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Ultramafic soils and species sorting in the flora of New Caledonia

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Running headline: Species sorting in the flora of New Caledonia

SUMMARY

1. Island floras are generally characterized by disharmony due to uneven representations of plant groups. This has usually been explained by the unequal capacity of plants to disperse and colonize islands, but it has been suggested that the ecology of the recipient islands may also be important.
2. We investigated the phylogenetic structure of the flora of New Caledonia, a biodiversity hotspot in the South-West Pacific, to examine the phylogenetic pattern of a disharmonic flora and to test two competing hypotheses: disharmony due to uneven dispersability versus disharmony due to uneven ability to adapt to the ultramafic soils that are widespread on the archipelago and constrain plant growth.
3. Dispersal did not seem to be a significant factor as plant families with low levels of endemism and thus high effective dispersal capacities tended to be under-represented.
4. We identified several clusters of over-represented families, such as the COM clade (Celastrales, Oxalidales and Malpighiales), in which nickel hyperaccumulation (a syndrome associated with ultramafic soils) was particularly common. We indeed found a positive association between hyperaccumulation and over-representation. Therefore, ultramafic soils may have been a major force for species sorting in the flora of New Caledonia.
5. Because we think that most colonizers were naïve to ultramafic soils before they reached the archipelago, the over-represented groups in New Caledonia may have possessed an exaptation to ultramafic soils, which has facilitated their settlement and diversification.

6. *Synthesis*. This study supports that beyond dispersal, ecology is an important factor in determining the success of different plant groups to colonize an island. In the case of New Caledonia, exaptation to ultramafic soils is likely a primary cause of ecological filtering.

Key-words: island biogeography, phylogenetic clustering, phylogenetic community structure, phylogenetic niche conservatism, serpentine, species selection

INTRODUCTION

“... the overriding role that the ecology of the recipient island plays in dispersal cannot be strongly enough stressed.”

(Carlquist 1974, p. 81)

Island biotas have long inspired evolutionary biologists, from the conception of the theory of evolution by Darwin to the now common reference to islands as “evolutionary laboratories” (Carlquist 1974). They have often served as models for the study of adaptive radiation (Givnish & Sytsma 1997; Schluter 2000), and more recently for sympatric speciation (Savolainen *et al.* 2006). MacArthur & Wilson (1963) have offered a simple theory to explain the formation of island biotas. Later extended by Hubbell’s neutral theory (2001), insular biodiversity is seen as an equilibrium between immigration, extinction, and local speciation. The composition of an insular biota may be disharmonic (Carlquist 1974, p.6) due to the over- or under-representation of particular groups. Disharmony of island biotas has generally been attributed to variation in dispersal capacity among groups, but local ecological conditions may be an alternative explanation.

Phylogenetic studies in various plant groups have recently revealed surprising cases of long-distance dispersal between land masses that were distant and/or non-contiguous, but which nevertheless offered similar ecological conditions: dispersal of *Ourisia* from the Andes to the temperate flora of New Zealand (Meudt & Simpson 2006), dispersal of *Carex* between poles (Vollan *et al.* 2006), and dispersal of Iridaceae, Orchidaceae, Poaceae and Restionaceae from the Cape Province to Eastern African Mountains (Galley *et al.* 2007). Using 45 groups of vascular plants of the southern Hemisphere, Crisp *et al.* (2009) found evidence for phylogenetic biome conservatism, which is a tendency for plant lineages to occupy the same biome after transoceanic dispersal. Such study supports the paradigm suggested by Donoghue

(2008) that “It’s easier to move than to evolve.” Therefore, in the process of the formation of an island flora, rare immigrants that arrive from regions with ecological conditions similar to those present on the island may have a greater success in colonization relative to more common immigrants with poorly matched requirements.

New Caledonia, an archipelago in the south-west Pacific, represents an excellent model for investigations of island biogeography. This biodiversity hotspot (Myers *et al.* 2000) is ecologically unique because of the abundance on the main island of ultramafic soils (Proctor 2003), which support an unusual flora (Jaffré 1993; Morat 1993). Because of the unusual ecological conditions of this archipelago, the impact of the local ecology on the composition of this island flora is more likely to be detected.

Relatively few studies have considered ecology and historical biogeography of islands simultaneously (Wiens & Donoghue 2004). Here we investigate the phylogenetic structure (Webb 2000) of the entire flora of New Caledonia to search for phylogenetic patterns in its disharmony and to identify clades that are over- or under-represented. We then address factors that may be responsible for species sorting (Vrba 1984; Vrba & Gould 1986), also referred to in a broader sense as species selection (Jablonski 2008; Rabovsky & McCune 2010) or selective immigration in the context of an island (Lomolino 1996). In this study we aimed to investigate the relative roles of dispersal and prevailing ecological conditions in the origin of disharmony in this archipelago. Just as fire may be an important cause for phylogenetic clustering in a Mediterranean flora (Verdú & Pausas 2007), we aimed to test if ultramafic soils have constrained immigration to New Caledonia.

MATERIAL and METHODS

MODEL SYSTEM: NEW CALEDONIA

Located in the south-west Pacific, with an area of c. 19 000 km², New Caledonia comprises one main island (c. 16 000 km²) surrounded by several smaller ones and is situated c. 1500 km east of Australia. It was once part of Gondwana and split from Australia c. 80 million years ago (McLoughlin 2001). However, the deep sea deposits of the early tertiary indicate that the island was well under sea level for a long time, from the late Cretaceous to the early Eocene (Aitchison *et al.* 1995; Picard 1999; Pelletier 2006). The island emerged in the middle-late Eocene (c. 35-45 million years ago), when the ophiolitic nappe covered the entire island (Pelletier 2006). Thus far, no evidence has been found to support the continuous persistence of a biota somewhere on the island or on putative islands in the vicinity, which could have served as refugia (Grandcolas *et al.* 2008). This implies that all plant species colonized the newly emerged island through long-distance dispersal from surrounding sources (Thorne 1965; Pelletier 2006; Grandcolas *et al.* 2008). All results from molecular clock analyses on New Caledonian radiation are consistent with a post-emersion origin of the New Caledonian biota (Murienne *et al.* 2005; Grandcolas *et al.* 2008).

The most likely origin of New Caledonian lineages is Australia, firstly because of its proximity, but also because it is able to offer high numbers of propagules due to its large size. Strong affinities have indeed been found between the two floras (Morat 1993) and confirmed by phylogenetic analysis of families such as the Cunoniaceae (Bradford & Barnes 2001) or Sapotaceae (Bartish *et al.* 2005). Beyond their similarities, some striking differences are also observed such as the absence or poor representation in New Caledonia of some genera that are extremely diverse and abundant in Australia (e.g. *Acacia*, *Eucalyptus*). Disharmony of the New Caledonian flora is particularly striking when comparing two families such as Cunoniaceae and Asteraceae (Fig. 1).

The most common explanation for disharmony in island biota is the different capacity of groups to disperse and colonize islands. However, long-distance dispersal is a rare

phenomenon which is difficult to observe (Nathan *et al.* 2008) and has generally been estimated indirectly (Ouborg *et al.* 1999). Thus, to measure dispersability, we chose to use ‘non-endemism’ as a surrogate. Species that are indigenous, but not endemic, to an island are likely to have arrived at or dispersed out of this island recently, or recent gene flow has occurred preventing genetic drift and speciation. Thus, groups that disperse easily are expected to have a lower level of endemism and a greater number of non-endemic species. This has indeed been observed in the New Zealand flora (McGlone *et al.* 2001), where groups with small propagules (minute seeds and spores) such as orchids and ferns have a lower level of endemism.

The major ecological feature of New Caledonia is the abundance of ultramafic soils, which have several characteristics that are limiting for plant growth: low fertility (low N, P, K), high Mg:Ca ratio, high concentrations of heavy metals (Co, Cr, Ni, etc.), and low water-holding capacity; in addition, fire is more frequent in vegetation on such substrates (Proctor 2003). Ultramafic soils currently cover one-third of the surface of the main island, but likely covered a significant majority of the island surface when it emerged in the Tertiary (Pelletier 2006). These soils clearly constrain the distribution of plant species within the archipelago (Jaffré *et al.* 1987; Morat 1993) as well as their genetic structure (Pillon *et al.* 2009a; see also Jourand *et al.* 2010 for an example in fungi), and the peculiar flora of New Caledonia suggests that not all plant groups are equally able to develop in such environment. Some plants growing on ultramafic soils have developed particular syndromes: they accumulate in their tissue heavy metals such as Ni or Mn in anomalous concentration (e.g. Jaffré *et al.* 1976). New Caledonia has the largest concentration of heavy metal hyperaccumulators, comparable to that of Cuba (Brooks 1998).

DATA

To test for a phylogenetic pattern of over-representation in the flora of New Caledonia, we considered all of the world's angiosperm families (N=440) and took their total number of species worldwide from Stevens (2001 onwards) and number of indigenous and endemic species in New Caledonia from Jaffré *et al.* (2001), and total number of indigenous species in Australia from Hnatiuk (1990). Although the latter two lists are considered outdated, they are not expected to bias estimations of disharmony between the Australian and the New Caledonia flora. In addition to indigenous species, endemics species were used as they are expected to be free of cryptogenic species (e.g. species of doubtful indigenous status that may actually be ancient human introduction, intentional or not); the latter may not be randomly distributed among families. We used the complete family tree of Davies *et al.* (2004), available from the Phylomatic website (Webb & Donoghue 2005). The number of nickel-hyperaccumulating species within each family was established from the list of Brooks (1998).

COMPARATIVE ANALYSES

To assess if one family was more or less represented than expected in New Caledonia, we compared separately the observed number of indigenous and endemic species with the expected numbers of each if the flora of New Caledonia were a random set of the Australian flora (null model). For instance, if 10% of the Australian angiosperms are orchids, 10% of indigenous and endemic New Caledonian angiosperms should be orchids. This null model therefore assumes equal chance of plants to disperse and to settle in New Caledonia, i.e. equal dispersal capacities and no ecological filtering. We used a normal distribution to detect families that significantly deviated from this null model and were therefore under- or over-represented in New Caledonia.

To test for phylogenetic correlation with over-representation we calculated for each family the following representation index:

$$R = \ln\left(\frac{N_{obs} + 1}{N_{exp} + 1}\right)$$

where N_{obs} is the number of indigenous or endemic species observed in New Caledonia, and N_{exp} is the number of indigenous or endemic species expected in New Caledonia under a null model. We searched for phylogenetic signal in the variation of the representation index by using Phylocom (Webb *et al.* 2008). Nodes which have significantly higher or lower means of the representation index (Tmn, mean value of trait across all descendant terminal taxa) than expected were identified by comparison with 1000 randomizations of the index value across the tips of the tree (threshold 5%) and mapped onto a phylogenetic tree using Dendroscope (Huson *et al.* 2007). K statistics of Blomberg *et al.* (2003), which measures the amount of phylogenetic signal across traits and trees, were calculated with the Picante package (Kembel *et al.* 2010) in R (R Development Core Team 2008). Although values of K above 1 are expected for a character evolving in a Brownian motion model of evolution on a phylogenetic tree, this is rarely observed in real data (Blomberg *et al.* 2003). Different trait types exhibit different values in empirical studies, which rank from highest to lowest K values as follows: body size, morphology, life history, physiology and behaviour (Blomberg *et al.* 2003). To test the impact of dispersability on disharmony, we calculated the correlation coefficient between the representation index for all families that are represented in New Caledonia with the proportion of endemic species and with the number of non-endemic species in this flora.

To test for the impact of ultramafic soils on disharmony, we tested whether there was an association between significant over-representation and a hyperaccumulation index calculated for each family and defined as follows:

$$H = \ln\left(\frac{Ni_{obs} + 1}{Ni_{exp} + 1}\right)$$

where $N_{i_{obs}}$ is the number of nickel-hyperaccumulating species recorded in a given family according to Brooks (1998), and $N_{i_{exp}}$ is the number of nickel-hyperaccumulating species expected if they were randomly distributed across angiosperms (species evenly distributed among families according to their total species number). We calculated phylogenetic independent contrasts (Felsenstein 1985) between the representation index R and the hyperaccumulation index H using the PDAP Package (Midford *et al.* 2005) implemented within Mesquite (Maddison & Maddison 2009).

RESULTS

Families that have a number of indigenous species that is significantly higher or lower than expected under the null model are listed in Supporting Information (Appendix S1) and mapped onto a phylogenetic tree in Fig. 2, which also shows nodes with significant deviation from random in the value of the mean representation index. Results obtained with endemic species are very similar and are shown in the Supporting Information (Appendix S2), where patterns of disharmony of the New Caledonian flora in comparison to the entire world flora are also shown.

There is an overall congruence between nodes with mean representation values that were significantly higher than expected by chance and significantly over-represented families which tend to occur in the same clade. For instance, Laurales (Magnoliids) and seven orders within Eudicots, including Ericales, Apiales, Gentianales, Sapindales and the COM clade (Celastrales, Oxalidales and Malpighiales, Zhu *et al.* 2007), contain altogether 63% of the 57 nodes with mean representation values that were significantly higher than expected by chance and 52% of the 71 over-represented families. Although these groups encompass altogether only 16% of the species of the angiosperms of Australia, they contain 51% and 60% of indigenous and endemic species of New Caledonia. Ninety-four percent of the 53 nodes with

mean representation values that were significantly lower than expected by chance and 66% of the 47 significantly under-represented families were found in Monocots and in four orders of Eudicots: Caryophyllales, Asterales, Lamiales and Fabales. The proportions of Monocots in the Australian flora and the indigenous and endemic flora of New Caledonia are 21%, 18% and 11%, respectively. Caryophyllales, Fabales, Asterales and Lamiales contain 34% of the Australian flora but only 10% and 7%, respectively, of the indigenous and endemic flora of New Caledonia. The nodes for which the divergence contributed most to overall variation in representation index for endemic and indigenous species are given in Table 1.

K statistics of phylogenetic signal were equal to 0.564 and 0.579 for the representation index for indigenous and endemic species, respectively, and 0.525 for the occurrence of nickel-hyperaccumulating species. These figures are comparable to those observed in a wide range of life history and physiological traits and higher than those observed for behaviour traits considered as most labile (Blomberg *et al.* 2003), and they indicate the existence of a phylogenetic signal in the composition of the New Caledonian flora.

Phylogenetic independent contrasts showed a significant correlation between the hyperaccumulation index and the representation indexes for both indigenous ($r=0.112$, $p=0.0094$, $d.f.=333$) and endemic ($r=0.199$, $p<0.001$, $d.f.=333$) species. Thus, representation in the flora of New Caledonia was positively correlated with the occurrence of nickel-hyperaccumulating species in families. The proportion of species endemic to New Caledonia within families was positively correlated with the representation index for indigenous ($r=0.512$, $p<0.001$) and endemic ($r=0.738$, $p<0.001$) species. The number of non-endemic species was negatively correlated with the representation index for indigenous ($r=-0.118$, $p=0.07$) and endemic ($r=-0.176$, $p=0.015$) species.

DISCUSSION

PHYLOGENETIC SIGNAL IN THE DISHARMONY OF THE NEW CALEDONIAN FLORA AND EVIDENCE FOR SPECIES SORTING

The comparative analysis shows that the most represented and the least represented groups in the New Caledonian flora are not randomly distributed within the angiosperm phylogenetic tree. Some groups are particularly well represented and form the major component of the New Caledonian flora: the COM clade (Celastrales, Oxalidales and Malpighiales), Sapindales, Gentianales, Apiales, Ericales and Laurales. K values for representation indices for indigenous and endemic species and the occurrence of nickel-hyperaccumulating species confirm the existence of a phylogenetic signal (Blomberg *et al.* 2003).

A possible explanation for this phylogenetic pattern is the importance of biogeography. New Caledonia could be the cradle of over-represented groups, thus explaining their abundance there. However, as the island was sunk into deep water in the Tertiary (Pelletier 2006), its biota could not have occurred there prior to the emersion c. 35-45 million years ago, and most angiosperms families are older than this. Even assuming a vicariant origin of the New Caledonian flora (a hypothesis less and less supported, Grandcolas *et al.* 2008), which would be c. 80 million years, corresponding to the split period between New Caledonia and Australia (McLoughlin 2001), the overall biota of New Caledonia is too young to be the birth place of entire orders. Thus the over-representation of large and ancient clades in New Caledonia can not be explained by an origin within the archipelago.

Areas other than Australia may have served as sources of plant lineages in New Caledonia, particularly New Guinea, but probably to a lesser extent (Morat 1993; Marsch *et al.* 2009). Furthermore, when comparing the New Caledonian flora with the world flora, we identified the same large clades that were under-represented (Asterales, Fabales, Lamiales,

Asterales and Monocots) or over-represented (COM clade, Apiales, Ericales, Gentianales, Sapindales, Appendix S2). Thus the disharmony observed in New Caledonia is grossly the same whether we postulate Australia as the sole source of plant lineage or the entire world flora. The comparison with the world flora only shows a lower phylogenetic signal in over- and under-represented families that appear less clustered because of obvious biogeographical constraints. For example, Brassicaceae seem under-represented, but this family is mostly diversified in temperate areas of the northern hemisphere, whereas Myrtaceae and Proteaceae seem over-represented, but these two families are well -diversified in Australia. Biogeography may thus explain the over- or under-representation of some families, but not of larger clades. Therefore, we think that the phylogenetic pattern observed in the disharmony of the New Caledonian flora is explained by variation among plant lineages in their capacities to disperse, settle, maintain and diversify in New Caledonia, i.e. species sorting (Vrba 1984; Vrba & Gould 1986).

POTENTIAL CAUSES OF SPECIES SORTING

Dispersal

The most represented groups in New Caledonia might be characterized by a high-dispersability that allowed them to colonize the island first and more often. Plant groups with great capacity of dispersal show lower levels of endemism in the New Zealand flora (McGlone *et al.* 2001). Ferns and angiosperm families with small seeds, such as Asteraceae, Poaceae and Orchidaceae (Harper *et al.* 1970), have indeed lower levels of endemism than other families and are represented by numerous non-endemic genera, suggesting a large number of colonization events. Nevertheless, the first two families are significantly under-represented in New Caledonia. When comparing Asteraceae and Cunoniaceae (Fig. 1), the first family is characterized by many more events of colonization but is nevertheless less

diversified on the island. More generally, endemism was positively correlated with representation in the New Caledonian flora, suggesting that dispersal may not be the major factor explaining its disharmony.

Determining the role of dispersal in the making of the New Caledonian biota is a difficult issue to tackle. According to Carlquist (1974), the major means of colonization of remote islands are: air flotation, dispersal by birds (internally or externally) and oceanic drift (by flotation or on raft). The first would favor small seeds, whereas large seeds are more often associated with zoochory or water-dispersed mangroves (Moles *et al.* 2005b). Furthermore, seed mass is often strongly correlated with ecology, especially habit (Moles *et al.* 2005a; Moles *et al.* 2005b), and therefore confounding effects can be expected for teasing apart dispersal and niche conservatism effects. In addition, island plants may evolve towards reduced dispersability, and seed size can evolve drastically after colonization (Carlquist 1974). The most diverse families in New Caledonia, Myrtaceae and Rubiaceae, are both well-represented by species with small wind-dispersed seeds and large fleshy fruits. Molecular phylogenies have shown that some genera with wind-dispersed seeds such as *Metrosideros* (Myrtaceae, Wright *et al.* 2000) or *Spiraeanthemum* (Cunoniaceae, Pillon *et al.* 2009b) as well as genera with large fleshy fruits such as *Syzygium* (Myrtaceae, Biffin *et al.* 2006), *Diospyros* (Ebenaceae, Duangjai *et al.* 2009) or *Planchonella* (Sapotaceae, Swenson *et al.* 2007) colonized the island on multiple occasions. Further data are needed on seed and fruit characteristics in New Caledonian plants, particularly for the many small families restricted or mostly found on this archipelago, and phylogenetic analyses are needed to determine the exact number of colonization events of each family. However, our observations do not support a major role for dispersal in the disharmony of the New Caledonian flora, and this may be because of the relatively ancient age of its biota that allowed even the least likely events of dispersal to happen and because other forces may be operating.

The influence of ultramafic soils

As New Caledonia emerged in the Tertiary, the island was largely covered by the ophiolitic nappe (Pelletier 2006). The weathering of this geological assemblage mostly composed of peridotites resulted in the formation of ultramafic soils (“serpentine”), which are challenging for plant growth (Proctor 2003). Thus, colonizing plants had to face the double challenge to first disperse over long distances and then to be able to grow on the ultramafic soils of the island. One can expect that this represented two major obstacles for successful immigrants. However, it is possible that some species may readily have a higher potential to adapt to such soils, as previously suggested by Kruckeberg (1986): “There is substantial evidence that populations have both the potential—by being preadapted—to tolerate unusual edaphic situations and often do become tolerant to them.” This was also suggested by Jaffré *et al.* (1987) for New Caledonian plants.

Nickel hyperaccumulation may be seen as a symptom of such groups that are preadapted to ultramafic soils, and this could explain the positive and significant association between hyperaccumulation and over-representation in the New Caledonian flora. Two angiosperm genera, *Phyllanthus* s.l. including *Glochidion* (Phyllanthaceae, Kathriarachchi *et al.* 2006) and *Psychotria* (Rubiaceae), contain a large number of nickel-hyperaccumulating species (24 and 32, respectively) distributed across several continents (Reeves 2003). These two genera are actually the two most diverse genera of the New Caledonian flora and belong to groups that are over-represented: Malpighiales and Gentianales. Although both genera are large with more than 1 000 species, most of the families of comparable size do not have as many nickel-hyperaccumulating species. Nickel-hyperaccumulating *Phyllanthus* s.l. species are known from Cuba, New Caledonia, Dominican Republic, Puerto Rico, Indonesia and the Philippines (Reeves 2003). Cuban and New Caledonian *Phyllanthus* are not closely related (Kathriarachchi *et al.* 2006), so the hyperaccumulation trait evolved at least twice. The broad

geographic distribution of the genus suggests a much larger number of appearances of this characteristic. Similarly, nickel-hyperaccumulating species of *Psychotria* are known from Cuba, Puerto Rico, Australia and New Caledonia, and multiple evolution of the trait is likely. Thus, these genera seem more efficient at adapting to ultramafic soils. Among the over-represented clades in New Caledonia, nickel-hyperaccumulating plants are known from the three orders Celastrales, Oxalidales and Malpighiales of the COM clade, Sapindales, Gentianales, Ericales, but have not so far been found in Apiales and Laurales. The COM clade itself contains 42% of the angiosperm species known to hyperaccumulate nickel according to Brooks (1998). In the Asteraceae and Fabaceae, two under-represented families, the numbers of hyperaccumulating species are rather modest, considering the large species numbers in these families. Also, nickel hyperaccumulation should not be considered as a necessary condition to ultramafic soils adaptation ; it is rather a possible symptom of adaptation to ultramafic soils. Most adapted species are tolerant by excluding and not by hyperaccumulating heavy metals. Indeed, heavy metals are only one of the several constraints occurring in those soils since plants also have to deal with a high Mg:Ca ratio, poor fertility and drought. Consequently, plants associated with such soils often have small and/or tough leaves (Read *et al.* 2006). The multiple independent origins of characters such as adaptation to ultramafic soils and heavy-metal hyperaccumulation within one given clade is paralleled by the multiple evolution of symbiosis allowing atmospheric nitrogen fixation in the ‘nitrogen-fixing clade’ within Rosids (Soltis *et al.* 1995), mycoheterotrophy in Dioscoreales (Merckx *et al.* 2006), C₄ metabolisms in grasses (Christin *et al.* 2007), aerial parasitism in Santalales (Vidal-Russel & Nickrent 2008), among other examples.

Exaptation to ultramafic soils

It might be hypothesized that the most represented clades in New Caledonia are those that present a potential pre-adaptation or rather an exaptation to ultramafic soils. According to

Gould & Vrba (1982), exaptations are “features that now enhance fitness but were not built by natural selection for their current role.” The distinction between these two hypotheses lies in whether or not the plants that colonized New Caledonia were already growing on ultramafic soils on their original landmasses. Ultramafic soils are also found in Eastern Australia (Batianoff *et al.* 1991; Batianoff *et al.* 2000), but they cover a small inland surface and have a relatively small flora (552 indigenous species), that is not well differentiated. Only 18 species are restricted to the serpentine of Central Queensland, and only two nickel-hyperaccumulating species are recorded there (Batianoff *et al.* 2000). In these areas, there is no record of several well diversified and over-represented families in New Caledonia, such as Cunoniaceae or Elaeocarpaceae, or the set of genera represented in the two areas is rather distinct for families such as Rubiaceae and Loganiaceae. However, it is possible that some groups used to be present on the Australian ultramafic soils and are not found there anymore. Furthermore, such soils are also recorded in areas such as the Philippines and New Guinea, but these floras are much less well studied (Proctor 2003) and less similar to that of New Caledonia (Marsch *et al.* 2009). Overall, most of these areas have one or several of the following features that suggest that they were not likely sources of propagules to colonize New Caledonia: small surface, poor flora, inland location, remoteness from New Caledonia. To our knowledge, no phylogenetic study to date has described a close relationship between any New Caledonian group and non-New Caledonian groups that grow on ultramafic soils. As indicated by the evolution of nickel-hyper-accumulation in distant areas in the genera *Phyllanthus* and *Psychotria*, cases of convergence are likely to be common. Thus, we believe that most plant groups were naïve to ultramafic soils when they reached New Caledonia, and their phylogenetic clustering would be evidence for exaptation of larger clades. Such groups would have been much more successful in colonizing New Caledonia and would have settled and diversified first. As erosion removed the layer of ultramafic soils, these groups that had

already settled on the island would have had an advantage over long-distance, over-water dispersers in the invasion of adjacent non-ultramafic soils. Further phylogenetic studies are needed to see how many times each clade has colonized New Caledonia to tease apart the impact of ultramafic soils on their success in settling and their success in diversifying in New Caledonia.

Only a few studies suggest a role for some ecological filter for shaping island biota, apart from high dispersability. However, while studying plants of the California chaparral, Ackerly (2004) found that small leaves, a generally accepted adaptation to Mediterranean-type climate, were already present in the ancestor of the chaparral lineage growing in cool temperate or subtropical conditions. He thus stated that “ancestors of chaparral taxa had already acquired appropriate traits that contributed to their success under Mediterranean-type climates.” In the case of ultramafic soils, it has been suggested that plants adapted to drought may have a greater ability to grow on such soils (Brady *et al.* 2005). Some similarities have been found in the response of plants to water stress and heavy metal stress, which can both involve small organic acids, amino acids and small peptides (Bhatia *et al.* 2005; Sharma & Dietz 2006; Yang *et al.* 2009), and the exaptation to ultramafic soils may lie in these physiological pathways.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 *List of families under-or over-represented in the New Caledonian flora.*

Appendix S2 *Representation of New Caledonian families mapped on the phylogenetic tree of the angiosperms, calculated for endemic species, or in comparison to the world flora.*

Table 1. Divergences making the largest contributions to the overall variation of the representation index. APA clade = Alseuosmiaceae+Phellinaceae+Argophyllaceae. COM clade = Celastrales+Oxalidales+Malpighiales. Nitrogen-fixing clade= Rosales+Fagales+Cucurbitales+Fabales

Rank	Divergences
	<i>Indigenous species</i>
1	Magnoliids vs. Eudicots
2	APA clade vs. Asteraceae+Calyceraceae+Goodeniaceae
3	COM clade vs. nitrogen-fixing clade
4	Paracryphiales vs. Asterales
	<i>Endemic species</i>
1	Magnoliids vs. Eudicots
2	APA clade vs. Asteraceae+Calyceraceae+Goodeniaceae
3	Magnoliids+Eudicots vs. Monocots+Ceratophyllales
4	COM clade vs. nitrogen-fixing clade

Fig. 1. Contrasting pattern of diversification of New Caledonian Cunoniaceae (88 species), Australian Cunoniaceae (36 species) and New Caledonian Asteraceae (34 species). Each bar represents the species richness of a genus, arranged in decreasing order. The seven genera of Cunoniaceae of New Caledonia probably represent each a single independent event of dispersal on New Caledonia (Bradford & Barnes 2001; Bradford 2002) with the exception of *Spiraeanthemum*, which likely arrived twice (Pillon *et al.* 2009b). Most of the Australian genera of Cunoniaceae represent phylogenetic independent lineages (Bradford & Barnes 2001), and none of the New Caledonia genera of Asteraceae are endemic, representing at least as many events of colonization of New Caledonia. Therefore, diversification of New Caledonian Cunoniaceae was more intense than that of Australian Cunoniaceae and of New Caledonian Asteraceae. Asteraceae in Australia are represented by 899 species and 143 genera; the mean species number per genus is six and the largest genus has 99 species. Species numbers are taken from Hnatiuk (1990), Jaffré *et al.* (2001), Bradford *et al.* (2004) and Pillon (2008).

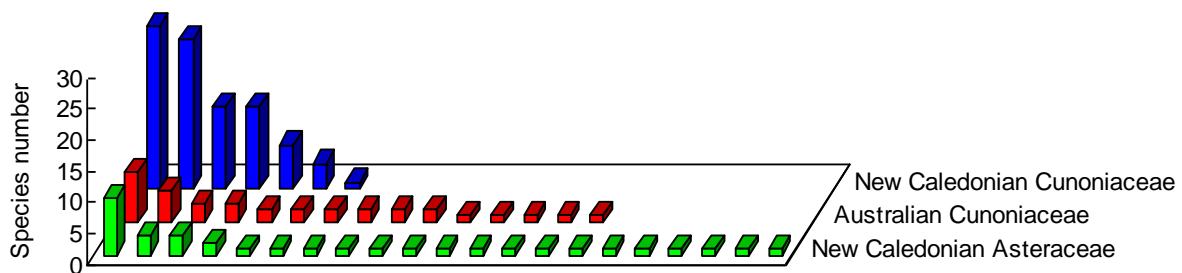


Fig. 2. Representation of New Caledonian families mapped on the phylogenetic tree of the angiosperms. The left-hand-side tree shows nodes that have a significantly higher (red square) or lower (blue square) mean representation index than expected. The right-hand-side tree shows families that are significantly over-represented (red branches) or under-represented (blue branches) in the flora of New Caledonia. Representation has been calculated for indigenous species of New Caledonia in comparison to the indigenous Australian flora.

