

RESEARCH IN CONTEXT

# High endemism and stem density distinguish New Caledonian from other high-diversity rainforests in the Southwest Pacific

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- **Background and Aims** The biodiversity hotspot of New Caledonia is globally renowned for the diversity and endemism of its flora. New Caledonia's tropical rainforests have been reported to have higher stem densities, higher concentrations of relictual lineages and higher endemism than other rainforests. This study investigates whether these aspects differ in New Caledonian rainforests compared to other high-diversity rainforests in the Southwest Pacific.
- **Methods** Plants (with a diameter at breast height  $\geq 10$  cm) were surveyed in nine 1-ha rainforest plots across the main island of New Caledonia and compared with 14 1-ha plots in high-diversity rainforests of the Southwest Pacific (in Australia, Fiji, Papua New Guinea and the Solomon Islands). This facilitated a comparison of stem densities, taxonomic composition and diversity, and species turnover among plots and countries.
- **Key Results** The study inventoried 11 280 stems belonging to 335 species (93 species ha<sup>-1</sup> on average) in New Caledonia. In comparison with other rainforests in the Southwest Pacific, New Caledonian rainforests exhibited higher stem density (1253 stems ha<sup>-1</sup> on average) including abundant palms and tree ferns, with the high abundance of the latter being unparalleled outside New Caledonia. In all plots, the density of relictual species was  $\geq 10$  % for both stems and species, with no discernible differences among countries. Species endemism, reaching 89 % on average, was significantly higher in New Caledonia. Overall, species turnover increased with geographical distance, but not among New Caledonian plots.
- **Conclusions** High stem density, high endemism and a high abundance of tree ferns with stem diameters  $\geq 10$  cm are therefore unique characteristics of New Caledonian rainforests. High endemism and high spatial species turnover imply that the current system consisting of a few protected areas is inadequate, and that the spatial distribution of plant species needs to be considered to adequately protect the exceptional flora of New Caledonian rainforests.

**Keywords:** Endemism hotspot, New Caledonia, island, Oceania, Pacific rainforests, palms, plot network, relictual lineages, species richness, trees, tree ferns, tropical forest.

## INTRODUCTION

Endemism hotspots, areas that harbour a disproportionately high number of species restricted to that region, are considered of high importance in the fields of biogeography, conservation and evolution (Carnaval *et al.*, 2009; Kier *et al.*, 2009; Myers *et al.*, 2000; Sandel *et al.*, 2011). Their continued relevance to various fields is illustrated by a recent volume on *Endemism Hotspots* in *Annals of Botany* (Harrison and Noss, 2017, and references therein). This special issue highlighted the pivotal role of climatic stability (Molina-Venegas *et al.*, 2017; Sandel *et al.*, 2017) and the presence of various microclimates (Bátori *et al.*, 2017; Keppel *et al.*, 2017) in maintaining high endemism.

Oceanic islands have cooler, wetter and less seasonal (more stable) climates than mainlands, probably due to the effects of the surrounding ocean (Weigelt and Kref, 2013). Provided

they are geologically old and topographically complex, they can harbour a considerable number of endemic species (Kier *et al.*, 2009; Keppel *et al.*, 2016). Due to their isolation from the mainland, islands also often have unique species, such as large, flightless birds and evolutionary relicts (Carlquist, 1972; Trewick *et al.*, 2007).

The floras of many islands in the Pacific, especially that of New Caledonia, exemplify the phenomenon of high endemism and vulnerability of island biodiversity (Morrison, 2012; Keppel *et al.*, 2014). New Caledonia's flora is globally renowned for its diversity and endemism and the archipelago constitutes the smallest global biodiversity hotspot (Myers *et al.*, 2000; Mittermeier *et al.*, 2005), being home to 3371 vascular plant species of which approx. 75 % are endemic (Morat *et al.*, 2012). The density of endemic vascular plant species (2519 species for 18 500 km<sup>2</sup>) is the highest in the world (Kier *et al.*,

2009) and many plant families that are rare on a global scale occur in New Caledonia (Williams *et al.*, 1994).

In addition to high biodiversity and endemism, New Caledonia's flora is highly distinct (Morat *et al.*, 2012; Pillon *et al.*, 2010). It includes *Parasitaxus ustus* (Podocarpaceae), the only parasitic conifer (de Laubenfels, 1959), and *Amborella trichopoda* (Amborellaceae), the sole surviving sister species of all living angiosperms (Albert *et al.*, 2013). The flora is characterized by (1) high representation of relict taxa including gymnosperms (46 species, 15 genera and five families) and basal angiosperms *sensu lato*, i.e. the ANA (Amborella, Nymphaeales, Austrobaileyales) grade, Chloranthales and magnoliids (109 species, 22 genera and ten families) (Morat *et al.*, 2012), (2) disharmony (over- and under-representation of groups compared to surrounding continental areas, i.e. Australia; Pillon *et al.*, 2010) and (3) extensive radiations of several genera, e.g. *Phyllanthus* (Phyllanthaceae, 113 species), *Psychotria* (Rubiaceae, 85 species) and *Syzygium* (Myrtaceae, 70 species). The presence of relict taxa, disharmonic biotas and radiations of certain groups are typical of island biotas (Carlquist, 1974; Keppel *et al.*, 2009).

Tropical rainforests make the greatest contribution to the diversity and endemism of New Caledonia's flora. The remaining 3800 km<sup>2</sup> of New Caledonian rainforests (about 25 % of their original area, see Jaffré *et al.*, 1998) contain about 62 % of the total plant diversity, with about 83 % being endemic (Jaffré *et al.*, 2009; Morat *et al.*, 2012). Other important vegetation types include maquis (shrublands), containing about 34 % of the total plant diversity (90 % endemism) and tropical dry forests (10 % of diversity, 59 % endemism).

Despite their uniqueness and diversity, the structure, composition and diversity of New Caledonian rainforest communities, especially at the stand level, remain poorly known. Jaffré and Veillon (1995) reported higher stem density and lower species density in New Caledonia compared to rainforests in the Malay Archipelago and Papua New Guinea. A recent analysis of an extensive 20 × 20-m plot network supported the claims of high stem density and species diversity as characteristics of New Caledonian rainforests (Ibanez *et al.*, 2014). While this latest analysis provided the first large-scale synthesis of the structural and floristic diversity of New Caledonian rainforests, the small plot size did not allow detailed investigation of the structure of communities or allow robust comparison with rainforests in other regions (see Grytnes and Felde, 2014; Ibanez *et al.*, 2016).

This paper describes the composition, diversity and structure of New Caledonian rainforest communities through the analysis of nine 1-ha plots. These results are compared with other tropical rainforests in the Southwest Pacific known to have high diversity (see Keppel *et al.*, 2010). While the composition, diversity and structure of rainforests in other regions around the world are relatively well known (Phillips *et al.*, 1994), this paper provides the first such overview for the Southwest Pacific region. Based on literature (Jaffré and Veillon, 1995; Morat *et al.*, 2012; Ibanez *et al.*, 2014), we expected New Caledonian rainforests to have higher endemism, stem densities and concentrations of relictual lineages than other rainforests in the Southwest Pacific.

## MATERIAL AND METHODS

### New Caledonia

New Caledonia (20–23°S, 164–167°E) is an archipelago located in the Southwest Pacific, just above the tropic of Capricorn, about 1500 km east of Australia and 2000 km north of New Zealand. The main island of New Caledonia (Grande Terre) includes a central mountain range with peaks of 1628 m in the north (Mont Panié) and 1618 m in the south (Mont Humboldt). Mean annual precipitation ranges from over 4000 mm yr<sup>-1</sup> on mountain tops and some lowlands of the windward east coast, to less than 1000 mm yr<sup>-1</sup> in the lowlands of the leeward west coast where the last fragments of dry forest stand (Gillespie and Jaffré, 2003).

The unique New Caledonian flora is thought to be inherited from a complex biogeographical history. Indeed, the main island of New Caledonia is a fragment of continental crust (Zealandia) that separated from Australia and drifted to the north-east, reaching its current position about 45 Mya (Neall and Trewick, 2008). This drift culminated in obduction during which New Caledonia was totally immersed and covered with ophiolites (see Neall and Trewick, 2008). Hence, its flora results from long- or short-distance recolonization and diversification events after New Caledonia re-emerged about 37 Mya (Grandcolas *et al.*, 2008; Espeland and Muriénne, 2011; Pillon, 2012).

Ultramafic substrates cover about one-third of New Caledonia, mainly in the southern part of the Grande Terre. Soils derived from ultramafic substrates are challenging for plants because of the low levels of macronutrients, such as nitrogen, phosphorous, potassium or calcium, and high levels of potentially phytotoxic metals, such as nickel, chromium or manganese (see Jaffré, 1980; Kazakou *et al.*, 2008). Although ultramafic substrates have played a key role in shaping the New Caledonian flora (e.g. Pillon *et al.*, 2010), we focus here on the less-studied rainforests occurring on non-ultramafic (volcano-sedimentary) substrates (Birnbaum *et al.*, 2015).

### Plot network and plant survey

Between March 2013 and October 2016, nine 1-ha plots (100 × 100 m) were established in mixed rainforests on volcano-sedimentary substrates in the Northern Province of New Caledonia. The locations of the plots were chosen to maximize the spatial coverage as well as the range of elevation and rainfall covered by the plots (Fig. 1). Two plots were located in the protected areas of Aoupinié and Panié (wilderness areas, IUCN category Ib). Plots were located between 240 and 880 m a.s.l. and between 1575 and 2995 mm mean annual precipitation and, where possible, away from evidence of recent disturbance (Table 1).

All stems with a diameter at breast height (dbh; at 1.3 m) ≥ 10 cm were tagged with a permanent number. Most plants were identified in the field. Samples of plants that could not be identified were collected and identified using voucher specimens at the herbarium of Nouméa (NOU) and/or literature (Aubréville *et al.*, 1967–present). Plants were classified into five main groups following the APG IV system of flowering

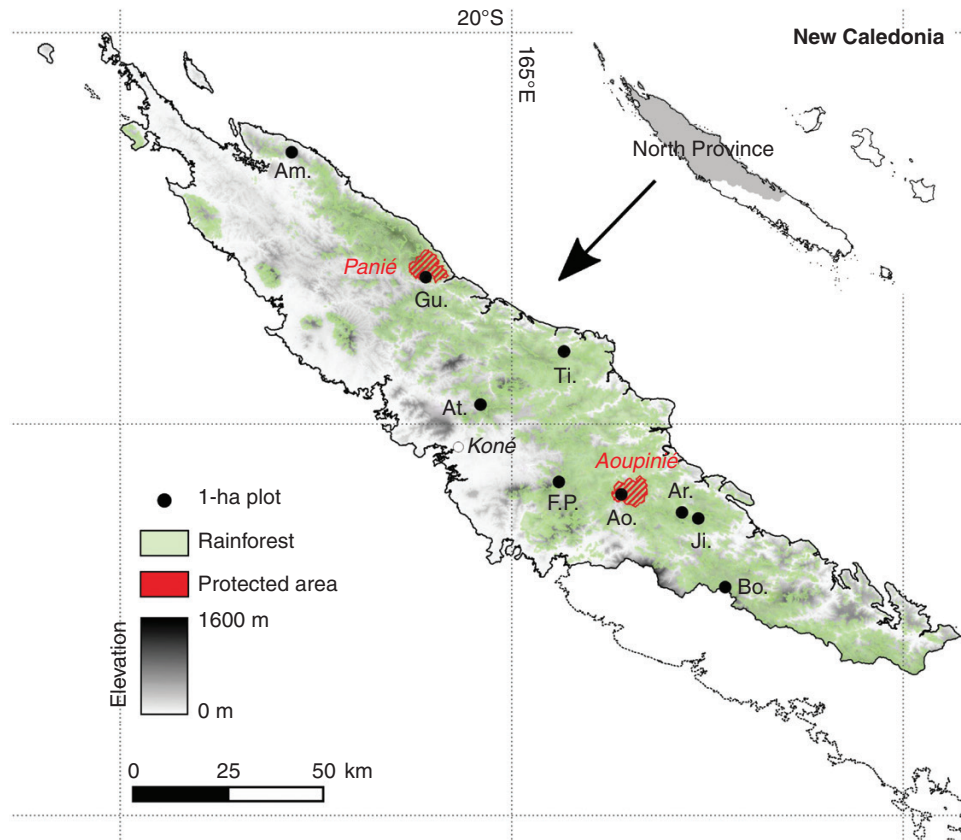


FIG. 1. Location of the nine 1-ha plots in the North Province of New Caledonia (SW Pacific). Protected areas are 'wilderness areas' (IUCN category Ib). Am. = Amoss, Ao. = Aoupinié, Ar. = Arago, At. = Atéu, Bo. = Bouirou, F. P. = Forêt Plate, Ji. = Jiève, Gu. = La Guen and Ti. = Tiwaé.

TABLE 1. *Site descriptions*

Country	Reference	Site	Long. (°E)	Lat. (°S)	Elevation (m)	Disturbance
New Caledonia	This study	Amoss	164.44	−20.31	480	No evidence of recent disturbances
		Aoupinié	165.28	−21.18	885	No evidence of recent disturbances
		Arago	165.48	−21.24	485	No evidence of recent disturbances
		Atéu	164.92	−20.95	775	No evidence of recent disturbances
		Bouirou	165.55	−21.42	540	Selective logging until the 1980s
		Forêt Plate	165.12	−21.15	510	Selective logging until the 1980s
		Jiève	165.44	−21.23	375	Old fire opening at the edge of the plot
		La Guen	164.78	−20.63	580	Traces of old settlement (about 100 years ago)
		Tiwaé	165.13	−20.81	240	Close to forest edge & domestic wood uptake
						Disturbed by cyclone Rona in 1999
Australia	Laidlaw <i>et al.</i> (2007)	Cape Tribulation (Thompson Creek)	145.44	−16.11	50	No evidence of recent disturbances
		Eungella	148.61	−21.02	720	No evidence of recent disturbances
		Paluma	146.18	−18.95	1000	No evidence of recent disturbances
		Atherton Tableland	145.62	−17.10	685	No evidence of recent disturbances
Fiji	Keppel <i>et al.</i> (2010)	Savura	178.44	−18.07	80–160	No evidence of recent disturbances
		Kubulau	178.98	−16.81	120–206	No evidence of recent disturbances
		Gau	179.28	−18.01	98–260	No evidence of recent disturbances
Papua New Guinea	Laidlaw <i>et al.</i> (2007)	Oomis	146.80	−6.68	65	Limited domestic wood uptake
		Baitabag	145.78	−5.13	100	Limited domestic wood uptake
	Keppel <i>et al.</i> (2010)	Sewa	150.99	−10.06	110–370	No evidence of recent disturbances
		Halowia	150.61	−6.08	100–220	No evidence of recent disturbances
Solomon Islands	Keppel <i>et al.</i> (2010)	Lauru	156.81	−6.97	35–130	No evidence of recent disturbances
		Kolombangara	157.12	−7.89	120–205	No evidence of recent disturbances
		Tetepare	157.55	−8.72	140–175	No evidence of recent disturbances



plant classification (The Angiosperm Phylogeny Group, 2016): ferns, gymnosperms, basal angiosperms (including here the Amborellales as well as the Austrobaileyales, Canellales, Chloranthales, Laurales, Magnoliales and Piperales), monocots (including here Arecales, Asparagales and Pandanales) and eudicots. Plot data are stored in the Global Forest Biodiversity Initiative (GFBI, [www.gfbinitiative.org](http://www.gfbinitiative.org)).

#### *Comparison with other tropical rainforests in the Southwest Pacific*

Stem density, taxonomic composition and diversity, and species turnover of rainforest communities in the nine New Caledonian 1-ha plots were compared with 14 1-ha plots located in the Southwest Pacific. These plots, described by Keppel *et al.* (2010) and Laidlaw *et al.* (2007), were located in countries known to have high species diversity in rainforests: Australia, Fiji, Papua New Guinea and the Solomon Islands (Table 1). Note that plots from Keppel *et al.* (2010) consist of four 50 × 50-m plots in close proximity (within 2 km<sup>2</sup> in the same forest system) pooled together.

#### *Floristic composition*

For each plot the number of stems was computed and the number of species, genera and families was inventoried in each plant group (ferns, gymnosperms, basal angiosperms, monocots and eudicots). Wilcoxon rank sum tests were used to test whether the composition of New Caledonian plots differed from the other plots. A non-metric multidimensional scaling (NMDS) was then performed using the *metaMDS* function of the *vegan* package in R (Oksanen *et al.*, 2013). NMDSs were computed using Bray–Curtis dissimilarity indices based on the presence/absence of species, genera or families. Permutational analysis of variance (PERMANOVA, *adonis* function) was used to assess how much country identities affected floristic dissimilarities as well as hierarchical classification (*hclust* function with Ward's grouping method) to assess the floristic affinities between plots.

#### *Diversity*

Because the diversity in a plot (alpha diversity) is highly dependent on the number of individuals sampled, rarefaction curves were compiled to compare diversity indices between plots using the *iNEXT* R package (Chao and Jost, 2012; Chao *et al.*, 2014). We chose to use Hill numbers (or effective numbers of species, see Hill, 1973) as diversity indices (see; Jost 2006; Ellison, 2010). Hill numbers (noted  ${}^qD$ ) weigh the number of species ( $S$ ) by the relative abundance of species ( $p_i$ ) according to a constant  $q$ :

$${}^qD = \left( \sum_{i=1}^S p_i^q \right)^{1/(1-q)}$$

When  $q = 0$ , all species have the same weight and  ${}^0D$  corresponds to the species richness, when  $q = 1$ , species are weighted by their relative abundance and  ${}^1D$  can be interpreted as the effective number of abundant species (also known as Shannon diversity) and when  $q = 2$ , the non-abundant species have little weight and  ${}^2D$  can be interpreted as the effective number of dominant species (also known as Simpson diversity). Rarefaction curves allow us to compare Hill numbers (with  $q = 0, 1$  and  $2$ ) for a given number of sampled individuals and also to estimate the completeness of the species inventory in the sites; that is, the more the curve trends to an asymptote, the more the sampling of species richness is complete (Gotelli and Colwell, 2010). Here, we compared Hill numbers estimated for 1000 trees. Finally, we compared species turnover (beta diversity) by computing Bray–Curtis dissimilarities after controlling for geographical distance between plots. The relationships between floristic dissimilarities and geographical distances were tested using Mantel tests.

## RESULTS

#### *Stem density*

A total of 11 280 stems with a dbh ≥ 10 cm were inventoried in the nine 1-ha plots in New Caledonia, with an average of 1253 stems ha<sup>-1</sup> and a range of 885 (Forêt Plate) to 1605 (Aoupinié) stems ha<sup>-1</sup> (Table 2). All plots (except Forêt Plate) had densities >1000 stems ha<sup>-1</sup>, which has only been reported for two plots outside New Caledonia (both in Australia). Plots from New Caledonia had significantly higher stem density than those from other countries (729 plants ha<sup>-1</sup> on average, Wilcoxon rank sum test,  $P < 0.001$ ), and was twice that observed in Papua New Guinea and the Solomon Islands (518 and 607 stems ha<sup>-1</sup> on average, respectively).

#### *Floristic composition*

A total of 335 species were identified in the New Caledonian plots, with 304 (90.7 %) being endemic to New Caledonia (Table 2, see Supplementary Data, Online Resource 1). A 1-ha plot had on average 95 species (and 42 families), ranging from 79 (La Guen) to 110 (Arago) species. Endemism ranged from 81 % in Forêt Plate to almost 100 % in Aoupinié (only two non-endemic native species). Ferns and monocots together accounted for 14 species (four species per plot on average) and basal angiosperms for 33 species (12 species per plot on average). Species density per plot in New Caledonia was not significantly different from other countries in the Southwest Pacific (Wilcoxon rank sum test,  $P = 0.25$ ), but family density per plot as well as endemism rates were significantly higher in New Caledonia (Wilcoxon rank sum test,  $P < 0.001$ ).

The large range in stem density on New Caledonia resulted, in part, from the varying abundance of monocots (particularly palms, Arecaceae) and tree ferns (Cyatheaceae and Dicksoniaceae) that represented about 12.6 and 3.2 %, respectively, of all inventoried plants and occurred in all sites except Forêt Plate. Basal angiosperms occurred in all plots with an average relative abundance of 10.8 %. Gymnosperms occurred in only two plots, and were relatively abundant in Forêt Plate

TABLE 2. Stem, species, genera and family densities in the main plant groups. Total densities (Eudicots/Monocots/Basal angiosperms/Gymnosperms/Ferns).

Country	Site	No. of stems	No. of species	No. of genera	No. of families	Species endemism (%)
New Caledonia	Amoss	1473 (1285/52/83/0/46)	94 (81/4/8/0/1)	76 (63/4/8/0/1)	43 (35/1/6/0/1)	89
	Aoupinié	1605 (1134/119/259/0/63)	87 (68/1/15/0/3)	59 (49/1/7/0/2)	41 (32/1/6/0/2)	98
	Arago	1347 (995/188/117/0/29)	110 (91/3/15/0/1)	73 (61/3/8/0/1)	42 (35/1/5/0/1)	93
	Atéu	1152 (591/444/80/0/35)	88 (71/1/14/0/2)	62 (49/1/10/0/2)	43 (33/1/7/0/2)	84
	Bouirou	1186 (798/158/118/1/111)	103 (84/1/13/1/4)	73 (60/1/8/1/3)	44 (34/1/6/1/2)	88
	Forêt Plate	885 (778/0/80/15/0)	100 (89/0/10/1/0)	70 (62/0/7/1/0)	41 (35/0/5/1/0)	81
	Jiève	1044 (957/4/78/0/4)	98 (86/3/8/0/1)	73 (63/3/6/0/1)	44 (36/2/5/0/1)	85
	La Guen	1286 (646/409/164/0/67)	79 (59/4/13/0/3)	54 (43/4/5/0/2)	38 (30/1/5/0/2)	91
	Tiwaé	1302 (1014/46/238/0/4)	97 (83/1/12/0/1)	59 (51/1/6/0/1)	40 (33/1/5/0/1)	90
	Average	1253 (911/158/135/2/40)	95 (79/2/12/0/2)	67 (56/2/7/0/1)	42 (34/1/6/0/1)	89
Australia	Thompson Creek	861 (541/182/134/4/0)	115 (86/2/26/1/0)	79 (68/2/8/1/0)	35 (29/1/4/1/0)	71
	Eungella	1194 (684/231/276/0/3)	40 (26/2/10/0/2)	28 (20/1/6/0/1)	19 (15/1/2/0/1)	87
	Paluma	1064 (721/0/343/0/0)	68 (51/0/17/0/0)	48 (40/0/8/0/0)	27 (24/0/3/0/0)	84
	Atherton Tableland	676 (367/0/306/0/3)	91 (62/0/28/0/1)	61 (48/0/12/0/1)	27 (22/0/4/0/1)	82
	Average	949 (578/103/265/1/2)	79 (56/1/20/0/1)	54 (44/1/9/0/1)	27 (23/1/3/0/1)	81
Fiji	Savura	915 (662/4/232/10/7)	121 (97/2/18/3/1)	67 (54/1/8/3/1)	47 (36/2/5/3/1)	54
	Kubulau	839 (693/3/122/20/1)	92 (78/1/11/1/1)	50 (43/0/7/0/0)	37 (30/1/4/1/1)	54
	Gau	752 (372/0/279/92/9)	86 (66/0/17/2/1)	64 (52/0/9/2/1)	42 (34/0/5/2/1)	57
	Average	835 (576/2/211/41/6)	100 (80/1/15/2/1)	60 (50/0/8/2/1)	42 (33/1/5/2/1)	55
Papua New Guinea	Oomis	484 (341/22/108/13/0)	97 (72/4/20/1/0)	64 (48/4/1/1/0)	36 (29/2/4/1/0)	—
	Baitabag	449 (387/1/57/4/0)	110 (96/1/12/1/0)	74 (65/1/7/1/0)	34 (29/1/3/1/0)	—
	Sewa	609 (466/0/137/6/0)	67 (56/0/10/1/0)	33 (27/0/5/1/0)	30 (25/1/3/1/0)	—
	Halowia	528 (462/1/63/2/0)	96 (77/1/17/1/0)	43 (34/1/7/1/0)	31 (26/1/3/1/0)	—
	Average	518 (414/6/91/6/0)	93 (75/2/15/1/0)	54 (44/2/8/1/0)	33 (27/1/3/1/0)	—
Solomon Islands	Lauru	662 (505/120/36/0/1)	119 (98/7/13/0/1)	55 (45/2/7/0/1)	35 (29/1/4/0/1)	14
	Kolombangara	537 (402/1/134/0/0)	80 (66/1/13/0/0)	35 (30/0/5/0/0)	29 (26/0/3/0/0)	8
	Tetepare	621 (463/45/113/0/0)	72 (66/2/4/0/0)	37 (32/1/4/0/0)	28 (25/1/2/0/0)	8
	Average	607 (457/55/94/0/0)	90 (77/3/10/0/0)	42 (36/1/5/0/0)	31 (27/1/3/0/0)	10

(15 *Agathis moorei*, Araucariaceae). The Arecaceae (1419 stems, eight species) and Sapindaceae (1156 stems, 22 species) were the most abundant families, while the Myrtaceae (576 stems, 33 species) was the most diverse family (Fig. 2). The genera *Burretiockentia* (Arecaceae; 899 stems, one species), *Cupaniopsis* (Sapindaceae; 645 stems, seven species), *Dysoxylum* (Meliaceae; 661 stems, eight species) and *Garcinia* (Clusiaceae; 627 stems, eight species) were the most abundant, and *Syzygium* (Myrtaceae; 145 stems, 18 species), *Cryptocarya* (Lauraceae; 436 stems, 13 species) and *Ficus* (Moraceae; 271 stems, 11 species) were the most diverse (Fig. 2).

Palms were also abundant in Australia and the Solomon Islands, with densities being 11.3 and 9.1 % on average, respectively. Tree ferns with dbh  $\geq 10$  cm were generally less abundant outside New Caledonia (Table 2). Basal angiosperms had higher relative abundances outside New Caledonia, reaching 29.0 % in Australia. The abundance of gymnosperms was low in Australia, Solomon Islands and New Caledonia compared with Fiji and Papua New Guinea, where they had relatively high densities (4.9 and 1.4 %, respectively).

The floristic composition of New Caledonian plots was different from plots elsewhere in the Southwest Pacific, with average Bray–Curtis dissimilarities being 0.79 and 0.51 at the genus and family level, respectively (Fig. 3). Generally, the genus/family composition was more similar within than among countries, with country of plot location explaining 62 and 65 % of the variability in Bray–Curtis dissimilarities at the genus and family level, respectively (PERMANOVA,  $P < 0.001$ ). Plots within New Caledonia generally had low Bray–Curtis dissimilarities (0.43 and 0.27 at the genus and family level,

respectively) although La Guen and Aoupinié seemed to form a distinct grouping for both genus and family composition.

### Diversity

In New Caledonia, species density ranged from 75 to 105 species per 1000 inventoried plants (92 species on average). Atéu, Amoss and La Guen were the least diverse plots (Table 3) and were dominated by few species (low Shannon and Simpson diversity) compared to the more diverse plots of Forêt Plate, Tiwaé and Arago, which had more dominant species. For instance, in Atéu and Amoss the two most abundant species – *Burretiockentia vieillardii* (444 stems) and *Apodytes clusiifolia* (89 stems) in Atéu and *Garcinia vieillardii* (377 stems) and *Calophyllum caledonicum* (224 stems) in Amoss – represented  $>40$  % of all inventoried stems. In contrast, the two most abundant species in Arago (*Calophyllum caledonicum* and *Cyphokentia macrostachya*) represented  $<12$  % of all inventoried stems. Standardized diversity estimates did not differ visually among countries (Fig. 4) and Hill numbers (rarefied to 1000 stems) did not differ significantly as a function of country identities (Wilcoxon rank sum test,  $P > 0.05$ , see Table 3).

On a regional scale, species dissimilarity (Bray–Curtis index computed on species presence/absence) globally increased with the log-transformed geographical distances (Mantel test,  $r = 0.34$ ,  $P = 0.002$ ) while on a shorter geographical range ( $< 170$  km) this relationship was not significant within New Caledonia (Mantel test,  $P = 0.739$ , Fig. 5). In New Caledonia,

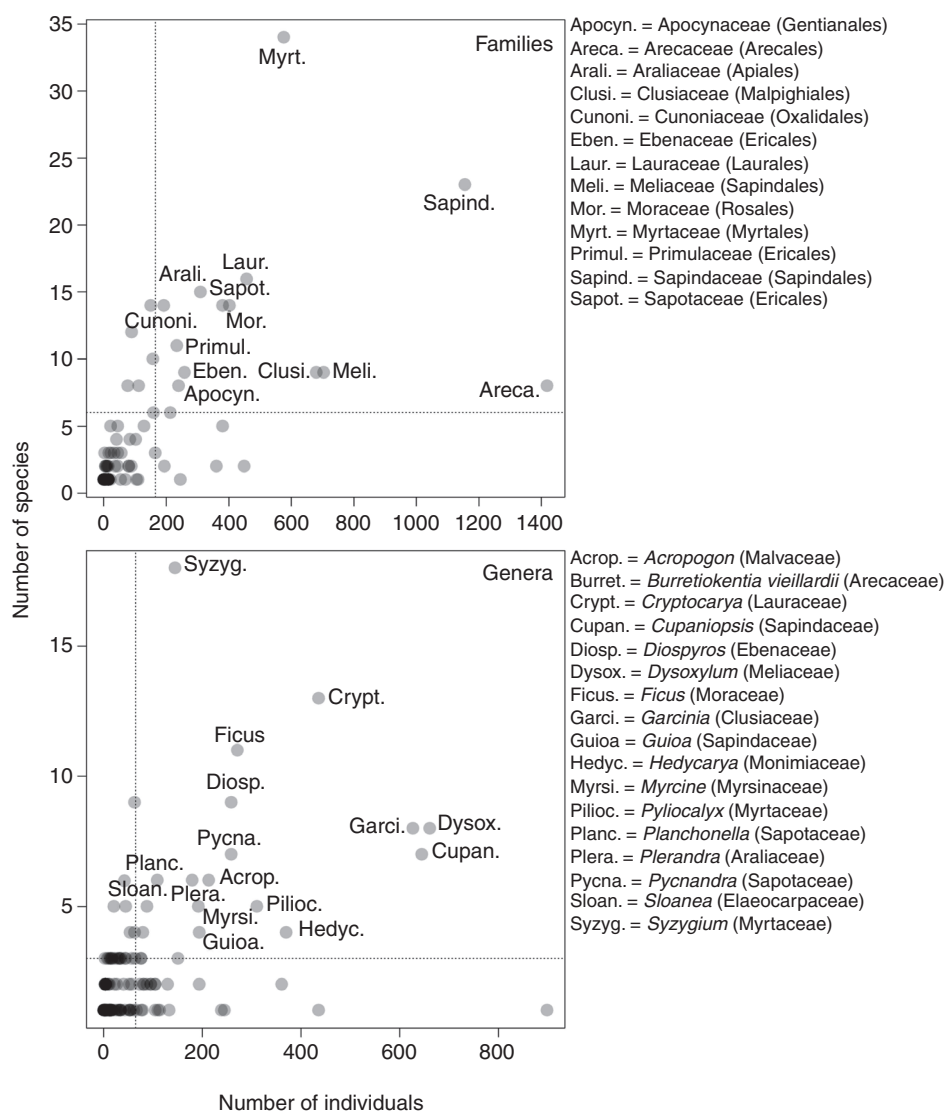


FIG. 2. Diversity (number of species) and abundance (number of individuals) of each family and genus in the New Caledonian plots. Dotted lines represent the third quartiles of the distribution of diversity and abundance. Names are only indicated for the most abundant and diverse families or genera.

the most similar plots (Bray–Curtis index = 0.45) were Boirou and Atéu, located 83 km apart, while the most dissimilar plots (Bray–Curtis index = 0.81) of Jiève and Aoupinié were only 16 km apart.

## DISCUSSION

### Stem density

These results indicate that New Caledonian rainforests have higher stem densities (1253 stems  $\text{ha}^{-1}$  on average) than other high-diversity rainforests in the Southwest Pacific (728 stems  $\text{ha}^{-1}$  on average). Similar stem densities (1256 stems  $\text{ha}^{-1}$  in Col d'Amieu based on 12 plots of 0.25 ha) have been reported in New Caledonia by Jaffré and Veillon (1995). The higher stem densities (1526 stems  $\text{ha}^{-1}$  across Grande Terre based on 87 plots of 0.04 ha) that were reported by Ibanez *et al.* (2014) are

likely to be an overestimation due to the small plot size and because plots were placed in homogeneous (closed canopy) forest patches, avoiding tree gaps which are natural features of tropical rainforests (Lang and Knight, 1983; Poorter *et al.*, 1994). Furthermore, Jaffré and Veillon (1995) and Ibanez *et al.* (2014) did not find major structural differences between plots located on ultramafic and non-ultramafic substrates, suggesting that high stem density is a common characteristic of New Caledonian tropical rainforests. Such high stem densities (i.e. >1000 stems  $\text{ha}^{-1}$ ) have also been reported in Mascarene Islands in La Réunion (Strasberg, 1996) and Mauritius (Florens *et al.*, 2012). On a global scale, Phillips *et al.* (1994) reported much lower stem densities in the Neotropics (630 stems  $\text{ha}^{-1}$  on average), Africa (618 stems  $\text{ha}^{-1}$  on average) and Southeast Asia (538 stems  $\text{ha}^{-1}$  on average).

The frequent tropical cyclones affecting New Caledonia as well as La Réunion and Mauritius (one or two cyclones per year on average) could explain the high stem densities, as these

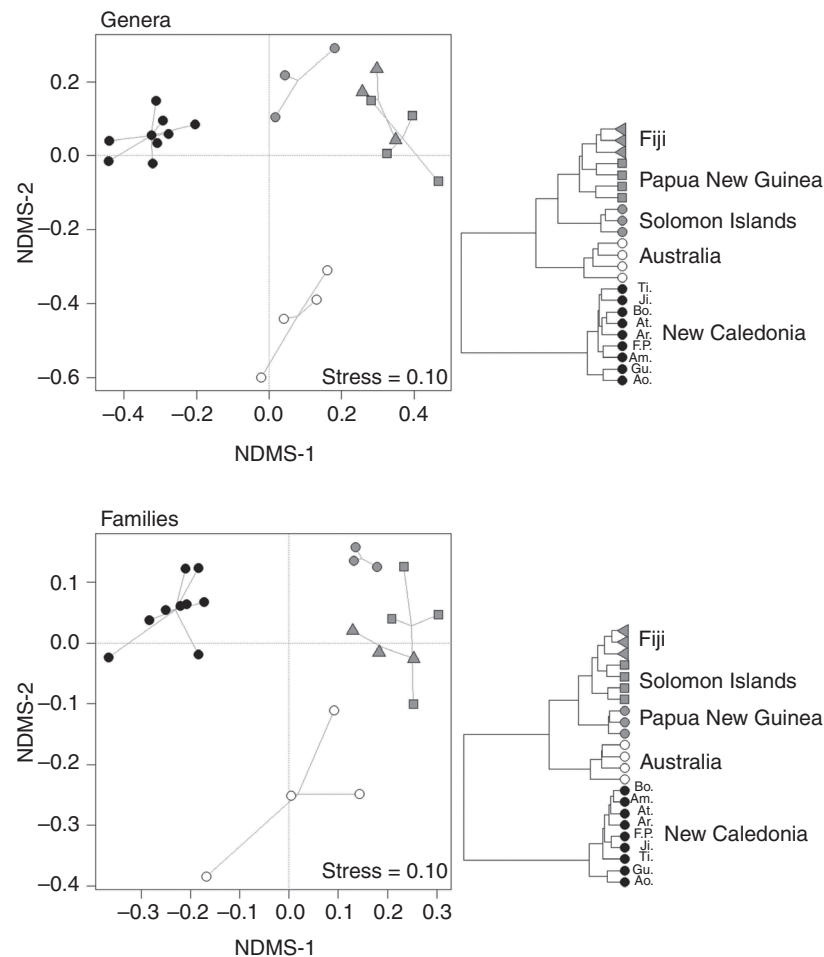


FIG. 3. Ordination (non-metric multidimensional scaling) and hierarchical classification trees (Ward's grouping method) according to the composition (Bray–Curtis dissimilarity performed on the presence/absence of genera and families) of 23 plots in Australia, Fiji, New Caledonia, Papua New Guinea and the Solomon Islands. For New Caledonian plots Am. = Amoss, Ao. = Aoupinié, Ar. = Arago, At. = Atéu, Bo. = Bouirou, F. P. = Forêt Plate, Ji. = Jiève, Gu. = La Guen and Ti. = Tiwaé.

repeated canopy disturbances would provide more opportunity for regeneration (Burslem *et al.*, 2000; Franklin *et al.*, 2004; Turton, 2008; Webb *et al.*, 2011). Indeed, cyclones are less frequent and less intense in Australia, Fiji and, to a larger extent, in the Solomon Islands and Papua New Guinea, compared to New Caledonia (Dowdy *et al.*, 2012). Regions in the Southwest Pacific experiencing higher frequencies of cyclones do seem to have higher stem densities (Keppel *et al.*, 2010). Cyclone frequency, in addition to topographic exposure (Boose *et al.*, 1994), could also be a contributing factor to the two-fold variation in stem density observed within New Caledonia in this study. Although our dataset is too small (nine plots) to identify the drivers of this variability, it supports the suggestion that stem density tends to increase with elevation in New Caledonia (Ibanez *et al.*, 2014). This pattern may be explained by changes in the following environmental parameters with increasing elevation: (1) decreasing temperature reducing plant growth and maximum size (e.g. Takyu *et al.*, 2005), (2) increasing precipitation and decreasing dry-season length (e.g. Slik *et al.*, 2010) and (3) increasing exposure to wind and cyclones affecting large trees (Lugo, 2008).

#### Floristic composition

The abundance of tree ferns with dbh  $\geq 10$  cm (40 stems  $\text{ha}^{-1}$  on average) was another unique characteristic of New Caledonian rainforests. Although high abundance of tree ferns has also been reported from Fiji (Keppel *et al.*, 2005), tree ferns in that study were mostly  $<10$  cm in dbh. Keppel *et al.* (2005) and other studies (e.g. Guariguata, 1990; Bystriakova *et al.*, 2011) have associated high abundances of tree ferns with high frequency of natural disturbances. Therefore, the high frequency of cyclones may also explain the abundance of tree ferns in New Caledonian rainforests.

Palms are another abundant plant group in New Caledonian rainforests. As in Ibanez *et al.* (2014), palms (Arecaceae) were the most abundant family (13 % of all inventoried plants) and *Burretio kentia vieillardii* was by far the most abundant species (8 % of all inventoried plants). The dominance of palms, as well as the high spatial variation in their abundance, is characteristic of tropical rainforests (see Eiserhardt *et al.*, 2011) and was also observed in the rainforests of Australia and the Solomon Islands. The variability in the local abundance of palms is likely to result from local-scale heterogeneity, complex interactions



TABLE 3. Hill numbers estimated for 1000 plants using rarefaction [95 % confidence intervals]

Country	Site	$q = 0$ (Richness)	$q = 1$ (Shannon diversity)	$q = 2$ (Simpson diversity)
New Caledonia	Amoss	86 [81–92]	24 [22–25]	10 [9–11]
	Aoupinié	79 [74–84]	36 [35–38]	24 [22–25]
	Arago	103 [97–110]	57 [54–59]	40 [37–43]
	Atéu	86 [80–92]	19 [17–21]	6 [5–7]
	Bouirou	100 [94–106]	44 [41–47]	25 [22–28]
	Forêt Plate	105 [95–114]	52 [48–55]	34 [31–38]
	Jiève	98 [89–107]	39 [36–42]	24 [21–26]
	La Guen	75 [69–80]	27 [25–29]	15 [14–17]
	Tiwaé	93 [88–98]	52 [50–55]	38 [35–40]
	Average	92	39	24
Australia	Atherton Tableland	101 [91–112]	43 [39–47]	25 [23–28]
	Thompson Creek	121 [111–131]	38 [34–42]	18 [16–20]
	Eungella	39 [34–43]	18 [17–19]	13 [12–14]
	Paluma	67 [61–73]	36 [34–39]	25 [23–27]
	Average	82	34	20
Fiji	Gau	92 [84–100]	38 [35–42]	20 [17–23]
	Kubulau	97 [87–108]	39 [36–43]	21 [18–24]
	Savura	124 [115–132]	58 [53–62]	28 [24–33]
	Average	104	45	23
Papua New Guinea	Baitabag	145 [127–164]	71 [63–79]	39 [32–45]
	Halowia	125 [109–141]	25 [20–29]	7 [6–8]
	Oomsis	127 [109–146]	58 [51–64]	33 [27–39]
	Sewa	79 [68–90]	25 [22–28]	13 [12–15]
	Average	119	45	23
Solomon Islands	Kolombangara	102 [86–117]	38 [34–43]	22 [19–25]
	Lauru	142 [127–157]	52 [46–58]	27 [23–30]
	Makira	82 [73–92]	30 [27–33]	18 [16–20]
	Average	107	40	22

between edaphic, topographic or hydrological preferences, small-scale disturbance histories (such as tree-fall gaps), and dispersal limitation (see Eiserhardt *et al.*, 2011).

The over-representation of ‘relictual’ groups, such as basal angiosperms and gymnosperms, is considered a key characteristic of the New Caledonian flora (Morat *et al.*, 2012). However, this over-representation is not reflected in our study based on nine 1-ha plots, showing that the relative species diversity and abundance of relictual groups at the stand scale is considerable (10–30 %) across the Southwest Pacific, with no significant difference among countries. In contrast, most of the diverse and abundant families in New Caledonia (Araliaceae, Clusiaceae, Lauraceae, Meliaceae, Moraceae, Myrtaceae, Sapindaceae, Sapotaceae) are over-represented (except Meliaceae and Myrtaceae) compared to Australia (Pillon *et al.*, 2010). The presence and abundance of these groups attests to the uniqueness of the New Caledonian rainforest flora.

### Diversity

Despite the high stem density, species density in New Caledonia was similar to other rainforests in species-rich regions of the Southwest Pacific. Average species density was 95 species ha<sup>-1</sup>, which is very close to the average of 97 species ha<sup>-1</sup> found by Jaffré and Veillon (1995) in Col d’Amieu. Overall species density in the Southwest Pacific was lower than in the upper reaches of the Amazon and in Southeast Asia, but higher than in African rainforests (Phillips *et al.*, 1994). However, values comparable to the diversity of the Amazon and Southeast Asia have been reported for Crater Mountain in Papua New

Guinea with 174 and 228 species ha<sup>-1</sup> (Wright *et al.*, 1997; Weiblen, 1998).

The most notable feature of New Caledonian rainforests is their extraordinarily high endemism (Kier *et al.*, 2009; Morat *et al.*, 2012; Pillon *et al.*, 2017). This was reflected in the 1-ha plots of this study, which had an average endemism of 89 %. The processes leading to such high endemism are still not fully understood. According to island biogeographical theory (MacArthur and Wilson, 1967; Whittaker *et al.*, 2008), the high endemism could result from both isolation (1220 km east of Australia) and the age of emergence of Grande Terre (about 37 Mya). By comparison, Fiji is more isolated (2630 km east of Australia) and younger (Viti Levu, the main island of Fiji, probably emerged about 5–16 Mya; see Neall and Trewick, 2008), but has lower endemism than New Caledonia (about 50–60 %; see Keppel *et al.*, 2010, 2011). Additionally, high niche diversity (edaphic and climatic) promoting major radiations in several plant groups has been invoked as a contributing factor to the high endemism in New Caledonian rainforests (edaphic and climatic; see, for example, Pillon *et al.*, 2009; Barrabé *et al.*, 2014; Paun *et al.*, 2016).

Similar to other endemism hotspots (Harrison and Noss, 2017), relative climatic stability may have contributed to the high endemism in New Caledonia. Pillon *et al.* (2017) indeed suggested that the high number of endemic genera (62–91) in New Caledonia could have been caused by their extinction outside the island during periods of unfavourable climate. For example, Australian rainforests are believed to have experienced severe contractions and associated extinctions during the Pleistocene glaciation (e.g. Byrne *et al.*, 2011).



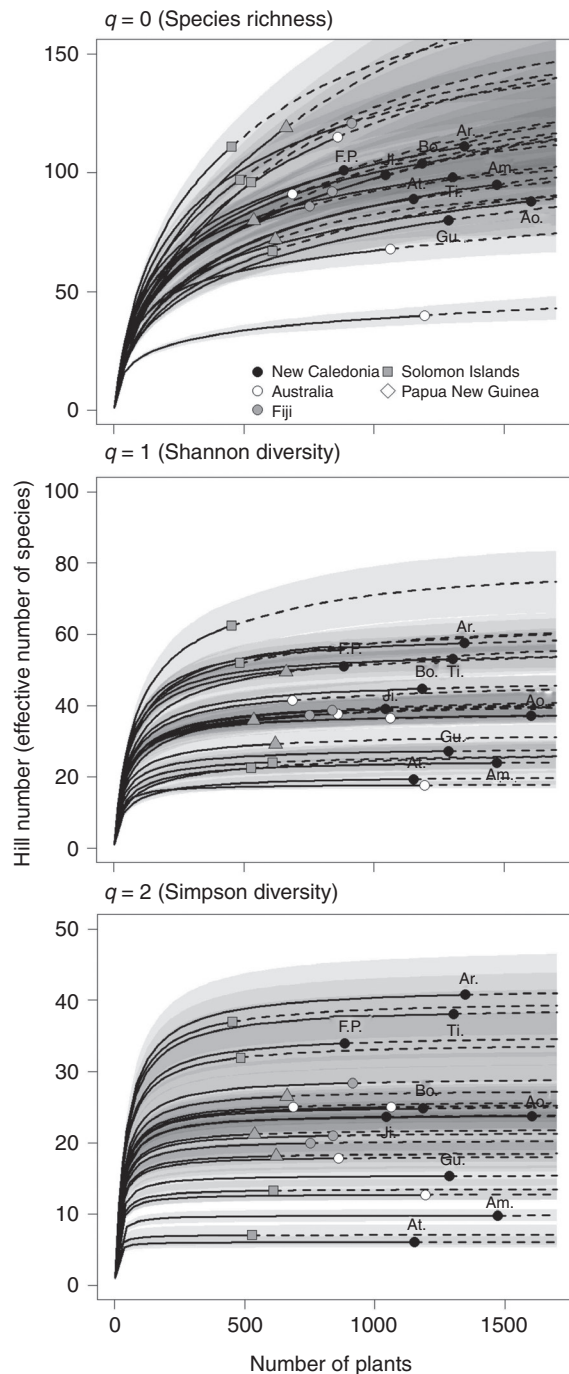


FIG. 4. Individual-based rarefaction curves, where each curve represents one 1-ha plot. Points represent the observed number of species as a function of the number of inventoried individuals. Solid black lines represent interpolations, dotted black lines represent extrapolations and grey areas represent the associated 95 % confidence intervals (from 100 bootstrap resamplings). For New Caledonian plots Am. = Amoss, Ao. = Aoupinié, Ar. = Arago, At. = Atéu, Bo. = Bouirou, F. P. = Forêt Plate, Ji. = Jiève, Gu. = La Guen and Ti. = Tiwaé.

New Caledonian rainforests showed high spatial species turnover that was not correlated to geographical distances between plots. This pattern was observed over short geographical distances (<170 km). Species turnover usually increases

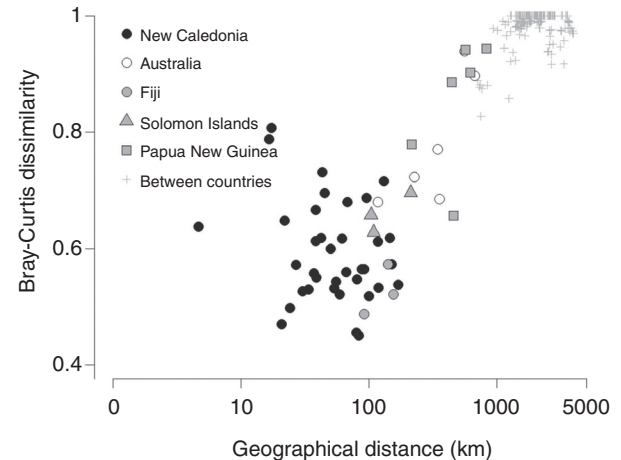


FIG. 5. Spatial turnover in species composition (Bray–Curtis dissimilarities based on species presence/absence) as a function of log-transformed geographical distances.

with geographical distance between plots due to increasing dissimilarities in environmental conditions, dispersal limitation and speciation processes (Condit *et al.*, 2002; Tuomisto *et al.*, 2003; Soininen *et al.*, 2007). While we lack sufficient plot data for other Pacific countries, this observation has important implications for the distribution and evolution of plant biodiversity in New Caledonia. Different interacting processes may explain this high spatial species turnover that is not related to geographical distance: (1) the topographical complexity of New Caledonia drives steep environmental gradients over relatively short distances (Jaffré, 1993), (2) cyclones and other disturbances such as fires produce a mosaic of different dynamic stages harbouring different floras (e.g. Rigg *et al.*, 1998; Enright *et al.*, 1999), (3) poor dispersal capacity associated with important geographical barriers promotes allopatric speciation (e.g. Paun *et al.*, 2016), and (4) climatic variation and isolation of populations into topographical refugia during the Pleistocene has promoted allopatric speciation and restricted species ranges around refugia (e.g. Pintaud *et al.*, 2001; Poncet *et al.*, 2013; Pouteau *et al.*, 2015).

## CONCLUSION

Rainforests in the Southwest Pacific can be highly diverse, even on a global scale, displaying higher species richness than African rainforests. They are home to many endemic species that are abundant elements of the flora and they therefore constitute important endemism hotspots. Several of these endemics are palaeoendemics (i.e. belong to ‘relictual’ groups, such as basal angiosperms and gymnosperms) and the stabilizing effect of the ocean on the regional climate may have contributed to the persistence of these taxa.

High stem densities, endemism and abundance of tree ferns, as well as high spatial species turnover, are characteristics of New Caledonian rainforests. We suggest that high frequency of cyclones contributes to high stem densities and abundance of tree ferns while topographical complexity and refugial dynamics of rainforest contraction and expansion during Pleistocene glacial cycles probably contributed to high endemism. However,

more detailed studies are required to assess the importance of these processes.

With less than 5 % of their area located in protected areas, New Caledonian rainforests are one of the least protected forest types within a global biodiversity hotspot (Gillespie *et al.*, 2012). Expanding existing protected areas would be unlikely to result in the adequate protection of the majority of rainforest species due to high levels of species turnover across New Caledonia. Our results therefore support the assertion by Jaffré *et al.* (1998) that the current system of protected areas in New Caledonia is inadequate. A better understanding of the drivers of spatial species turnover and the identification of phytogeographical regions could help to optimize species conservation by developing a network of protected areas that maximizes the number of species protected (Pouteau and Birnbaum, 2016).

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## SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of Online Resource 1: List of inventoried plant species in New Caledonian plots.

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