIAN ENDEMIC GENERA OF VASCULAR PLANTS

Endemic genera are shown in bold on first appearance. We follow here a linear sequence based on APG IV (2016) and consider all the endemic genera listed in Morat *et al.* (2012) and the few others described or re-instated after that publication. For non-monotypic genera, we indicated in parenthesis the number of species (a) included in the cited phylogenetic studies and the total number of species per genus (b) as follows: *genus* (a/b). Numbers of species in endemic genera are taken from Munzinger *et al.* (2016). All of the endemic genera formed a monophyletic clade in the cited phylogenetic studies unless otherwise stated.

### FERNS

#### Gleicheniaceae

The monotypic ***Stromatopteris*** Mettenius is the only genus of fern endemic to New Caledonia. In molecular phylogenetic analyses including all genera of Gleicheniaceae, *Stromatopteris* is recovered with strong support as sister to the Indo-Pacific *Gleichenia* Sm. (Pryer *et al.*, 2004; Lehtonen, 2011).

### GYMNOSPERMS

## Podocarpaceae

The monotypic *Parasitaxus* de Laub. is the only known parasitic gymnosperm and is involved in an original type of parasitism with another podocarp [*Falcatifolium taxoides* (Brongn. & Gris) de Laub., also endemic to New Caledonia] that may also involve a fungus partner (Feild & Brodribb, 2005). In a molecular phylogenetic analysis including all genera of Podocarpaceae, *Parasitaxus* forms a moderately supported clade with *Manoao* Molloy (New Zealand) and *Lagarostrobos* Quinn (Tasmania), both monotypic, although their exact relationships are unresolved. *Parasitaxus* may be sister to the other two taxa (Sinclair *et al.*, 2002). A close relationship between these three genera was confirmed by Lu *et al.* (2014), but their relationships are not resolved.

## Cupressaceae

Phylogenetic data have demonstrated that the monotypic *Neocallitropsis* Florin is nested in the Australian and New Caledonian *Callitris* Vent. (Pye, Gadek & Edwards, 2003). This lineage is the sister group to the New Caledonian *C. sulcata* Schltr. (*C. neocaledonica* Dümmer was not included). Consequently, the sole species, *N. pancheri* (Carrière) de Laub., was recently transferred to *Callitris* (Byng, 2015).

## Taxaceae

The monotypic *Austrotaxus* Compton is the only representative of its family in the Southern Hemisphere. In a phylogenetic framework including all the genera of the family, Cheng *et al.* (2000) found that this genus was sister to the rest of tribe Taxeae (*Taxus* L., *Pseudotaxus* W.C.Cheng, from Eurasia, Malesia and North America) with strong support. This latter relationship was confirmed by Lu *et al.* (2014).

## ANGIOSPERMS

### AMBORELLALES, Amborellaceae

*Amborella* Baill. (monotypic) is now usually accepted as the sister lineage to all angiosperms (Qiu *et al.*, 1999; Soltis *et al.*, 2011), although a few analyses have recovered Nymphaeales as its sister group (e.g. Goremykin *et al.*, 2003). *Amborella trichopoda* Baill. is the first New Caledonian endemic plant to have had its genome entirely sequenced (Amborella Genome Project, 2013).

## MAGNOLIIDS

### LAURALES

#### Atherospermataceae

In a phylogenetic analysis including all genera of Atherospermataceae, the monotypic *Nemuaron* Baill. is recovered as sister to the Australian monotypic *Atherosperma* Labill. (Renner, Foreman & Murray, 2000).

#### Monimiaceae

Renner *et al.* (2010) recovered the monotypic *Kibaropsis* Vieill. ex Jérémie in clade III, which also includes the Oceanian *Levieria* Becc. and *Hedycarya* J.R.Forst. & G.Forst. Support in this clade is moderate, but *Hedycarya* appears polyphyletic, with *Kibaropsis* and *Levieria* nested inside it. *Kibaropsis* seems closer to the New Zealand *H. arborea* J.R.Forst. &



G.Forst. (bootstrap 65%) rather than the New Caledonian *H. cupulata* Baill. Generic delimitation in this group requires further investigations.

#### Lauraceae

*Adenodaphne* S.Moore (1/4) has been recovered as the sister group to two species of *Litsea* Lam. from Japan and China with moderate support (Chanderbali, van der Werff & Renner, 2001). Delimitation in *Litsea* (c. 400 species) and its allied genera requires clarifications (e.g. Fijridiyanto & Murakami, 2009). Since morphological confusions are possible between *Adenodaphne* and *Litsea*, also present in New Caledonia (Kostermans, 1974), their distinctiveness needs to be critically assessed.

#### MONOCOTS

##### LILIALES, Campynemataceae

Campynemataceae comprise only two genera, the Tasmanian monotypic *Campynema* Labill. and the New Caledonian *Campynemanthe* Baill. (1/3) that have been recovered as sister groups in phylogenetic analyses (Vinnersten & Bremer, 2001; Mennes *et al.*, 2015).

##### ASPARAGALES, Orchidaceae

The exact placement of some of the endemic genera (all terrestrial) is still somewhat uncertain, mostly because a number of related genera in this diverse family have not yet been included in any molecular phylogenetic analysis. This is particularly true for subtribe Goodyerinae (Chase *et al.*, 2015). *Clematepistephium* N.Hallé and *Eriaxis* Rchb.f. (both monotypic, tribe Vanilleae) are sister groups and together seem to be sister to the East Asian-New Guinean *Lecanorchis* Blume (Cameron, 2009). *Pachyplectron* Schltr. (1/3), has been

recovered as sister to the rest of tribe Goodyerinae (Alvarez-Molina & Cameron, 2009).

*Gonatostylis* Schltr. (1/2) seems to be sister to *Odontochilus* Blume (synonym *Pristiglottis* Cretz. & J.J.Sm.; Alvarez-Molina & Cameron, 2009), although the sampling of genera of Goodyerinae and *Odontochilus* spp. is limited in this study. The latter genus is found in Asia and the Pacific, including New Caledonia. *Gonatostylis* is also morphologically similar to the mycotrophic *Danhatchia* Garay & Christenson (Ormerod & Cribb, 2003) from New Zealand and Australia, which has never been included in any molecular phylogenetic studies.

*Achlydosa* M.AClem. & D.L.Jones (monotypic) has been found to be sister to the Australasian *Pterostylis* R.Br. (Cisternas *et al.*, 2012), the sole other member of subtribe Pterostylidinae (Chase *et al.*, 2015), also present in New Caledonia. *Coilochilus* Schltr. (monotypic) is sister to *Cryptostylis* R.Br. (Kores *et al.*, 2001), the sole other member of subtribe Cryptostylidinae (Chase *et al.*, 2015) from South-east Asia and the Pacific, including New Caledonia.

#### ARECALES, Arecaceae

The taxonomic updates by Pintaud & Baker (2008), associated with a complete generic-level phylogenetic analysis of the family (Baker *et al.*, 2009), resulted in a significant decrease in the number of palm genera in New Caledonia, placing in synonymy six endemic genera. More recently, *Pritchardiopsis* Becc. (monotypic) was placed in synonymy with *Saribus* Blume (Bacon & Baker, 2011; Bacon, Baker & Simmons, 2012), that occurs in South-east Asia and the Pacific. There are currently eight endemic palm genera recognized in New Caledonia, all members of tribe Areceae. Subtribe Clinospermatinae are endemic to New Caledonia and is composed of *Clinosperma* Becc. (4/4) and *Cyphokentia* Brongn (2/2). The study by Baker *et al.* (2011), including all of the species of Areceae, confirmed that the two genera are reciprocally monophyletic. Subtribe Archontophoenicinae include *Actinokentia* Dammer

(2/2), *Chambeyronia* Vieill. (2/2) and *Kentiopsis* Brongn. (4/4), the Australian *Archontophoenix* H.Wendl. & Drude, and the Papuan *Actinorhytis* H.Wendl. & Drude, but relationships and generic delimitations between the three New Caledonian genera and *Archontophoenix* remain unclear, including the monophyly of *Chambeyronia* and *Kentiopsis* (Domenech *et al.*, 2014). *Basselinia* Vieill. (3/14), *Burretiokentia* Pic.Serm. (2/5) and *Cyphophoenix* H.Wendl. ex Benth. & Hook.f (3/4) are placed in subtribe Basseliniinae. The phylogenetic study by Baker *et al.* (2011) suggested that *Cyphophoenix nucele* H.E.Moore could be sister to *Burretiokentia*, whereas two other *Cyphophoenix* spp, form a clade sister to the Melanesian genus *Physokentia* Becc. This study also indicates that three *Basselinia* spp. and the Lord Howe Island endemic *Hedyscepe* H.Wendl. & Drude form a polytomy, although *Hedyscepe* has been assigned to a different subtribe, Rhopalostylidinae. Further work is needed to clarify the taxonomic circumscriptions of the genera in subtribes Archontophoenicinae and Basseliniinae.

#### POALES, Poaceae

The dwarf bamboo *Greslania* Balansa (2/3) has been recovered with strong support as sister to an Australasian clade composed of *Cyrtochloa* S.Dransf., *Dinochloa* Buse, *Mullerochloa* K.M.Wong, *Neololeba* Widjaja, *Parabambusa* Widjaja, *Pinga* Widjaja and *Sphaerobambos* S.Dransf. (Chokthaweeapanich, 2014).

#### EUDICOTS

#### PROTEALES, Proteaceae

In a molecular phylogenetic tree including all genera of Proteaceae (Sauquet *et al.*, 2009), *Beaupreopsis* Virost (monotypic) formed a strongly supported clade with the Tasmanian genus

*Cenarrhenes* Labill. (monotypic) and the Malagasy genus *Dilobeia* Thou. (two species), and the last two are moderately supported as sister groups. *Beauprea* Brongn. & Gris (9/13) is monophyletic (He, Lamont & Fogliani, 2016) and is strongly supported as the sister lineage to tribe Proteeae (*Protea* L. and *Faurea* Harv. from Africa; Sauquet *et al.*, 2009). The two species of New Caledonian *Knightia* R.Br. are not related to the type species of this genus from New Zealand and are instead placed in an endemic genus *Eucarpha* (R.Br.) Spach (1/2) by Weston & Barker (2006), although the nomenclatural combinations have never been published. *Eucarpha* is strongly supported as the sister group to the eastern Australian *Triunia* L.A.S.Johnson & B.G.Briggs (Sauquet *et al.*, 2009). *Kermadecia* Brongn. & Gris (3/4) and *Sleumerodendron* Viot (monotypic) are part of a well-supported subtribe Gevuiniinae (Mast *et al.*, 2008) in which they form a well-supported clade with *Turrillia* A.C.Sm. (1/3, Fiji, Vanuatu). There is a weak support for a sister relationship between *Turrillia* and *Kermadecia*, which are in turn sister to *Sleumerodendron* (Mast *et al.*, 2008). The species of these three morphologically close genera (Viot, 1967; Smith & Haas, 1975) were all once placed in *Kermadecia* and further evidence for their reciprocal monophyly is desirable. *Virotia* L.A.S.Johnson & B.G.Briggs (2/6) is part of subtribe Virotiinae (Mast *et al.*, 2008) with *Athertonia* L.A.S.Johnson & B.G.Briggs (Queensland) and *Helicopsis* Sleumer (Indo-Malesia); their relationships are unresolved. *Garnieria* Brongn. & Gris (monotypic) is nested in the larger Australian genus *Persoonia* Michx. with the New Zealand endemic *Toronia* L.A.S.Johnson & B.G.Briggs and the south-western Australian *Acidonia* L.A.S.Johnson & B.G.Briggs (Weston & Porter, unpub. data, cited in Weston & Barker, 2006).

ROSIDS

FABALES

## Fabaceae

Egan *et al.* (2016) found that *Arthroclianthus* Baill. (2/19) and *Nephrodesmus* Schindl. (2/5) were sister groups and reciprocally monophyletic in tribe Desmodieae.

## Polygalaceae

*Balgoya* Morat & Meijden (monotypic) is generally placed in tribe Moutabeae and the study of Persson (2001), which included only a short *trnL* sequence for this genus, failed to resolve its phylogenetic position in the family or to confirm its placement in this tribe.

## ROSALES

### Rhamnaceae

The recently described *Jaffrea* H.C.Hopkins & Pillon (2/2, Hopkins *et al.*, 2015a) is sister to *Emmenosperma* F.Muell. (occurring in Malesia, Australia, New Caledonia and Fiji).

### Moraceae

In a molecular phylogenetic analysis including 32 of 37 genera of Moraceae, Zerega *et al.* (2005) found strong support for a sister relationship between the New Caledonian endemic *Sparattosyce* Bureau (1/2) and the New Guinean *Antiaropsis* K.Schum (two species).

### FAGALES, Myricaceae

In a molecular phylogenetic analysis including all genera of Myricaceae, Herbert *et al.* (2006) found strong support for a placement of *Canacomyrica* Guillaumin (monotypic) as the sister group to the rest of this widespread family.

#### CELASTRALES, Celastraceae

In a phylogenetic study including all genera of tribe Celastreae (Simmons *et al.*, 2008), *Salaciopsis* Baker f. (3/6) occupies an unresolved position between several multigeneric clades. *Menepetalum* Loes. (2/4) is sister to *Dinghousia* R.H.Archer from Queensland and *Dicarpellum* (Loes.) A.C.Sm. (2/4) is sister to *Hypsophila* F.Muell., also from Queensland (Coughenour *et al.*, 2010; Simmons *et al.*, 2012b). *Peripterygia* Loes. (monotypic) forms a weakly supported clade with the Australasian *Siphonodon* Griff. and *Crossopetalum* P.Browne (West Indies, Africa), but their exact relationships are unresolved (Simmons *et al.*, 2012a).

#### OXALIDALES, Cunoniaceae

In a phylogenetic study including all but two genera of Cunoniaceae, *Codia* J.R.Forst. & G.Forst. is recovered with strong support as the sister group to the Australian *Callicoma* Andrews (Hopkins, Rozefelds & Pillon, 2013) and is probably monophyletic (15/15, Pillon *et al.*, 2009a; Pillon pers. obs.). The phylogenetic position of *Hooglandia* McPherson & Lowry (monotypic) is unresolved somewhere among the early branches of the phylogenetic tree for Cunoniaceae (Sweeney, Bradford & Lowry, 2004; Hopkins *et al.*, 2013; Hopkins, Pillon & Hoogland, 2014). The latter genus has some morphological affinities with *Aistopetalum* Schltr. (McPherson & Lowry, 2004; H.C. Hopkins, pers. comm.), a genus of two species occurring in New Guinea that has not yet been included in any molecular phylogenetic study. *Pancheria* Brongn. & Gris (3/27) is placed in tribe Cunonieae and its relationship to *Cunonia*

L. (New Caledonia, southern Africa) and *Weinmannia* L. (pantropical) is unclear, although it might be sister to both (Bradford, 2002).

## MALPIGHIALES

### Clusiaceae

In a phylogenetic study including all but one genus of Clusiaceae, Ruhfel *et al.* (2011) recovered *Montrouziera* Pancher ex Planch. & Triana (2/6) as sister group to the South American *Platonia* Raf. with low support.

### Salicaceae

In a phylogenetic study of former Flacourtiaceae (Alford, 2005), *Lasiochlamys* Pax & K.Hoffm. (1/11) was found to be nested in *Xylosma* G.Forst. (America, Asia and Pacific). However, because the single species sampled, *L. reticulata* Pax & K.Hoffm., was sister to a *Xylosma* sp. from New Caledonia (*X. vincentii* Guillaumin), the author thought there might be a possible misidentification or a possible plastid capture confounding the phylogenetic signal. *Lasiochlamys* differs from *Xylosma* in having petals (Lescot, 1980), but otherwise the two genera are similar and the presence/absence of petals has been shown to be highly homoplasious in this family (Alford, 2005).

### Euphorbiaceae

In the analysis of Horn *et al.* (2012) including all the genera of tribe Euphorbieae, the monotypic *Neoguillauminia* Croizat is sister to the Australian *Calycopeplus* Planch. (five species) and these two genera are in turn sister to the large genus *Euphorbia* L. In the study of Tokuoka (2007), *Cocconerion* Baill. (1/2) is sister to *Baloghia* Endl. (Australia, New

Caledonia, Norfolk and Lord Howe Islands). The distinction between the two genera may warrant further investigations. *Bocquillonia* Baill. (1/14) is nested with strong support in the pantropical *Alchornea* Sw. (Wurdack, Hoffmann & Chase, 2005), although the latter study included a single species of *Bocquillonia* and two of *Alchornea*. Webster (1994) thought that most genera of subtribe Alchorneinae are only weakly separated from *Alchornea*. *Myricanthe* Airy Shaw (monotypic) has never been included in any molecular phylogenetic study and was classified as a close relative to *Cocconerion*, the Australian *Bertya* Planch. and the Bornean endemic *Borneodendron* Airy Shaw based on morphological similarities (Webster, 1994).

#### Picrodendraceae

In the analysis of Tokuoka & Tobe (2006) including only four genera of Picrodendraceae (out of c. 24), *Scagea* McPherson (1/2) is sister to the rest of the family. *Longetia* Baill. (monotypic) has not yet been included in any molecular phylogenetic studies.

#### MYRTALES, Myrtaceae

*Carpolepis* (J.W.Dawson) J.W.Dawson (3/3) is nested in *Metrosideros* Banks ex Gaertn. (Wright *et al.*, 2000; Pillon *et al.*, 2015), a genus widespread across the Pacific Islands (including New Caledonia), of which it is now considered a synonym (Pillon *et al.*, 2015). *Cloezia* Brongn. & Gris (1/6) is placed with strong support with tribe Tristanieae (Australasia, Biffin *et al.*, 2010), although its exact sister group has not been identified, but it may be sister to the entire tribe. In the analysis by Snow *et al.* (2011), *Kanakomyrtus* N.Snow (3/6, tribe Myrteae) is polyphyletic with its species mixed with those of the genera *Rhodomirtus* (DC.) Rchb. (South-east Asia and Pacific), *Pilidiostigma* Burret (Australasia) and *Octamirtus* Diels (Malesia). The monotypic *Myrtastrum* Burret is part of the “Australasian group” of Myrteae and is the earliest diverging lineage in this clade (T.N.C. Vasconcelos, pers. comm.).



*Arillastrum* Pancher ex Baill. (monotypic) is well supported as sister to *Corymbia* K.D.Hill & L.A.S.Johnson + *Angophora* Cav. in Eucalypteae (Australasia) (Thornhill *et al.*, 2015). Tribe Xanthostemoneae is composed of three genera all represented in New Caledonia [*Pleurocayptus* Brongn. & Gris (two species), *Purpureostemon* Gugerli (monotypic) and the much larger *Xanthostemon* F.Muell. (also Australia, New Guinea, Philippines, eastern Indonesia and Solomon Islands)]. The first two have never been included in any molecular phylogenetic analysis and morphological data suggest that *Pleurocalyptus* could be nested in *Xanthostemon* (Wilson, 2011).

#### CROSSOSOMATALES, Strasburgeriaceae

The monospecific genus *Strasburgeria* Baill., once considered the sole member of Strasburgeriaceae, has been recovered as sister to the New Zealand endemic *Ixerba* A.Cunn. (Cameron, 2003) in the poorly known order Crossossomatales.

#### SAPINDALES

##### Sapindaceae

Sapindaceae are highly diverse in New Caledonia with four endemic genera: *Gongrodiscus* Radlk. (3/3), *Loxodiscus* Hook.f. (monotypic), *Podonephelium* Baill. (7/9), and *Storthocalyx* Radlk. (4/5). Buerki *et al.* (2012) have formally tested the monophyly and phylogenetic relationships of these endemic genera by including representatives into a generic level phylogenetic analysis of Sapindaceae (Buerki *et al.*, 2009). This study confirmed the monophyly of all the endemic genera, which belong to two different phylogenetic lineages: the *Cupania* L. group (Sapindoideae) and the *Dodonaea* Mill. group (Dodonaeoideae). In the *Cupania* group, *Gongrodiscus* and *Storthocalyx* were inferred as closely related together with

one species of the polyphyletic genus *Sarcotoechia* Radlk. from Australia; however, this relationship has to be clarified by sampling more DNA regions. *Podonephelium* belongs to another clade in the *Cupania* group and is sister to the widely distributed genus *Alectryon* Gaertn. (Malesia, Australia, New Caledonia, New Zealand and Hawaii). In the *Dodonaea* group, the monotypic *Loxodiscus* is supported as sister to a clade comprising *Harpullia* Roxb. (India, south-eastern China, Malesia to Australia, New Caledonia and Pacific Islands), *Cossinia* Comm. ex Lam. (Mascarenes, New Caledonia, eastern Australia, Fiji), *Diplopeltis* Endl. (north-western Australia) and *Dodonaea* (mainly in Australia, Malesia, New Guinea, Caribbean and Madagascar).

#### Rutaceae

Appelhans *et al.* (2014) found that *Comptonella* Baker f. (4/8), *Dutaillyea* Baill. (1/2) and *Picrella* Baill. (2/3) were nested in the larger and more widespread *Melicope* J.R.Forst. & G.Forst. (South-east Asia and Pacific), being close to the New Caledonian members of this genus. The authors suggested that *Duttaillioopsis* T.G.Hartley (monotypic) may also be nested in *Melicope*, although it has not been included in any molecular phylogenetic studies.

*Oxanthera* Montrouz. (2/5) is nested in the large genus *Citrus* L. (Bayer *et al.*, 2009).

*Boronella* Baill. (2/4) is nested in the Australian *Boronia* Sm. (Bayly *et al.*, 2013) and its species have now been transferred into this genus (Bayly *et al.*, 2015). *Crossosperma*

T.G.Hartley (1/2) has been recovered with strong support as sister to the Australian *Acradenia* Kippist (both species included). The relationship between *Myrtopsis* O.Hoffm. (2/8) and a number of Australian genera placed in tribe Boronieae, some of medium size [*Leionema* (F.Muell.) Paul G.Wilson, *Phebalium* Vent., *Philotheca* Rudge], are unresolved.

*Neoschmidia* T.G.Hartley (1/2) is recovered as sister to a diverse clade of Australasian genera including *Halfordia* F.Muell. and *Myrtopsis* (Bayly *et al.*, 2013).

## MALVALES

### Malvaceae

In a phylogenetic study including all the genera of subfamily Sterculioideae, Wilkie *et al.* (2006) recovered *Acropogon* Schltr. (2/25) as a member of the moderately supported *Brachychiton* Schott & Endl. clade. The relationships between *Acropogon*, *Brachychiton* (Australia-New Guinea), *Argyrodendron* (Endl.) Klotzsch (Australia) and *Franciscodendron* B.Hyland & Steenis (Australia) are unresolved. In a phylogenetic study including all eight genera of tribe Lasiopetaleae (Whitlock *et al.*, 2011), *Maxwellia* Baill. (monotypic) formed a strongly supported clade with *Hannafordia* F.Muell. (Australia) and a group of four genera (*Thomasia* J.Gay, *Lysiosepalum* F.Muell., *Lysiopetalum* K.Schum., *Guichenotia* J.Gay; all Australian), but their exact relationships are unresolved.

### Thymelaeaceae

The phylogenetic relationships of *Deltaria* Steenis (monotypic) and *Solmsia* Baill. (1/2) with the genera *Lethedon* Spreng. (New Caledonia, Australia), *Gonystylus* Teijsm. & Binn. (South-east Asia) and *Arnhemia* Airy Shaw (Australia) in subfamily Gonystyloideae are unresolved (Beaumont *et al.*, 2009).

## SANTALALES

### Balanophoraceae

In a phylogenetic study of Balanophoraceae, *Hachettea* Baill. (monotypic) was recovered as sister to the New Zealand endemic *Dactylanthus* Hook.f. (Su *et al.*, 2015).

## Santalaceae

In a phylogenetic analysis including all of the accepted genera of Santalaceae (Der & Nickrent, 2008), *Amphorogyne* Stauffer & Hurlim. (1/3) and *Daenikera* Hurlim. & Stauffer (monotypic) are retrieved as sister and inferred as sister to the rest of tribe Amphorogyneae. *Elaphanthera* N.Hallé (monotypic) was considered as a synonym of *Exocarpos* Labill. (South-east Asia and Pacific) by Der & Nickrent (2008), but the single species of this genus has not yet been included in a molecular phylogenetic framework.

## ASTERIDS

## ERICALES

## Sapotaceae

Since the earliest monograph was published (Aubréville, 1967), New Caledonian Sapotaceae have been the subject of major generic rearrangements over the past few years (Bartish *et al.*, 2005; Swenson *et al.*, 2008; Swenson, Nylander & Munzinger, 2013) and several genera once considered as endemic to New Caledonia have been placed in synonymy (*Corbassona* Aubrév., *Leptostylis* Benth., *Ochrothallus* Pierre ex Baill., *Pyriluma* Aubrév., *Sebertia* Pierre ex Engl. and *Trouettia* Pierre ex Baill.) or now include species from outside New Caledonia (*Pichonia* Pierre). The expanded *Pycnandra* Benth. has emerged as the largest endemic genus of New Caledonia with 59 described species. It is sister to the Australian *Niemeyera* F.Muell. (Swenson *et al.*, 2013) and a study including 60 of 68 presumed species (some undescribed) indicated that it is monophyletic (Swenson *et al.*, 2015).

## Primulaceae

The recently described monotypic genus *Mangenotiella* M.Schmid (Schmid, 2012) has not yet been included in any phylogenetic study. There has been little phylogenetic work on woody Primulaceae (but see Strijk *et al.*, 2014), and *Mangenotiella* needs to be critically compared with *Tapeinosperma* Hook.f. (also present in New Caledonia) and *Discocalyx* Mez (South-east Asia to Pacific), the distinctness of which has been questioned (e.g. Smith, 1973).

## Ericaceae

The phylogenetic relationships between *Cyathopsis* Brongn. & Gris (1/3) and a number of other genera of the Styphelieae are unresolved (Quinn *et al.*, 2005; Puente-Lelièvre *et al.*, 2015), although an analysis based on the nuclear ITS region alone suggests a weakly supported sister relationship with the Australian *Lissanthe* R.Br.

## ICACINALES, Oncothecaceae

*Oncotheca* Baill. (1/2) is the only genus of Oncothecaceae. Oncothecaceae were not placed in any order in APG III (2009), because most phylogenetic studies had failed to clarify an exact position in lamiids (Bremer *et al.*, 2002; Cameron, 2003; González *et al.*, 2007; Soltis *et al.*, 2011; Byng *et al.*, 2014). A recent study using complete plastid genomes recovered this genus as sister to a narrowly defined Icacinaeae (Stull *et al.*, 2015) and it was placed in Icacinales in APG IV (2016) to reflect this finding.

## GENTIANALES

### Rubiaceae

*Morierina* Vieill. (2/2) and *Thiollierea* Montrouz. (12/12, previously included under *Bikkia*

Reinw., but reinstated by Barrabé *et al.*, 2011), form a well-supported clade, sister to an alliance of several Caribbean genera mainly occurring in Cuba with high support (*Ceratopyxis* Hook.f., *Eosanthe* Urb., *Phialanthus* Griseb. and *Schmidtottia* Urb.; Manns & Bremer, 2010). Although Manns & Bremer (2010) placed *Morierina montana* Vieill. as sister to two *Thiollierea* spp., uncertainties remain about the internal topology of the ‘*Morierina-Thiollierea*’ clade since an unpublished study, based on a complete species sampling and five DNA loci, has shown unresolved interspecific and intergeneric relationships (Mouly, pers. comm.). *Guettarda* L. has been revealed to be polyphyletic (Achille *et al.*, 2006). Of the 20 New Caledonian species, only the type species *G. speciosa* L. belongs to *Guettarda* s.s. The other species should be included in *Antirhea* Juss., *Guettardella* Benth., *Timonius* DC., *Tinadendron* Achille and a new endemic genus, ***Gea*** Achille ined. (2/6). Robust morphological characters support the last genus, composed of six species (Achille, pers. comm.), although this genus is unpublished and its monophyly has not been demonstrated. The monotypic *Normandia* Hook.f. was found to be nested in *Coprosma* J.R.Forst. & G.Forst. (Anderson, Rova & Andersson, 2001), but this study was based on an incorrect DNA sequence (Markey, Lord & Orlovich, 2004). Recently, *Normandia* has been excluded from this genus with strong support and placed as the possible sister-group of the large alliance formed by *Coprosma* and *Nertera* Gaertn. (Markey *et al.*, 2004; Cantley *et al.*, 2014).

#### Apocynaceae

In the analysis of Potgieter & Albert (2001), *Cerberiopsis* Vieill. ex Pancher & Sebert (1/3) is strongly supported as sister to *Cerbera* L. (Indian Ocean, Australasia, Pacific). Livshultz *et al.* (2007) found *Artia* Guillaumin (1/4) to be sister to the Australasian *Parsonsia* R.Br. noting the similarities between the two genera and acknowledging that only a few *Parsonsia* spp. were included in the phylogenetic analysis. The two genera are in turn nested in the

Neotropical *Prestonia* R.Br. Therefore, generic delimitations need to be further evaluated in this group. *Artia* was not considered as an endemic genus in Morat *et al.* (2012), but this was an error.

#### LAMIALES, Gesneriaceae

In a phylogenetic analysis including all of the genera of tribe Coronanthereae, Woo *et al.* (2011) found that *Depanthus* S.Moore (1/2) was either sister to the Australian *Lenbrassia* G.W.Gillett or to the Lord Howe island endemic *Negria* F.Muell.

#### AQUIFOLIALES, Stemonuraceae

*Gastrolepis* Tiegh. (two species) has not yet been included in any molecular phylogenetic analysis.

#### ASTERALES

##### Alseuosmiaceae

In a phylogenetic analysis published by Lundberg & Bremer (2003) *Platyspermatium* Guillaumin (monotypic) was inferred as sister to the rest of the family (four out of five genera included). *Periomphale* Baill. (monotypic) was once synonymized with *Wittsteinia* F.Muell., a view latter rejected by Tirel & Jérémie (1996). Unpublished phylogenetic analyses support the latter conclusion (A. Mouly, pers. comm.).

##### Phellinaceae

*Phelline* Labill. (3/14) is the only genus of Phellinaceae, which form a clade with Alseuosmiaceae and Argophyllaceae in Asterales (Kårehed *et al.*, 1999). The relationships

between these three small and poorly known families are unclear. Phellinaceae were placed with strong support as sister to Argophyllaceae in the analysis of Tank & Donoghue (2010), but in the analysis of Soltis *et al.* (2011) including more DNA regions, they were placed as sister to a weakly supported clade including Alseuosmiaceae and Argophyllaceae.

#### PARACRYPHIALES, Paracryphiaceae

*Paracryphia* Baker f. (monotypic) was once considered as the sole member of Paracryphiaceae, which has been expanded to include *Sphenostemon* Baill. and *Quintinia* A.DC. (APG III, 2009). There is strong support for a sister-group relationship between *Paracryphia* and *Sphenostemon* from Australia, New Guinea and New Caledonia (Tank & Donoghue, 2010; Soltis *et al.*, 2011).

#### APIALES

##### Myodocarpaceae

Myodocarpaceae have a centre of diversity in New Caledonia and include only two genera, which are reciprocally monophyletic (Nicolas & Plunkett, 2009): the endemic New Caledonian *Myodocarpus* Brongn. & Gris (4/10) and *Delarbrea* Vieill. (Malesia to New Caledonia).

##### Apiaceae

In a phylogenetic study including 40 of the 42 genera previously placed in subfamily Hydrocotyloideae, Nicolas & Plunkett (2009) found that *Apiopetalum* Baill. (2/2) was sister to *Actinotus* Labill. (Australasian) in the newly circumscribed subfamily Mackinlayoideae.



## DISCUSSION

How many endemic genera of vascular plants occur in New Caledonia?

Current phylogenetic evidence suggests that the monophyly of 30 New Caledonian endemic genera still needs to be confirmed or has been challenged (Table 1) and eight are clearly nested in larger, more widespread genera; some have been synonymized since Morat *et al.* (2012). In most problematic cases, the endemic genera are nested in a larger more widespread genus (e.g. *Neocallitropsis* nested in *Callitris*, and *Comptonella*, *Dutaillyea* and *Picrella* in *Melicope*) or their distinction from such genera needs further testing (e.g. *Lasiochlamys* vs. *Xylosma*, *Kibaropsis* vs. *Hedycarya*). This latter situation mirrors previous results obtained from the New Zealand flora (Garnock-Jones, 2014) and matches the expectations of Stuessy *et al.* (2014). In several cases, the evidence that an endemic genus is nested in a larger one has been known for a long time (e.g. *Oxanthera* nested in *Citrus*), but the synonymy and the necessary taxonomic changes are still pending. There are currently few cases of endemic genera that are polyphyletic (the recently described *Kanakomyrtus* and potentially *Chambeyronia* and *Kentiopsis*). Although many species in endemic genera are yet to be included in phylogenetic studies to confirm monophyly, the small size of most endemic genera makes polyphyly unlikely. In a few cases, some endemic genera may be better merged, although further evidence may still be required (e.g. *Thiollierea/Morierina*, *Chambeyronia/Actinokentia/Kentiopsis*, *Kermadecia/Sleumerodendron*). The distinctiveness and monophyly of eight genera remain to be evaluated by molecular analyses.

The flora of New Caledonia is still incompletely known as indicated by its increasing number of known endemic species over time: 2423 (Jaffré *et al.*, 2001), 2519 (Morat *et al.*, 2012) and 2544 (Munzinger *et al.*, 2016). Many important families in New Caledonia have not yet been monographed in the local flora “*Flore de la Nouvelle-Calédonie*” or elsewhere. As for other tropical areas, herbaria around the world probably house a large number of New

Caledonian species awaiting description (Bebber *et al.*, 2010) and this may include a few novel genera. Future phylogenetic works may also reveal new endemic genera to be resurrected or described, e.g. the recently segregated *Jaffrea* (Rhamnaceae) or, in Sapindaceae, the New Caledonian species of the Palaeotropical *Arytera* and *Cupaniopsis* appear to be phylogenetically distinct (Buerki *et al.*, 2012). As increasing knowledge is gathered regarding the phylogenetic relationships of the endemic genera, critical morphological comparison with their closest relatives becomes easier. Some of the monotypic genera may lose their rank to reduce redundancy similar to the expanded concepts of Strasburgeriaceae and Paracryphiaceae (Angiosperm Phylogeny Group III, 2009) that reduced the number of endemic families from five to three.

Current evidence indicates that between 62 and 91 genera endemic to New Caledonia probably satisfy the criterion of monophyly (Table 1) and this probably represents a conservative estimate of the actual number of endemic genera. These genera have on average 4.7–4.9 species, with a median of 2; 26–35 of them are monotypic and they encompass 12.0–16.7% of the endemic flora of New Caledonia.

Comparison of the New Caledonian endemic generic flora with those of other Pacific islands

New Zealand may have between 28 and 44 endemic genera after considering phylogenetic evidence (Garnock-Jones, 2014). Eastern Polynesia (French Polynesia and the Cook Islands) has 12 endemic genera according to Meyer (2004); however, the endemic *Sclerotheca* A.DC. and *Apetahia* Baill. (Campanulaceae) may be merged since *Sclerotheca* is nested in *Apetahia* (Givnish *et al.*, 2009; Pillon *et al.* unpublished) and are morphologically similar (Florence, 1997). The endemic *Tahitia* Burret (Malvaceae) may be considered as a synonym of *Christiana* DC. (Kubitzki, 1995) and *Plakothira* J.Florence (Loasaceae) is nested in *Klaprothia* Kunth (Weigend *et al.*, 2004). Samoa has only two endemic genera according

to Whistler (2011): *Sarcopygme* Setch. & Christoph. (Rubiaceae) and *Solfia* Rechinger (Arecaceae). However, recent phylogenetic evidence challenged their distinctiveness so that the first genus is now a synonym of *Morinda* L. (Razafimandimbison & Bremer, 2011) and the second is a synonym of *Balaka* Becc. (Zona & Baker, 2014). Fiji has seven endemic genera according to *Flora Vitiensis Nova* (Smith, 1996): *Amaroria* A.Gray (Simaroubaceae), *Degeneria* I.W.Bailey & A.C.Sm. (Degeneriaceae), *Gillespiea* A.C.Sm., *Hedstromia* A.C.Sm., *Squamellaria* Becc., *Sukunia* A.C.Sm. (Rubiaceae) and *Pimia* Seem. (Malvaceae). *Amaroria* is nested in *Soulamea* Lam. (Clayton *et al.*, 2007) and *Pimia* is a synonym of *Commersonia* J.R.Forst. & G.Forst. (Dorr & Cheek, 2011). *Gillespiea* has never been included in any molecular study, *Hedstromia* belongs to a large *Psychotria* L. clade the limits of which remain unclear and requires further work (Barrabé *et al.*, 2014) and *Squamellaria* is a peculiar lineage of subtribe Hydnohytinae and is now considered to be present on Vanuatu and the Solomon Islands (Chomicki & Renner, 2016). *Sukunia*, sometimes considered as a synonym of *Atractocarpus* Schltr. & K.Krause (Puttock & Quinn, 1999), was viewed as distinct more recently (Mouly *et al.*, 2014). Note that Degeneriaceae are endemic to Fiji. There is no conspectus for the flora of Vanuatu, but it seems to host only one endemic genus: *Carpoxydon* H.Wendl. & Drude (Arecaceae). We still lack a flora treatment for the Solomon islands, but Thorne (1969) listed five endemic genera in this region: *Allowoodsonia* Markgr. (Apocynaceae), *Cassidispermum* Hemsl. (Sapotaceae), *Kajewskiella* Merr. & L.M.Perry (Rubiaceae), *Rehderophoenix* Burret and *Strongylocaryum* Burret (Arecaceae). *Cassidispermum* is thought to be a synonym of *Burckella* Pierre (Govaerts *et al.*, 2015), *Rehderophoenix* is a synonym of *Drymophloeus* Zipp. and *Strongylocaryum* is a synonym of *Ptychosperma* Labill. (Govaerts *et al.*, 2016). The Hawaiian islands have 35 endemic vascular plant genera (Wagner, Herbst & Sohmer, 1999; Palmer, 2003), a number that needs to be

revised and should be considered as an upper estimate. Stuessy *et al.* (2014) suggested that only 22 may be recognized after careful examination.

Most Pacific archipelagos have only a few endemic genera, the number tending to decrease with the progress of phylogenetic analyses. Larger numbers are found in New Caledonia, New Zealand and Hawaii. Even when considering lower estimates, New Caledonia still has by far the largest number of endemic genera in the Pacific region. It also has three endemic families (and one order, Amborellales); only Fiji also has an endemic family.

Why are there so many endemic genera in New Caledonia?

New Caledonia has a rich and unique flora (Morat *et al.*, 2012) with 3389 species, of which 75.1% are endemic (Munzinger *et al.*, 2016). It can therefore also be expected to have a higher number of endemic genera. These two levels of endemism may share a number of identical causes. New Caledonia is geographically isolated, has a relatively large surface (c. 18,600 km<sup>2</sup>) and is chiefly composed of a single large island (rather than many small ones) and might therefore be expected to harbour more species than an archipelago of equivalent surface, but composed of a greater number of smaller islands (Diamond, 1975). It also lies entirely in the tropical belt, compared to, e.g., New Zealand, which is at a higher latitude and can be expected to have a comparatively less species-rich flora (Gaston, 2000). Beyond such trivial explanations, there may be other factors that have favoured a greater accumulation of endemic genera in New Caledonia than in any other Pacific islands.

Endemic genera as relicts

Endemic genera may be relicts of larger and once widespread clades, in which species from outside the island may have been driven to extinction and New Caledonia may have

offered particular conditions to accumulate many such relicts. Indeed, 26 to 35 of these genera are monotypic and most of them have few species (only eight to 12 have ten or more species), suggesting that they may be declining globally rather than actively diversifying. Several endemic genera have a sister group in remote areas (South Africa, South America, Caribbean) that do not seem to be intuitive source areas for the New Caledonian flora. Such biogeographical disjunctions may be easier to explain by extinctions in areas adjacent to New Caledonia.

Although its biodiversity may not be as old as it was previously estimated, New Caledonia is still much older than any other islands in the Pacific region besides New Zealand (Table 2). Communities on New Caledonia may have had sufficient time to reach saturation as indicated by slowing-down of diversification and density-dependent diversification observed in several groups (Espeland & Murienne, 2011; Pillon, 2012; Swenson *et al.*, 2015). There is, however, not yet any evidence from molecular dating (Pillon, 2012) or the fossil record (which is sparse and requires a critical review; Guillaumin, 1919) supporting the continuous coverage of vegetation since the emergence of the island in the Eocene. Nevertheless, rainforests may have been continuously present for a long period of time, including through the Quaternary climatic oscillations (Pintaud, Jaffré & Puig, 2001; Poncet *et al.*, 2013; Pouteau *et al.*, 2015). In contrast, nearby Australia, which probably served as a source for most of the island flora (Morat, 1993) went through dramatic climatic changes during the Tertiary, particularly aridification, that may have driven to extinction many plant lineages, most notably in the rainforest (Holloway, 1979; Byrne *et al.*, 2011; Crisp & Cook, 2013; Sniderman, Jordan & Cowling, 2013), some of them being putative close relatives of New Caledonian species. Indeed, a number of genera restricted to New Caledonia nowadays have a fossil record in Australia and/or New Zealand: *Beauprea* (Pocknall & Crosbie, 1988), *Codia* (Barnes & Hill, 1999), *Amphorogyne*, *Paracryphia* and *Phelline* (Pole, 2010). New

Caledonian conifers also suffered lower extinction rates than in other areas (Condamine, Leslie & Antonelli, 2016).

New Caledonia is well known for its ultramafic substrates that offer challenging conditions for plant growth and host the unique ‘maquis’ vegetation (Isnard *et al.*, 2016). We found that the majority of the endemic genera (59–85) are found on ultramafic substrates and 25–36 of the endemic genera are restricted to them (or almost so), whereas only three to six avoid them (Table 1). Ultramafic substrates cover about one third of New Caledonia and host about half of the indigenous flora; 36% of the species are restricted to this substrate (Isnard *et al.*, 2016). Therefore, the number of endemic genera restricted to these substrates is unexpectedly high regarding their surface and species richness. Ultramafic substrates probably covered the entire island as it emerged (Pelletier, 2006) and probably acted as ecological filter in the making of this island flora (Pillon *et al.*, 2010). This double insularity may have protected the earliest settlers by limiting the rate of immigration (Jaffré *et al.*, 1987), slowing down the turnover in this community and allowing relicts to survive. The high diversity of conifers in New Caledonia, often considered as less competitive than angiosperms, and their strong bias towards ultramafic substrates (Jaffré, Munzinger & Lowry, 2010) and the limited number of invasive species recorded on such soils (Meyer *et al.*, 2006) support this hypothesis.

#### Endemic genera as the product of adaptive radiations

Adaptive radiation on islands implies the diversification of one colonizer into an array of species occupying a variety of niches and differing by morphological and physiological traits associated with those niches (Schluter, 2000). Carlquist (1965: 134) cited only a few examples of adaptive radiations in New Caledonia: *Araucaria*, *Dacrydium* Lamb, *Podocarpus* L’Hér. ex Pers. (all relatively small radiations of conifers), *Phyllanthus* L. (multiple

colonization events, Kathriarachchi *et al.*, 2006) and *Tieghemopanax* R.Vig. (now included in *Polyscias* J.R.Forst. & G.Forst., see Eibl, Plunkett & Lowry, 2001). When morphological differences are sufficient, the offspring of an adaptive radiation may be treated as different genera, but this does not seem to be common in New Caledonia. There are currently only four to six pairs of sister endemic genera: *Clematepistephium* & *Eriaxis*, *Clinosperma* & *Cyphokentia*, *Amphorogyne* & *Daenikera*, *Arthroclianthus* & *Nephrodesmus* and, possibly, *Morierina* & *Thiollierea* and *Kermadecia* & *Sleumerodendron*. There is no clade of three or more endemic genera (but see *Pycnandra* below).

*Eriaxis* and *Clematepistephium* (both monotypic) have remarkably different habits. The first is an erect herb not exceeding 50 cm (inflorescence excluded) mostly found in maquis, whereas the second is a long rainforest vine reaching several meters (Hallé, 1977). *Clinosperma* (four species) and *Cyphokentia* (two species) differ by the presence/absence of membranous ramenta and didymous/not didymous anthers (Pintaud & Baker, 2008), but these cannot be easily connected with putative ecological differences. *Amphorogyne* spp. (three) are root parasitic chlorophyllous shrubs and trees reaching several meters, whereas *Daenikera* (monotypic) is a parasitic, aphyllous, purplish shrub not exceeding 60 cm (Hallé, 1988). *Nephrodesmus* (19 species) and *Arthroclianthus* (five species) differ by the position of the corolla wings (cover the keel in *Arthroclianthus* vs. do not cover the keel in *Nephrodesmus*), and their fruit morphology (sustained by a stipe vs. not sustained by a stipe; H. Vandrot, comm. pers.). These latter genera do not differ in terms of ecology, although *Arthroclianthus* has a greater ecological amplitude. *Morierina* (two species) and *Thiollierea* (12 species) differ in flower morphology (tubular with long and reflexed lobes vs. campanulate with short lobes), inflorescence structure (straight and subtending on a stiff axis with leafy bracts vs. pendant and generally on a flexible axis without leafy bracts) and type of anthers (not twisted vs. twisted, Barrabé *et al.*, 2011), suggesting a shift in pollination syndrome (moths vs. birds,

Motley, Wurdack & Delprete, 2005). The first is mostly found in rainforests, whereas the second is generally in maquis; both are restricted to ultramafic substrates. *Kermadecia* (four species) and *Sleumerodendron* (one species) and *Turrillia* (Vanuatu & Fiji) are similar vegetatively and ecologically and their flowers differ only in small points (Virost, 1967; Smith & Haas, 1975).

These pairs of sister genera account only for a small number of species (24 at most for *Arthroclianthus-Nephrodesmus*). The morphological and ecological differences are relatively modest in three cases (*Clinosperma & Cyphokentia*, *Arthroclianthus & Nephrodesmus*, *Kermadecia & Sleumerodendron*) and do not obviously qualify as adaptive radiations. The fact that two are relatively species-poor (*Clematopistephium & Eriaxis*, *Amphorogyne & Daenikera*) suggests that they are relicts rather than actively diversifying lineages. This contrasts with Hawaii that has several multi-generic plant radiations: the silversword alliance (three genera, 28 species; Baldwin, 1997), lobeliads (six genera, 126 species; Givnish *et al.*, 2009) and mints (three genera, 60 species, Lindqvist & Albert, 2002). The Macaronesian islands have a large radiation of Crassulaceae (four genera, 63 species; Mort *et al.*, 2002). Adaptive radiations seem to have contributed little to the formation of endemic genera in New Caledonia. The largest monophyletic clade in New Caledonia is a group of *Psychotria* (c. 78 species, Barrabé *et al.*, 2014) with modest morphological diversity that is not easily correlated with the ecology of the different species. The largest endemic genus, *Pycnandra*, is composed of six subgenera (Swenson *et al.*, 2015), most of which were once recognized as genera. However, apart from subgenus *Lepostylis*, the delimitation of these subgenera has changed considerably since the time when they were ranked as genera (Swenson *et al.*, 2008). The homoplasy of most morphological characters explored so far (Swenson *et al.*, 2015) probably made the classification of this group complicated. Since the subgenera of *Pycnandra* are difficult to characterize morphologically (Swenson & Munzinger, 2009, 2016; Swenson *et al.*,



2015) and do not show clear ecological differences, *Pycnandra* does not seem to be comparable to the multigeneric adaptive radiations from Hawaii or the Macaronesian islands cited above. With the current evidence at hand, most New Caledonian plant lineages may be considered as mere “radiation” or, in a few cases, “explosive radiation” (e.g. *Psychotria*) rather than “adaptive radiation” (Givnish, 2015).

It remains unclear why the New Caledonian flora has few dramatic examples of adaptive radiation, but it may be linked to the fact that the vegetation is largely composed of woody plant species (Virot, 1956), whereas most convincing examples of adaptive radiation in plants are herbaceous or ancestrally herbaceous (Givnish, 2010). “Increased woodiness” is a commonly observed syndrome on islands, whereby herbaceous ancestors become shrubs or trees after colonizing islands [Carlquist, 1965 (chapter 8), 1974 (chapter 10)], but this is almost unseen in New Caledonia and the rest of Melanesia (Carlquist, 1974: 409). Many large herbaceous families are under-represented in New Caledonia, including Asteraceae, Campanulaceae, Cyperaceae, Lamiaceae and Poaceae (Pillon *et al.*, 2010). The paucity of Asteraceae is particularly striking, especially on the ultramafic soils (Carlquist, 1965: 42), whereas they are well represented in many island floras, producing several remarkable adaptive radiations (Carlquist, 1965: 204). When New Caledonia emerged, it was probably entirely covered with ultramafic substrate which may have filtered the successful immigrants (Pillon *et al.*, 2010) and primarily woody plants may be more competitive than herbs on ultramafic substrates.

The relative ancient age of New Caledonia may also explain the lack of dramatic adaptive radiation by allowing enough time for a diverse cohort of immigrants to reach the island. The diversity of Asteraceae on islands may be explained by their ability to disperse long distances and their weediness and evolutionary lability (Carlquist, 1965: 204), whereas trees may be poor dispersers (Carlquist, 1965: 189). As time passes, even the least likely

dispersal might happen and, for example, new immigrant tree species may outcompete those that evolved from herbaceous colonizers. The available data from molecular dating suggest that arrivals of colonizers were spread in time rather than being synchronous and close to the putative emergence time of New Caledonia (Pillon, 2012). On New Caledonia, we may be observing a mature flora, in which continuous immigration has progressively thinned out the earlier adaptive radiations. Such processes have not yet taken place in the other more recent Pacific islands.

Despite its complex environmental gradients, New Caledonia may not offer ecological conditions as diverse as other islands, particularly in terms of climate. Hawaiian islands display a diverse range of climatic conditions (Carlquist, 1980: 63), some extreme, offering considerable opportunities for adaptive radiations. New Caledonia lies entirely in the tropical belt and its highest peak (Mt Panié, 1628 m) is lower than that of several Pacific archipelagos (Table 2). Although its mountain tops host some distinctive plant communities that may be exposed to frost (Bradford & Jaffré, 2004; Munzinger, McPherson & Lowry, 2008), those are still dense and largely shrubby and do not display distinctive vegetative forms such as large rosette and cushion plants.

It has long been recognized that a striking ecological feature of New Caledonia is the diversity of its soils (Jaffré, 1993) and this could have been a major driver for plant diversification (Pillon *et al.*, 2009a,b). However this might have been translated into physiological diversity more than morphological attributes and hence a rather cryptic mode of adaptive radiation (e.g. Pillon *et al.*, 2014).

Finally, New Caledonia also displays few dramatic examples of plant-pollinator co-evolution that could compare to, for example, Hawaiian lobeliads and Hawaiian honeycreepers (Carlquist, 1965: 131). There is an interesting case of mutualism reported between the large genus *Phyllanthus* and *Epicephala* moths (Kawakita & Kato, 2004), but it

did not result in spectacular variations in flower morphology. Pollination syndromes have not been thoroughly investigated in New Caledonia (but see Carpenter, Read & Jaffré, 2003; Kato & Kawakita, 2004; Donovan *et al.*, 2013; Hopkins *et al.*, 2015b) and some patterns might have been overlooked. It is possible that the pollination guild of New Caledonia is more depauperate than elsewhere (Carpenter *et al.*, 2003; Pauly & Munzinger, 2003). Also, most of the lineages in which zygomorphic flowers are found are under-represented in the flora of New Caledonia: monocots, Asterales, Fabales and Lamiales (Pillon *et al.*, 2010), and this may have reduced the opportunities for specific plant-pollinator interactions.

## CONCLUSIONS

New Caledonia may have a total of between 62 and 91 endemic genera. Many of these genera have still not been included in molecular phylogenetic studies and the delimitation of others needs further work, and some other genera may be revealed in the future. This number of endemic genera is far greater than in any other Pacific archipelago. Endemic genera may be the result of extinctions outside the island, evolutionary changes on the island or both. In the case of New Caledonia, the first phenomenon may have been the preponderant force. The relative ancient age of the island, a putative climatic stability and a possible protective role of ultramafic substrate against new colonizers may have been key factors in the accumulation of relict lineages. In contrast, evidence for adaptive radiations is limited and this may be linked to the modest contribution of primarily herbaceous lineages to the composition of flora or the limited ecological contrasts on the island beside the diversity of soils. Beyond the now famous *Amborella*, New Caledonia hosts a large number of unique relicts of conservation significance, as can be expected in old, climatically buffered, infertile landscapes (OCBILs, Hopper, 2009; Hopper, Silveira & Fiedler, 2016). Endemic genera may be in some cases the sole survivor of ancient lineages and the age and phylogenetic diversity of these taxa will be

discussed in a forthcoming paper. It can be anticipated that this will magnify the conservation significance of the ultramafic substrates of New Caledonia, which host most endemic genera and where the preservation of the native ecosystems is most conflicted (Pascal *et al.*, 2008). Updated conservation assessments for these unique lineages are urgently needed to set conservation priorities and preserve these unique branches of the tree of life.

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Table 1. Phylogenetic status of the vascular plant endemic genera endemic to New Caledonia. Column 1. Distinctiveness has been confirmed by phylogenetic studies with thorough sampling (all closely related genera have been included). Available data suggest that the genus is monophyletic (or in several cases monotypic or species-poor) and it seems unlikely that it is nested in another one. Column 2. All current evidence support the distinctiveness of the genus, although sampling of related genera may not be exhaustive or resolution in phylogenetic relationships may be low, or the phylogenetic study is not published yet. Column 3. There is some evidence that the genus may not be monophyletic or may be nested in another one or that the genus is closely related to a large genus that has not been thoroughly sampled yet, also present in New Caledonia or not, for which delimitation may be problematic, and in which the candidate genus could be nested. Column 4. The genus has been found to be nested in another genus with strong support or has been synonymized since the publication of Morat *et al.* (2012). Column 5. The genus has never been included in any molecular phylogenetic study and there are no DNA sequences available in GenBank. Underlined genera: restricted to ultramafic substrates (or almost so). Highlighted genera: never found on ultramafic substrates (or almost so). Numbers in parenthesis are species numbers according to Munzinger *et al.* (2016).

Status confirmed		Likely	Need further work	To be synonymized	Never investigated
<u>Achlydosa</u> (1) <u>Amborella</u> (1) <u>Amphorogyne</u> (3) <u>Apiopetalum</u> (2) <u>Arillastrum</u> (1) <u>Austrotaxus</u> (1) <u>Beauprea</u> (13) <u>Beaupreopsis</u> (1) <u>Campynemanthe</u> (3) <u>Canacomyrca</u> (1) <u>Clematepistephium</u> (1) <u>Clinosperma</u> (4) <u>Cloezia</u> (6) <u>Codia</u> (15) <u>Coilochilus</u> (1) <u>Cyphokentia</u> (2) <u>Daenikera</u> (1) <u>Depanthus</u> (2) <u>Dicarpellum</u> (4) <u>Eriaxis</u> (1) <u>Eucarpha</u> (2) <u>Gongrodiscus</u> (3) <u>Hachettea</u> (1) <u>Hooglandia</u> (1)	<u>Jaffrea</u> (2) <u>Loxodiscus</u> (1) <u>Menepetalum</u> (4) <u>Montrouziera</u> (6) <u>Myodocarpus</u> (10) <u>Myrtastrum</u> (1) <u>Nemuaron</u> (1) <u>Neoguillauminia</u> (1) <u>Neoschmidia</u> (2) <u>Oncotheca</u> (2) <u>Pachyplectron</u> (3) <u>Pancheria</u> (27) <u>Paracryphia</u> (1) <u>Parasitaxus</u> (1) <u>Phelline</u> (14) <u>Platyspermatum</u> (1) <u>Podonephelium</u> (9) <u>Pycnandra</u> (59) <u>Salaciopsis</u> (6) <u>Sparattosyce</u> (2) <u>Storthocalyx</u> (5) <u>Strasburgeria</u> (1) <u>Stromatopteris</u> (1) <u>Viotia</u> (6)	<u>Acropogon</u> (25) <u>Arthroclianthus</u> (19) <u>Balgoya</u> (1) <u>Cerberiopsis</u> (3) <u>Crossosperma</u> (2) <u>Cyathopsis</u> (3) <u>Gonatosstylis</u> (2) <u>Greslania</u> (3) <u>Maxwellia</u> (1) <u>Normandia</u> (1) <u>Nephrodesmus</u> (5) <u>Peripterygia</u> (1) <u>Periomphale</u> (1) <u>Scagea</u> (2)	<u>Actinokentia</u> (2) <u>Adenodaphne</u> (4) <u>Artia</u> (4) <u>Basselinia</u> (14) <u>Bocquillonina</u> (14) <u>Burretiokentia</u> (5) <u>Chambeyronia</u> (2) <u>Cocconerion</u> (2) <u>Cyphophoenix</u> (4) <u>Deltaria</u> (1) <u>Gea</u> (6) <u>Kanakomyrtus</u> (6) <u>Kentiopsis</u> (4) <u>Kermadecia</u> (4) <u>Kibaropsis</u> (1) <u>Lasiochlamys</u> (11) <u>Morierina</u> (2) <u>Myrtopsis</u> (8) <u>Sleumerodendron</u> (1) <u>Solmsia</u> (2) <u>Thiollierea</u> (12)	<u>Comptonella</u> (8) <u>Dutaillyea</u> (2) <u>Garnieria</u> (1) <u>Oxanthera</u> (5) <u>Picrella</u> (3)	<u>Dutailliopsis</u> (1) <u>Elaphanthera</u> (1) <u>Gastrolepis</u> (2) <u>Longetia</u> (1) <u>Mangenotiella</u> (1) <u>Myricanthe</u> (1) <u>Pleurocalyptus</u> (2) <u>Purpureostemon</u> (1)
				Synonymized since Morat <i>et al.</i> (2012)	
				<u>Boronella</u> (4) <u>Carpolepis</u> (3) <u>Neocallitropsis</u> (1) <u>Pritchardiopsis</u> (1)	

Table 2. Statistics for different archipelagos in the Pacific Ocean.

Archipelago	New Caledonia	New Zealand	Solomon Islands	Vanuatu	Fiji	Samoa	French Polynesia and Cook Islands	Hawaiian Islands
Surface (km <sup>2</sup> )	18,576	268,021	28,400	12,190	18,274	3,030	3,916	16,636
Age of biota (Myr)	37 <sup>a</sup>	25 <sup>b</sup>	?	5 <sup>c</sup>	7-16 <sup>d</sup>	13,5 <sup>e</sup>	≈18 <sup>f</sup>	mostly ≤5 <sup>g</sup>
Highest elevation (m)	1,628	3,754	2,332	1,879	1,325	1,858	2,241	4,207
Number of vascular plant species	3,389 <sup>h</sup>	2,221 <sup>i</sup>	?	?	1,315 <sup>j</sup>	550 <sup>k</sup>	651 <sup>m</sup>	1,207 <sup>n</sup>
Specific endemism (%)	75.1 <sup>8</sup>	78 <sup>i</sup>	?	?	62 <sup>j</sup>	31 <sup>k</sup>	70.9 <sup>m</sup>	88 <sup>n</sup>
Number of endemic genera	61-91	28-44	?2	1	1-5	0	≈ 9	22-35

<sup>a</sup>Grandcolas *et al.* (2008), <sup>b</sup>Trewick *et al.* (2007), <sup>c</sup>Zielske & Haase (2014a), <sup>d</sup>Zielske & Haase (2014b), <sup>e</sup>Ewart (1988), <sup>f</sup>Maury *et al.* (2014), <sup>g</sup>Price & Clague, <sup>h</sup>Munzinger *et al.*, <sup>i</sup>Breitwieser *et al.* (2012), <sup>j</sup>Heads, <sup>k</sup>angiosperms only, Whistler (2011), <sup>m</sup>French Polynesia only, Florence in Morat *et al.* (2012), <sup>n</sup>Gustafson *et al.* (2014).

Figure 1. Some representatives of New Caledonia endemic genera: A. *Loxodiscus coriaceus* Hook.f. (Sapindaceae), B. *Pancheria robusta* Guillaumin (Cunoniaceae), C. *Platyspermatium crassifolium* Guillaumin (Alseuosmiaceae), D. *Thiollierea kaalaensis* (N.Hallé & Jérémie) Barrabé & Mouly, E. *Hachettea austrocaledonica* Baill. (Balanophoraceae), F. *Campynemanthe viridiflora* Baill. (Campynemataceae). Photograph credits: V. Hequet (A), Y. Pillon (B, C, D, F), L. Barrabé (E).

