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Cryptic adaptive radiation in tropical forest trees in New Caledonia

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Summary

- The causes of the species richness of tropical trees are poorly understood, in particular the roles of ecological factors such as soil composition. The nickel-hyperaccumulating tree genus *Geissois* (Cunoniaceae) from the South-West Pacific was chosen as model of diversification on different substrates.
- We investigated the leaf element compositions, spatial distributions, and phylogeny of all species of *Geissois* occurring on New Caledonia.
- We found that New Caledonian *Geissois* descended from a single colonist and diversified relatively quickly into 13 species. Species on ultramafic and non-ultramafic substrates showed contrasting patterns of leaf element composition and range overlap. Those on non-ultramafic substrates were largely sympatric but had distinct leaf element compositions. In contrast, species on ultramafic substrates showed similar leaf element composition, but occurred in many cases exclusively in allopatry. Further, earlier work showed that at least three out of these seven species use different molecules to bind nickel.
- *Geissois* qualifies as a cryptic adaptive radiation, and may be the first such example in a lineage of tropical forest trees. Variation in biochemical strategies for coping with both typical and adverse soil conditions may help to explain the diversification and coexistence of tropical forest trees on similar soil types.

Keyword: Adaptive radiation, aluminium hyperaccumulator, island, New Caledonia, nickel hyperaccumulator, rainforest trees, serpentine, ultramafic

Introduction

The great diversity of species in tropical rainforests is a widely known fact and enigma, especially the coexistence, side by side, of many species of trees that have the same basic requirements. The coexistence of morphologically similar congeneric species in particular is puzzling (Richards, 1969; Leigh *et al.*, 2004). A growing number of studies indicate that substrates have a strong impact on the composition of tree communities and on the spatial distribution of individual plants within communities (John *et al.*, 2007; Anderson *et al.*, 2010; Schreeg *et al.*, 2010; Katabuchi *et al.*, 2012). Further, soils have played a pivotal role in plant speciation in other vegetation types such as the fynbos and the succulent karoo of the Cape region (Schnitzler *et al.*, 2011). Because most studies of rainforest plants have focused on communities, few have addressed niche partitioning among congeneric species. Fine *et al.* (2005) suggested that soils played a major role in the diversification of *Protium* in Amazonian forests; however, for sister species pairs that occur over large geographic scales (i.e. continents), it is difficult to exclude the possibility of earlier phases of allopatry in their divergence history. In contrast, when diversification has occurred on small oceanic islands, ecological speciation with gene flow is the most logical explanation (Savolainen *et al.*, 2006; Papadopulos *et al.*, 2011), demonstrating the value of such systems to test this hypothesis.

New Caledonia, an archipelago in the south-west Pacific is renowned for its rich, unique and threatened flora (Morat *et al.*, 2012). Although it is geologically a continental island, having drifted from Australia, New Caledonia was entirely submerged from the end of the Cretaceous until 37 My ago (Cluzel *et al.*, 1998; Pelletier, 2006), and all studies to date support the post-immersion origin of its biota (Grandcolas *et al.*, 2008; Cruaud *et al.*, 2012; Pillon, 2012). Thus, the history of the island's flora is comparable to that of true oceanic islands (e.g. volcanic islands) or “Darwinian” islands (Grandcolas *et al.*, 2008) sensu Gillespie & Roderick (2002). Nonetheless, the rich flora of New Caledonia is short of dramatic examples of adaptive radiation, particularly when compared to the Hawaiian or Macaronesian Islands (see examples in Givnish, 2010). Few radiations display the diversity of growth forms typically associated with ecological divergence. One notable exception is the genus *Oxera* (Lamiaceae), which contains a variety of life-forms: monocaule shrubs, tangled shrubs and vines that range from slightly to very woody (Mabberley & de Kok, 2004). Further, there are no convincing examples of radiations involving divergence in floral morphology associated with different pollination syndromes aside from *Oxera*, some orchids, and genera engaged in specific plant-pollinator mutualisms such as *Ficus* (Cruaud *et al.*, 2012) and *Phyllanthus* (including *Glochidion*, Kawakita & Kato, 2004). This paucity may be linked to the under-representation of lineages with zygomorphic flowers such as monocots, Asterales, Fabales, and Lamiales in New Caledonia (Pillon *et al.*, 2010).

The primary distinguishing feature of New Caledonia’s terrestrial environment is the abundance of ultramafic substrates that cover one third of the surface of the main island. Soils that develop on ultramafic rocks (including serpentine) have several characteristics that are limiting for plant growth, including low availability of N, P and K, a high Mg/Ca ratio, high concentrations of heavy metals (e.g. Co, Cr, Ni) and variable but often low water-holding capacity; in addition, fire seems to play an important role in vegetation dynamics (Jaffré, 1980; Proctor, 2003). Because of these edaphic characteristics, New Caledonia might be considered an Old Climatically Buffered Infertile Landscape (OCBIL, Hopper, 2009) or an Old Stable Landscape (OSL, Mucina & Wardell-Johnson, 2011), where elevated nutritional specialization is expected. Ultramafic substrates have been implicated as a cause of the disharmonic nature of the New Caledonian flora, for example the under-representation of monocots and Lamiales or the overrepresentation of Magniolianae and Malpighiales (Pillon *et al.*, 2010). Clades that are well represented in New Caledonia have a high frequency of nickel-hyperaccumulating species (Jaffré *et al.*, 2013), a trait associated with ultramafic substrates (Reeves & Baker, 2000). The ability to grow on ultramafic substrates, and possibly metal hyperaccumulation, may have been exaptations (Pillon *et al.*, 2010); i.e. these traits appeared in non-New Caledonian ancestors growing on normal soils and turned out to be advantageous when colonizing the island which was probably entirely covered with ultramafic rocks when it first emerged (Pelletier, 2006). Other types of substrate found in New Caledonia include limestone and mostly old metamorphic or sedimentary rocks (including greywacke, schist and shale) that can be hard to characterize. It is often accepted that the variety of New Caledonian soils is an important factor underlying the diversity of the flora (Jaffré, 1993). How plants have adapted to these different edaphic conditions is poorly known, but the few studies that have addressed this problem suggest the involvement of high trait lability, hybrid speciation, and cryptic species among other possibilities (de Kok, 2002; Pillon *et al.*, 2009b; Pillon *et al.*, 2009c).

In this study, we focus on the genus *Geissois* (Cunoniaceae), a lineage of trees that are known to hyperaccumulate nickel (Jaffré *et al.*, 1979). We studied the leaf element composition and geographic distributions of 13 species in New Caledonia to examine associations among leaf element composition, soil type and degree of sympatry. Molecular phylogenetics and molecular clocks were also applied in order to test the single origin of the genus on the island, to estimate the speed of its diversification, and to determine if New Caledonian *Geissois* qualifies as an adaptive radiation.

Materials and Methods

The genus *Geissois*

The genus *Geissois* Labill. comprises 19 species, all occurring in Melanesia (Hopkins *et al.*, 2013): 13 species in New Caledonia, four in Fiji, one in Vanuatu, and one in the Temotu Province of the Solomon Islands (Fig. 1). Species of *Geissois* are tall shrubs to large trees primarily found in rainforests and forest edges but also in secondary vegetation, including savanna (generally dominated by *Melaleuca quinquinervia*) and maquis (scrubby vegetation on ultramafic rocks). The genus is characterized by its palmate, opposite leaves (3 to 11 leaflets), its conspicuous intrapetiolar stipules, and its relatively uniform flowers and inflorescences (Hopkins, 2008; Fogliani *et al.*, 2009). The flowers are red and show some minor variation in size and pubescence. They are arranged in bottle brush-like racemes that are axillary or borne on branches, and project stiffly from the stem or are sometimes pendulous. The racemes are simple (or trident in *G. hirsuta*), and may be solitary or in clusters. They attract a wide range of nectarivorous birds (Barré *et al.*, 2010) as well as bats, geckos and insects (Hopkins *et al.*, in press). The fruits are capsules, and the small winged seeds are dispersed by wind. Most species are distinguished by leaflet and stipule characters, including the number, size and shape of the leaflets, the size and shape of the stipules, and type of pubescence, as well as the presence of domatia (Hopkins *et al.*, in press); none of these characters has any obvious adaptive value (cf Ashton, 1969).

Leaf element composition

To take into account recent advances in *Geissois* systematics (Hopkins, 2006; Hopkins, 2007; Hopkins & Pillon, 2011), we updated the information in Jaffré *et al.* (1979) with new measurements. Herbarium specimens have been shown to be a useful source of samples for the analysis of leaf element composition (Brooks *et al.*, 1977). Therefore, we obtained small leaf samples (~1g) at the Herbier de la Nouvelle-Calédonie (NOU) at IRD Nouméa. We sampled up to five specimens per species whenever possible, and more for species found on a range of soil types (Supporting Information Table S1). No samples were taken from herbarium sheets when doing so would have affected the quality of the information provided by that sheet, and this constrained our choice of samples for some species. Some species are naturally rare and represented by only a few specimens, e.g. the critically endangered *G. belema* and G. *bradfordii*, therefore fewer samples were included for such species. Otherwise, we tried to maximize the geographical coverage of each species' range. The samples were ground to a powder, and 0.25-0.3g was dry-ashed at 500°C for 5.5 hours and re-suspended in 25 mL of 1M HCl before being run on a Varian Vista MPX ICP-OES at the UH Hilo Analytical Lab. We measured concentrations of seven elements: Al, Ca, Cr, Fe, Mg, Ni, and P in each leaf sample. Samples with a value of iron above 500 ppm were conservatively excluded, because of possible soil contamination (Reeves & Baker, 2000 recommended a threshold of 1000 ppm). Data were then log-transformed and standardized. We performed Non-Metric Multidimensional Scaling (NMDS) in PAST (Hammer *et al.*, 2001) to obtain a graphical representation of the variation within and among species in leaf elemental content. We used Hotelling's pairwise comparison in PAST to test for differences in leaf element composition among species.

Species distributions

Species distributions were established from a list of specimens of *Geissois* (Hopkins *et al.*, in press) largely based on the collection of the NOU herbarium. A convex polygon was drawn to represent the distribution of each species, and its surface area was calculated; overlap between those polygons and the ocean was nonexistent to negligible. We also calculated the percentage of geographic range overlap for each pair of species by dividing the area of overlap by the area of the species with the smaller range. Using the range of the more restricted species yielded the maximum estimate of sympatry, and thus the most conservative estimate of allopatry, in each case.

Phylogenetic analyses

For phylogenetic reconstruction, we supplemented and re-analyzed data from Pillon (2011). Because of the persistence of multiple ITS copies in many Cunoniaceae, and the low level of variation of plastid genes, we sequenced a single plastid locus, *trnL-F*, and two nuclear genes, *ncpGS* and *PHYC*, using the protocols described in Pillon *et al*. (2009a). Sequences were available for all New Caledonia species known at that time plus *Geisssois denhamii* from Vanuatu. We added to this dataset *trnL* and *PHYC* sequences for the recently described *G. belema* and the Fijian *G. ternata*, and a *trnL* sequence of the Fijian *G. superba* from Genbank (Supporting information Table S4). Best fit substitution models for *trnL*, *PHYC* and *ncpGS* were HKY, HKY+γ and HKY+γ according to JModeltest analyses (Posada, 2008). No evidence for recombination was found in either the *PHYC* or the *ncpGS* datasets using GARD (Kosakovsky Pond *et al.*, 2006), assuming no site-to-site variation (most sensitive setting). For each dataset, we ran two-million generations of Markov Chain Monte Carlo (MCMC) in MrBayes (Ronquist

& Huelsenbeck, 2003), sampling the tree every 1,000 generations, using the appropriate substitution models and a 500,000-generation burnin; convergence was checked in Tracer (Rambaut & Drummond, 2007). In order to combine the *PHYC* and *ncpGS* datasets, where some species are represented by multiple accessions or heterozygotes, we used *BEAST (Heled & Drummond, 2010). We twice ran a 500-million-generation MCMC, with appropriate substitution models, a Yule process for tree reconstruction starting with a UPGMA tree, and a strict molecular clock, sampling one tree every 500,000 generations and with a burnin of 100-million generations.

In order to estimate a date for the origin of the radiation of New Caledonian *Geissois*, we applied a molecular clock analysis on a reduced combined dataset of *ncpGS* and *PHYC*. In spite of the availability of an almost complete generic sampling for plastid genes (Bradford & Barnes, 2001; Hopkins *et al.*, 2013) and the rich fossil record of Cunoniaceae in Australia (Barnes *et al.*, 2001), the absence of variation in plastid genes within New Caledonian *Geissois* (Supporting Information Fig. S4), as in other New Caledonian Cunoniaceae genera (Pillon, pers. obs.), precluded the dating of the crown radiation. To simplify the analyses, we limited the sampling within *Geissois* by avoiding heterozygote accessions but making sure to sample the deepest split within New Caledonian *Geissois* as well as two other genera of New Caledonian Cunoniaceae : *Codia* and *Spiraeanthemum* (group *brongniartianum*, Pillon *et al.*, 2009a). We ran two analyses of 100-million generations MCMC in BEAST v.1.7.5 (Drummond *et al.*, 2012), applying appropriate substitution models, a lognormal clock, and a Yule tree prior using an input ultrametric tree obtained from r8s (Sanderson, 2003), sampling a tree every 100,000 generations and with a burnin of 10-million generations. Prior age at the root (divergence Cunoniaceae-Brunelliaceae) followed a normal distribution with a mean of 86 My and a standard deviation of

2 My. This age was obtained by Heibl & Renner (2012) for the divergence between Cunoniaceae and its putative sister group (Brunelliaceae, Cephalotaceae, Elaeocarpaceae). A similar age of 83 My was obtained independently for the same node by Xi et al. (2012). All BEAST analyses were run on Lifeportal (University of Oslo), and convergence of the runs was checked in Tracer. Speciation rates were calculated using equation 4 of Magallón & Sanderson (2001).

Results

Low levels of iron were observed in all leaf samples of *Geissois* (max 230 ppm) with the exception of one sample of *G. pruinosa* var *pruinosa* (*MacKee 45227*, 924 ppm), which was excluded from subsequent analyses because of suspicion of contamination with soil. All species of *Geissois* naturally present on ultramafic substrates were found to be nickel hyperaccumulators (Ni content >1,000 ppm), with the notable exception of the recently described *G. belema* (Supporting Information Fig. S1). All species absent from ultramafic substrates had low nickel content, suggesting that the high levels reported previously in *G. montana* and *G. racemosa* by Jaffré *et al.* (1979) were likely to result from confusion at a time where the taxonomy of the genus was not well understood. In fact, for *G. hippocastanifolia*, *G. polyphylla* and *G. montana,* nickel was undetectable in four out of five samples. Only one individual of *G. balansae*, from near Ponerihouen (*Haudricourt 817*, vague locality, no ecological information) had a relatively high nickel concentration (571 ppm). This finding suggests that this plant was growing on or in the vicinity of ultramafic substrate, although the species is not reported from this habitat. High nickel content was observed in all accessions of *G. pruinosa* var *intermedia*, a taxon that is reported only in the north-east, usually on non-ultramafic substrate. Lastly, we report here for the first time evidence that *G. polyphylla* is an Al hyperaccumulator; four of five individuals sampled had values equal to or above 1,000 ppm, and no other species of *Geissois* reached this threshold (see Apendix S5).

Non-Metric Multidimensional Scaling (NMDS) on all elements analyzed allowed a relatively clear separation between species found on ultramafic substrates and those found on non-ultramafic ones (Fig. 2). Overlaps were due to: *G. hirsuta*, which seems to be the only species unambiguously present on both soil types, the one sample of *G. balansae* with an unusually high Ni content, and *G. belema*, which grows on ultramafic substrates but does not hyperaccumulate nickel. Each of the five species restricted to non-ultramafic substrate had a largely distinct elemental profile, with only slight overlap between *G. polyphylla* and *G. hippocastanifolia*, and a larger overlap between *G. montana* and *G. balansae*. Although all of these species had similar nickel concentrations in their leaves, they varied considerably in the concentrations of other elements such as Al, Ca, Mg. Species from Vanuatu, Fiji and the Solomon Islands, all of which occur on non-ultramafic substrates, had elemental profiles that fell within the range of *G. balansae* (Supporting Information Fig. S2). The geographic ranges of species from non-ultramafic substrates in New Caledonia were highly overlapping (Fig. 3, Supporting Information Table S3 & Fig. S3). The only exception was the species pair, *G. montana-G. balansae*, the first of which occurred northward from Mt Aoupinié and the second southward from Mt Aoupinié. In contrast to the near-unique elemental profiles of non-ultramafic species, those restricted to ultramafic substrate showed highly overlapping leaf element compositions; no species had a distinct profile (Fig. 2), even if the widespread and ecologically variable *G. pruinosa* was excluded. Also in contrast to non-ultramafic species, the geographic distributions of taxa on ultramafic substrate tended to be more disjunct (Fig. 3, Supporting

Information Table S3 & Fig. S3). For example, *G. bradfordii* and *G. velutina* are restricted to the far south, *G. magnifica* to the east coast, *G. lanceolata* to the west coast, and *G. belema* to the northern island of Art.

Little variation was found in the *trnL* dataset (Supporting Information Fig. S4) with all the New Caledonian species having identical DNA sequences except for *G. hippocastanifolia*, which differed by a single base; the two Fijian species shared one substitution. The *PHYC* tree (Supporting Information Fig. S5) was also poorly resolved with only two groups supported within *Geissois*: *G. hippocastanifolia* + *G. polyphylla* and *G. denhamii* (Vanuatu) + *G. ternata* (Fiji). In the *ncpGS* tree (Supporting Information Fig. S6), *G. hippocastanifolia* and *G. polyphylla* formed a clade that is sister to the rest of the species of New Caledonia plus *G. denhamii* (Vanuatu). Several species had multiple distant alleles, and some represented by multiple accessions were not monophyletic. The combined *PHYC-npcGS* analysis in *BEAST (Fig. 4) also recovered *G. hippocastanifolia* and *G. polyphylla* as sister species, forming a clade that was sister to the rest of the genus (*G. racemosa* group), including all other New Caledonian species and *G. denhamii* (Vanuatu). Internal supports within the *G. racemosa* group were low. The molecular clock analysis on a combined *PHYC-npcGS* dataset (Supporting Information Fig. S7) indicated an age of 7.3 My (3.5-12.8 My) for the crown of *Geissois* (Table 1).

Discussion

New Caledonia is well known for its diverse flora; however, no dramatic cases of adaptive radiation have been documented thus far. We show here that *Geissois* satisfies the criteria of an adaptive radiation (Schluter, 2000): common ancestry, rapid speciation, correlation between phenotype and environment, and trait utility. The difference between New Caledonian *Geissois* and classic examples of adaptive radiation is the lack of apparent niche separation in *Geissois*, which occurs on just two broad soil types. Radiation of this genus within the small land area of New Caledonia's main island appears to have involved divergence of metal uptake mechanisms on ultramafic substrates and character displacement, or ultra-fine partitioning of edaphic niches, by species on non-ultramafic substrates.

Common ancestry−Molecular phylogenetic analyses provide support for the monophyly of *Geissois*; all New Caledonian species belong to a single clade and are likely to be descended from a single colonist. Subsequently, it seems that a unique dispersal event towards neighboring islands gave rise to the endemic species of Vanuatu and Fiji. *Geissois polyphylla* and *G. hippocastanifolia* are recovered as sister species, and are in turn sister to the *Geissois racemosa* group (all other New Caledonian species, including the morphologically divergent *G. hirsuta* and extra-New-Caledonian species). All species growing on ultramafic substrates belong to the *G. racemosa* group. This clade was poorly resolved, and several species were not recovered as monophyletic in the *ncpGS* analysis. The lack of cohesion of the individual species in this group suggests either hybridization among species or retention of ancestral polymorphisms, both of which are consistent with recent divergence.

Rapid speciation−Diversification of *Geissois* occurred at a rate of 0.26 sp.My^{-1}(Table 1). This rate is similar to that of other New Caledonian plant radiations (Pillon, 2012), which may be considered modest among known plant radiations. Nevertheless, when taking into account the small surface area of the island, *Geissois* had a diversification rate per unit area of 1.5 x 10^{-5} sp.My^{-1}.km^{-2}. This is comparable to rates reported for rapid island radiations such as Hawaiian *Bidens* and Macaronesian *Echium*, and higher than the rates reported for large continental radiations such as Andean *Lupinus* and Eurasian *Dianthus* (Knope *et al.*, 2012). This figure is especially significant considering that the archipelago is dominated by one large island and is therefore far less fragmented and hence less suited for allopatric speciation than most archipelagos.

Correlation between phenotype and environment −Although the variation in vegetative traits that characterize the different species of *Geissois* in New Caledonia shows no clear relationship with ecology, the variation in leaf element composition among species is more readily associated with the environment. All *Geissois* species growing on ultramafic substrates except *G. belema* are nickel hyperaccumulators, species absent from non-ultramafic substrates have a higher Al content, and *G. polyphylla* qualifies as Al hyperaccumulator. As a group, species from ultramafic substrates were elementally distinct from those on non-ultramafic ones when considering all elements together. The contrast between these groups is not likely to be due solely to plasticity given that some species occurring sympatrically on ultramafic substrates, and thus likely experiencing equal nickel availability, displayed different levels of Ni concentration, for example *G. velutina* and *G. pruinosa* var *pruinosa*. In addition, previous greenhouse experiments found that the non-ultramafic *G. montana* is sensitive to watering with a nickel solution whereas the ultramafic taxon *G. pruinosa* var *pruinosa* is resistant (L. Richard, Y. Pillon & H. Amir pers. obs.), indicating a genetic basis for tolerance to this heavy metal. Although nickel tolerance and hyperaccumulation are different processes, the former is a pre-requisite for the latter, in natural settings at least. Understanding the mechanisms that underlie the variation among *Geissois* species in the ability to hyperaccumulate nickel will nevertheless require testing under controlled conditions.

Trait utility−Little is known about the evolutionary significance of nickel hyperaccumulation in *Geissois*. In other plant groups, however, nickel hyperaccumulation is suggested to confer resistance to herbivory (Boyd, 2007), pathogens (Hörger *et al.*, 2013) or drought (Bhatia *et al.*, 2005). There is less information on the significance of aluminium hyperaccumulation (Jansen *et al.*, 2002), although it has been suggested as a mechanism to deter herbivory. This idea has not been well tested, however, and was not supported in a field study in the Philippines including six aluminium hyperaccumulator and one nickel hyperaccumulators (Proctor *et al.*, 2000). In the aluminium hyperaccumulator, *Melastoma malabathricum*, an increase in oxalate concentration in the rhizosphere enabled solubilization of aluminium phosphate, and an increase in plant phosphorus was associated with an increase in plant aluminium (Watanabe & Osaki, 2002). In the current study, the single aluminium hyperaccumulator species, *G. polyphylla*, also had the highest phosphorus content. It is possible, therefore, that this species has developed a similar mechanism to increase phosphorus uptake. Similarly nickel hyperaccumulation could also be a byproduct of a different physiological pathway rather than an end in itself.

Diversification on non-ultramafic substrates–Our data suggest character displacement within *Geissois*, at least on non-ultramafic substrates, where largely sympatric species exhibit different elemental signatures (Fig. 2, Supporting Information Table S5). The geology of New Caledonia is fairly complex, and non-ultramafic rocks of the main island include old and often poorly delimited geological layers. As such, we cannot exclude the possibility that different species of *Geissois* with overlapping distributions have preferences for different soils (micro-habitats), which could explain the variation in leaf element composition among them. However, in areas such as Col d'Amieu, *G. balansae*, *G. polyphylla* and *G. racemosa* can grow within a few meters of each other. Furthermore, *G. hippocastanifolia* and *G. montana* are often sympatric (Mandjélia, Aoupinié) and can hybridize as suggested by the intermediate morphology of one specimen (*Pillon* 81, Mandjélia). It is possible that these species differentially exploit available soil nutrients (cf. Richards, 1969), and this may explain their coexistence. Testing this hypothesis would require analysis of individuals growing in controlled conditions. Interestingly the only two non-ultramafic species that have somewhat similar leaf element compositions, *G. montana* and *G. balansae*, are largely allopatric. Further, even though *G. hirsuta* has a broad ecology (occurring on both ultramafic and non-ultramafic substrates), its elemental signature is different from those of at least *G. hippocastanifolia*, *G. montana* and *G. polyphylla* (Fig. 2, Supporting Information Table S2). The fact that the allopatric *G. denhamii* (Vanuatu), *G. ternata* (Fiji) and *G. pentaphylla* (Solomon Islands) have relatively similar elemental signatures, that are in turn similar to the New Caledonian *G. balansae*, suggests that the variation in elemental signatures observed among species on non-ultramafic substrates in New Caledonia is not the result of random processes but rather of character displacement to minimize competition. The phylogenetic position of *G. polyphylla* indicates that aluminium hyperaccumulation is a derived character that evolved in New Caledonia, as it is not found in other species of the *Geissois* nor in the closely related *Pseudoweinmannia* and *Lamanonia* (Nogueira & Haridasan, 1997). The character is, however, found in several less closely related genera of Cunoniaceae in Australia (Jansen *et al.*, 2002).

Diversification on ultramafic substrates−Species growing on ultramafic substrates had largely overlapping elemental signatures, including high Ni content; however, the mechanisms by which they attain these signatures may be different. In a study of the nickel-binding ligand in several hyperaccumulating taxa, Callahan *et al.* (2012) found that *G. bradfordii*, *G. hirsuta* and *G. pruinosa* var *pruinosa* had distinct metabolite profiles. Although in all species nickel was bound to nicotianamine, this metal was also bound to serine in *G. bradfordii*, to citric acid in *G. pruinosa* var *pruinosa* and to citric acid and galacturonic acid in *G. hirsuta*. Therefore, despite having similar levels of nickel in their tissues, these species appear to possess different mechanisms for nickel storage. Surprisingly, *Geissois belema* does not seem to accumulate nickel; this might be explained by the fact that it grows on highly weathered ferralitic soils where nickel is not available in significant amounts (Jaffré & L'Huillier, 2010).

In contrast to non-ultramafic substrates that are almost continuous on the main island, ultramafic substrates represent a highly fragmented environment. Their patchy distribution across the island is likely to have favored allopatric speciation and may explain the weaker ecological differentiation observed in some cases, through reduced interspecific competition. Of all 13 species in New Caledonia, *G. bradfordii* is the only one that seems to have an obviously narrow ecology, being restricted to the bank of a river in an ultramafic area. This rupicolous species has narrow leaflets as expected in plants with such ecology (van Steenis, 1981). Interestingly, it occurs in the south of the island, as do some other rupicolous Cunoniaceae in the genera *Spiraeanthemum*, *Cunonia* and *Pancheria* (Hopkins *et al.*, in press).

Widespread species−Only two species of *Geissois* are broadly distributed and documented on both ultramafic and non-ultramafic substrates. *Geissois pruinosa* is a species complex most commonly found on ultramafic substrates. Although several records suggested the presence of var *intermedia* on non-ultramafic rocks in the north-east, all of the samples analyzed in the current study had a high Ni content, suggesting that they were collected on ultramafic substrates. Serpentine rocks are patchily distributed in the north-east, and it may be that *G. pruinosa* always has access to nickel and may be more strictly associated with ultramafic substrates than previously thought. Further fieldwork is required to re-evaluate the ecology of this species.

Geissois hirsuta is therefore the only species unambiguously present on both types of soil, and it is both morphologically distinct from other species and uniform throughout its range. Thus, the presence of cryptic species is not indicated (cf. *Spiraeanthemum*, Pillon *et al.*, 2009b). Rather, it could represent an interesting model for studies of the genetic basis of adaptation to ultramafic conditions. Aside from these two widespread species, each species of *Geissois* possesses a unique combination of ecology, elemental signature, and geographic distribution (Table 2). Therefore, only the mechanism by which these two species remain distinct remains unexplained by this study, although pollinators may play a role (see below).

Reproductive isolation−It is not clear how reproductive barriers evolved within *Geissois* to isolate so many species within such a small geographic area, but the variation observed in soils, leaf element composition and mechanism of metal accumulation may be associated with reduced fitness of interspecific hybrids (i.e., postzygotic barriers). Postzygotic barriers may then promote the evolution of prezygotic barriers through reinforcement (Widmer *et al.*, 2009), which would be consistent with the differential flowering peaks among some *Geissois* species observed in the field but undetected in the herbarium (Hopkins *et al.*, in press). Variation in flowering time may also be linked directly to differences in substrate (Savolainen *et al.*, 2006), particularly if associated with water availability (Borchert, 1994). With a single possible exception, there is no evidence of diversification in *Geissois* through adaptation to different pollinators. The uniquely widespread non-edaphic specialist *G. hirsuta* has distinct pendant, trident-shaped inflorescences that may attract a distinct suite of pollinators. Pollinator isolation might perhaps maintain the distinctiveness of this species in spite of its ecological and geographical overlap with so many other species of the genus. Further work is needed to test these ideas.

In conclusion, the radiation of *Geissois* on New Caledonia was the result of the rapid diversification from a single progenitor. Speciation was facilitated by the sharp contrast between non-ultramafic and ultramafic substrates where nickel–hyperaccumulating species evolved. On non-ultramafic substrates, species display broad geographic overlap but generally have distinct elemental signatures, suggesting specialization to different microhabitats within this variable soil type or, more likely, different preferences for soil nutrients. In contrast, on ultramafic substrates, allopatry may have been more important for diversification. However, even though species displayed similar elemental signatures, preliminary biochemical work suggests that different mechanisms evolved within *Geissois* to deal with ultramafic conditions. New Caledonia *Geissois* may be the first confirmed case of adaptive radiation in trees. There are only a modest number of confirmed cases of adaptive radiation in plants, and most involve herbs or plants that were ancestrally herbs (Givnish, 2010). Few studies have been able to determine how congeneric tree species partition the ecological space within a given geographical area (Cavender-Bares *et al.*, 2004). Our study suggests that a large part of the diversity within a lineage of tropical forest trees may be hidden in their less-visible interactions with different soils and their different mechanisms of nutrient and metal uptake. These results need to be confirmed in other plant groups and in other geographical areas where contrasts in soil conditions may not be as sharp as in New Caledonia.

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Supporting information

Table S1. Results of leaf element analyses on dry leaf samples.

Table S2. Results of Hotelling pairwise comparisons of leaf element compositions of *Geissois* species.

Table S3. Pairwise percentage overlap of the geographic distributions of New Caledonian *Geissois* species.

Table S4. Index of collections used for molecular phylogenetics analyses with voucher information and Genbank accession numbers.

Table S5. Principal ecological and elemental characteristics of *Geissois* species mentioned in the text.

Figure S1. Nickel concentrations in leaves of New Caledonian *Geissois* species.

Figure S2. NMDS of leaf element composition of all New Caledonian *Geissois* species restricted to non-ultramafic soils and species from Vanuatu, Fiji and Solomon Islands.

Figure S3. Distribution maps of the New Caledonian species of *Geissois*.

Figure S4. Half-compatible consensus tree of the tribe Geissoieae based on *trnL* sequence data.

Figure S5. Half-compatible consensus tree of the tribe Geissoieae based on *PHYC* sequence data.

Figure S6. Half-compatible consensus tree of *Geissois* based on *ncpGS* sequence data.

Figure S7. Chronogram of the family Cunoniaceae based on BEAST analysis of *PHYC* & *ncpGS* data.

Table 1. Crown age for some Cunoniaceae radiations in New Caledonia. Diversification rate per km^2 is calculated for the main island only (16,372 km^2); *Geissois belema*, which is endemic to Art Island, was therefore excluded from the calculation of diversification rate.

	Species number	Crown age median [95% confidence interval] (My)	Diversification rate ($sp.My^{-1}$)	Diversification rate ($sp.My^{-1}$ km^{-2})
New Caledonian *Geissois*	13	7.3 [3.5-12.8]	0.26	$1.5\ 10^{-5}$
Codia	14	5.3 [2.5-9.4]	0.37	$2.2\ 10^{-5}$
Spiraeanthemum group *brongniartianum*	6	6.3 [2.3-12.1]	0.17	$1.1\ 10^{-5}$

Table 2. Pairwise ecological, elemental and geographical differences between species of New Caledonia *Geissois*. S=no substrate overlap (ultramafic vs. non-ultramafic substrate), E=no elemental overlap (no overlaps between polygons in NMDS analysis of leaf element composition), e=minor elemental overlap (for the species pair *G. hippocastanifolia*/*G. polyphylla*), G=no geographical overlap of species distributions, g=geographical overlap of less than 5%. *pruinosa* includes both varieties (*pruinosa*, *intermedia*).

	balansae	*belema*	*bradfordii*	*hippocastanifolia*	*hirsuta*	*lanceolata*	*magnifica*	*montana*	*polyphylla*	*pruinosa*	*racemosa*	*trifoliolata*	*velutina*
balansae													
belema	S/-/G												
bradfordii	S/E/G	-/E/G											
hippocastanifolia	-/E/-	S/E/G	S/E/G										
hirsuta	-/-/-	-/-/G	-/E/-	-/E/-									
lanceolata	S/E/-	-/E/G	-/E/G	S/E/G	-/-/-								
magnifica	S/E/G	-/E/G	-/E/G	S/E/g	-/-/-	-/-/G							
montana	-/-/G	S/E/G	S/E/G	-/E/-	-/E/-	S/E/G	-/E/G						
polyphylla	-/E/-	S/E/G	S/E/G	-/e/-	-/E/-	S/E/g	S/E/G	-/E/-					
pruinosa	-/-/-	-/E/G	-/-/-	-/E/-	-/-/-	-/-/-	-/-/-	-/E/-	-/E/-				
racemosa	-/E/-	S/E/G	S/E/G	-/E/-	-/-/-	-/E/-	S/E/-	-/E/-	-/E/-	-/E/			
trifoliolata	-/E/-	-/E/G	-/E/G	-/E/G	-/-/-	-/E/G	-/-/G	-/E/G	-/E/-	-/-/-	-/E/-		
velutina	S/-/g	-/E/G	-/E/-	S/E/G	-/-/-	-/E/G	-/-/G	S/E/G	S/E/G	-/-/-	S/E/G	-/E/G	

Figure 1. Distributions of the genus *Geissois* in the South-West Pacific and the closely related genera *Karrabina* and *Pseudoweinmannia* in Australia (both disjunct between northern Queensland and southern Queensland-northern New South Wales). *Lamanonia*, the fourth genus of the tribe Geissoieae, occurs in South America (not shown).

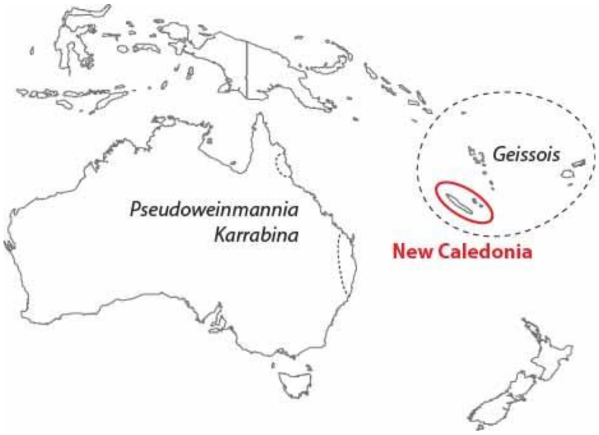

Figure 2. NMDS of leaf element composition of New Caledonian *Geissois* species. *ba =Geissois balansae*, *be= G. belema*, *br=G. bradfordii*, *hip=G. hippocastanifolia*, *hir=G. hirsuta*, *l=G. lanceolata*, *ma=G. magnifica*, *mo= G. montana*, *po=G. polyphylla*, *pr=G. pruinosa* (all varieties), *t= G. trifoliolata*, *ra= G. racemosa*, *v= G. velutina*.

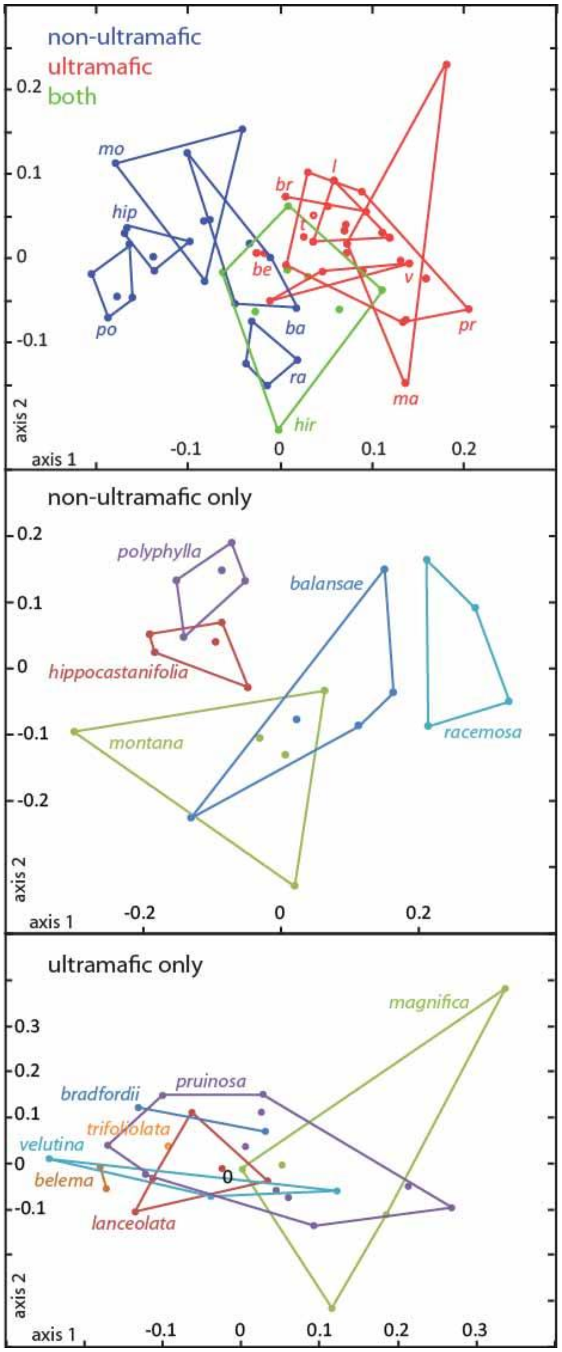

Figure 3. Example of distributions of selected *Geissois* species in New Caledonia, showing broad sympatry among species on non-ultramafic substrates (left-hand map), and allopatry of species on ultramafic substrates (right-hand map). Areas in red are ultramafic rocks.

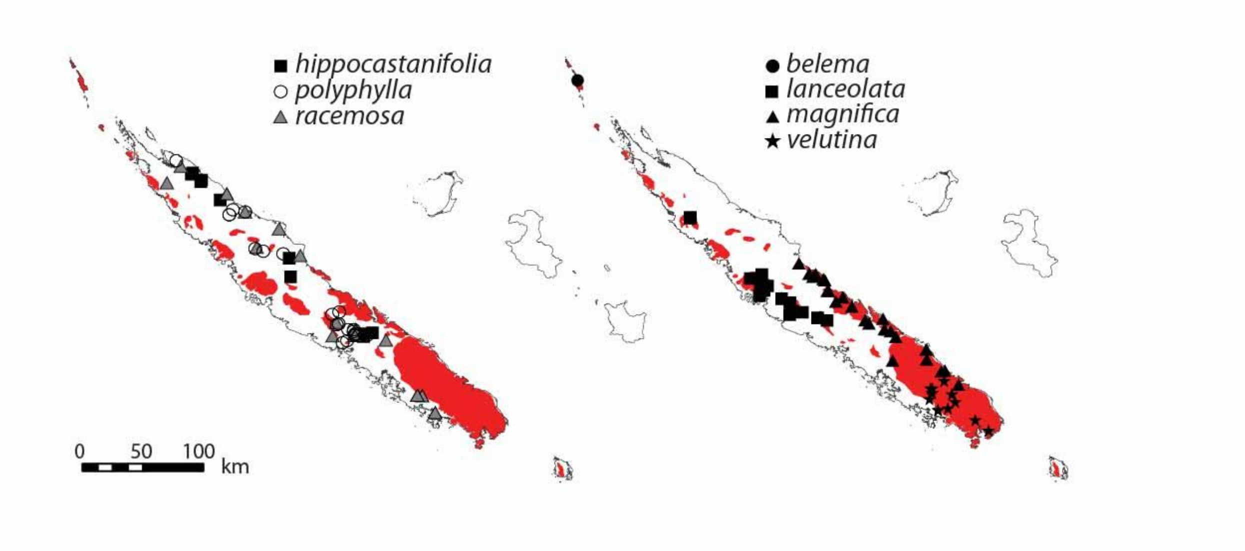

Figure 4. Half compatible consensus tree of *Geissois* obtained from the combined *PHYC-ncpGS* analysis in *BEAST. Numbers at nodes indicate posterior probabilities above 0.5. var *int*.= var. *intermedia*. Substrate preferences are indicated: UM: ultramafic, NUM: non-ultramafic, UM-NUM: both types. Hyperaccumulation of aluminium or nickel is indicated by Al or Ni, respectively. *Geisois belema* is not included here because only the *PHYC* sequence was available.