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

Thomas Ibanez1*, E. Blanchard1, V. Hequet1, G. Keppel1, M. Laidlaw4, R. Pouteau1, H. Vandrot1 and P. Birnbaum1,5

1 Institut Agronomique néo-Calédonien (IAC), Diversité biologique et fonctionnelle des écosystèmes terrestres, BPA5, 98848 Nouméa, New Caledonia, 2 Institut de Recherche pour le Développement (IRD), UMR AMAP, BPA5, 98848 Nouméa, New Caledonia, 3 School of Natural and Built Environments, University of South Australia, Mawson Lakes Campus, GPO Box 2471, Adelaide, South Australia 5001, Australia, 4 Queensland Herbarium, Department of Science, Information Technology and Innovation, Toowong, Queensland 4066, Australia and 5 Cirad, UMR AMAP, 34398 Montpellier, France

*For correspondence. Email ibanez@iac.nc

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 ≥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⁻¹ on average) in New Caledonia. In comparison with other rainforests in the Southwest Pacific, New Caledonian rainforests exhibited higher stem density (1253 stems ha⁻¹ 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 ≥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 ≥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 Kreft, 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 km²) is the highest in the world (Kier et al., 2009; Keppel et al., 2016).
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 Parasitoxis usit (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 relictual 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 magnolids (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 relictual 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 km² 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 endemism (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⁻¹ on mountain tops and some lowlands of the windward east coast, to less than 1000 mm yr⁻¹ 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 Murienne, 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).


<table>
<thead>
<tr>
<th>Country</th>
<th>Reference</th>
<th>Site</th>
<th>Long. (°E)</th>
<th>Lat. (°S)</th>
<th>Elevation (m)</th>
<th>Disturbance</th>
</tr>
</thead>
<tbody>
<tr>
<td>New Caledonia</td>
<td>This study</td>
<td>Amoss</td>
<td>164.44</td>
<td>−20.31</td>
<td>480</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aoupinié</td>
<td>165.28</td>
<td>−21.18</td>
<td>885</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Arago</td>
<td>165.48</td>
<td>−21.24</td>
<td>485</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Atéu</td>
<td>164.92</td>
<td>−20.95</td>
<td>775</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bouirou</td>
<td>165.55</td>
<td>−21.42</td>
<td>540</td>
<td>Selective logging until the 1980s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Forêt Plate</td>
<td>165.12</td>
<td>−21.15</td>
<td>510</td>
<td>Selective logging until the 1980s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Jiève</td>
<td>165.44</td>
<td>−21.23</td>
<td>375</td>
<td>Old fire opening at the edge of the plot</td>
</tr>
<tr>
<td></td>
<td></td>
<td>La Guen</td>
<td>164.78</td>
<td>−20.63</td>
<td>580</td>
<td>Traces of old settlement (about 100 years ago)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tiwae</td>
<td>165.13</td>
<td>−20.81</td>
<td>240</td>
<td>Close to forest edge &amp; domestic wood uptake</td>
</tr>
<tr>
<td>Australia</td>
<td>Laidlaw et al. (2007)</td>
<td>Cape Tribulation (Thompson Creek)</td>
<td>145.44</td>
<td>−16.11</td>
<td>50</td>
<td>Disturbed by cyclone Rona in 1999</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Eungella</td>
<td>148.61</td>
<td>−21.02</td>
<td>720</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Paluma</td>
<td>146.18</td>
<td>−18.95</td>
<td>1000</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Atherton Tableland</td>
<td>145.62</td>
<td>−17.10</td>
<td>685</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td>Fiji</td>
<td>Keppel et al. (2010)</td>
<td>Savura</td>
<td>178.44</td>
<td>−18.07</td>
<td>80–160</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Kubulau</td>
<td>178.98</td>
<td>−18.01</td>
<td>120–206</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gau</td>
<td>179.28</td>
<td>−18.01</td>
<td>98–260</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td>Papua New Guinea</td>
<td>Laidlaw et al. (2007)</td>
<td>Oomis</td>
<td>146.80</td>
<td>−6.68</td>
<td>65</td>
<td>Limited domestic wood uptake</td>
</tr>
<tr>
<td></td>
<td>Keppel et al. (2010)</td>
<td>Baitabag</td>
<td>145.78</td>
<td>−5.13</td>
<td>100</td>
<td>Limited domestic wood uptake</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sewa</td>
<td>150.99</td>
<td>−10.06</td>
<td>110–370</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Halowia</td>
<td>150.61</td>
<td>−6.08</td>
<td>100–220</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Kolombangara</td>
<td>157.12</td>
<td>−7.89</td>
<td>120–205</td>
<td>No evidence of recent disturbances</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tetepare</td>
<td>157.55</td>
<td>−8.72</td>
<td>140–175</td>
<td>No evidence of recent disturbances</td>
</tr>
</tbody>
</table>
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^2 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 (helust 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 et al., 2014). Hill numbers (noted ^qD) weigh the number of species (S) by the relative abundance of species (p_i) according to a constant q:

\[ qD = \left( \sum_i p_i^q \right)^{1/(1-q)} \]

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.
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, Tiwae and Arago, which had more dominant species. For instance, in Atéu and Amoss the two most abundant species – *Burretioptenia vieillardii* (444 stems) and *Apodytes clusii* (89 stems) in Atéu and *Garcinia vieillardii* (89 stems) in Atéu and *Calophyllum caledonicum* (645 stems) – represented >40% of all inventoried stems. In contrast, the two most abundant species in Arago (*Calophyllum caledonicum* and *Cyphekentia 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 (Manel test, \( r = 0.34, P = 0.002 \)) while on a shorter geographical range (< 170 km) this relationship was not significant within New Caledonia (Manel test, \( P = 0.739 \), Fig. 5). In New Caledonia,
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 ha−1 on average) than other high-diversity rainforests in the Southwest Pacific (728 stems ha−1 on average). Similar stem densities (1256 stems 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 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 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 ha−1 on average), Africa (618 stem ha−1 on average) and Southeast Asia (538 stem 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
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 ≥ 10 cm (40 stems 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 Burretiokentia 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...
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\(^{-1}\), which is very close to the average of 97 species ha\(^{-1}\) 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\(^{-1}\) (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).
Ibanez et al. — What makes New Caledonian rainforests so different?

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 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; Porchet 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 phyogeographical 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).

ACKNOWLEDGMENTS

This study was funded by the Agency for Economic and Environmental Development (DDEE) of the North Province of New Caledonia. Plots were established with the help of many people to whom we are most grateful. Assistance in the field was notably provided by Céline Chambrey, Dimitri Justeau, Elias Ganivet, Gendrilla Wairimavute, Grégroie Blanchard, Thomas Bouteaux, Jean-Jérôme Cassan, Juliane Kaoh, Marie Dubreuil and Pierre Lemaistre. We also thank Jacqueline Fambart-Tinel and all the team of the Nounéa herbarium (NOU) for technical support. We thank Janet Franklin and one anonymous reviewer for their helpful comments on the manuscript.

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.

LITERATURE CITED


Ibanez et al. — What makes New Caledonian rainforests so different?