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ARTICLE *in* MOLECULAR PHYLOGENETICS AND EVOLUTION · FEBRUARY 2014

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# New Caledonian lineages of *Psychotria* (Rubiaceae) reveal different evolutionary histories and the largest documented plant radiation for the archipelago



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## ARTICLE INFO

### Article history:

Received 21 February 2013

Revised 23 October 2013

Accepted 24 October 2013

Available online 5 November 2013

### Keywords:

Dispersal mode

Diversification

Island colonization

New Caledonia

Phylogenetic dating

*Psychotria* s.l.

## ABSTRACT

New Caledonia is a remote archipelago of the South-West Pacific, whose flora is rich, distinctive, and disharmonic. The interest of botanists has long been attracted by the spatio-temporal origin of this flora, but little attention has been paid to the modes of colonization and the diversification processes that have led to the archipelago's modern flora. To date, no explosive plant radiation has yet been highlighted for New Caledonia. A dated phylogenetic framework on the second richest New Caledonian genus – *Psychotria* s.l. and its allied genera (tribes Psychotrieae and Palicoureeae, Rubiaceae; ca. 85 species) – is provided in this study to explore its patterns of colonization and diversification in the archipelago. This study is based on a comprehensive species sampling, two nuclear and four plastid loci. Results show that New Caledonia was colonized four times by *Psychotria* and its allied genera during the Neogene long after its mid-Eocene re-emergence from the sea. The Pacific clade of Psychotrieae, one of the largest plant diversifications in the Pacific islands and the Indo-Pacific region, is absent from New Caledonia, possibly due to niche competition. Although the four lineages colonized New Caledonia relatively simultaneously during the Neogene, they express different evolutionary histories, as revealed by unevenness in species richness and net diversification rates. The genus *Geophila* has not diversified on New Caledonia, as a non-endemic single species has been documented in the archipelago. The genus *Margaritopsis* had a moderate level of diversification (four species) similar to that on other Pacific islands. The *Psychotria* clade NC1 appears to be a relictual lineage, which probably underwent a drastic extinction, with a narrow ecological habitat and dispersal limitations. The *Psychotria* clade NC2 is the largest and youngest New Caledonian plant radiation, and has undergone the fastest recorded diversification of any endemic lineage in the archipelago, and could be the result of a 'non-adaptive radiation', originating from Australian rainforests.

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## 1. Introduction

New Caledonia is a remote archipelago in the South-West Pacific, located approximately 1300 km from Australia and 1450 km from New Zealand. Its flora has for many years attracted the interest of botanists studying its temporal and geographic origins (e.g. Morat et al., 1986; Morat et al., 1984; Morat et al., 1994; reviewed

in Grandcolas et al., 2008). The main island (=Grande Terre) is considered to be a small or several pieces of the original Gondwana landmass (Ladiges and Cantrill, 2007) separated from Australia around 80 million years ago (hereafter Ma; Neall and Trewick, 2008; Pelletier, 2006). During its drift, due to the opening of the Tasman Sea, it underwent a deep sub-marine immersion (Paris, 1981; Pelletier, 2006; Picard, 1999). Preceding its emergence, estimated at 37 Ma (Cluzel et al., 1998; Cluzel et al., 2012), New Caledonia, was subducted by the Pacific plate and entirely covered by an ophiolitic layer, whose derived soils (=ultramafic soils) have constraining chemical and physical properties for plant growth (Jaffré, 1980; Jaffré et al., 1987; L'Huillier et al., 2010). Orogenesis

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and weathering of this ultramafic layer, allowing resurgence of old metamorphic substrates (predating the Gondwanan break-up), and sedimentary rocks deposited during immersion (Cluzel et al., 1998; Chevillotte et al., 2006), led to the establishment of a mosaic of soils on the territory (Jaffré et al., 1993; Paris, 1981; Schmid, 1982). Currently, ultramafic soils are fragmented into a large unit in the south and south-east of the main island and several small isolated massifs in the North-West. The uplift of the Loyalty ridge to the east of Grande Terre led to the recent emergence of the four coral limestone Loyalty Islands (from the Pleistocene; see Pelletier, 2006, and references therein). This complex geological history, combined with insularity, a strong climatic zonation, and sharp elevation gradient, has strongly influenced the development of numerous unique ecosystems, and a mosaic of habitats (Jaffré, 1993; Morat et al., 1981; Schmid, 1982). As a consequence of these factors, the New Caledonian flora is highly diverse (3371 species occurring on 18,600 km<sup>2</sup>; Morat et al., 2012), distinctive (74.4% of endemic species; Morat et al., 2012), and disharmonic (i.e. some groups are over-represented compared to neighboring areas, as Australia, e.g. Cunoniaceae, Rubiaceae, or Sapindaceae, whereas others are species-poor, e.g. Asteraceae, Ericaceae, or Lamiaceae; Jaffré, 1980; Pillon et al., 2010). Many authors also regard the archipelago as a biogeographic region well apart from the rest of the South-West Pacific and Australia (Keppel et al., 2009; Mueller-Dombois and Fosberg, 1998; Takhtajan et al., 1986; Thorne, 1963).

Based on geological evidence, none of the lineages of the actual New Caledonian flora are likely to have been present in the archipelago for more than 37 Ma (Pelletier, 2006), and therefore lineages must have colonized the island by either long or short distance dispersal (i.e. in a steeping-stones manner; Keppel et al., 2009). In this context, the hypothesis of a Gondwanan origin of the New Caledonian flora is increasingly being questioned (Cruaud et al., 2012; Grandcolas et al., 2008; Murienné et al., 2005; Pillon, 2012). Recent studies showed that New Caledonian plant lineages colonized the archipelago between the start of re-emergence in the mid-Eocene and present day, but their times of arrival do not appear to be synchronous and have rather ranged over time (Cruaud et al., 2012; Pillon, 2012). Currently, no large, recent and rapid diversification of a plant lineage has been documented for New Caledonia (Pillon, 2012). The most species-rich genera of the island could therefore constitute good candidates to test whether explosive plant diversification has taken place on the island. With the exception of the genus *Pycnanandra* Benth. (Sapotaceae, ca. 57 species), where a decrease in net diversification rate has been observed through time (Espeland and Murienné, 2011), no other studies attempted to infer the diversification rate of a large New Caledonian plant lineage. Most other large genera, composed of more than 30 species, investigated so far seem to have colonized the archipelago on multiple occasions, e.g. *Diospyros* L. (Ebenaceae, 32 species in New Caledonia; Duangjai et al., 2009), *Phyllanthus* L. (Phyllanthaceae, 116 species, including three *Glochidion* J.R. Forst. & G. Forst. species; Kathriarachchi et al., 2006), *Planchonella* Pierre (Sapotaceae, 36 species; Swenson et al., 2007), and *Syzygium* Gaertn. (Myrtaceae, 70 species; Biffin et al., 2006); and therefore represent a collection of smaller diversifications rather than a single (or few) large ones.

The genus *Psychotria* L. s.l. (Rubiaceae, subfamily Rubioideae) is currently considered to be the second most speciose plant genus in New Caledonia, with all 85 members endemic to the archipelago (Barrabé et al., in press; Guillaumin, 1948; Morat et al., 2012). This richness reflects a global trend, as *Psychotria* is the fifth largest plant genus on earth (Frodin, 2004) with no fewer than 1800 tropical species (Davis et al., 2009). The polyphyly of the genus has been demonstrated through recent worldwide molecular phylogenetic studies (Andersson, 2001, 2002a; Barrabé et al., 2012;

Nepokroeff et al., 1999). All species currently placed in *Psychotria* s.l. belong to one of two sister-tribes, Psychotrieae (including the type species *P. asiatica* L.; Davis et al., 2001) and Palicoureeae (Andersson, 2002a; Barrabé et al., 2012; Bremer and Eriksson, 2009; Razafimandimbison et al., 2008). The studies of Andersson (2001, 2002a) and Barrabé et al. (2012), based on very limited samplings of New Caledonian taxa (i.e. seven species), suggested the existence of at least four distinct colonization events of Psychotrieae–Palicoureeae in the archipelago (=Psy–Pal here after). To date no other attempt has been previously undertaken to include in a molecular phylogenetic framework all the remaining species of New Caledonian *Psychotria* (i.e. 78 species), which have been suggested to belong to Psychotrieae according to recent morpho-taxonomic investigation (Barrabé et al., in press). Their phylogenetic placement and their monophyly thus remain to be investigated. Consequently, assumptions about the geographic origin and the time of arrival in the archipelago are difficult to make for a substantial part of New Caledonian *Psychotria* since no recent phylogenetic approach has been applied for them. The diversification and colonization (number and timing of events) of New Caledonian *Psychotria* s.l. (ca. 85 species) is investigated here based on an extensive taxon sampling and a Bayesian dating framework (using six DNA loci). A number of hypotheses are carefully examined to explain the success of *Psychotria* s.l. on the island, including the tempo of diversification, dispersal ability and ecological limitations (using species distribution modeling). We hope that this study will provide a valuable contribution towards the understanding of the diversification processes of plants that have led to the establishment of the New Caledonian flora.

## 2. Material and methods

### 2.1. Sampling strategy for the establishment of phylogenetic relationships

To investigate the phylogenetic placement of New Caledonian taxa within Psy–Pal, and to establish relationships among them, the ingroup sampling was composed of 31 New Caledonian species (out of 85 species) encompassing the morphological and ecological range of the group. The sampling was then completed by other species belonging to Psychotrieae and Palicoureeae to ensure adequate representation of the large diversity of both tribes (Andersson, 2001, 2002a, 2002b; Nepokroeff et al., 1999). The sampling of Palicoureeae was almost identical to Barrabé et al. (2012): 41 species of the 45 sequenced in this last study were included. The sampling of Psychotrieae was composed of species from the Pacific region, Asia, Africa and America, and also representatives of nine genera that have been shown phylogenetically and morphologically to be closely related to *Psychotria*: *Amaracarpus* Blume, *Calycosia* A.Gray, *Cremocarpon* Boiv. ex Baill., *Hedstromia* A.C.Sm., *Hydnophytum* Jack, *Myrmecodia* Jack, *Psathura* Comm. ex A.Juss., *Squamellaria* Becc., and *Trigonopyren* Bremek. (Andersson, 2002a; Davis and Bridson, 2001, 2004; Nepokroeff et al., 1999; Piesschaert, 2001; Smith and Darwin, 1988). A total of 148 species were used in the Psy–Pal sampling (=core Psy–Pal dataset), including 55 species whose sequences were generated from previous phylogenetic studies (Table 1). Finally two species of *Prismatomeris* Thwaites (belonging to the closely related tribe Rubioideae; Razafimandimbison et al., 2008) were selected as outgroup taxa following Razafimandimbison et al. (2008) and Rydin et al. (2009).

### 2.2. Sampling strategy for divergence time estimations

A two-step approach was adopted to estimate molecular divergence times of New Caledonian *Psychotria* following Renner (2005)

and Tosh et al. (in press). In each step, the dating analyses were applied to a comprehensive sampling of lineages at the generic and/or tribe level to avoid inaccuracies in estimating branch lengths (Linder et al., 2004; Poux et al., 2008).

In the first step (Rubioidae dataset), three plastid regions (the non-coding *rps16* intron, the *trnT-F* region, and the coding *ndhF*) were used for 111 taxa including: (1) a pruned sampling of the core Psy–Pal dataset (i.e. 82 species, Table 1) and (2) 29 representatives of all the other major Rubioidae lineages, selected as described below, and whose sequences were downloaded from GenBank (Table 1). This allowed incorporating the single reliable Rubioidae fossil (see below) as a calibration point to estimate the divergence times within the Psy–Pal. Although a large fossil record of Rubiaceae has been identified (Graham, 2009), only four fossils are currently widely used to calibrate divergence analyses (Antonelli et al., 2009; Bremer, 2009; Manns et al., 2012; Smedmark et al., 2010; Tosh et al., in press). Only one of which, a pollen fossil from the Lower Eocene, belongs to subfamily Rubioidae and has been assigned to the genus *Faramea* Aubl. (Graham, 1985). According to the most recent molecular phylogenies of Rubioidae (Bremer and Eriksson, 2009; Razafimandimbison et al., 2008; Rydin et al., 2009), *Faramea* belongs to the tribe Coussareeae, which is sister to a clade comprising the Spermacoceae alliance and the Psychotriaceae alliance (the latter includes tribes Psychotriaceae and Palicoureeae). To confidently place this fossil several species of each tribe of both alliances were sampled, together with six species of Coussareeae (including four *Faramea* species; Table 1) to constitute the 29 Rubioidae species, whose *Coccyzelum condalia* was considered as the most external outgroup species.

In the second step, four plastid and two nuclear ribosomal DNA regions (*rps16*, *trnT-F*, *ndhF*, the intergenic spacer *trnH-psbA*, and the nuclear internal and external transcribed spacers ITS and ETS) were used for the entire core Psy–Pal dataset (i.e. 150 species). The estimate of the divergence time between Psy–Pal and *Prismatomeris* recovered during the first step of the analysis was used as a secondary calibration point.

### 2.3. Preparation of datasets

All sequences were generated by using the DNA extraction, amplification and sequencing protocols for ITS and the four plastid regions (*ndhF*, *rps16*, *trnT-F* and *trnH-psbA*) described in Barrabé et al. (2012). The ETS region was sequenced using the primers ETS Psy1/18S-ETS (Baldwin and Markos, 1998; Nepokroeff et al., 2003), and following the same protocols as for ITS. The program Sequencher v.4.10.1 (Gene Codes Corp., Ann Arbor, Michigan, USA) was used to assemble complementary sequencing strands and verify software base-calling. Each DNA region was initially aligned automatically using MUSCLE (www.ebi.ac.uk/tools/msa/muscle), and subsequently manually adjusted in MEGA5 (Tamura et al., 2011). Inversions, found in plastid regions, were removed and coded as missing data. Ambiguous regions were removed from all DNA alignments by using the BMGE software (Criscuolo and Gribaldo, 2010), following the approach described in Barrabé et al. (2012; Table 2). Even after this latter step, large poly A/T regions in the *rps16* sequences remained and were manually removed.

### 2.4. Preliminary phylogenetic analyses

Preliminary single-locus and combined phylogenetic inferences were carried out using maximum likelihood (ML) and Bayesian Markov Chain Monte Carlo (MCMC) analyses for both the Rubioidae and core Psy–Pal datasets. Best-fit models for each DNA region were identified using jModelTest (Posada, 2008) based on the Akaike criterion (Table 2). The combined datasets were

partitioned to allow each locus to have its specific model parameters (Nylander et al., 2004; Ronquist and Huelsenbeck, 2003). The ML analyses were performed in RAXML (Stamatakis, 2006) using the Vital-IT facility (phylobench.vital-it.ch/raxml-bb). To evaluate node support a bootstrap analysis (BS; Felsenstein, 1985) was performed using 100 replicates. A clade with a BS value > 95% was considered well supported. The Bayesian MCMC analyses were performed as in Barrabé et al. (2012) and ran twice under MrBayes v.3.1.2 (Ronquist and Huelsenbeck, 2003). The burn-in period per run was set to  $5 \times 10^6$  generations for both datasets. The remaining trees were used to construct a half-compatible consensus tree and its associated estimate Bayesian posterior probabilities (PP), corresponding to a 50% majority rule consensus tree. A clade with a PP value > 0.95 was considered well supported. We checked for the absence of supported incongruence (PP > 0.95) between pairs of single locus analysis in both datasets before combining DNA regions for the ML, Bayesian MCMC and dating analyses.

### 2.5. Bayesian divergence times estimates

The temporal evolution of *Psychotria* s.l. was estimated using the Bayesian MCMC approach implemented in BEAST v.1.6.2 for both the Rubioidae and core Psy–Pal datasets (Drummond and Rambaut, 2007). DNA regions were combined and partitions were set as in the preliminary Bayesian MCMC analyses (see above). An uncorrelated relaxed molecular clock model was selected to allow estimates of independent rate variation across branches following a lognormal distribution, because an evolution rate stable over time generally misleads hypotheses of divergence times (Yoder and Yang, 2000). As the study was conducted at the species-level, the Yule process was implemented for the tree prior as recommended in the BEAST manual, assuming a constant speciation rate per lineage. The mean of the branch rates (UCLD.mean) was set to follow a uniform distribution. Based on the results of preliminary combined Bayesian MCMC analyses, the taxon subsets were defined as follows. In the Rubioidae dataset, four groups were forced to be monophyletic: (1) the entire dataset (allowing root calibration); (2) the four species of *Faramea*; (3) tribe Coussareeae (including the *Faramea* clade, thus allowing for fossil calibration); and (4) the clade comprising the Spermacoceae and Psychotriaceae alliances. In the core Psy–Pal dataset, three groups were forced to be monophyletic: (1) the entire dataset; (2) both species of *Prismatomeris*; and (3) the clade comprising Psychotriaceae and Palicoureeae. To satisfy constraints of each taxon subset, one all-compatible tree, generated in the preliminary Bayesian MCMC analysis under MrBayes, was rendered ultrametric in TreeEdit v.1.0a10 (Rambaut and Charleston, 2002) and used as a starting tree in BEAST. The MCMC was run for 25 million generations and sampled every 1000 generations. The analysis for each dataset was conducted four times. Convergence of runs and adequate MCMC sampling were checked using Tracer v.1.5 (Rambaut and Drummond, 2009). The first  $15 \times 10^6$  generations of each run for the Rubioidae dataset and  $10 \times 10^6$  generations for the core Psy–Pal dataset were discarded as burn-in. The remaining trees were summarized using a Maximum Clade Credibility target tree in Treannotator v.1.6.2 (Drummond and Rambaut, 2007), as well as Bayesian posterior probability (PP), median height (=age estimate) and the 95% highest posterior density heights interval (95% HPD) of each node.

### 2.6. Fossil constraints and secondary calibration

#### 2.6.1. The Rubioidae dataset

Two constraints were used for the Rubioidae dataset: a fossil calibration point and a secondary calibration point (Hedges and Kumar, 2004). Several studies supported a multi-fossil dating



approach to better estimate divergence times (e.g. Renner, 2005; Sauquet et al., 2012). However, in the case of New Caledonian *Psychotria* the incorporation of unreliable fossils could have involved poor priors (Near et al., 2005; Parham et al., 2012) and therefore a single-fossil approach was retained by selecting the pollen fossil of *Faramaea* (see above). Considering uncertainties of estimating an accurate age for this fossil, the boundary between Middle and Upper Eocene was used (37.2 Ma; Gradstein and Ogg, 2004; Walker and Geissman, 2009). This age was calibrated to the *Faramaea* crown node to avoid underestimation of node age estimates (Smedmark et al., 2010), and we used a lognormal prior distribution with default settings.

The second calibration point was the divergence time between Coussareeae and the clade comprising the Spermacoceae and Psychotrieae alliances, estimated from a previous study (=stem age of Coussareeae; Bremer and Eriksson, 2009) and was attributed to the root to avoid unrealistic values of its time estimates (Sanders and Lee, 2007). A uniform prior distribution was calibrated by using a lower bound of 54.3 Ma and an upper bound of 76.6 Ma, which correspond to the 95% HPD of Bremer and Eriksson (2009), with a mean value of 65.4 Ma.

#### 2.6.2. The core Psy–Pal dataset

The use of a secondary calibration point can lead to an underestimation of divergence times (Sauquet et al., 2012) and to the accumulation of estimated error (Renner, 2005); but in the absence of a reliable fossil, it is the only way to assess age estimates (Hedges and Kumar, 2004; Ho, 2007). The divergence time between *Prismatommeris* and Psy–Pal estimated in the analysis of the Rubioideae dataset was assigned to the root node of the tree generated from this dataset, following a uniform distribution and by using a lower bound of 35.5 Ma and an upper bound of 58.4 Ma, which correspond to the 95% HPD of this divergence time, with a median value of 46.65 Ma (Appendix A).

#### 2.7. Net and relative diversification rates

To obtain an overall estimate of the pattern of diversification of New Caledonian Psy–Pal, net diversification rates were calculated following Magallón and Sanderson (2001). This approach allows the comparison of values with those of other New Caledonian plant groups provided in Pillon (2012).

Eq. (7) of Magallón and Sanderson (2001) was chosen to calculate net diversification rates using the median crown ages estimated in the BEAST analyses (for further explanation see Pillon (2012)), and using their 95% HPD to take uncertainty into account. These rates were then calculated at two extreme values of relative extinction (extinction assumed to be null, equal to 0, and then assumed to be high, equal to 0.9) using the R packages LASER (Rabosky, 2006) and GEIGER (Harmon et al., 2008). Net diversification rates were likewise estimated on a per-unit-area and a per-unit-log(area) basis following Knope et al. (2012) to allow comparisons with rapid plant diversifications from other remote islands (by using a total area of 18,600 km<sup>2</sup> for lineages occurring throughout the entire New Caledonian archipelago and 16,600 km<sup>2</sup> for those occurring only on Grande Terre).

Moreover, to test whether species richness varies significantly from random among any Psy–Pal lineages present in New Caledonia the number of species in each lineage was compared with a broken stick distribution (MacArthur, 1957) using the biodiversity calculator of Danoff-Burg ([http://www.columbia.edu/itc/cerc/danoff-burg/MBD\\_Links.html](http://www.columbia.edu/itc/cerc/danoff-burg/MBD_Links.html)). We also tested the difference in species richness between the New Caledonian Psy–Pal and their sister-clades using Eq. (3) of Slowinsky and Guyer (1993), which is regarded as a conservative test (McConway and Sims, 2004; Paradis, 2012). To allow calculating these estimates and to ensure that their

first basal splits in dating trees were assessed, we preliminary estimated their species richness, and those of their sister-clades, according to Guillaumin (1930), Morat et al. (2012), Barrabé et al. (2012), Barrabé (2013), and Barrabé (in press).

#### 2.8. Geographic distributions and ecological data

The geographic distribution of each ingroup species was provided at both a large scale (global and centered on the Pacific region) and a fine scale (New Caledonia). The global distribution of each species was scored from the World Checklist of Rubiaceae (Govaerts et al., 2012) and displayed on the BEAST topology obtained using the core Psy–Pal dataset. The geographic range of New Caledonian species was retrieved from the databases of the herbaria of Noumea (VIROT) and the Museum National d'Histoire Naturelle, Paris (SONNERAT). Herbarium specimen records were used and their geographic coordinates databased, error-corrected for distribution, and then incorporated into a geographic information system (GIS; ArcGis v. 10). Three ecological GIS layers were selected and combined allowing visualization of putative ecological specializations for New Caledonian lineages, as delimited in the phylogenetic analyses. These three ecological parameters are generally considered to have the most strongly correlated with plants distribution across New Caledonia (Jaffré, 1993; Morat, 1993; Pintaud and Jaffré, 2001; Veillon, 1993): (1) the main types of geological substrates (three classes: volcano-sedimentary and metamorphic rocks, ultramafic, and coral limestone, as provided by the DIMENC, New Caledonia); (2) elevation (three classes: 0–300 m, 300–800 m, and >800 m, provided by the DITTT, New Caledonia); and (3) rainfall rates (three classes: 0–1250 mm, 1250–2000 mm, and >2000 mm, provided by Météo France, New Caledonia, based on mean values between 1999 and 2010).

#### 2.9. Species distribution modeling

Additional species distribution modeling analyses were carried out using the presence-only MaxEnt Species Distribution Modeling (Phillips et al., 2006) to test whether any lineages among New Caledonian Psy–Pal appear to be specialized to one or more ecosystems. The three GIS ecological layers (see above) were used for the modeling analyses. These layers were represented with a 500 m resolution. The dataset, composed of coordinates for all species of New Caledonian Psy–Pal, was set as occurrence data to calibrate the corresponding modeling. All the features available were included in the model and 10,000 random background points were used for statistical analyses of the predictive power. We used 25% randomly selected occurrence data as a testing dataset. Suitable regularization values, included to reduce overfitting, were selected automatically by the program. Fifty iterations were performed. To evaluate the relative contribution of each variable to the model a jackknife test of variable importance was performed (Phillips et al., 2006).

### 3. Results

Single gene and combined BEAST phylogenetic trees inferred from both the Rubioideae and Psy–Pal datasets showed no supported incongruence and were congruent with those of both the ML (data not shown) and Bayesian MCMC combined analyses (Appendices B–D; Fig. 1). Only the phylogenetic results of the core Psy–Pal dataset will be presented and discussed hereafter given that the broader Psy–Pal sampling of this dataset allows a sharper establishment of phylogenetic relationships of New Caledonian taxa with the remainder Psy–Pal species (Figs. 1 and 2–C). These analyses revealed the existence of four New Caledonian Psy–Pal

Table 1

List of taxa investigated in this study, voucher information, dataset, country origin, and accession numbers.

Taxa	Rubioideae dataset	Psy-Pal dataset	Sample	Herbarium	ndhF	rps16	trnHpsbA	trnTF	ITS	ETS	Tribe	Rubioideae intra level	Country/area
<i>Amaracarpus muscifer</i> A.C. Sm.	×	×	Barrabé & Tuiwawa 1109	NOU	KF675995*	KF676083*	KF676261*	KF676171*	KF675907*	KF675790*	PSY	PSY ALL	Fiji
<i>Amaracarpus nematopodus</i> (F. Muell.) P.I. Forst. 1	×	×	Barrabé et al. 1030	NOU	JX155105 <sup>19</sup>	JX155152 <sup>19</sup>	JX155192 <sup>19</sup>	JX155011 <sup>19</sup>	JX155060 <sup>19</sup>	KF675791*	PSY	PSY ALL	Australia
<i>Amaracarpus nematopodus</i> (F. Muell.) P.I. Forst. 2	×	×	Pillon 1072	NOU	JX155119 <sup>19</sup>	JX155166 <sup>19</sup>		JX155026 <sup>19</sup>	JX155074 <sup>19</sup>		PSY	PSY ALL	Vanuatu
<i>Calycosia cf. petiolata</i> A. Gray	×	×	Buerki et al. 166	NOU	KF675996*	KF676084*	KF676262*	KF676172*	KF675908*	KF675792*	PSY	PSY ALL	Fiji
<i>Carapichea ligularis</i> (Rudge) Delprete	×	×				AF147567 <sup>8</sup>			AF149390 <sup>1</sup>		PAL	PSY ALL	America
<i>Chassalia catatii</i> Drake ex Bremek.	×	×	Razafimandimbison 480	UPS	AM945283 <sup>13</sup>	AM945331 <sup>13</sup>		AM945363 <sup>13</sup>	AM945218 <sup>13</sup>		PAL	PSY ALL	Madagascar
<i>Chassalia</i> sp. 1MADA		×	Ramandimbimanana 140	K	JX155138 <sup>19</sup>	JX155181 <sup>19</sup>			JX155092 <sup>19</sup>		PAL	PSY ALL	Madagascar
<i>Chassalia</i> sp. 1VIET		×	HNK 610	K	JX155132 <sup>19</sup>	JX155177 <sup>19</sup>	JX155218 <sup>19</sup>	JX155039 <sup>19</sup>	JX155087 <sup>19</sup>		PAL	PSY ALL	Vietnam
<i>Chassalia</i> sp. 2MADA		×	Callmander 307	K	JX155147 <sup>19</sup>			JX155054 <sup>19</sup>	JX155100 <sup>19</sup>		PAL	PSY ALL	Madagascar
<i>Chassalia</i> sp. 2VIET		×	Briggs 114	K	JX155135 <sup>19</sup>	JX155179 <sup>19</sup>	JX155219 <sup>19</sup>	JX155042 <sup>19</sup>	JX155090 <sup>19</sup>		PAL	PSY ALL	Vietnam
<i>Chassalia</i> sp. SUMA		×	De Kok 1297	K	JX155133 <sup>19</sup>	JX155178 <sup>19</sup>		JX155040 <sup>19</sup>	JX155088 <sup>19</sup>		PAL	PSY ALL	Sumatra
<i>Chazaliella abrupta</i> (Hiern) E.M.A. Petit & Verdc. 1	×	×	Davis 2924	K	JX155134 <sup>19</sup>		JX155217 <sup>19</sup>	JX155041 <sup>19</sup>	JX155089 <sup>19</sup>		PAL	PSY ALL	Tanzania
<i>Chazaliella abrupta</i> (Hiern) E.M.A. Petit & Verdc. 2		×	Bremer 3081	UPS	JX155148 <sup>19</sup>		JX155227 <sup>19</sup>	JX155055 <sup>19</sup>	JX155101 <sup>19</sup>		PAL	PSY ALL	Tanzania
<i>Coccocypselum condalia</i> Pers.	×		Pirani & Bremer 4891	SPF	EU145420 <sup>14</sup>	EU145499 <sup>14</sup>		EU145547 <sup>14</sup>			COU		? America
<i>Coelospermum monticola</i> Baill. ex Guillaumin	×		Ohansson 87	S	AM945255 <sup>13</sup>	AF001438 <sup>5</sup>		AM945334 <sup>13</sup>			MOR	PSY ALL	New Caledonia
<i>Coprosma pumila</i> Hook.f.	×		Forbes s.n.	S	FJ695294 <sup>17</sup>	FJ695262 <sup>17</sup>		FJ695405 <sup>17</sup>			ANT	SPE ALL	Tasmania
<i>Coussarea hydrangeifolia</i> (Benth.) Benth. & Hook.f. ex Müll.Arg.	×		Fuentes 5504	GB	EU145422 <sup>14</sup>	EU145501 <sup>14</sup>		EU145549 <sup>14</sup>			COU		? America
<i>Craterispermum</i> sp. 2MADA	×		Razafimandimbison and Ravelonarivo 656	SPF	AM945274 <sup>13</sup>	AM945323 <sup>13</sup>		AM945354 <sup>13</sup>			CRA	PSY ALL	Madagascar
<i>Craterispermum</i> sp. 3MADA	×		No collector name, 24169-SF	P	AM945275 <sup>13</sup>	AM945324 <sup>13</sup>		AM945355 <sup>13</sup>			CRA	PSY ALL	Madagascar
<i>Cremocarpon boivinianum</i> Baill.	×	×	Mouly 696	P	KF675997*	KF676085*	KF676263*	KF676173*	KF675909*	KF675793*	PSY	PSY ALL	Mayotte
<i>Cremocarpon lantzii</i> Bremek.		×	McPherson 18327	MO	KF675998*	KF676086*	KF676264*	KF676174*	KF675910*	KF675794*	PSY	PSY ALL	Madagascar
<i>Damnacanthus macrophyllus</i> Siebold ex Miq.	×		Fukuoka 8792	P	AM945257 <sup>13</sup>	AM945308 <sup>13</sup>		AM945336 <sup>13</sup>			MIT	PSY ALL	Japan
<i>Danais xanthorrhoea</i> (K. Schum.) Bremek.	×		Bremer 3079	UPS	AJ236293 <sup>6</sup>	AM117297 <sup>16</sup>		AM117357 <sup>16</sup>			DAN	SPE ALL	Tanzania
<i>Dunnia sinensis</i> Tutcher	×		Yangchun 10, Ge et al. 2002	not provided	EU145442 <sup>14</sup>	EU145515 <sup>14</sup>		EU145583 <sup>14</sup>			DUN	SPE ALL	China
<i>Fareamea crassifolia</i> Benth.	×		Jansen-Jacobs et al. 3882	GB		HM042567 <sup>18</sup>		HM042587 <sup>18</sup>			COU		Guyana
<i>Fareamea multiflora</i> A. Rich.	×		Andersson 2041/Bremer et al. 3331	S/UPS	EU145424 <sup>14</sup>	AF004048 <sup>5</sup>		AF102422 <sup>4</sup>			COU		? America
<i>Fareamea torquata</i> Müll.Arg.	×		Stahl 3021	GB		HM042568 <sup>18</sup>		HM042588 <sup>18</sup>			COU		Ecuador
<i>Fareamea trinervia</i> K. Schum. & Donn.Sm.	×		Gomez-Lavrito 8374	CR		AM900598 <sup>15</sup>		HM042589 <sup>18</sup>			COU		Costa Rica
<i>Gaertnera</i> sp. MADA	×		Bremer et al. 4008	UPS	AM945260 <sup>13</sup>	AM945310 <sup>13</sup>		AM945339 <sup>13</sup>			GAE	PSY ALL	Madagascar
<i>Galium album</i> Mill.	×		Andersson 2201/Bremer 3321	UPS	FJ695299 <sup>17</sup>	AF004050 <sup>5</sup>					SPE	SPE ALL	? Europa
<i>Geophila obvallata</i> Didr.	×	×			AM945259 <sup>13</sup>	AF369845 <sup>8</sup>		EU145569 <sup>14</sup>	AM945196 <sup>13</sup>		PAL	PSY ALL	Africa
<i>Geophila repens</i> (L.) I.M. Johnst.		×	Munzinger 3649	NOU	JX155124 <sup>19</sup>		JX155210 <sup>19</sup>	JX155031 <sup>19</sup>	JX155079 <sup>19</sup>		PAL	PSY ALL	Vanuatu
<i>Gynochthodes coriacea</i> Blume	×		Ridsdale XVII.C.103	L	AM945253 <sup>13</sup>	AM117311 <sup>16</sup>		AJ847407 <sup>12</sup>			MOR	PSY ALL	?
<i>Hedstromia latifolia</i> A.C. Sm.	×	×	Barrabé et al. 1090	NOU	KF675999*	KF676087*	KF676265*	KF676175*	KF675911*	KF675795*	PSY	PSY ALL	Fiji
<i>Hodgkinsonia frutescens</i> C.T. White	×	×	Baba et al. 786	NOU	JX155106 <sup>19</sup>	JX155153 <sup>19</sup>	JX155194 <sup>19</sup>	JX155012/ JX155013 <sup>19</sup>	JX155061 <sup>19</sup>	KF675796*	PAL	PSY ALL	Australia
<i>Hydnophytum cf. longistylum</i> Becc.	×	×	McPherson 19437	NOU	JX155123 <sup>19</sup>	JX155170 <sup>19</sup>	JX155209 <sup>19</sup>	JX155030 <sup>19</sup>	JX155078 <sup>19</sup>	KF675797*	PSY	PSY ALL	Vanuatu
<i>Hydnophytum</i> sp. AUST		×	Barrabé & Rigault 1041	NOU	KF676000*	KF676088*	KF676266*	KF676176*	KF675912*	KF675798*	PSY	PSY ALL	Australia
<i>Hymenocoleus hirsutus</i> (Benth.) Robbr.	×	×				AF369848 <sup>8</sup>			AF072018 <sup>7</sup>		PAL	PSY ALL	Africa
<i>Kohautia caespitosa</i> Schnizl.	×		Bremer et al. 42566B	UPS	FJ695303 <sup>17</sup>	AM117324 <sup>16</sup>		EU145573 <sup>14</sup>			SPE	SPE ALL	? Africa

(continued on next page)

Table 1 (continued)

Taxa	Rubioideae dataset	Psy-Pal dataset	Sample	Herbarium	ndhF	rps16	trnHpsbA	trnTF	ITS	ETS	Tribe	Rubioideae intra level	Country/area
<i>Margaritopsis acutifolia</i> C. Wright in Sauvalle	×	×	Ekman 10248	UPS		AF001340 <sup>5</sup>	JX155230 <sup>19</sup>	EU145568 <sup>14</sup>	AM945198 <sup>13</sup>		PAL	PSY ALL	Cuba
<i>Margaritopsis astrellantha</i> (Wernham) L. Andersson		×	Zappi 938	K	JX155142 <sup>19</sup>	JX155185 <sup>19</sup>	JX155225 <sup>19</sup>	JX155047/ JX155048 <sup>19</sup>	JX155096 <sup>19</sup>		PAL	PSY ALL	Brazil
<i>Margaritopsis boliviana</i> (Standl.) C.M. Taylor		×	Zappi 973	K	JX155143 <sup>19</sup>	JX155186/ JX155187 <sup>19</sup>	JX155220 <sup>19</sup>	JX155049/ JX155050 <sup>19</sup>	JX155097 <sup>19</sup>		PAL	PSY ALL	Brazil
<i>Margaritopsis guianensis</i> (Bremek.) C.M. Taylor		×	Zappi 980	K	JX155144 <sup>19</sup>	JX155188 <sup>19</sup>		JX155051/ JX155052 <sup>19</sup>	JX155098 <sup>19</sup>		PAL	PSY ALL	Brazil
<i>Margaritopsis kappleri</i> (Miq.) C.M. Taylor	×	×	Zappi 921	K	JX155141 <sup>19</sup>	JX155184 <sup>19</sup>	JX155224 <sup>19</sup>	JX155046 <sup>19</sup>	JX155095 <sup>19</sup>		PAL	PSY ALL	Brésil
<i>Mouretia larsenii</i> Tange	×		Beusekom et al. 4743	P	FJ695306 <sup>17</sup>	FJ695267 <sup>17</sup>		FJ695410 <sup>17</sup>			ARG	SPE ALL	? Asia
<i>Myrmecodia tuberosa</i> Jack	×	×	Andreasen 341	UPS	KF676001*	KF676089*	KF676267*	KF676177*	KF675913*	KF675799*	PSY	PSY ALL	Cult. Bergianska Bot. Gard. New Caledonia
<i>Normandia neocaledonica</i> Hook.f.	×		Munzinger 532	MO	FJ695315 <sup>17</sup>	AF257931 <sup>2</sup>		EU145543 <sup>14</sup>			ANT	SPE ALL	Brésil
<i>Notopleura tapajozensis</i> (Standl.) Bremek.	×	×	Zappi 869	K	JX155140 <sup>19</sup>	JX155183 <sup>19</sup>	JX155223 <sup>19</sup>	JX155045 <sup>19</sup>	JX155094 <sup>19</sup>	KF675800*	PAL	PSY ALL	Brésil
<i>Paederia majungensis</i> Homolle ex Puff	×		Nilsson et al. D152	UPS	FJ695319 <sup>17</sup>	DQ662209 <sup>10</sup>		DQ662155 <sup>10</sup>			PAE	SPE ALL	Madagascar
<i>Palicourea crocea</i> (Sw.) Schult. in J.J. Roemer & J.A. Schultes	×	×	Cordio 2736	SP	AM945280 <sup>13</sup>	AF147510 <sup>1</sup>		AM945259 <sup>13</sup>	AF149322 <sup>1</sup>		PAL	PSY ALL	America
<i>Pentodon pentandrus</i> (Schumach. & Thonn.) Vatke	×		Bremer 3082	UPS	FJ695323 <sup>17</sup>	AF003612 <sup>5</sup>		FJ695419 <sup>17</sup>			SPE	SPE ALL	Zanzibar
<i>Plocama pendula</i> Aiton	×		Andreasen 1	UPS	FJ695329 <sup>17</sup>	FJ695276 <sup>17</sup>		DQ662162 <sup>10</sup>			PUT	SPE ALL	Canary
<i>Prismatomeris albidiflora</i> Thwaites	×	×	Marie 89	P	AM945270 <sup>13</sup>	AM945320 <sup>13</sup>		AM945351 <sup>13</sup>	AM945205 <sup>13</sup>		PRI	PSY ALL	Cambodge
<i>Prismatomeris beccariana</i> (Baill. ex K. Schum.) J.T. Johanss.	×	×	Ridsdale 2461	L	AM945271 <sup>13</sup>	AF331652 <sup>3</sup>		AM945352 <sup>13</sup>	AM945206 <sup>13</sup>		PRI	PSY ALL	?
<i>Psathura terniflora</i> A.Rich. ex DC.	×	×	Coode 4698	K	KF676002*	KF676090*	KF676268*	KF676260*	KF675914*	KF675801*	PSY	PSY ALL	Maurice
<i>Psychotria</i> aff. <i>tephrosantha</i> A. Gray		×	Buerki et al. 175	NOU	KF676003*	KF676091*		KF676178*	KF675915*		PSY	PSY ALL	Fiji
<i>Psychotria amboniana</i> K. Schum		×	Luke 8344	UPS	AM945281 <sup>13</sup>	AM945328 <sup>13</sup>		AM945360 <sup>13</sup>	AM945215 <sup>13</sup>		PSY	PSY ALL	Kenya
<i>Psychotria ammericola</i> Guillaumin	×	×	Barrabé 590	NOU	KF676004*	KF676092*	KF676269*	KF676179*	KF675916*	KF675802*	PSY	PSY ALL	New Caledonia
<i>Psychotria aeneityensis</i> Guillaumin		×	Pillon 1127	NOU	JX155120 <sup>19</sup>	JX155167 <sup>19</sup>	JX155207 <sup>19</sup>	JX155027 <sup>19</sup>	JX155075 <sup>19</sup>	KF675803*	PAL	PSY ALL	Vanuatu
<i>Psychotria archboldiana</i> Fosberg	×	×	Buerki et al. 170	NOU	JX155113 <sup>19</sup>	JX155160 <sup>19</sup>	JX155201 <sup>19</sup>	JX155020 <sup>19</sup>	JX155068 <sup>19</sup>	KF675804*	PAL	PSY ALL	Fiji
<i>Psychotria asiatica</i> L.	×	×	Davis s.n.	K	JX155127 <sup>19</sup>			JX155034 <sup>19</sup>	JX155082 <sup>19</sup>	KF675805*	PSY	PSY ALL	Hong Kong
<i>Psychotria baillonii</i> Schltr.		×	Barrabé 627	NOU	KF676005*	KF676093*	KF676270*	KF676180*	KF675917*	KF675806*	PSY	PSY ALL	New Caledonia
<i>Psychotria baladensis</i> (Baill.) Guillaumin		×	Barrabé et al. 894	NOU	KF676006*	KF676094*	KF676271*	KF676181**	KF675918*	KF675807*	PSY	PSY ALL	New Caledonia
<i>Psychotria brachylaena</i> (Baill.) Guillaumin		×	Barrabé et al. 643	NOU	KF676007*	KF676095*	KF676272*	KF676182*	KF675919*	KF675808*	PSY	PSY ALL	New Caledonia
<i>Psychotria calothyrsa</i> (Baill.) Guillaumin	×	×	Barrabé 688	NOU	KF676008*	KF676096*	KF676273*	KF676183*	KF675920*	KF675809*	PSY	PSY ALL	New Caledonia
<i>Psychotria camptopus</i> Verdc.	×	×	Maurin 38	K	JX155129 <sup>19</sup>	JX155174 <sup>19</sup>	JX155214 <sup>19</sup>	JX155036 <sup>19</sup>	JX155084 <sup>19</sup>	KF675810*	PSY	PSY ALL	Cameroon
<i>Psychotria cardiochlamys</i> (Baill.) Schltr. 1	×	×	Barrabé & Rigault 579	NOU	KF676009*	KF676097*	KF676274*	KF676184*	KF675921*	KF675811*	PSY	PSY ALL	New Caledonia
<i>Psychotria cardiochlamys</i> (Baill.) Schltr. 2		×	Dagostini et al. 1439	NOU		KF676098*	KF676275*	KF676185*		KF675812*	PSY	PSY ALL	New Caledonia
<i>Psychotria carnea</i> (G. Forst.) A.C. Sm. 1		×	Barrabé & Tuiwawa 1113	NOU	JX155110 <sup>19</sup>	JX155157 <sup>19</sup>	JX155198 <sup>19</sup>	JX155017 <sup>19</sup>	JX155065 <sup>19</sup>	KF675813*	PAL	PSY ALL	Fiji
<i>Psychotria carnea</i> (G. Forst.) A.C. Sm. 2		×	Barrabé et al. 1123	NOU	JX155111 <sup>19</sup>	JX155158 <sup>19</sup>	JX155199 <sup>19</sup>	JX155018 <sup>19</sup>	JX155066 <sup>19</sup>	KF675814*	PAL	PSY ALL	Fiji
<i>Psychotria</i> cf. <i>araiosantha</i> A.C. Sm. & S.P. Darwin	×	×	Barrabé et al. 1135	NOU	KF676010*	KF676099*	KF676276*	KF676186*	KF675922*	KF675815*	PSY	PSY ALL	Fiji
<i>Psychotria</i> cf. <i>confertifolia</i> A.C. Sm.	×	×	Barrabé & Tuiwawa 1110	NOU	KF676011*	KF676100*	KF676277*	KF676187*	KF675923*	KF675816*	PSY	PSY ALL	Fiji
<i>Psychotria</i> cf. <i>impercepta</i> A.C. Sm. & S.P. Darwin	×	×	Barrabé et al. 1086	NOU	JX155108 <sup>19</sup>	JX155155 <sup>19</sup>	JX155196 <sup>19</sup>	JX155015 <sup>19</sup>	JX155063 <sup>19</sup>	KF675817*	PSY	PSY ALL	Fiji
<i>Psychotria</i> cf. <i>vaccinioides</i> Valetton	×	×	John 10072	K	KF676012*	KF676101*	KF676278*	KF676188*	KF675924*	KF675818*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria</i> cf. <i>tephrosantha</i> A. Gray	×	×	Buerki et al. 171	NOU	KF676013*	KF676102*	KF676279*	KF676189*	KF675925*	KF675819*	PSY	PSY ALL	Fiji
<i>Psychotria</i> cf. <i>trichostoma</i> Merr. & L.M. Perry	×	×	Pillon 1057	NOU	JX155118 <sup>19</sup>	JX155165 <sup>19</sup>	JX155206 <sup>19</sup>	JX155025 <sup>19</sup>	JX155073 <sup>19</sup>	KF675820*	PAL	PSY ALL	Vanuatu

<i>Psychotria coelospermum</i> F.M. Bailey	×	×	Barrabé & Rigault 1056	NOU	KF676014*	KF676103*	KF676280*	KF676190*	KF675926*	KF675821*	PSY	PSY ALL	Australia
<i>Psychotria collina</i> Labill.	×	×	Barrabé et al. 698	NOU	JX155117 <sup>19</sup>	JX155164 <sup>19</sup>	JX155205 <sup>19</sup>	JX155024 <sup>19</sup>	JX155072 <sup>19</sup>	KF675822*	PAL	PSY ALL	New Caledonia
<i>Psychotria comptonii</i> S. Moore	×	×	Barrabé & Rigault 1014	NOU	KF676015*	KF676104*	KF676281*	KF676191*	KF675927*	KF675823*	PSY	PSY ALL	New Caledonia
<i>Psychotria dallachiana</i> Benth. 1		×	Barrabé & Rigault 1048	NOU	KF676016*	KF676169*	KF676282*	KF676192*	KF675928*	KF675824*	PSY	PSY ALL	Australia
<i>Psychotria dallachiana</i> Benth. 2	×	×	Barrabé & Rigault 1053	NOU	KF676017*	KF676170*	KF676283*	KF676193*	KF675929*	KF675825*	PSY	PSY ALL	Australia
<i>Psychotria daphnoides</i> A. Cunn. ex Hook. var. <i>angustifolia</i> Benth.	×	×	Barrabé & Rigault 1039	NOU	KF676018*	KF676105*	KF676284*	KF676194*	KF675930*	KF675826*	PSY	PSY ALL	Australia
<i>Psychotria daphnoides</i> A. Cunn. ex Hook. var. <i>daphnoides</i>		×	Baba et al. 704	NOU	KF676019*	KF676106*	KF676285*	KF676195*	KF675931*	KF675827*	PSY	PSY ALL	Australia
<i>Psychotria declieuxioides</i> S. Moore	×	×	Barrabé & Nigote 937	NOU	KF676020*	KF676107*	KF676286*	KF676196*	KF675932*	KF675828*	PSY	PSY ALL	New Caledonia
<i>Psychotria eminiana</i> (Kuntze) E.M.A. Petit		×	Gereau 5795	MO	KF676021*	KF676108*	KF676287*	KF676197*		KF675829*	PSY	PSY ALL	Tanzania
<i>Psychotria exilis</i> A.C. Sm.		×	Barrabé et al. 1119	NOU	KF676022*	KF676109*	KF676288*	KF676198*	KF675933*	KF675830*	PSY	PSY ALL	Fiji
<i>Psychotria faguetii</i> (Baill.) Schltr.		×	Barrabé et al. 820	NOU	KF676023*		KF676289*		KF675934*	KF675831*	PSY	PSY ALL	New Caledonia
<i>Psychotria fitzalanii</i> Benth.	×	×	Barrabé & Rigault 1057	NOU	KF676024*	KF676110*	KF676290*	KF676199*	KF675935*	KF675832*	PSY	PSY ALL	Australia
<i>Psychotria flava</i> Oerst. ex Standl.		×	Chase 2268	K	KF676025*	KF676111*	KF676291*	KF676200*	KF675936*	KF675833*	PSY	PSY ALL	Mexico
<i>Psychotria forsteriana</i> A. Gray	×	×	Buerki et al. 162	NOU	JX155112 <sup>19</sup>	JX155159 <sup>19</sup>	JX155200 <sup>19</sup>	JX155019 <sup>19</sup>	JX155067 <sup>19</sup>	KF675834*	PAL	PSY ALL	Fiji
<i>Psychotria frondosa</i> S. Moore		×	Barrabé et al. 689	NOU	KF676026*	KF676112*	KF676292*	KF676201*	KF675937*	KF675835*	PSY	PSY ALL	New Caledonia
<i>Psychotria gabriellae</i> (Baill.) Guillaumin	×	×	Barrabé & Nigote 946	NOU	KF676027*	KF676113*	KF676293*	KF676202*	KF675938*	KF675836*	PSY	PSY ALL	New Caledonia
<i>Psychotria gneissica</i> S. Moore	×	×	Poullain & Cardineau 127	NOU	KF676028*	KF676114*	KF676294*	KF676203*	KF675939*	KF675837*	PSY	PSY ALL	New Caledonia
<i>Psychotria goniocarpa</i> (Baill.) Guillaumin		×	Barrabé 586	NOU	KF676029*	KF676115*	KF676295*	KF676204*	KF675940*	KF675838*	PSY	PSY ALL	New Caledonia
<i>Psychotria grandis</i> Sw.	×	×	Taylor 11745	MO	JX155125 <sup>19</sup>	JX155171 <sup>19</sup>	JX155211 <sup>19</sup>	JX155032 <sup>19</sup>	JX155080 <sup>19</sup>	KF675839*	PSY	PSY ALL	Caribbean
<i>Psychotria hawaiiensis</i> (A. Gray) Fosberg	×	×	Pillon 1425	NOU	KF676030*	KF676116*	KF676296*	KF676205*	KF675941*	KF675840*	PSY	PSY ALL	Hawaii
<i>Psychotria hivaoana</i> Fosberg	×	×	Meyer 3071	PAP	KF676031*	KF676117*	KF676297*	KF676206*	KF675942*	KF675841*	PSY	PSY ALL	French Polynesia
<i>Psychotria holtzii</i> (K. Schum.) E.M.A. Petit		×	Luke 8342	UPS		AM945330 <sup>13</sup>		AM945362 <sup>13</sup>	AM945217 <sup>13</sup>		PSY	PSY ALL	Kenya
<i>Psychotria insularum</i> A. Gray	×	×	Pillon 909	NOU	KF676032*	KF676118*	KF676298*	KF676207*	KF675943*	KF675842*	PSY	PSY ALL	Wallis & Futuna
<i>Psychotria iteophylla</i> Stapf		×	Axelius 303	S		AF410726 <sup>9</sup>		JN643465 <sup>20</sup>			PSY	PSY ALL	Borneo
<i>Psychotria kirkii</i> Hiern	×	×	Bremer 3102	UPS	AM945278 <sup>13</sup>	AM945327 <sup>13</sup>		AM945358 <sup>13</sup>	AM945214 <sup>13</sup>		PSY	PSY ALL	Cult. Uppsala Bot. Gard.
<i>Psychotria lepiniana</i> (Baill. ex Drake) Drake		×	Nadeaud 345	P	JX155104 <sup>19</sup>	JX155151 <sup>19</sup>	JX155193 <sup>19</sup>	JX155010 <sup>19</sup>	JX155059 <sup>19</sup>	KF675843*	PAL	PSY ALL	Society Islands
<i>Psychotria leptothyrsa</i> Miq.		×	Droz & Molem s.n.	CBSF	JX155149 <sup>19</sup>	JX155190 <sup>19</sup>	JX155228 <sup>19</sup>	JX155056 <sup>19</sup>	JX155102 <sup>19</sup>	KF675844*	PAL	PSY ALL	Papua New Guinea
<i>Psychotria leratii</i> Guillaumin		×	Dagostini et al. 1567	NOU	KF676081*	KF676119*	KF676299*	KF676208*	KF675944*	KF675845*	PSY	PSY ALL	New Caledonia
<i>Psychotria loniceroides</i> Sieber ex DC.		×	Barrabé & Rigault 1042	NOU	KF676033*	KF676120*	KF676300*	KF676209*	KF675945*	KF675846*	PSY	PSY ALL	Australia
<i>Psychotria lorentzii</i> Valetton		×	Puradyatmika 10460	K	KF676034*	KF676121*	KF676301*	KF676210*	KF675946*	KF675847*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria lyciiflora</i> (Baill.) Guillaumin	×	×	Barrabé & Barriole 747	NOU	JX155114 <sup>19</sup>	JX155161 <sup>19</sup>	JX155202 <sup>19</sup>	JX155021 <sup>19</sup>	JX155069 <sup>19</sup>	KF675848*	PSY	PSY ALL	New Caledonia
<i>Psychotria macroglossa</i> (Baill.) Guillaumin		×	Barrabé & Rigault 573	NOU	KF676035*	KF676122*	KF676302*	KF676211*	KF675947*	KF675849*	PSY	PSY ALL	New Caledonia
<i>Psychotria mapouriioides</i> DC.		×	Merello 1711	MO		KF676123*	KF676303*	KF676212*	KF675948*	KF675850*	PSY	PSY ALL	Caribbean
<i>Psychotria micralabastra</i> (Lauterb. & K. Schum.) Valetton	×	×	Takeuchi 16163	K	KF676036*	KF676124*	KF676304*	KF676213*	KF675949*	KF675851*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria microglossa</i> (Baill.) Guillaumin	×	×	Barrabé 585	NOU	KF676037*	KF676125*	KF676305*	KF676214*	KF675950*	KF675852*	PSY	PSY ALL	New Caledonia
<i>Psychotria micrococca</i> (Lauterb. & K. Schum.) Valetton		×	Droz & Molem s.n.	PSF	KF676038*	KF676126*	KF676306*	KF676215*	KF675951*	KF675853*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria milnei</i> (A. Gray) K. Schum.	×	×	Pillon 551	NOU	KF676039*	KF676127*	KF676307*	KF676216*	KF675952*	KF675854*	PSY	PSY ALL	Vanuatu
<i>Psychotria monanthos</i> (Baill.) Schltr.		×	Pillon 1370	NOU	KF676040*	KF676128*	KF676308*	KF676217*	KF675953*	KF675855*	PSY	PSY ALL	New Caledonia
<i>Psychotria naccado</i> Guillaumin		×	McPherson 19478	NOU	KF676041*	KF676129*	KF676309*	KF676218*	KF675954*	KF675856*	PSY	PSY ALL	Vanuatu
<i>Psychotria nummularioides</i> Baill. ex Guillaumin	×	×	Rigault & Barrabé 144	NOU	KF676042*	KF676130*	KF676310*	KF676219*	KF675955*	KF675857*	PSY	PSY ALL	New Caledonia
<i>Psychotria oleoides</i> (Baill.) Schltr.	×	×	Barrabé & Rigault 658	NOU	JX155121 <sup>19</sup>	JX155168 <sup>19</sup>	JX155208 <sup>19</sup>	JX155028 <sup>19</sup>	JX155076 <sup>19</sup>	KF675858*	PAL	PSY ALL	New Caledonia

(continued on next page)



Table 1 (continued)

Taxa	Rubioideae dataset	Psy–Pal dataset	Sample	Herbarium	ndhF	rps16	trnHpsbA	trnTF	ITS	ETS	Tribe	Rubioideae intra level	Country/area
<i>Psychotria pandurata</i> Verdc.	×	×	Davis 2915	K	KF676043*	KF676131*		KF676220*	KF675956*		PSY	PSY ALL	Tanzania
<i>Psychotria parkeri</i> Baker	×	×	Maurin 132	K	JX155130 <sup>19</sup>	JX155175 <sup>19</sup>	JX155215 <sup>19</sup>	JX155037 <sup>19</sup>	JX155085 <sup>19</sup>	KF675859*	PSY	PSY ALL	Madagascar
<i>Psychotria parvula</i> A. Gray		×	Tuiwawa et al. 4936	SUVA	KF676044*	KF676132*	KF676311*	KF676221*	KF675957*	KF675860*	PSY	PSY ALL	Fiji
<i>Psychotria poeppigiana</i> Müll.Arg.	×	×	Bremer 3330	UPS	AM945279 <sup>13</sup>	AF002748 <sup>5</sup>			AF149400 <sup>1</sup>		PAL	PSY ALL	Ecuador
<i>Psychotria poissoniana</i> (Baill.) Guillaumin ex S. Moore		×	Munzinger 5156	NOU	KF676045*	KF676133*	KF676312*	KF676222*	KF675958*	KF675861*	PSY	PSY ALL	New Caledonia
<i>Psychotria polioSTEMMA</i> Benth.		×	Barrabé & Rigault 1058	NOU	KF676046*	KF676134*	KF676313*	KF676223*	KF675959*	KF675862*	PSY	PSY ALL	Australia
<i>Psychotria pritchardii</i> Seem.	×	×	Barrabé et al. 1124	NOU	KF676078*	KF676165*	KF676347*	KF676257*	KF675992*	KF675903*	PSY	PSY ALL	Fiji
<i>Psychotria raivavaensis</i> Fosberg	×	×	Meyer 3088	PAP	KF676047*	KF676135*	KF676314*	KF676224*	KF675960*		PSY	PSY ALL	French Polynesia
<i>Psychotria rupicola</i> (Baill.) Schltr. 1	×	×	Barrabé et al. 547	NOU	KF676048*	KF676136*	KF676315*	KF676225*	KF675961*	KF675863*	PSY	PSY ALL	New Caledonia
<i>Psychotria rupicola</i> (Baill.) Schltr. 2	×	×	Barrabé & Rigault 662	NOU	KF676049*	KF676137*	KF676316*	KF676226*	KF675962*	KF675864*	PSY	PSY ALL	New Caledonia
<i>Psychotria rupicola</i> (Baill.) Schltr. 3	×	×	Barrabé & Rigault 655	NOU	KF676050*	KF676138*	KF676317*	KF676227*	KF675963*	KF675865*	PSY	PSY ALL	New Caledonia
<i>Psychotria samoana</i> K. Schum.		×	Bristol 2128	K	JX155136/ JX155137 <sup>19</sup>	JX155180 <sup>19</sup>	JX155221 <sup>19</sup>	JX155043 <sup>19</sup>	JX155091 <sup>19</sup>	KF675866*	PAL	PSY ALL	Samoa
<i>Psychotria sarmentosa</i> Blume 1		×	Jacobs	C		AF410751 <sup>9</sup>		JN643530 <sup>20</sup>			PSY	PSY ALL	Sumatra
<i>Psychotria sarmentosa</i> Blume 2		×	Boeea 6609	S		AF410739 <sup>9</sup>		JN643506 <sup>20</sup>			PSY	PSY ALL	Borneo
<i>Psychotria schlechteriana</i> K. Krause	×	×	Barrabé et al. 712	NOU	JX155115 <sup>19</sup>	JX155162 <sup>19</sup>	JX155203 <sup>19</sup>	JX155022 <sup>19</sup>	JX155070 <sup>19</sup>	KF675867*	PSY	PSY ALL	New Caledonia
<i>Psychotria schliebenii</i> E.M.A. Petit		×	Luke 8348	UPS	AM945282 <sup>13</sup>	AM945329 <sup>13</sup>		AM945361 <sup>13</sup>	AM945216 <sup>13</sup>		PSY	PSY ALL	Kenya
<i>Psychotria serpens</i> L.		×	Xuejun s.n.	K	KF676051*	KF676139*	KF676318*	KF676228*		KF675868*	PSY	PSY ALL	China
<i>Psychotria</i> sp. 1AUST		×	Weston 888	(Syd. Bot. Gard. 862980)	JX155131 <sup>19</sup>	JX155176 <sup>19</sup>	JX155216 <sup>19</sup>	JX155038 <sup>19</sup>	JX155086 <sup>19</sup>	KF675869*	PAL	PSY ALL	Australia
<i>Psychotria</i> sp. 1FIJI		×	Barrabé 1060	NOU	JX155107 <sup>19</sup>	JX155154 <sup>19</sup>	JX155195 <sup>19</sup>	JX155014 <sup>19</sup>	JX155062 <sup>19</sup>	KF675870*	PAL	PSY ALL	Fiji
<i>Psychotria</i> sp. 1NC	×	×	Munzinger 4963	NOU	JX155116 <sup>19</sup>	JX155163 <sup>19</sup>	JX155204 <sup>19</sup>	JX155023 <sup>19</sup>	JX155071 <sup>19</sup>	KF675871*	PAL	PSY ALL	New Caledonia
<i>Psychotria</i> sp. 1PNG		×	De Kok 1157	K	KF676052*	KF676140*	KF676319*	KF676229*	KF675964*	KF675872*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria</i> sp. 1THAI	×	×	Larsen et al. 43366	P	KF676053*		KF676320*	KF676230*	KF675965*	KF675873*	PSY	PSY ALL	Thailand
<i>Psychotria</i> sp. 1VANU	×	×	McPherson 19425	NOU	JX155122 <sup>19</sup>	JX155169 <sup>19</sup>		JX155029 <sup>19</sup>	JX155077 <sup>19</sup>	KF675874*	PAL	PSY ALL	Vanuatu
<i>Psychotria</i> sp. 1VIET	×	×	Davis 4031	K	JX155126 <sup>19</sup>	JX155172 <sup>19</sup>	JX155212 <sup>19</sup>	JX155033 <sup>19</sup>	JX155081 <sup>19</sup>	KF675875*	PAL	PSY ALL	Vietnam
<i>Psychotria</i> sp. 2AUST	×	×	Barrabé et al. 1032	NOU	KF676054*	KF676141*	KF676321*	KF676231*	KF675966*	KF675876*	PSY	PSY ALL	Australia
<i>Psychotria</i> sp. 2FIJI	×	×	Barrabé et al. 1100	NOU	KF676055*	KF676142*	KF676322*	KF676232*	KF675967*	KF675877*	PSY	PSY ALL	Fiji
<i>Psychotria</i> sp. 2NC	×	×	Munzinger 4174	NOU	KF676056*	KF676143*	KF676323*	KF676233*	KF675968*	KF675878*	PSY	PSY ALL	New Caledonia
<i>Psychotria</i> sp. 2PNG	×	×	De Kok 1159	K	KF676057*	KF676144*	KF676324*	KF676234*	KF675969*	KF675879*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria</i> sp. 2THAI	×	×	Larsen et al. 43407	P	KF676058*	KF676145*	KF676325*	KF676235*	KF675970*	KF675880*	PSY	PSY ALL	Thaïlande
<i>Psychotria</i> sp. 2VANU	×	×	Pillon 563	NOU	KF676059*	KF676146*	KF676326*	KF676236*	KF675971*	KF675881*	PSY	PSY ALL	Vanuatu
<i>Psychotria</i> sp. 2VIET	×	×	HNK 614	K	JX155128 <sup>19</sup>	JX155173 <sup>19</sup>	JX155213 <sup>19</sup>	JX155035 <sup>19</sup>	JX155083 <sup>19</sup>	KF675882*	PAL	PSY ALL	Vietnam
<i>Psychotria</i> sp. 3AUST		×	Barrabé & Rigault 1035	NOU	KF676060*	KF676167*	KF676327*	KF676237*	KF675972*	KF675883*	PSY	PSY ALL	Australia
<i>Psychotria</i> sp. 3FIJI	×	×	Buerki et al. 161	NOU	KF676061*	KF676147*	KF676328*	KF676238*	KF675973*	KF675884*	PSY	PSY ALL	Fiji
<i>Psychotria</i> sp. 3NC	×	×	Barrabé et al. 922	NOU	KF676062*	KF676148*	KF676329*	KF676239*	KF675974*	KF675885*	PSY	PSY ALL	New Caledonia
<i>Psychotria</i> sp. 3PNG	×	×	De Kok 1179	K	KF676063*	KF676149*	KF676330*	KF676240*	KF675975*	KF675886*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria</i> sp. 3VANU	×	×	Pillon 1117	NOU	KF676064*	KF676150*	KF676331*	KF676241*	KF675976*	KF675887*	PSY	PSY ALL	Vanuatu
<i>Psychotria</i> sp. 3VIET		×	Briggs 98	K	KF676065*	KF676151*	KF676332*	KF676242*	KF675977*	KF675888*	PSY	PSY ALL	Vietnam
<i>Psychotria</i> sp. 4AUST	×	×	Barrabé & Rigault 1034	NOU	KF676066*	KF676152*	KF676333*	KF676243*	KF675978*	KF675889*	PSY	PSY ALL	Australia
<i>Psychotria</i> sp. 4NC		×	Munzinger 2237	NOU	KF676067*	KF676153*	KF676334*	KF676244*	KF675979*	KF675890*	PSY	PSY ALL	New Caledonia
<i>Psychotria</i> sp. 4PNG		×	Bau LAE 88424	K	KF676068*	KF676154*	KF676335*	KF676245*	KF675980*	KF675891*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria</i> sp. 4VIET	×	×	HNK 2274	K	KF676069*	KF676155*	KF676336*	KF676246*	KF675981*	KF675892*	PSY	PSY ALL	Vietnam
<i>Psychotria</i> sp. 5PNG		×	Sands 7317	K	KF676082*	KF676156*	KF676337*	KF676247*	KF675982*	KF675893*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria</i> sp. 5VIET		×	HNK 2625	K	KF676070*	KF676157*	KF676338*	KF676248*	KF675983*	KF675894*	PSY	PSY ALL	Vietnam
<i>Psychotria</i> sp. 6PNG		×	Johns 10343	K	KF676071*	KF676158*	KF676339*	KF676249*	KF675984*	KF675895*	PSY	PSY ALL	Papua New Guinea

<i>Psychotria</i> sp. 7PNG		×	Edwards 4052	K	KF676072*	KF676159*	KF676340*	KF676250*	KF675985*	KF675896*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria</i> sp. 8PNG	×	×	Johns 8721	K	KF676073*	KF676160*	KF676341*	KF676251*	KF675986*	KF675897*	PSY	PSY ALL	Papua New Guinea
<i>Psychotria</i> sp. BRAZ		×	Zappi 978	K	KF676074*	KF676161*	KF676342*	KF676252*	KF675987*	KF675898*	PSY	PSY ALL	Brazil
<i>Psychotria submontana</i> Domin		×	Barrabé et al. 1044	NOU		KF676168*	KF676343*	KF676253*	KF675988*	KF675899*	PSY	PSY ALL	Australia
<i>Psychotria temehaniensis</i> J.W. Moore	×	×	Mouly 403	P	KF676075*	KF676162*	KF676344*	KF676254*	KF675989*	KF675900*	PSY	PSY ALL	French Polynesia
<i>Psychotria trisulcata</i> (Baill.) Guillaumin	×	×	Barrabé et al. 902	NOU	KF676076*	KF676163*	KF676345*	KF676255*	KF675990*	KF675901*	PSY	PSY ALL	New Caledonia
<i>Psychotria wagapensis</i> Guillaumin	×	×	Barrabé et al. 833	NOU	KF676077*	KF676164*	KF676346*	KF676256*	KF675991*	KF675902*	PSY	PSY ALL	New Caledonia
<i>Reada membranacea</i> Gillespie	×	×	Barrabé et al. 1093	NOU	JX155109 <sup>19</sup>	JX155156 <sup>19</sup>	JX155197 <sup>19</sup>	JX155016 <sup>19</sup>	JX155064 <sup>19</sup>		PAL	PSY ALL	Fiji
<i>Rudgea stipulacea</i> (DC.) Steyerl.		×	Zappi 986	K	JX155145/ JX155146 <sup>19</sup>	JX155189 <sup>19</sup>	JX155226 <sup>19</sup>	JX155053 <sup>19</sup>	JX155099 <sup>19</sup>	KF675904*	PAL	PSY ALL	Brazil
<i>Schizocolea linderi</i> (Hutch. & Dalziel) Bremek.	×		Adam 789	P	FJ695335 <sup>17</sup>	AM945309 <sup>13</sup>		AM945338 <sup>13</sup>			SCHI	PSY ALL	Liberia
<i>Schradera subandina</i> K. Krause	×		Clark & Watt 878	QCNE	AM945264 <sup>13</sup>	AM945313 <sup>13</sup>		AM945343 <sup>13</sup>			SCHR	PSY ALL	?
<i>Sherardia arvensis</i> L.	×		K. Andreasen 345 / Wallander 51	SBT	FJ695337 <sup>17</sup>	AF004082 <sup>5</sup>		EU145571 <sup>14</sup>			RUB	SPE ALL	?/Italy
<i>Squamellaria imberbis</i> (A. Gray) Becc.	×	×	Barrabé et al. 1099	NOU	KF676079*	KF676166*	KF676348*	KF676258*	KF675993*	KF675905*	PSY	PSY ALL	Fiji
<i>Theligonum cynocrambe</i> L.	×		Reutersward & Forsslund 2	S	FJ695340 <sup>17</sup>	FJ695281 <sup>17</sup>		FJ695427 <sup>17</sup>			THE	SPE ALL	?
<i>Triainolepis mandrarensis</i> Homolle ex Bremek.	×		Razafimandimbison 521	UPS	FJ695341 <sup>17</sup>	AM266899 <sup>11</sup>		AM266985 <sup>11</sup>			KNO	SPE ALL	Madagascar
<i>Trigonopyren</i> sp. MADA		×	Razanajatovo 146	K	KF676080*		KF676349*	KF676259*	KF675994*	KF675906*	PSY	PSY ALL	Madagascar

Superscript numbers refer to the place where sequences first appeared: \* This study; <sup>1</sup> Andersson and Taylor (unpublished); <sup>2</sup> Andersson et al. (unpublished); <sup>3</sup> Andersson (unpublished); <sup>4</sup> Struwe et al. (1998); <sup>5</sup> Andersson and Rova (1999); <sup>6</sup> Bremer et al. (1999); <sup>7</sup> Nepokroeff et al. (1999); <sup>8</sup> Andersson (2001); <sup>9</sup> Andersson (2002a); <sup>10</sup> Backlund et al. (2007); <sup>11</sup> Karehed and Bremer (2007); <sup>12</sup> Khan et al. (2008); <sup>13</sup> Razafimandimbison et al. (2008); <sup>14</sup> Rydin et al. (2008); <sup>15</sup> Smedmark et al. (2008); <sup>16</sup> Bremer and Eriksson (2009); <sup>17</sup> Rydin et al. (2009); <sup>18</sup> Smedmark et al. (2010); <sup>19</sup> Barrabé et al. (2012); <sup>20</sup> Lemaire et al. (2012). Abbreviations used: *Rubioideae* intra level: PSY ALL = Psychotrieae alliance, SPE ALL = Spermacoceae alliance; *Tribes*: ANT = Anthospermeae, ARG = Argostemmateae, COU = Coussareeae, CRA = Craterispermeae, DAN = Danaideae, DUN = Dunnieae, GAR = Gaertnereae, KNO = Knoxieae, MIT = Mit-chelleae, MOR = Morindeae, PAE = Paederieae, PAL = Palicoureeae, PRI = Pristomerideae, PSY = Psychotrieae, PUT = Putorieae, RUB = Rubieae, SCHI = Schizocoleae, SCHR = Schradereae, SPE = Spermacoceae, THE = Theligoneae.

**Table 2**

Characteristics of the DNA partitions and BMGE software settings used in the phylogenetic and dating analyses of the Rubioideae dataset and the core Psy–Pal dataset.

	Rubioideae dataset				core Psy–Pal dataset					
	<i>trnT-F</i>	<i>rps16</i>	<i>ndhF</i>	Total	<i>trnT-F</i>	<i>rps16</i>	<i>ndhF</i>	<i>trnH-psbA</i>	ITS	ETS
DNA region nature	Plastid	Plastid	Plastid gene		Plastid	Plastid	Plastid gene	Plastid	Nuclear	Nuclear
Number of taxa	107	108	105	111	145	142	140	126	144	117
Number of alignment characters	2884	1312	2091	6287	2466	1160	2070	988	769	463
Similarity matrix	PAM250	PAM250	PAM250		PAM250	PAM250	PAM250	PAM250	PAM250	PAM250
Sliding windows size	1	1	3		1	1	3	1	1	1
GAP rate cut-off	0.75	0.75	0.2		0.75	0.75	0.2	0.75	0.2	0.2
Number of included characters	1600	705	2043	4348	1658	747	2043	388	690	407
Evolution models	F81 + I + G	F81 + G	SYM + G		F81 + G	SYM + I + G	GTR + G	F81 + G	GTR + G	GTR + I + G

lineages, of which three are supported as monophyletic (PP = 1; Fig. 1). Two lineages belonged to Palicoureeae. The first is composed of a single non-endemic species, *Geophila repens*, which has a pantropical distribution (Fig. 2A). The second, the *Margaritopsis* clade NC, included four species from New Caledonia and one from Vanuatu (*Psychotria* sp. 1VANU; Fig. 2A). The other two lineages belonged to Psychotrieae (within *Psychotria* s.s. sensu Andersson, 2002a) and are endemic to New Caledonia (*Psychotria* clade NC1 and *Psychotria* clade NC2; Fig. 2C).

### 3.1. Phylogeny of Psychotrieae–Palicoureeae and clades geographic distributions

Within Palicoureeae, the phylogenetic BEAST combined analysis of the core Psy–Pal dataset retrieved the seven major lineages of Barrabé et al. (2012) whose only two occur in New Caledonia (five lineages with PP > 0.95; Fig. 2A). Among them, the *Chassalia/Geophila/Hymenocoleus* clade included two sister-species: *Geophila obvallata*, sampled in Africa, and *G. repens*, sampled in Vanuatu, but also occurring in New Caledonia (PP = 1; Fig. 2A). The Indo-Pacific *Margaritopsis* clade (PP = 1) included the well-supported *Margaritopsis* clade NC (PP = 1), sister to the *Leptothyrsa* clade with a low support value (PP = 0.6; Fig. 2A). Within Psychotrieae six major lineages were highly supported: *Cremocarpon* clade, Pacific clade, and *Psychotria* clades I, II, III and IV sensu Andersson (all with PP = 1; Fig. 2B and C; Andersson, 2002a). The *Cremocarpon* clade (PP = 1; Fig. 2B) included species of *Cremocarpon* (including the type species: *C. boivinianum*), *Psathura* and *Trigonopyren* all from the Malagasy region. The *Psychotria* clades I, II and III formed a well-supported monophyletic group (PP = 1) including species from the Neotropics, Africa and South-East Asia. The Pacific clade (PP = 1; Fig. 2B) is distributed in South-East Asia, Malesia and the Pacific Islands (but is not occurring in New Caledonia) and included species of *Amarcarpus*, *Calycosia*, *Hedstromia*, *Hydnophytum*, *Myrmecodia*, *Psychotria*, and *Squamellaria*. The *Psychotria* clade IV (PP = 1; Fig. 2C) occurs in South-East Asia, Malesia and the Pacific Islands, and is especially rich in New Caledonia. The *Psychotria* clade NC1 included three New Caledonian species, *P. comptonii*, *P. declieuxioides* and *P. rupicola* (PP = 1) and was inferred sister to all remaining members of *Psychotria* clade IV (i.e. *Psychotria* clade IP; PP = 1). The *Psychotria* clade NC2 (PP = 1) included all of the 23 remaining New Caledonian species in our sampling. The *Psychotria* clade NC2 was sister to the Australian *Psychotria* clade A2 (PP = 0.99; Fig. 2C). The latter two clades were sister to the Australian *Psychotria* clade A1 (PP = 0.99).

### 3.2. Divergence time estimations and diversification estimates

To investigate diversification patterns of Psy–Pal in New Caledonia, we first retrieved divergence times from BEAST analyses and secondly applied several estimates to the four Psy–Pal lineages present in the archipelago.

#### 3.2.1. Species richness estimates of the four New Caledonian lineages and their sister-clades

The genus *Geophila* in New Caledonia is composed of a single non-endemic species, *G. repens* (Guillaumin, 1930, 1948; Morat et al., 2012). The *Margaritopsis* clade NC and the *Psychotria* clade NC1 include each a total of four species (Barrabé, 2013). Based on preliminary phylogenetic results including all species of Psy–Pal occurring in the archipelago (Barrabé, 2013), the *Psychotria* clade NC2 likely encompasses all of the remaining New Caledonian species (described and undescribed) currently placed in *Psychotria*, and consequently would include ca. 78 species.

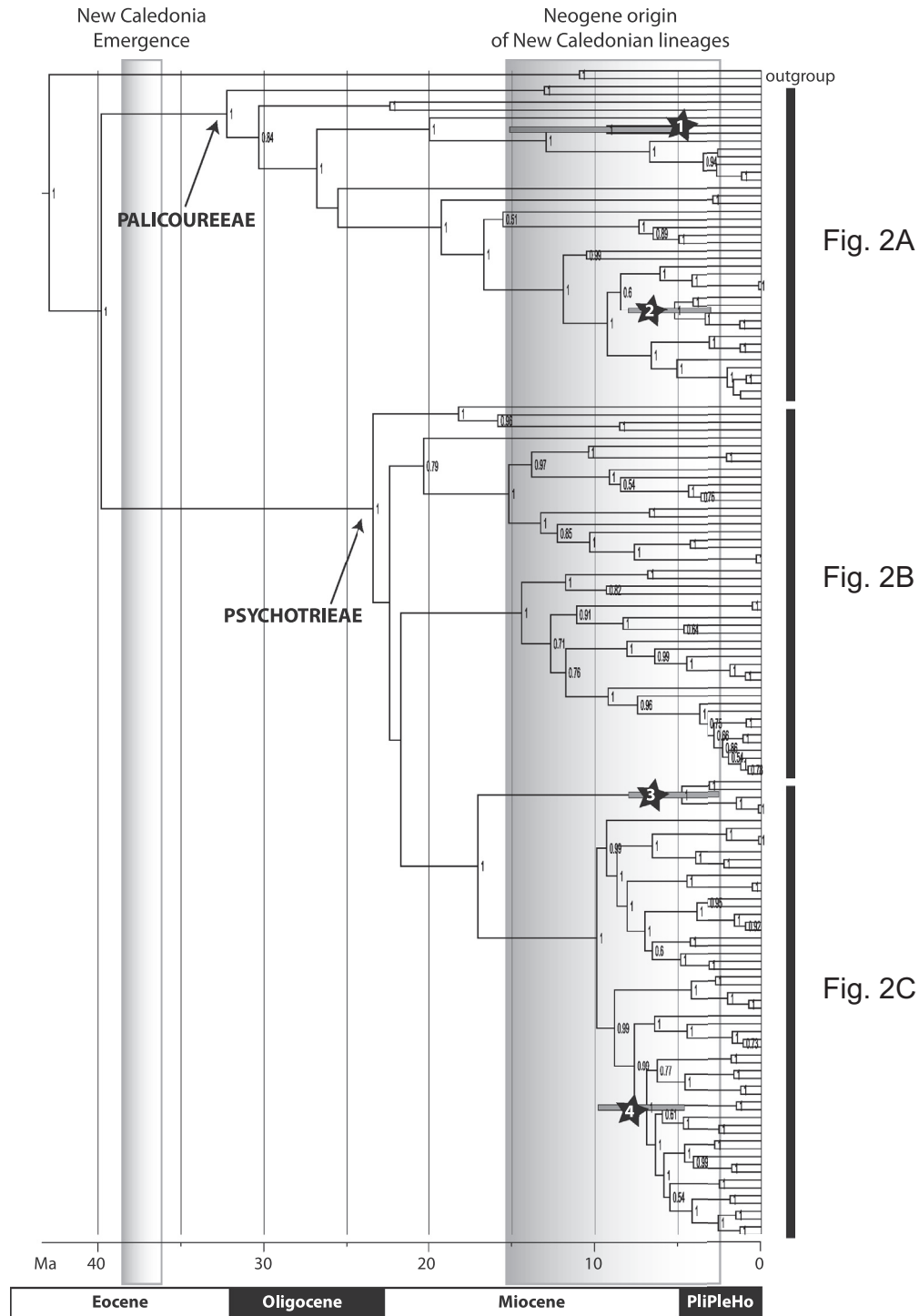
The sister-clade (*Psychotria* clade A2) of the *Psychotria* clade NC2 comprised four (from our phylogenetic sampling; Fig. 2C) to nine species (i.e. all non-climbing Australian *Psychotria* less the four species of the *Psychotria* clade A1 and *P. sp. 2AUST*; Cooper and Cooper, 2004). The sister-clade of the *Margaritopsis* clade NC is composed of four to 34 species, depending on its phylogenetic placement. This placement was recovered as ambiguous within the Indo-Pacific *Margaritopsis* clade (Barrabé et al., 2012), including either four species if retrieved sister to the *Leptothyrsa* clade (Fig. 2A), or 34 species if retrieved sister to all the remaining species of the Indo-Pacific *Margaritopsis* clade. The sister-clade (*Psychotria* clade IP) of the *Psychotria* clade NC1, composed of all remaining species of the *Psychotria* clade IV, had at least 136 species (from our phylogenetic sampling; Fig. 2C).

#### 3.2.2. Divergence time estimates

The BEAST analysis showed that the four New Caledonian lineages all appeared during the Neogene, relatively simultaneously. The median divergence time estimates are 9.3, 8.47, 17.06 and 7.63 Ma for the stem nodes of *Geophila repens*, *Margaritopsis* clade NC, *Psychotria* clade NC1 and *Psychotria* clade NC2, respectively. For the crown nodes, the median divergence time estimates are 5.21, 4.78 and 6.9 Ma for the *Margaritopsis* clade NC, the *Psychotria* clade NC1 and the *Psychotria* clade NC2, respectively (Fig. 1 and Table 3).

#### 3.2.3. Net diversification rate estimates

Net diversification rates estimated from median crown ages are 0.133, 0.145 and 0.53 species/Ma for the *Margaritopsis* clade NC, the *Psychotria* clade NC1 and the *Psychotria* clade NC2, respectively for a null extinction, and 0.039, 0.04, and 0.31 species/Ma, respectively for a high extinction (Table 4). No net diversification rates were provided for the *Geophila repens* because it is the single species of the genus occurring in the archipelago. With respect to per-unit-area, diversification rates are estimated to be between  $1.36 \times 10^{-6}$ – $1.25 \times 10^{-5}$ ,  $1.49 \times 10^{-6}$ – $1.25 \times 10^{-5}$ , and  $1.16 \times 10^{-5}$ – $4.27 \times 10^{-5}$  species/Ma/km<sup>2</sup>, for the *Margaritopsis* clade NC, the *Psychotria* clade NC1 and the *Psychotria* clade NC2, respectively (Table 4). At a per-unit-log(area), diversification rates were estimated to be between  $0.26 \times 10^{-2}$ – $0.23 \times 10^{-1}$ ,  $0.26 \times 10^{-2}$ – $0.28 \times 10^{-1}$ , and  $0.22 \times 10^{-1}$ – $0.81 \times 10^{-1}$  species/Ma/(log)km<sup>2</sup>, respectively (Table 4).



**Fig. 1.** BEAST maximum credibility cladogram of tribes Palicoureeae and Psychotrieae based on the core Psy–Pal dataset. Bayesian posterior probabilities (PP) are indicated for each node when superior to 0.5. Stars indicate New Caledonian lineages: (1) *Geophila repens*; (2) *Margaritopsis* clade NC; (3) *Psychotria* clade NC1; (4) *Psychotria* clade NC2. Grey node bars correspond to the 95% highest posterior density and are only provided for clades that include New Caledonian species. The abbreviation PliPleHo, used on the geological scale, corresponds to the epoch of Pliocene, Pleistocene, and Holocene.

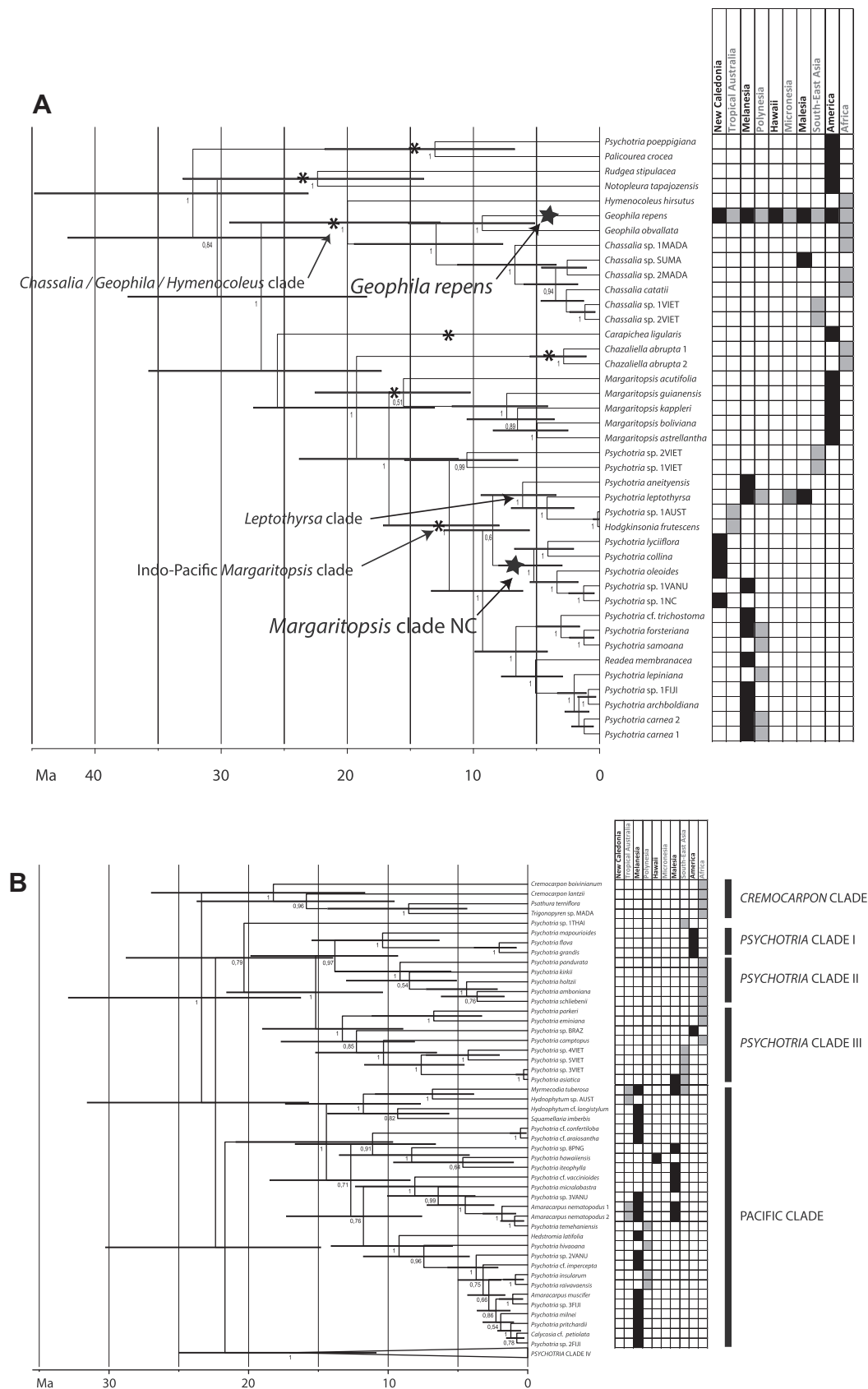
### 3.2.4. Relative diversification rates

The species distribution among the four New Caledonian Psy–Pal lineages differed significantly from a broken stick distribution ( $p = 0.0009$ ; MacArthur, 1957). The application of Eq. (3) of Slowinsky and Guyer (1993) showed that the *Margaritopsis* clade NC had less species than its sister-clade ( $p = 0.57$ – $0.91$ ; Table 4). As the sister-clade of *Psychotria* clade NC1 had more species, the test was assessed for the *Psychotria* clade IP ( $p = 0.027^*$ ; Table 4). The *Psychotria* clade NC1 therefore had significantly fewer species than

its sister-clade. Only the *Psychotria* clade NC2 had significantly or marginally significantly more species than its sister-clade the *Psychotria* clade A2 ( $p = 0.049^*$ – $0.105$ ; Table 4).

### 3.3. Distribution and ecology of New Caledonian lineages, and species distribution modeling

The geographic range of New Caledonian Psy–Pal lineages is shown in Fig. 3. Species of both the *Margaritopsis* clade NC and



**Fig. 2.** Details of the BEAST maximum clade credibility chronogram of tribes Palicoureeae and Psychotrieae based on the core Psy-Pal dataset. Bayesian posterior probabilities (PP) are indicated for each node when superior to 0.5. Stars indicate New Caledonian lineages. Asterisk indicates the seven Palicoureeae clades delimited in Barrabé et al., 2012. Grey node bars correspond to the 95% HPD. The geographic distribution of each taxon of the sampling is provided and follows the biogeographic units of Mueller-Dombois and Fosberg (1998) and Keppel et al. (2009). (A) Chronogram of Palicoureeae. (B) Chronogram of Psychotrieae, part I (Cremocarpus clade, Pacific clade, Psychotria clades I, II and III). (C) Chronogram of Psychotrieae, part II (Psychotria clade IV).



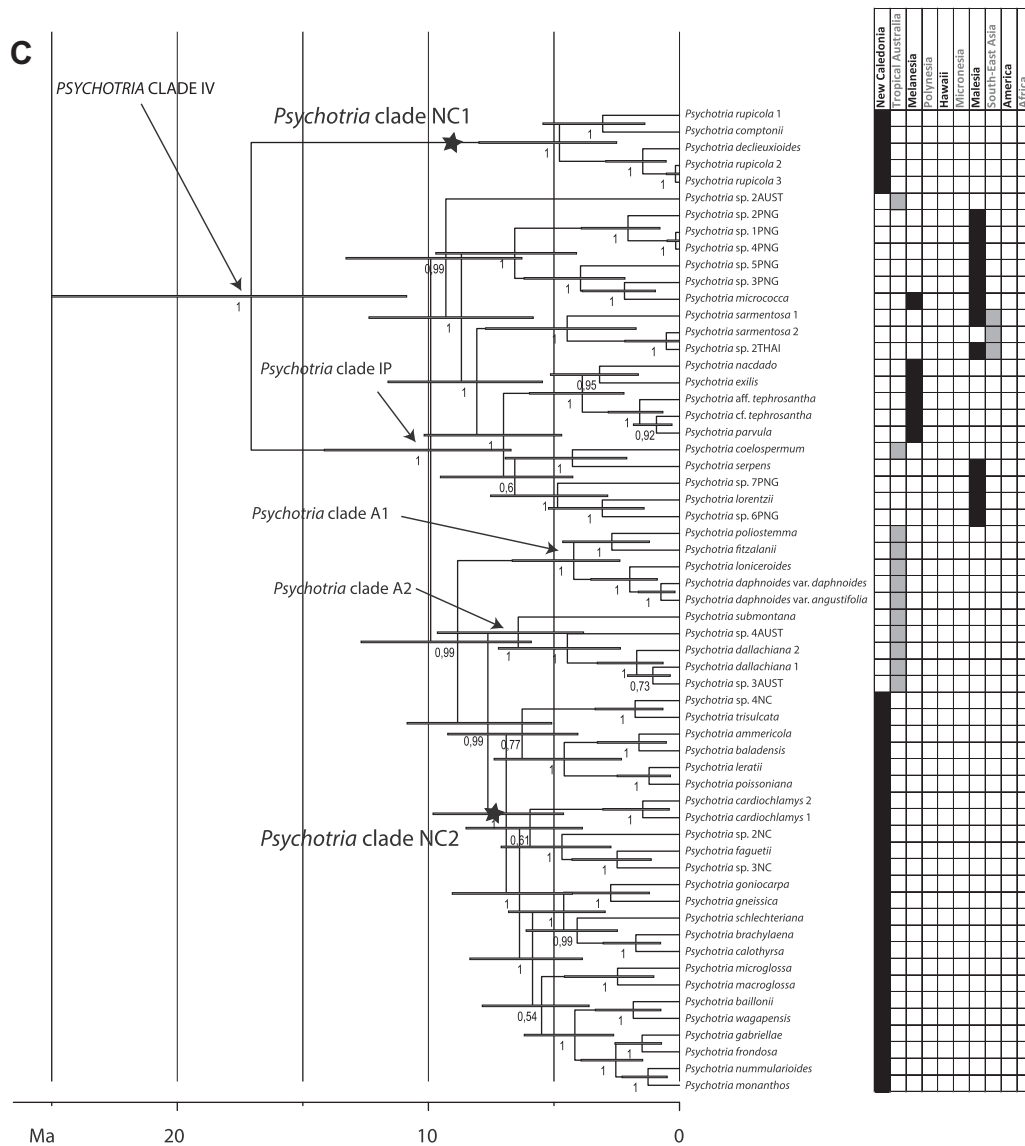


Fig. 2 (continued)

the *Psychotria* clade NC2 are widely distributed over the archipelago (i.e. Grande Terre and the Loyalty Islands) and occupied a large diversity of habitats. Collectively these species extended from sea

level to high elevations, in localities with low to high rainfall rates, and on all kinds of geological substrates (Fig. 3B and D). The four species of the *Psychotria* clade NC1 are strictly restricted to

Table 3

Divergence time estimates resulting from BEAST dating analysis of the core Psy-Pal dataset. The abbreviation NA corresponds to non available data.

	Stem age (Ma)	95% HPD stem age (Ma)	Crown age (Ma)	95% HPD crown age (Ma)
Palicoureeae	39.81	30.55–54.43	32.24	23.1–44.8
Chassalia/Geophila/Hymenocoleus clade	26.83	18.46–37.38	19.98	12.64–29.33
Geophila repens	9.3	5.15–15.15	NA	NA
Indo-Pacific <i>Margaritopsis</i> clade	11.92	7.96–17.14	9.27	6.09–13.33
<i>Margaritopsis</i> clade NC	8.47	5.56–12.33	5.21	2.97–7.99
Psychotrieae	39.81	30.55–54.43	23.37	16.27–32.9
Cremocarpon clade	23.37	16.27–32.9	18.22	11.67–26.96
Pacific clade	21.69	14.84–30.24	14.43	9.67–20.9
<i>Psychotria</i> clade I	13.82	9.31–19.84	10.4	6.35–15.46
<i>Psychotria</i> clade II	13.82	9.3–19.84	9.15	5.5–13.82
<i>Psychotria</i> clade III	15.19	10.4–21.57	13.28	8.94–19
<i>Psychotria</i> clade IV	21.69	14.84–30.24	17.06	10.86–25.01
<i>Psychotria</i> clade NC1	17.06	10.86–25.01	4.78	2.5–7.99
<i>Psychotria</i> clade IP	17.06	10.86–25.01	9.91	6.71–14.15
<i>Psychotria</i> clade A1	8.84	5.9–12.68	4.21	2.37–6.66
<i>Psychotria</i> clade A2	7.63	5.09–10.85	6.42	3.82–9.64
<i>Psychotria</i> clade NC2	7.63	5.09–10.85	6.9	4.62–9.82

**Table 4**  
Biological, ecological and diversification characteristics of the four New Caledonian Psychotrieae–Palicoureeae lineages. The abbreviation NA corresponds to non available data.

	<i>Geophila repens</i>	<i>Margaritopsis</i> clade NC	<i>Psychotria</i> clade NC1	<i>Psychotria</i> clade NC2
<i>Characteristics</i>				
Number of species	1	4	4	78
Phylogenetic status	N/A	Paraphyletic (1 Vanuatu species)	Monophyletic	Monophyletic
Habit	Creeping herbs with stolons	Shrubs to small trees	Shrubs to small trees	Shrubs to small trees
Fruits type	Drupe	Drupe	Dry, schizocharp	Drupe
Dispersal mode	Endozoochory	Endozoochory	Barochory	Endozoochory
Substrate	Ultramafic, volcano-sedimentary	Ultramafic, volcano-sedimentary, limestone	Ultramafic	Ultramafic, volcano-sedimentary, limestone
Vegetation type	Rainforest	Rainforest, dry forest, maquis, etc.	Maquis	Rainforest, dry forest, maquis, etc.
<i>Age estimates</i>				
Stem age (Ts, Ma)	9.3	8.47	17.06	7.63
95% HPD stem age (Ma)	[5.15–15.15]	[5.56–12.33]	[10.86–25.01]	[5.09–10.85]
Crown age (Tc, Ma)	N/A	5.21	4.78	6.9
95% HPD crown age (Ma)	N/A	[2.97–7.99]	[2.5–7.99]	[4.62–9.82]
Ts–Tc (Ma)	N/A	3.26	12.28	0.73
<i>Net diversification rates</i>				
Median crown age, extinction = 0 (species/Ma)	N/A	0.133	0.145	0.53
Median crown age, extinction = 0.9 (species/Ma)	N/A	0.039	0.04	0.31
95% HPD crown age, extinction = 0 (species/Ma)	N/A	[0.087–0.23]	[0.087–0.28]	[0.37–0.79]
95% HPD crown age, extinction = 0.9 (species/Ma)	N/A	[0.025–0.068]	[0.025–0.081]	[0.215–0.46]
Per-unit-area (species/Ma/km <sup>2</sup> )	N/A	$1.36 \times 10^{-6}$ – $1.25 \times 10^{-5}$	$1.49 \times 10^{-6}$ – $1.25 \times 10^{-5}$	$1.16 \times 10^{-5}$ – $4.27 \times 10^{-5}$
Per-unit-log(area) (species/Ma/(log)km <sup>2</sup> )	N/A	$0.26 \times 10^{-2}$ – $0.23 \times 10^{-1}$	$0.26 \times 10^{-2}$ – $0.28 \times 10^{-1}$	$0.22 \times 10^{-1}$ – $0.81 \times 10^{-1}$
<i>Test of Slowinsky and Guyer</i>				
Richness of sister-clade	N/A	4 or 34	At least 136	4 or 9
p-Value (* = significant if < 0.05)	N/A	0.57–0.91	0.98 (reverse p-value of the sister-clade = 0.027*)	0.049*–0.105

ultramafic soils of the southeastern part of Grande Terre (Fig. 3C), and are found exclusively in a specific shrubby vegetation type, referred to as ‘maquis miniers’ (Barrabé, 2013). The only species of *Geophila* occurring in New Caledonia (i.e. *G. repens*) has only been recorded in four localities in the southeastern, northwestern and northeastern parts of Grande Terre, on both ultramafic and volcano-sedimentary soils (Fig. 3A).

Analyses of species distribution modeling using MaxEnt were only conducted for the *Psychotria* clade NC1, because it is the only lineage (of the four studied here) specialized to a specific vegetation type and a geological substrate. The results revealed that its potential habitat was not exclusively present in the southeastern part of Grande Terre but also in the ultramafic isolated massifs of the northwestern coast (Fig. 4).

#### 4. Discussion

In an archipelago, as New Caledonia, a plant lineage is the result of opposite evolutionary forces, leading to a continual species turn-over through time (MacArthur and Wilson, 1967; Simberloff, 1974; Whittaker and Fernández-Palacios, 2007): immigration (or colonization, a species gain from outside, decomposed in two step: the arrival from outside and the establishment; Silvertown, 2004a), speciation (a species gain inside) and extinction (a species loss inside). These diversification processes are driven by intrinsic and extrinsic factors, as well as punctuated by climatic and/or geological events (Barracough et al., 1998; Slowinsky and Guyer, 1993; Whittaker and Fernández-Palacios, 2007). Through the example of the Psy–Pal, we will attempt to explain their evolutionary history in the New Caledonian archipelago by linking these foregoing evolutionary forces with biotic and abiotic factors.

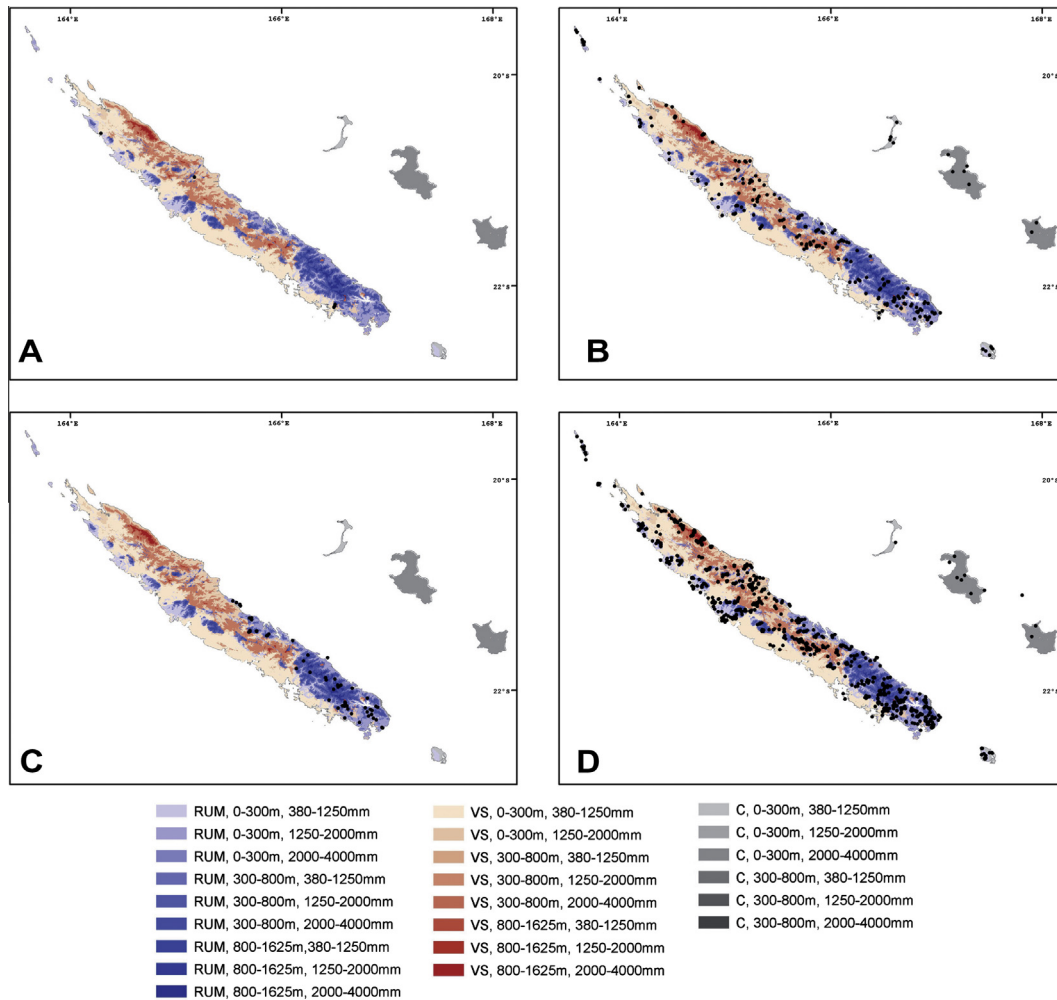
##### 4.1. Multiple colonizations of New Caledonia by Psychotrieae–Palicoureeae lineages during the Neogene

The Psy–Pal lineages successfully colonized the New Caledonian archipelago four times: *Geophila repens*, the *Margaritopsis* clade NC, the *Psychotria* clade NC1, and the *Psychotria* clade NC2 (Fig. 2A–C). These colonizations were almost synchronous (Table 3) and occurred between the Middle Miocene and Pliocene, long after the re-emergence of the Grande Terre (Fig. 1). This timing of colonization is in agreement with the results of recent reviews (Cruaud et al., 2012; Pillon, 2012). These lineages remain relatively recent for the archipelago as some palms groups or the clade *Kermadecia* Brongn. & Gris – *Sleumerodendron* R.Virot (Proteaceae), compared to other groups (e.g. *Planchonella*, *Pycnan-dra*, or some *Metrosideros* Banks ex Gaertn. clades) whose origins were estimated almost contemporary to the New Caledonia’s re-emergence (Bartish et al., 2011; Pillon, 2012). The relative synchronous of their respective arrival and establishment of these lineages in New Caledonia could reflect an intense environmental changes that occurred during the Neogene (Chevallotte et al., 2006), that could have led to the replacement of established plant species by the newly competitive colonizers, perhaps including members of Psy–Pal.

##### 4.2. Colonization in New Caledonia

###### 4.2.1. The four New Caledonian lineages: differential colonization successes

New Caledonia is a relatively remote archipelago and its colonization would be favoured by several appropriate adaptations e.g. involving in long-distance dispersal (Carlquist, 1967). *Geophila repens*, members of the *Margaritopsis* clade NC and the



**Fig. 3.** Geographic range of the four Psychotriaceae–Palicoeae lineages present in New Caledonia. Each rectangle indicates a special ecological niche and registers from left to right: substrate type (RUM: ultramafic, in blue; VS: volcano-sedimentary, in red; C: coral limestone, in gray), elevational range, rainfall range. (A) *Geophila* clade; (B) *Margaritopsis* clade NC; (C) *Psychotria* clade NC1; (D) *Psychotria* clade NC2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

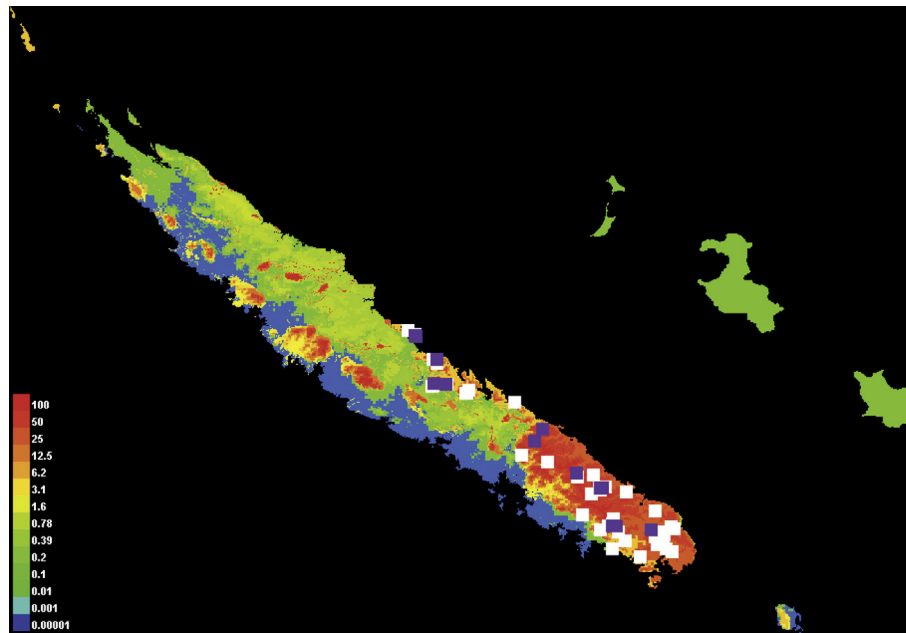
*Psychotria* NC2 clades have drupaceous fruits, suggesting dispersal by endozoochory (Fig. 5; Bremer and Eriksson, 2009). This mode is generally considered more likely for tropical islands than anemochory or hydrochory (Carlquist, 1967; Givnish, 2010; Howe and Smallwood, 1982), and therefore could have conferred high dispersal ability to these lineages enabling them to disperse to New Caledonia and to invade the Indo-Pacific region (Fig. 2A and C). Fruits of these species do not exceed 2 cm long (Barrabé, 2013), indicating that they are not dispersed by large birds (Carpenter et al., 2003). These lineages are then not conditioned by the size of their biotic vectors, which would explain their success in colonizing the archipelago. The *Psychotria* clade NC2 originated in Australia (as suggested by the basal Australian grade of clades A1 and A2; Fig. 2C), a pattern shared with other families in New Caledonia: Ebenaceae (Duangjai et al., 2009; Turner et al., 2013), Ericaceae (Wagstaff et al., 2010), Sapindaceae (Buerki et al., 2012a) and Sapotaceae (Bartish et al., 2005; Swenson et al., 2007; Swenson et al., 2008).

The colonization success of the *Psychotria* clade NC1 in New Caledonia remains difficult to explain since species of this lineage possess schizocarpic fruits (Fig. 5). These dried fruits are certainly dispersed by simple gravity (Bremekamp, 1958) with known limitations (e.g. short-distance dispersal from the mother plant, or high competition between seedlings) if no association with a second dispersal mode is recorded (Castro et al., 2010). In the Psy–Pal

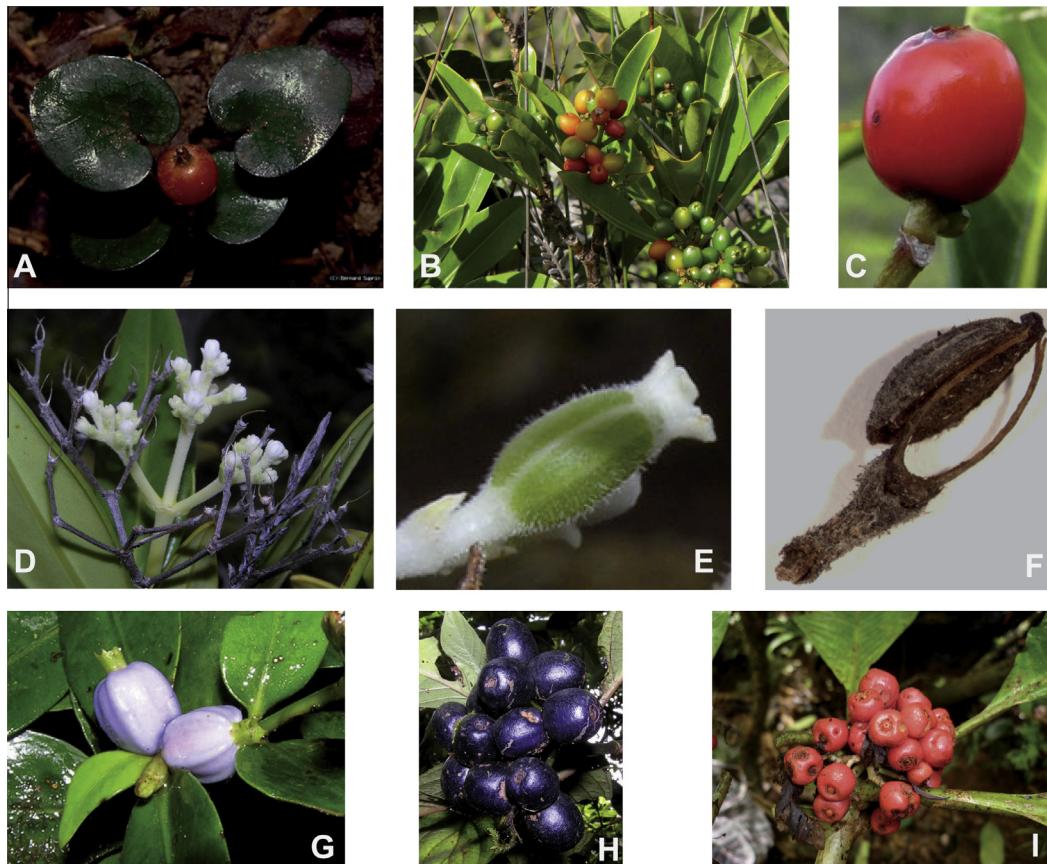
clade, this fruit type only occurs in the *Psychotria* clade NC1 and the *Cremocarpon* clade, whose limited distribution range (New Caledonia and the West Indian Ocean, respectively; Bremekamp, 1958; Piesschaert, 2001) could be explained by their dispersal mode. However, a previous hypothesis suggesting a close relationship between the Malagasy/Comoran *Cremocarpon* and *Psychotria rupicola* (belonging to the *Psychotria* clade NC1) based on their morphological characters is rejected by our results (Fig. 2B and C). The fruits of taxa in the *Psychotria* clade NC1 could have lost their ability to disperse over long-distances after settling in New Caledonia (i.e. evolution from ancestral drupes to extant schizocarps; Carlquist, 1967), an hypothesis which could be set out to test in future investigation. Otherwise, the colonization of the *Psychotria* clade NC1 could have been favoured by hazardous or punctuated events, such as transport via air currents (e.g. tropical depressions; Gillespie et al., 2012).

#### 4.2.2. The Pacific clade: failure of arrival or settlement?

The Pacific clade includes more than 340 species (Andersson, 2002a; Barrabé, 2013; Davis and Bridson, 2001, 2004; Govaerts et al., 2012; Huxley and Jebb, 1991). This clade invaded the Indo-Pacific region by taking advantage of an endozoochorous mode of dispersal (drupaceous fruits; Fig. 5; Andersson, 2002a; Piesschaert, 2001), but it is absent in New Caledonia (Fig. 2B). The Pacific clade represents one of the most species-rich lineages of Psy–Pal



**Fig. 4.** Potential ecological habitat of the *Psychotria* clade NC1, resulting from modeling analysis using Maxent. White and purple squares indicate occurrences of species belonging to the clade (purple squares are those used to test the modeling). The color code shown on the left corresponds to the probability distribution. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 5.** Examples of fruit types encountered in the four New Caledonian lineages of Psychotrieae–Palicoureeae and the Pacific clade. (A) *Geophila repens*. – (B and C) *Margaritopsis* clade NC. – (D–F) *Psychotria* clade NC1. – (G and H) *Psychotria* clade NC2. – (I) Pacific clade.

(Andersson, 2002a; Nepokroeff et al., 1999), and is a major plant radiation for the Indo-Pacific region, comparable in size to *Cyrtandra* J.R. Forst. & G. Forst. (ca. 600 species; Clark et al., 2009; Cronk et al., 2005). The large diversification of the Pacific clade, which

appears to have started around ca. 14.4 Ma, might have been promoted by the abrupt warming during the Mid-Miocene Climatic Optimum (Böhme, 2003), as observed in several other plant lineages (see e.g. Buerki et al., 2012b; Zhou et al., 2012), or by the



emergence of the majority of Pacific volcanic islands during this period (Clark et al., 2009; Neall and Trewick, 2008).

The absence of the Pacific clade in New Caledonia might be more linked to environmental local specificities than to the isolation of the archipelago. The members of this clade are shrubs and small trees or epiphytes, mostly recorded from rainforest understories (e.g. Lorence and Wagner, 2005; Smith and Darwin, 1988; Sohmer, 1988; Sohmer and Davis, 2007). Even if this clade is older than the others found on New Caledonia, its absence could be explained by ecological niche competition (MacArthur and Wilson, 1967; Simberloff, 1974; Silvertown, 2004a, 2004b; Silvertown et al., 2005; Walker and Valentine, 1984). The New Caledonian forest understory may have been occupied by other plant groups (e.g. the other *Psychotria* lineages), which colonized and diversified in New Caledonia before the Pacific clade, thus preventing its establishment when it reached the archipelago. A similar scenario is observed in Gesneriaceae, where the shrubby genus *Coronanthera* Vieill. ex C.B. Clarke successfully settled in New Caledonia, and then diversified throughout the entire archipelago, whereas the widely distributed *Cyrtandra* is absent on the archipelago except for a single species restricted to the Loyalty islands (Morat et al., 2012).

More than 140 species belonging to the Pacific clade are epiphytes (i.e. subtribe Hydnophytinae; Barrabé, 2013; Govaerts et al., 2012; Huxley and Jebb, 1991) whose growth requires high average annual rainfall. The climate in New Caledonia is drier on average than in neighboring archipelagos (Jaffré, 1993; Morat et al., 1981) and may not be favorable to ligneous epiphytes. This situation is paralleled in two other shrubby epiphytic groups, *Medinilla* Gaudich. ex DC. (Melastomataceae; Clausen and Renner, 2001; Thorne, 1969) and *Benstonea* Callm. & Buerki (Pandanaeae; Buerki et al., 2012c; Callmander et al., 2012), which are also well represented in the Indo-Pacific region, including Vanuatu and Fiji, but absent in New Caledonia.

#### 4.3. Comparison of diversification processes between New Caledonian lineages

Species are not evenly or randomly distributed among the four Psy–Pal lineages present on New Caledonia as indicated by the significant deviation from the broken stick distribution. Dissimilarities observed between net diversification rates, rates per-unit-area and species richness suggest different evolutionary processes between the lineages.

##### 4.3.1. The *Geophila* lineage: failure to diversify?

Although pantropical, the genus *Geophila* expresses a low world diversification with ca. 30 species (Govaerts et al., 2012; Piesschaert et al., 1999; Piesschaert, 2001). Only a single species, *G. repens*, colonized New Caledonia. This lack of species richness in the archipelago mirrors the pattern observed across the Pacific islands, as only this species occurs in the whole area (Barrabé, 2013; Govaerts et al., 2012). In New Caledonia, *G. repens* has a sparse distribution on Grande Terre (Fig. 3), according to herbarium records, which may be partly explained by undercollection of this discrete low forest-floor herbaceous plant. Although this species seems indifferent to soil type and rainfall (Fig. 3), it appears to be unable to diversify in the archipelago and also in the Pacific islands (Price and Wagner, 2004). Perhaps it arrived recently by human introduction given its low geographic density. Moreover, this species is a creeping herb, developing stolons suggesting vegetative reproduction, as all the remainder species of *Geophila* (Piesschaert, 2001; Robbrecht, 1975). *G. repens* could be involved in the early stages of forest establishment (Howe and Smallwood, 1982). This peculiar reproductive mode may be also the cause of high level of clonality, which allied to high dispersal ability, could induce a low diversification rate.

##### 4.3.2. The *Margaritopsis* clade NC: a lineage moderately diversified

Species richness of the *Margaritopsis* clade NC is low (i.e. four species) but similar to the remainder species of the genus, especially in the Pacific islands (e.g. three species in Vanuatu, eight in Fiji, and eight in Samoa; Barrabé et al., 2012), and even balanced with its sister-clade as revealed by the test of Slowinsky and Guyer ( $p$ -value = 0.57–0.91). This situation is paralleled in other genera, which exhibit similar geographic ranges and low levels of species richness in the Indo-Pacific region, as *Barringtonia* J.R. Forst. & G. Forst. (Lecythidaceae; Payson, 1967), *Weinmannia* L. (Cunoniaceae; Hopkins and Bradford, 1998) or *Serianthes* Benth. (Mimosoideae, Fabaceae; Nielsen et al., 1983). This pattern suggests high dispersal ability and low level of diversification of the genus *Margaritopsis* in the entire area (Barrabé et al., 2012). In New Caledonia the *Margaritopsis* clade NC shows a low rate of diversification (ca. 0.13 species/Ma, for a null extinction rate) similar to those inferred for *Pycnanthus* and *Dacrydium* Lamb. (Espeland and Murielle, 2011; Pillon, 2012), even if it occupies a wide range of habitats (all species are widespread, frequently encountered, with no apparent micro-endemism; Fig. 3; Barrabé, 2013). The presumed high dispersal ability of this lineage, allowing gene flow among distant populations of each species, might have narrowed speciation processes. The low diversification of this lineage could be also the result of a combination of recent dispersals and slow divergence of characters for each of its species. Moreover, all species of this lineage are nitrogen accumulators (M. Lebrun, comm. pers.). This evolutionary advantage could explain their high ability to be present in many habitats on poor soils, deficient in nitrogen nutrients, as on ultramafic substrates (L'Huillier et al., 2010).

##### 4.3.3. The *Psychotria* clade NC1: a relictual lineage

The stem age of *Psychotria* clade NC1 is older than that of the three other New Caledonian lineages (Middle vs. Late Miocene; Fig. 2C). Its sister-clade, the *Psychotria* clade IP, has a wide geographic distribution (i.e. the entire Indo-Pacific region). These phylogenetic characteristics suggest that it may represent a 'relictual lineage' within *Psychotria* clade IV ('broom and handle' clade; Crisp and Cook, 2009), as it does not possess a close relative in the region. It could be the only survivor of a lineage formerly more widespread in the region (Pole, 2010). The number of species of *Psychotria* clade NC1 (four species) is significantly lower than its sister-clade (i.e. they are highly imbalanced, test of Slowinsky and Guyer:  $p = 0.027^*$ ; Table 4), indicating a decrease of its speciation rate. Furthermore, its low species richness, slow net diversification rate (ca. 0.14 species/Ma, for a null extinction rate) and young crown age suggest that it may have been going extinct and that its diversification has only recently been initiated, after a phase of equilibrium.

The narrow distribution of this lineage (restricted to the southeastern part of the Grande Terre on ultramafic soils) is not in agreement with the species distribution modeling analyses that inferred a larger suitable range, extending to the northwestern part of the island (Fig. 4). The narrow distribution of this lineage is therefore more probably linked to a lesser effective dispersal mode than to ecological specialization (Fig. 4). In any case, this lineage is not ecologically diverse and is not able to disperse, which greatly reduce its chances to diversify.

##### 4.3.4. The *Psychotria* clade NC2: a case of explosive diversification

The diversification of the *Psychotria* clade NC2 has been explosive and confined to the New Caledonian archipelago (i.e. 78 species), reflecting highly imbalanced species richness with its sister-clade, compared to e.g. the *Margaritopsis* clade NC. This diversification occurred recently (during the Late Miocene), and in a relatively short time (as shown by the short branch leading to this clade indicating a radiation induced shortly after its arrival



in New Caledonia; Fig. 2C). Furthermore, this lineage is surprisingly well represented in ecosystems on ultramafic substrates (60% of the species, a half of which are exclusive to these areas; Barrabé, 2013) and even contains a nickel hyperaccumulating species (i.e. *Psychotria gabriellae*; Barrabé et al., in press; Jaffré and Schmid, 1974). In most cases, the species originating from Australia may have presented some exaptations ('pre-adaptations') to these substrates when they colonized New Caledonia (Pillon et al., 2010), as observed for *Codia* Forst. (14 species vs. the single species of *Callioma* Andrews in Australia; Bradford and Barnes, 2001) or *Pycnantha* (57 species vs. five Australian species; Swenson et al., 2008). Additionally, the number of species in this lineage is significantly higher than in its sister-clade (test of Slowinsky and Guyer:  $p = 0.049^* - 0.105$ ; Table 4), indicating an increase of its speciation rate in New Caledonia and/or a slow down in the Australian sister-clade. These imbalanced richness could be the mirror of range contraction for certain Australian species of *Psychotria*, present in the aseasonal-wet biomes (Bowman et al., 2010; Byrne et al., 2011; Byrne et al., 2008) consequent to the intense aridification in Australia during the Neogene; whereas other species may have dispersed and diversified in other islands, as in New Caledonia, where ecological conditions remained favorable (Crisp et al., 2004).

The pace of diversification in *Psychotria* clade NC2 is estimated to have been ca. four times higher than in the other New Caledonian Psy-Pal lineages (or even higher if one assumes a significant degree of extinction) and represents the highest documented rate for plants on the island (diversification rate of 0.53, for a null extinction; Table 4; Pillon, 2012). This situation is similar to that seen in other groups that have undergone insular diversifications (where per-unit-area and per-unit-log(area) rates are similar to New Caledonian *Psychotria*; Table 4): e.g. Hawaiian *Bidens* L. and Macaronesian *Echium* L. (Knoppe et al., 2012). Based on a novel dating from Baker and Couvreur (2012), the net diversification rate of New Caledonian palm lineages, previously suggested as the fastest diversification among the archipelago's plants (Pillon, 2012), would now be lower: 0.11 species/Ma for *Clinosperma* Becc. – *Cyphokentia* Brongn. (crown age of ca. 9.6 Ma), 0.22 species/Ma for *Burretioakentia* Pichi Sermolli – *Cyphophoenix* H. Wendl. ex Hook. f. (ca. 6.7 Ma), and 0.29 species/Ma for *Chambeyronia* Vieill. ex Brongn. & Gris – *Kentia* Brongn. (3.8 Ma). To our knowledge, the *Psychotria* NC2 clade represents therefore the most recent, fastest and largest diversification of any group of plants in New Caledonia. Furthermore it may have resulted from 'non-adaptive radiation' (Sanderson, 1998), as there is not a corresponding high level of morphological specialization associated with specific ecological adaptations.

#### 4.4. *Psychotria*, the largest plant radiation in New Caledonia

Even if the name *Psychotria* is applied just to the 78 species belonging to the *Psychotria* clade NC2, *Psychotria* would remain the second largest plant genus in New Caledonia. It would just surpassing *Syzygium* (69 species) if this last genus is expanded to include *Piliocalyx* Brongn. & Gris (eight species) which then appears to be the result of at least four separate colonization events (Biffin et al., 2006). The next largest genera are *Eugenia* L. (54 species), *Pycnantha* (52 species) and *Pittosporum* Banks ex Gaertn. (45 species; Morat et al., 2012). There are very few confirmed cases of clades composed of several endemic genera, as they all belong to palms (Pintaud and Baker, 2008) except *Morierina* Vieill. – *Thiolliera* Montrouz. (Barrabé et al., 2011; Motley et al., 2005) and possibly in Rutaceae (genera allied to *Melicope* J.R. Forst. & G. Forst.; Bayly et al., 2013), with significantly fewer species.

The only other possible larger plant diversification in New Caledonia is *Phyllanthus* (Phyllanthaceae), which includes 113 species Schmid (1991). Schmid distinguished seven groups among New Caledonian members of the genus and the phylogenetic study of

Kathriarachchi et al. (2006) included members of all except one of them (group 3, two species). They recovered four monophyletic and distinct New Caledonian lineages: group 1 (two species), group 2 (one species), group 5 (47 species) and group 6 + 7 (58 species). ITS data placed the latter two clades far apart, whereas they are sister-clades in their *matK* analysis. The latter results alone would suggest that morphological groups 5, 6 and 7 may form an endemic monophyletic lineage totalizing 105 species. However, species of group 5 have twice as many chromosomes as species from group 7 (Mangenot et al., 1977), which along with phylogenetic data, suggest an allopolyploid origin of group 5, one parent's being close to group 7 and the other one to an unidentified and unrelated lineage, and therefore implies two colonizations events of New Caledonia. The *Psychotria* clade NC2 is larger than either of those groups and thus may be considered as the largest plant diversification in New Caledonia.

## 5. Conclusions

The Psychotrieae–Palicoureeae clade constitutes a valuable model for testing differential evolutionary scenarios of the New Caledonian flora following its mid-Eocene re-emergence. This study highlighted the largest plant diversification of the archipelago, and which is also probably one of the largest in the Pacific islands, surpassed only by the Hawaiian Lobeliads (126 species; Givnish et al., 2009) and New Zealand *Veronica* (formerly *Hebe*, 100 species mostly confined to the island; Wagstaff et al., 2002). The arrival of the ancestor of *Psychotria* clade NC2 in New Caledonia was rapidly followed by its diversification, as it invaded empty habitats during its large expansion or outcompeted lineages already present. The environmental factors that have promoted its diversification still have to be determined to explain the dramatic diversification of the *Psychotria* clade NC2 since its arrival in New Caledonia in the Late Miocene.

## Acknowledgments

We are grateful to the members of the Laboratoire de Botanique et d'Ecologie Végétale Appliquées and the herbarium at IRD Nouméa (NOU, UMR AMAP), especially Gilles Dagostini, Williams Nigote, Tanguy Jaffré, Jacqueline Fambart-Tinel, Michèle Magat, Céline Grignon, Hervé Vandrot, Philippe Birnbaum, Céline Chambrey and Vanessa Hequet. We thank Yumiko Baba and Darren Crayn (Tropical Australian Herbarium of Cairns, James Cook University), Marika V. Tuiwawa, Alifereti Naikatini and Fiona Tuiwawa (South Pacific Regional Herbarium, University of the South Pacific of Suva), Isaac A. Rounds (Conservation International, Fiji), Jérôme Munzinger (IRD, Montpellier), Christopher Davidson and Sharon Christoph, Daniel and Irène Létocart, and Martin Callmander and Pete Lowry (Missouri Botanical Garden, Saint Louis) for their unconditional assistance with fieldworks in Australia and Fiji. We thank Clarisse Majorel and Laure Hannibal (Laboratoire des Symbioses Tropicales Méditerranéennes, IRD Nouméa) for their help with laboratory procedures; Edith Kapinos and Laszlo Csiba (Royal Botanic Gardens, Kew), Jean-Yves Meyer (Ministère de l'Éducation, de l'Enseignement Supérieur et de la Recherche, Gouvernement de Polynésie Française, Papeete), Alyse Rothrock Kuhlman (Missouri Botanical Garden, Saint Louis), Sylvain Razafimandimbison and Birgitta Bremer (Bergius Foundation, Stockholm), and Jean-Noël Labat † and Myriam Gaudeul (Museum National d'Histoire Naturelle, Paris) for assisting us with obtaining access to DNA samples. We are grateful to Céline Gomez (IRD Noumea, UMR ESPACE) for providing help with the Maxent analysis. For permission to conduct fieldwork, and collect and export specimens we thank the Direction de l'Environnement of the Province Sud and the Direction

du Développement économique et de l'Environnement of the Province Nord in New Caledonia, the Department of Environment and Resource Management of the Queensland Government in Australia, and the Department of Environment of the Government of Fiji. Material from Santo (Vanuatu) was collected during the Santo 2006 expedition. Part of work was funded through a three year grant from the CIRAD, and the BIONECA and ULTRABIO projects supported by a grant from the French Agence Nationale de la Recherche. We also wish to thank one anonymous reviewer, Pete Lowry, and the Editors of Molecular Phylogenetics and Evolution for providing useful comments that have improved the manuscript.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jmpev.2013.10.020>.

## References

- Andersson, L., 2001. *Margaritopsis* (Rubiaceae, Psychotriaceae) is a pantropical genus. *Syst. Geogr. Plants* 71, 73–85.
- Andersson, L., 2002a. Relationship and generic circumscriptions in the *Psychotria* complex (Rubiaceae, Psychotriaceae). *Syst. Geogr. Plants* 72, 167–202.
- Andersson, L., 2002b. Re-establishment of *Carapichea* (Rubiaceae, Psychotriaceae). *Kew. Bull.* 57, 363–374.
- Antonelli, A., Nylander, J.A.A., Persson, C., Sanmartín, I., 2009. Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proc. Natl. Acad. Sci.* 106, 9749–9754.
- Andersson, L., Rova, J.H., 1999. Therps16 intron and the phylogeny of the Rubioideae (Rubiaceae). *Pl. Syst. Evol.* 214, 161–186.
- Backlund, M., Bremer, B., Thulin, M., 2007. Paraphyly of Paederieae, recognition of Putorieae and expansion of Plocama (Rubiaceae–Rubioideae). *Taxon* 56, 315–328.
- Baker, W.J., Couvreur, T.L.P., 2012. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. II. Diversification history and origin of regional assemblages. *J. Biogeogr.* 40, 286–298.
- Baldwin, B.G., Markos, S., 1998. Phylogenetic utility of the external transcribed spacer (ETS) of 18S–26S rDNA: congruence of ETS and ITS trees of *Calycadenia* (Compositae). *Mol. Phylogenet. Evol.* 10, 449–463.
- Barrabé, L., Buerki, S., Mouly, A., Davis, A.P., Munzinger, J., Maggia, L., 2012. Delimitation of the genus *Margaritopsis* (Rubiaceae) in the Asian, Australasian and Pacific region, based on molecular phylogenetic inference and morphology. *Taxon* 61, 1251–1268.
- Barrabé, L., Mouly, A., Florence, J., in press. Psychotriaceae (Rubiaceae) Neocaledonicarum Specierum Nomenclator. Adansonia.
- Barrabé, L., Mouly, A., Lowry II, P.P., Munzinger, J., 2011. A morphological phylogenetic study of *Bikkia* (Rubiaceae): polyphyly necessitates reinstatement of the endemic New Caledonian genus *Thiollireia*. *Adansonia*, ser. 3 (33), 115–134.
- Barrabé, L., 2013. Systématique et Evolution du genre *Psychotria* (Rubiaceae) en Nouvelle-Calédonie. Université de la Nouvelle-Calédonie, Noumea. PhD Thesis.
- Barracough, T.G., Vogler, A.P., Harvey, P.H., 1998. Revealing the factors that promote speciation. *Philos. Trans. Roy. Soc. Lond. B Biol. Sci.* 353, 241–249.
- Bartish, I.V., Antonelli, A., Richardson, J.E., Swenson, U., 2011. Vicariance or long-distance dispersal: historical biogeography of the pantropical subfamily Chrysophylloideae (Sapotaceae). *J. Biogeogr.* 38, 177–190.
- Bartish, I.V., Swenson, U., Munzinger, J., Anderberg, A.A., 2005. Phylogenetic relationships among New Caledonian Sapotaceae (Ericales): molecular evidence for generic polyphyly and repeated dispersal. *Am. J. Bot.* 92, 667–673.
- Bayly, M.J., Holmes, G.D., Forster, P.J., Cantrill, D.J., Ladiges, P.Y., 2013. Major clades of Australasian Rutoideae (Rutaceae) based on rbcL and atpB sequences. *PLoS ONE* 8, e72493.
- Biffin, E., Craven, L.A., Crisp, M.D., Gadek, P.A., 2006. Molecular systematics of *Syzygium* and allied genera (Myrtaceae): evidence from the chloroplast genome. *Taxon* 55, 79–94.
- Böhme, M., 2003. The Miocene climatic optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 195, 389–401.
- Bowman, D.M.J.S., Brown, G.K., Braby, M.F., Brown, J.R., Cook, L.G., Crisp, M.D., Ford, F., Haberle, S., Hughes, J., Isagi, Y., Joseph, L., McBride, J., Nelson, G., Ladiges, P.Y., 2010. Biogeography of the Australian monsoon tropics. *J. Biogeogr.* 37, 201–216.
- Bradford, J.C., Barnes, R.W., 2001. Phylogenetics and classification of Cunoniaceae (Oxalidales) using chloroplast DNA sequences and morphology. *Syst. Bot.* 26, 354–385.
- Bremekamp, C.E.B., 1958. Monographie des genres *Cremocarpus* Boiv. ex Baill. et *Pyragra* Brem. (Rubiaceae). *Candollea* 16, 147–177.
- Bremer, B., 2009. A review of molecular phylogenetic studies of Rubiaceae. *Ann. Mo. Bot. Gard.* 96, 4–26.
- Bremer, B., Eriksson, T., 2009. Time tree of Rubiaceae: phylogeny and dating the family, subfamilies, and tribes. *Int. J. Plant Sci.* 170, 766–793.
- Bremer, B., Jansen, R.K., Oxelman, B., Backlund, M., Lantz, H., Kim, K.J., 1999. More characters or more taxa for a robust phylogeny—case study from the coffee family (Rubiaceae). *Syst. Biol.* 48, 413–435.
- Buerki, S., Forest, F., Callmander, M.W., Devey, D.S., Munzinger, J., 2012a. Phylogenetic inference of New Caledonian lineages of Sapindaceae: molecular evidence requires a reassessment of generic circumscriptions. *Taxon* 61, 109–119.
- Buerki, S., Jose, S., Yadav, S.R., Goldblatt, P., Manning, J.C., Forest, F., 2012b. Contrasting biogeographic and diversification patterns in two Mediterranean-type ecosystems. *PLoS ONE* 7, e39377.
- Buerki, S., Callmander, M.W., Devey, D.S., Chappell, L., Gallaher, T., Munzinger, J., Haevermans, T., Forest, F., 2012c. Straightening out the screw-pines: a first step in understanding phylogenetic relationships within Pandanaceae. *Taxon* 61, 1010–1020.
- Byrne, M., Steane, D.A., Joseph, L., Yeates, D.K., Jordan, G.J., Crayn, D., Aplin, K., Cantrill, D.J., Cook, L.G., Crisp, M.D., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P., Weston, P.H., 2011. Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *J. Biogeogr.* 38, 1635–1656.
- Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., Cooper, S., Donnellan, C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N., Wyrwoll, K.-H., 2008. Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Mol. Ecol.* 17, 4398–4417.
- Callmander, M.W., Lowry, P.P., Forest, F., Devey, D.S., Beentje, H., Buerki, S., 2012. *Benstonea* Callm. & Buerki (Pandanaceae): characterization, circumscription, and distribution of a new genus of screw-pines, with a synopsis of accepted species. *Candollea* 67, 323–345.
- Carlquist, S., 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific islands. *Bull. Torrey Bot. Club* 94, 129–162.
- Carpenter, R.J., Read, J., Jaffré, T., 2003. Reproductive traits of tropical rain-forest trees in New Caledonia. *J. Trop. Ecol.* 19, 351–365.
- Castro, S., Ferrero, V., Loureiro, J., Espadaler, X., Silveira, P., Navarro, L., 2010. Dispersal mechanisms of the narrow endemic *Polygala vayredae*: dispersal syndromes and spatio-temporal variations in ant dispersal assemblages. *Plant Ecol.* 207, 359–372.
- Chevillotte, V., Chardon, D., Beauvais, A., Maurizot, P., Colin, F., 2006. Long-term tropical morphogenesis of New Caledonia (Southwest Pacific): importance of positive epeirogeny and climate change. *Geomorphology* 81, 361–375.
- Clark, J.R., Wagner, W.L., Roalson, E.H., 2009. Patterns of diversification and ancestral range reconstruction in the southeast Asian–Pacific angiosperm lineage *Cyrtandra* (Gesneriaceae). *Mol. Phylogenet. Evol.* 53, 982–994.
- Clausing, G., Renner, S., 2001. Evolution of growth form in epiphytic Dissochaeteae (Melastomataceae). *Org. Divers. Evol.* 1, 45–60.
- Cruz, D., Chiron, D., Courme, M.-D., 1998. Discordeance de l'Eocène supérieur et événements pré-obduction en Nouvelle-Calédonie. *Comp. Rend. Acad. Sci. Paris, ser. 2 Sci. Terre ePlan.* 327, 485–491.
- Cruz, D., Maurizot, P., Collot, J., Sevin, B., 2012. An outline of the geology of New Caledonia; from Permian–Mesozoic Southeast Gondwanaland active margin to Cenozoic obduction and supergene evolution. *Episodes – Newsmag. Int. Union Geol. Sci.* 35, 72–86.
- Cooper, W., Cooper, W.T., 2004. Fruits of the Australian tropical rainforest. Melbourne, Nokomis Editions.
- Crisuolo, A., Gribaldo, S., 2010. BMGE (Block Mapping and Gathering with Entropy): a new software for selection of phylogenetic informative regions from multiple sequence alignments. *BMC Evol. Biol.* 10, 210.
- Crisp, M.D., Cook, L.G., 2009. Explosive radiation or cryptic mass extinction? Interpreting signatures in molecular phylogenies. *Evolution* 63, 2257–2265.
- Crisp, M.D., Cook, L.G., Steane, D., 2004. Radiation of the Australian flora: what can comparisons of molecular phylogenies across multiple taxa tell us about the evolution of diversity in present-day communities? *Philos. Trans. Roy. Soc. Lond. B Biol. Sci.* 359, 1551–1571.
- Cronk, Q.C.B., Kiehn, M., Wagner, W.L., Smith, J.E., 2005. Evolution of *Cyrtandra* (Gesneriaceae) in the Pacific Ocean: the origin of a supertramp clade. *Am. J. Bot.* 92, 1017–1024.
- Cruaud, A., Jabbour-Zahab, R., Genson, G., Ungricht, S., Rasplus, J.-Y., 2012. Testing the emergence of New Caledonia: fig wasp mutualism as a case study and a review of evidence. *PLoS ONE* 7, e30941.
- Davis, A.P., Bridson, D.M., 2001. A taxonomic revision of the genus *Dolianthus* (Rubiaceae). *Blumea* 46, 421–446.
- Davis, A.P., Bridson, D.M., 2004. A taxonomic revision of the genus *Amaracarpus* (Rubiaceae, Psychotriaceae). *Blumea* 49, 25–68.
- Davis, A.P., Bridson, D.M., Jarvis, C., Govaerts, R., 2001. The typification and characterization of the genus *Psychotria* L. (Rubiaceae). *Bot. J. Linn. Soc.* 135, 35–42.
- Davis, A.P., Govaerts, R., Bridson, D.M., Ruhsam, R., Moat, J., Brummitt, N., 2009. A global assessment of distribution, diversity, endemism and taxonomic effort in the Rubiaceae. *Ann. Mo. Bot. Gard.* 96, 68–78.
- Drummond, A.J., Rambaut, A., 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* 7, 214.
- Duangjai, S., Samuel, R., Munzinger, J., Forest, F., Wallnofer, B., Barfuss, M.H.J., Fischer, G., Chase, M.W., 2009. A multi-locus plastid phylogenetic analysis of the pantropical genus *Diospyros* (Ebenaceae), with an emphasis on the radiation and biogeographic origins of the New Caledonian endemic species. *Mol. Phylogenet. Evol.* 52, 602–620.

- Espeland, M., Muriene, J., 2011. Diversity dynamics in New Caledonia: towards the end of the museum model? *BMC Evol. Biol.* 11, 254.
- Felsenstein, J., 1985. Confidence-limits on phylogenies: an approach using the bootstrap. *Evolution* 39, 783–791.
- Frodin, D., 2004. History and concepts of big plant genera. *Taxon* 53, 741–752.
- Gillespie, R.G., Baldwin, B.G., Waters, J.M., Fraser, C.L., Nikula, R., Roderick, G.K., 2012. Long-distance dispersal: a framework for hypothesis testing. *Trends Ecol. Evol.* 27, 47–56.
- Givnish, T.J., 2010. Ecology of plant speciation. *Taxon* 23, 1–41.
- Givnish, T.J., Millam, K.C., Mast, A.R., Patterson, T.B., Theim, T.J., Hipp, A.L., Henss, J.M., Smith, J.F., Wood, K.R., Sytsma, K.J., 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proc. Roy. Soc. Lond. B Biol. Sci.*, 276–416.
- Govaerts, R., Ruhsam, M., Andersson, L., Robbrecht, E., Bridson, D., Davis, A.P., Schanzer, I., Sonké, B., 2012. World Checklist of Rubiaceae. Published on the Internet. <<http://apps.kew.org/wcsp/home.do>> (retrieved 01.08.12) Facilitated by the Royal Botanic Gardens, Kew.
- Gradstein, F., Ogg, J., 2004. Geologic time scale 2004 – why, how, and where next. *Lethaia* 37, 175–181.
- Graham, A., 1985. Studies in Neotropical paleobotany. IV. The eocene communities of Panama. *Ann. Mo. Bot. Gard.* 72, 504–534.
- Graham, A., 2009. Fossil record of the Rubiaceae. *Ann. Mo. Bot. Gard.* 96, 90–108.
- Grandcolas, P., Muriene, J., Robillard, T., Desutter-Grandcolas, L., Jourdan, H., Guilbert, E., Deharveng, L., 2008. New Caledonia: a very old Darwinian island? *Biol. Sci.* 363, 3309–3317.
- Guillaumin, A., 1930. Matériaux pour la flore de la Nouvelle-Calédonie. XXVII. Révision des Rubiacées. *Archives de Botanique, Mémoires*, Caen.
- Guillaumin, A., 1948. Flore analytique et synoptique de la Nouvelle-Calédonie, phanérogames. Office de la Recherche Scientifique Coloniale, Paris.
- Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E., Challenger, W., 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* 24, 129–131.
- Hedges, S.B., Kumar, S., 2004. Precision of molecular time estimates. *Trends Genet. Evol.* 20, 242–247.
- Ho, S.Y.W., 2007. Calibrating molecular estimates of substitution rates and divergence times in birds. *J. Avian Biol.* 38, 409–414.
- Hopkins, M.S., Bradford, J.C., 1998. A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific. 1. Introduction and an account of the species of Western Malesia, the Lesser Sunda Islands and the Moluccas. *Adansonia* 20, 5–41.
- Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13, 201–228.
- Huxley, C.R., Jebb, M.H.P., 1991. The tuberous epiphytes of the Rubiaceae 1: a new subtribe – the Hydnophytinae. *Blumea* 36, 1–20.
- Jaffré, T., 1980. Etude écologique du peuplement végétal des sols dérivés de roches ultrabasiques en Nouvelle-Calédonie. ORSTOM, Paris.
- Jaffré, T., 1993. The relationship between ecological diversity and floristic diversity in New Caledonia. *Biodivers. Lett.* 1, 82–87.
- Jaffré, T., Morat, P., Veillon, J.-M., 1993. Etude floristique et phytogéographique de la forêt sclérophylle de Nouvelle-Calédonie. *Bull. Mus. Natl. Hist. Nat., B. Adansonia*, ser. 4 (15), 107–146.
- Jaffré, T., Morat, P., Veillon, J.M., MacKee, H.S., 1987. Changements dans la végétation de la Nouvelle-Calédonie au cours du tertiaire: la végétation et la flore des roches ultrabasiques. *Bull. Mus. Natl. Hist. Nat., B. Adansonia*, ser. 4 (9), 365–391.
- Jaffré, T., Schmid, M., 1974. Accumulation du nickel par une Rubiaceae de Nouvelle-Calédonie, *Psychotria douarrei* (G. Beauvais) Däniker. *Compt. Rend. Acad. Sci.*, ser. 3. *Sci. Vie* 278, 1727–1730.
- Kårehed, J., Groeninkx, I., Dessein, S., Motley, T.J., Bremer, B., 2008. The phylogenetic utility of chloroplast and nuclear DNA markers and the phylogeny of the Rubiaceae tribe Spermacoeae. *Mol. Phyl. Evol.* 49, 843–866.
- Kathirarachchi, H., Samuel, R., Hoffmann, P., Mlinarec, J., Wurdack, K.J., Ralimana, H.N., Stuessy, T.F., Chase, M.W., 2006. Phylogenetics of tribe Phyllanthae (Phyllanthaceae; Euphorbiaceae sensu lato) based on nrITS and plastid matK DNA sequence data. *Am. J. Bot.* 93, 637–655.
- Keppel, G., Lowe, A.J., Possingham, H.P., 2009. Changing perspectives on the biogeography of the tropical South Pacific: influences of dispersal, vicariance and extinction. *J. Biogeogr.* 36, 1035–1054.
- Khan, S.A., Razafimandimbison, S.G., Bremer, B., Liede-Schumann, S., 2008. Sabiceae and Virentariae (Rubiaceae, Ixoroideae): one or two tribes? New tribal and generic circumscriptions of Sabiceae and biogeography of Sabiceae sl. *Taxon* 57, 7–23.
- Knope, M.L., Morden, C.W., Funk, V.A., Fukami, T., 2012. Area and the rapid radiation of Hawaiian *Bidens* (Asteraceae). *J. Biogeogr.* 39, 1206–1216.
- Ladiges, P.Y., Cantrill, D.J., 2007. New Caledonia–Australian connections: biogeographic patterns and geology. *Aust. Syst. Bot.* 20, 383–389.
- Lemaire, B., Lachenaud, O., Persson, C., Smets, E., Dessein, S., 2012. Screening for leaf-associated endophytes in the genus *Psychotria* (Rubiaceae). *FEMS microbio. ecol.* 81, 364–372.
- L'Huillier, L., Jaffré, T., Wulff, A., 2010. Mines et environnement en Nouvelle-Calédonie: les milieux sur substrats ultramafiques et leur restauration. Païta.
- Linder, H.P., Hardy, C.R., Rutschmann, F., 2004. Taxon sampling effects in molecular clock dating: an example from the African Restionaceae. *Mol. Phylogenet. Evol.* 35, 569–582.
- Lorence, D.H., Wagner, W.L., 2005. A revision of *Psychotria* (Rubiaceae) in the Marquesas Islands (French Polynesia). *Allertonia* 9, 1–37.
- MacArthur, R.H., 1957. On the relative abundance of birds species. *Proc. Natl. Acad. Sci.* 43, 293–295.
- MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.
- Magallón, S., Sanderson, M.J., 2001. Absolute diversification rates in angiosperm clades. *Evolution* 55, 1762–1780.
- Mangenot, G., Bancelhon, L., Mangenot, S., 1977. Caryologie du genre *Phyllanthus* (Euphorbiaceae, Phyllanthoideae). *Ann. Sci. Nat. Bot.* 18, 71–1116.
- Manns, U., Wikström, N., Taylor, C.M., Bremer, B., 2012. Historical Biogeography of the Predominantly Neotropical Subfamily Cinchonoideae (Rubiaceae): Into or Out of America. *Int. J. Plant Sci.* 173, 261–286.
- McConway, K.J., Sims, H.J., 2004. A likelihood-based method for testing for nonstochastic variation of diversification rates in phylogenies. *Evolution* 58, 12–23.
- Morat, P., 1993. Our knowledge of the flora of New Caledonia: endemism and diversity in relation to vegetation types and substrates. *Biodivers. Lett.* 1, 72–81.
- Morat, P., Jaffré, T., Tronchet, F., Munzinger, J., Pillon, Y., Veillon, J.-M., Chalopin, M., 2012. Le référentiel taxonomique Florical et les caractéristiques de la flore vasculaire indigène de la Nouvelle-Calédonie. *Adansonia* 34, 179–221.
- Morat, P., Jaffré, T., veillon, J.-M., 1981. Végétation. Atlas de la Nouvelle-Calédonie et dépendances, Office de la Recherche Scientifique et Technique Outre-Mer, Paris, plate 15.
- Morat, P., Jaffré, T., Veillon, J.-M., Mackee, H.S., 1986. Affinités floristiques et considérations sur l'origine des maquis miniers de la Nouvelle-Calédonie. *Bull. Mus. Natl. Hist. Nat., B. Adansonia*, ser. 4 (22), 133–182.
- Morat, P., Jansen, R.K., Veillon, J.-M., 1994. Richesse et affinités floristiques de la Nouvelle-Calédonie: conséquence directe de son histoire géologique. *Mém. Soc. Biogéogr.* 4, 111–123.
- Morat, P., Veillon, J.-M., Mackee, H.S., 1984. Floristic relationships of New Caledonian rainforest phanerogams. *Telopea* 2, 631–679.
- Motley, T.J., Wurdack, K.J., Delprete, P.G., 2005. Molecular systematics of the Catesbaeae–Chiococceae complex (Rubiaceae): flower and fruit evolution and biogeographic implications. *Am. J. Bot.* 92, 316–329.
- Mueller-Dombois, D., Fosberg, F.R., 1998. Vegetation of the Tropical Pacific Islands. Springer-Verlag, New York.
- Muriene, J., Grandcolas, P., Piulachs, M.D., Bellés, X., D'Haese, C., Legendre, F., Pellens, R., Guilbert, E., 2005. Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? *Cladistics* 21, 2–7.
- Neall, V.E., Treweek, S.A., 2008. The age and origin of the Pacific islands: a geological review. *Philos. Trans. Roy. Soc. Lond. B Biol. Sci.* 363, 3293–3308.
- Near, T.J., Meylan, P.A., Shaffer, H.B., 2005. Assessing concordance of fossil calibration points in molecular clock studies: an example using turtles. *Am. Nat.* 165, 137–146.
- Nepokroeff, M., Bremer, B., Systma, K.J., 1999. Reorganization of the genus *Psychotria* and tribe Psychotrieae (Rubiaceae) inferred from ITS and rbcL sequence data. *Syst. Bot.* 24, 5–27.
- Nepokroeff, M., Systma, K.J., Wagner, W.L., Zimmer, E.A., 2003. Reconstructing ancestral patterns of colonization and dispersal in the Hawaiian understory tree genus *Psychotria* (Rubiaceae): a comparison of parsimony and likelihood approaches. *Syst. Biol.* 52, 820–838.
- Nielsen, I., Guinet, P., Baretta-Kuipers, T., 1983. Studies in the Malesian, Australian and Pacific Ingeae (Leguminosae–Mimosoideae): the genera Archidendropsis, Wallaceodendron, Paraserianthes, Pararchidendron and Serianthes: Part 1. *Bull. Mus. Natl. Hist. Nat., B. Adansonia*, ser. 4 (5), 303–329.
- Nylander, J.A.A., Ronquist, F., Huelsenbeck, J.P., Nieves-Aldrey, J.L., 2004. Bayesian phylogenetic analysis of combined data. *Syst. Biol.* 53, 47–67.
- Paradis, E., 2012. Shift in diversification in sister-clade comparisons: a more powerful test. *Evolution* 66, 288–295.
- Parham, J.F., Donoghue, P.C.J., Bell, C.J., Calway, T.D., Head, J.J., Holroyd, P.A., Inoue, J.G., Irmis, R.B., Joyce, W.G., Ksepka, D.T., Patane, J.S.L., Smith, N.D., Tarver, J.E., van Tuinen, M., Yang, Z.H., Angielczyk, K.D., Greenwood, J.M., Hipsley, C.A., Jacobs, L., Makovicky, P.J., Muller, J., Smith, K.T., Theodor, J.M., Warnock, R.C.M., Benton, M.J., 2012. Best practices for justifying fossil calibrations. *Syst. Biol.* 61, 346–359.
- Paris, J.-P., 1981. Géologie de la Nouvelle-Calédonie: un essai de synthèse. Orléans.
- Payson, J.P.D.W., 1967. A monograph of the genus *Barringtonia* (Lecythidaceae). *Blumea* 15, 157–263.
- Pelletier, B., 2006. Geology of the New Caledonia region and its implications for study of the New Caledonian biodiversity. In: Payri, C., Richer de Forges, B. (Eds.), *Compendium of Marine Species from New Caledonia*, Forum Biodiversité des Ecosystèmes Coralliens, 30 octobre–4 novembre 2006. Institut de Recherche pour le Développement, Nouméa, Nouvelle-Calédonie, pp. 17–30.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modelling of species geographic distributions. *Ecol. Modell.* 190, 231–259.
- Picard, M., 1999. L'archipel neo-caledonien: 300 millions d'années pour assembler les pièces d'un puzzle géologique. Centre de Documentation Pédagogique de Nouvelle-Calédonie, Nouméa.
- Piesschaert, F., 2001. Carpology and Pollen Morphology of the Psychotrieae (Rubiaceae–Rubiaceae). Towards a New Tribal and Generic Delimitation. Katholieke Universiteit Leuven, Leuven, p. 495.
- Piesschaert, F., Robbrecht, E., Poulsen, A.D., Smets, E., 1999. Pyrene and pollen observations in the pantropical genus *Geophila* (Rubiaceae–Psychotrieae). *Nord. J. Bot.* 19, 93–100.
- Pillon, Y., 2012. Time and tempo of diversification in the flora of New Caledonia. *Bot. J. Linn. Soc.* 170, 288–298.
- Pillon, Y., Munzinger, J., Amir, H., Lebrun, M., 2010. Ultramafic soils and species sorting in the flora of New Caledonia. *J. Ecol.* 98, 1108–1116.



- Pintaud, J.-C., Baker, W.J., 2008. A revision of the palm genera (Arecaceae) of New Caledonia. *Kew. Bull.* 63, 61–73.
- Pintaud, J.-C., Jaffré, T., 2001. Patterns of diversity endemism in palms on ultramafic rocks in New Caledonia. *S. Afr. J. Sci.* 97.
- Pole, M., 2010. Was New Zealand a primary source for the New Caledonian flora? *Alcheringa* 34, 61–74.
- Posada, D., 2008. jModelTest: phylogenetic model averaging. *Mol. Biol. Evol.*, 1253–1256.
- Poux, C., Madsen, O., Glos, J., de Jong, W.W., Vences, M., 2008. Molecular phylogeny and divergences times of Malagasy tenrecs: influence of data partitioning and sampling on dating analysis. *BMC Evol. Biol.* 8, 102.
- Price, J.P., Wagner, W.L., 2004. Speciation in Hawaiian angiosperm lineages: cause, consequence, and mode. *Evolution* 58, 2185–2200.
- Rabosky, D.L., 2006. Likelihood methods for detecting temporal shifts in diversification rates. *Evolution* 60, 1152–1164.
- Rambaut, A., Charleston, M., 2002. TreeEdit v.1.0a10. <<http://tree.bio.ed.ac.uk/software/treedit/>>.
- Rambaut, A., Drummond, A.J., 2009. Tracer v.1.5. <<http://beast.bio.ed.ac.uk/tracer/>>.
- Razafimandimbison, S.G., Rydin, C., Bremer, B., 2008. Evolution and trends in the Psychotriaceae alliance (Rubiaceae) – a rarely reported evolutionary change of many-seeded carpels from one-seeded carpels. *Mol. Phylogenet. Evol.* 48, 207–223.
- Renner, S.S., 2005. Relaxed molecular clocks for dating historical plant dispersal events. *Trends Plant Sci.* 10, 550–558.
- Robbrecht, E., 1975. *Hymenocleus*, a new genus of Psychotriaceae (Rubiaceae) from Tropical Africa. *Bull. Jard. Bot. Natl. Belg.* 45, 273–300.
- Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19, 1572–1574.
- Rydin, C., Razafimandimbison, S.G., Khodabandeh, A., Bremer, B., 2009. Evolutionary relationships in the Spermacoceae alliance (Rubiaceae) using information from six molecular loci: insights into systematic affinities of *Neohymenopogon* and *Mouretia*. *Taxon* 58, 793–810.
- Sanders, K.L., Lee, M.S.Y., 2007. Evaluating molecular clock calibrations using Bayesian analyses with soft and hard bounds. *Biol. Lett.* 3, 275–279.
- Sanderson, M.J., 1998. Reappraising adaptive radiation. *Am. J. Bot.* 85, 1650–1655.
- Sauquet, H., Ho, S.Y.W., Gandolfo, M.A., Jordan, G.J., Wilf, P., Cantrill, D.J., Bayly, M.J., Bromham, L., Brown, G.K., Carpenter, R.J., Lee, D.M., Murphy, D.J., Sniderman, J.M.K., Udovicic, F., 2012. Testing the impact of calibration on molecular divergence times using a fossil-rich group: the case of *Nothofagus* (Fagales). *Syst. Biol.* 61, 289–313.
- Schmid, M., 1982. Endémisme et spéciation en Nouvelle-Calédonie. *Compt. Rend. Séances Soc. Biogéogr.* 48, 52–60.
- Schmid, M., 1991. *Phyllanthus*. In: Morat, P., MacKee, H.S. (Eds.), *Flore de la Nouvelle-Calédonie et dépendances*, vol. 17. Muséum National d'Histoire Naturelle, Paris, pp. 31–329.
- Smedmark, J.E., Rydin, C., Razafimandimbison, S.G., Khan, S.A., Liede-Schumann, S., Bremer, B., 2008. A phylogeny of Urophylleae (Rubiaceae) based on rps16 intron data. *Taxon* 57, 24–32.
- Silvertown, J., 2004a. Plant coexistence and the niche. *Trends Ecol. Evol.* 19, 605–611.
- Silvertown, J., 2004b. The ghost of competition past in the phylogeny of island endemic plants. *J. Ecol.* 92, 168–173.
- Silvertown, J., Francisco-Ortega, J., Carine, M., 2005. The monophyly of island radiations: an evaluation of niche pre-emption and some alternative explanations. *J. Ecol.* 93, 653–657.
- Simberloff, D.S., 1974. Equilibrium theory of island biogeography and ecology. *Ann. Rev. Ecol. Syst.* 5, 161–182.
- Slowinsky, J.B., Guyer, C., 1993. Testing whether certain traits have caused amplified diversification – an improved method based on a model random speciation and extinction. *Am. Nat.* 142, 1019–1024.
- Smedmark, J.E.E., Eriksson, T., Bremer, B., 2010. Divergence time uncertainty and historical biogeography reconstruction – an example from Urophylleae (Rubiaceae). *J. Biogeogr.* 37, 2260–2274.
- Smith, A.C., Darwin, S.P., 1988. Rubiaceae. In: Smith, A.C. (Ed.), *Flora vitiensis nova, Pacific Tropical Botanical Garden*, vol. 4. Lawai, Kauai, pp. 143–376.
- Sohmer, S.H., 1988. The nonclimbing species of the genus *Psychotria* (Rubiaceae) in New Guinea and the Bismarck Archipelago. *Bishop Mus. Bull. Bot.* 1, 1–339.
- Sohmer, S.H., Davis, A.P., 2007. The genus *Psychotria* (Rubiaceae) in the Philippine archipelago. *Sida Bot. Misc.* 27, 1–247.
- Stamatakis, A., 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22, 2688–2690.
- Struwe, L., Thiv, M., Kadereit, J.W., Pepper, A.S.R., Motley, T.J., White, P.J., Rova, J.H.E., Potgieter, K., Albert, V.A., 1998. *Saccifolium* (Saccifoliaceae), an endemic of Sierra de la Neblina on the Brazilian-Venezuelan border, is related to a temperate-alpine lineage of Gentianaceae. *Harvard Papers in Botany* 3, 199–214.
- Swenson, U., Lowry II, P.P., Munzinger, J., Rydin, C., Bartish, I.V., 2008. Phylogeny and generic limits in the *Niemeyera* complex of New Caledonian Sapotaceae: evidence of multiple origins of the anisomerous flower. *Mol. Phylogenet. Evol.* 49, 909–929.
- Swenson, U., Munzinger, J., Bartish, I.V., 2007. Molecular phylogeny of *Planchonella* (Sapotaceae) and eight new species from New Caledonia. *Taxon* 56, 329–354.
- Takhtajan, A., Crovello, T.J., Cronquist, A., 1986. *Floristics Regions of the World*. University of California Press, United States of America.
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., Kumar, S., 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol. Biol. Evol.* 28, 2731–2739.
- Thorne, R.F., 1963. Biotic distribution patterns in the tropical Pacific. In: Gressitt, J.L. (Ed.), *Pacific Basin Biogeography*. Bishop Museum Press, Honolulu, pp. 311–350.
- Thorne, R.F., 1969. Floristic relationships between New Caledonia and the Solomon Islands. *Philos. Trans. Roy. Soc. Lond. B Biol. Sci.* 255, 595–602.
- Tosh, J., Dessein, S., Buerki, S., Groeninckx, I., Mouly, A., Bremer, B., Smets, E.F., De Block, P., in press. Evolutionary history of the Afro-Madagascan *Ixora* species (Rubiaceae): species diversification and distribution of key morphological traits inferred from dated molecular phylogenetic trees. *Ann. Bot. (Oxford)*. <http://dx.doi.org/10.1093/aob/mct222>.
- Turner, B., Murphy, D.J., Duangjai, S., Temsch, E.M., Stockenhuber, R., Barfuss, M.H.J., Chase, M.W., Samuel, R., 2013. Molecular phylogenetics of New Caledonian *Diospyros* (Ebenaceae) using plastid and nuclear markers. *Mol. Phylogenet. Evol.* 69, 740–763.
- Veillon, J.-M., 1993. Protection of floristic diversity in New Caledonia. *Biodivers. Lett.* 1, 88–91.
- Wagstaff, S.J., Bayly, M.J., Garnock-Jones, P.J., Albach, D.C., 2002. Classification, origin, and diversification of the New Zealand hebes (Scrophulariaceae). *Ann. Mo. Bot. Gard.* 89, 38–63.
- Wagstaff, S.J., Dawson, M.L., Venter, S., Munzinger, J., Crayn, D.M., Steane, D.A., Lemson, K.L., 2010. Origin, diversification, and classification of the Australasian genus *Dracophyllum* (Richeeae, Ericaceae). *Ann. Mo. Bot. Gard.* 97, 235–258.
- Walker, T.D., Valentine, J.W., 1984. Equilibrium models of evolutionary species diversity and the number of empty niches. *Am. Nat.* 124, 887–899.
- Walker, J.D., Geissman, J.W., 2009. Geological Time Scale. Geological society of America, <<http://www.geosociety.org/science/timescale/timescl.pdf>>.
- Whittaker, R.J., Fernández-Palacios, J.M., 2007. *Island Biogeography*. Oxford University Press, New York.
- Yoder, A.D., Yang, Z., 2000. Estimation of primate speciation dates using local molecular clocks. *Mol. Biol. Evol.* 17, 1081–1090.
- Zhou, L., Su, Y.C.F., Thomas, D.C., Saunders, R.M.K., 2012. 'Out-of-Africa' dispersal of tropical floras during the Miocene climatic optimum: evidence from *Uvaria* (Annonaceae). *J. Biogeogr.* 39, 322–335.