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Structural and floristic diversity of mixed tropical rain forest in New Caledonia: new data from the New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN)

Thomas Ibanez, Jérôme Munzinger, Gilles Dagostini, Vanessa Hequet, Frédéric Rigault, Tanguy Jaffré & Philippe Birnbaum

Keywords
Alpha and beta diversity; Basal area; Environmental gradients; Floristic dissimilarity; Serpentine; Species richness; Stem density; Ultramafic substrates

Abbreviations
BC = Bray–Curtis dissimilarity index
NC-PIPPN = New Caledonian Plant Inventory and Permanent Plot Network; non-UM = Non-ultramafic substrates; UM = Ultramafic substrates

Nomenclature
Florical (Morat et al. 2012)

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Ibanez, T. (corresponding author, ibanez@iac.nc), **Munzinger, J.** (jerome.munzinger@ird.fr), **Dagostini, G.** (gilles.dagostini@ird.fr), **Hequet, V.** (vanessa.hequet@ird.fr), **Rigault, F.** (frederic.rigault@ird.fr), **Jaffré, T.** (tanguy.jaffre@ird.fr) & **Birnbaum, P.** (philippe.birnbaum@cirad.fr): Laboratoire de botanique et d'écologie végétale appliquées, Herbarium NOU, IRD, BPA5, 98848, Nouméa, New Caledonia
Ibanez, T. : IAC, BP73, 98890, Païta, New Caledonia
Munzinger, J. , **Dagostini, G.** , **Hequet, V.** , **Rigault, F.** & **Jaffré, T.** (tanguy.jaffre@ird.fr): IRD, UMR AMAP, 34398, Montpellier, France
Birnbaum, P. (philippe.birnbaum@cirad.fr): IAC/CIRAD, UMR AMAP, 34398, Montpellier, France
Rigault, F.: Current address: IRD, UMR IMBE, 13545, Aix en Provence, France

Abstract

Aims: To describe the structural and floristic diversity of New Caledonian mixed tropical rain forest and investigate its environmental determinants.

Location: New Caledonia (SW Pacific), a biodiversity hotspot.

Methods: Structural (stem density, basal area) and floristic characteristics (composition, species richness and dissimilarity) were investigated along environmental gradients (elevation, rainfall and slope) on different substrates (ultramafic and non-ultramafic) through the New Caledonian Plant Inventory and Permanent Plots Network (NC-PIPPN, 201 plots each measuring 20 m x 20 m).

Results: A total of 28,640 trees (DBH ≥5 cm) belonging to 749 species, 240 genera and 92 families were inventoried in the NC-PIPPN. The New Caledonian mixed rain forest studied was characterized as having high stem density, basal area and species richness, and many small stems (60% of the trees <10 cm DBH and almost a quarter of species did not exceed this threshold). More than one-third of the species were rare (i.e. inventoried in less than three plots or represented by fewer than three individuals) in the plot network and floristic dissimilarity was high (Bray–Curtis index >0.70). The presence of ultramafic (UM) and non- ultramafic substrates (non-UM) combined with altitudinal and rainfall gradients were the main drivers of floristic dissimilarity, whereas the effect of geographic distance between the plots was surprisingly low. Floristic dissimilarity was very high between UM and non-UM substrates from species up to family level. About 75% of the species occurred on a single substrate type. The mixed rain forest on UM and non-UM substrates differed in floristic composition but not in structure.

Conclusions: NC-PIPPN proved to be an effective tool for investigating the woody species richness of New Caledonia as containing *ca.* 46% of its non-herbaceous species. However, the network's design, and more specifically its small plots, restricts its capacity to capture beta diversity and forest structure. High species richness and floristic dissimilarity confirm that New Caledonian mixed rain forest is exceptionally rich.

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Introduction

The flora of New Caledonia is widely known for its exceptional richness and diversity (Morat et al. 2012) and this, combined with a high level of threat (Jaffré et al. 1998, 2010), makes it a major biodiversity hotspot (Myers 1988; Myers et al. 2000; Mittermeier et al. 2004). Studies focused on the origin, evolution and diversification of the New Caledonian biota have raised considerable interest and promoted substantial controversy. Its biota was first considered as a part of Gondwana (Thorne 1963), but this 'museum' theory has gradually given way to the 'recolonization' theory, according to which it results from recent (<37 Ma) long-distance recolonization and diversification events after total submersion and re-emergence of the main island (e.g. Murienne et al. 2005; Grandcolas et al. 2008; Murienne 2009; Espeland & Murienne 2011; Pillon 2012). Conversely, studies on ecosystems that support this diversity remain scarce. In particular, our knowledge of New Caledonian tropical rain forest – which is the most threatened ecosystem – is strikingly limited. If we are to better manage and conserve this exceptional biodiversity, we need to improve our knowledge of the environmental factors that determine the structural and floristic diversity of this forest (Jaffré 1993).

Very few studies in New Caledonia have investigated the structural and floristic diversity of mixed rain forest (e.g. Jaffré & Veillon 1995), some have compared mixed to mono-dominant rain forests (Read et al. 1995, 2000) and their results have suffered from a lack of extensive, standardized field surveys. Therefore, New Caledonian forests have long been classified on the basis of abiotic factors, namely nature of substrates (i.e. forest on ultramafic, volcano-sedimentary or calcareous rocks), elevation (low- to mid-elevation forest found below 1000 m or high-elevation forest above this threshold), rainfall (i.e. dry forest with less than 1100 $\text{mm}\cdot\text{yr}^{-1}$ and rain forest above this threshold) and slope (i.e. forest on steep slopes or not), rather than on clear structural and floristic characterization (Sarlin 1954; Jaffré 1993; Jaffré et al. 2008). Hence, an extensive and standardized vegetation survey is likely to provide clearer insights into the definition of rain forest types as well as a framework for understanding differences between them (Chytrý et al. 2011).

Forest ecosystems worldwide are commonly characterized by structural (e.g. stem density, basal area, canopy height) and floristic attributes (e.g. composition, richness, alpha and beta diversity). Extensive vegetation surveys, i.e. plant inventory and permanent plot networks, which are arguably the best way to assess such characteristics, have received increasing interest across the tropics, e.g. in South America (Malhi et al. 2002; Toledo et al. 2011; Blundo et al. 2012), Africa (Eilu et al. 2004; Picard et al. 2010), India (Davidar et al. 2008), Indonesia (Aiba & Kitayama 1999; Potts et al. 2002; Hadi et al. 2009) and the South Pacific (Webb et al. 2006; Keppel et al. 2010). Such networks offer new opportunities to study the environmental drivers of structural and floristic diversity and the long-term vegetation dynamics (Bakker et al. 1996). They also provide essential data to assess and compare large-scale diversity (ter Steege et al. 2006; De Caceres et al. 2012; Myers et al. 2013) and biomass (Peacock et al. 2007) distribution patterns.

Here, we present new data from the New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN) and investigate the environmental and spatial factors that determine structural and floristic variations across mixed tropical rain forest. The purpose of this study was to provide fresh information to clarify the definition of New Caledonian mixed rain forest and assess the usefulness of the NC-PIPPN as a tool to assess floristic and structural characteristics.

Methods

New Caledonia

New Caledonia is an archipelago in the South Pacific located just above the Tropic of Capricorn (20–23°S, 164–167°E), about 1500 km east of Australia and 2000 km north of New Zealand. The main island (about 400-km long and 40-km wide), called *Grande Terre*, is bisected by a continuous mountain chain whose highest peak reaches 1628 m in the north (*Mont Panié*) and 1618 m in the south (*Mont Humboldt*). Mean annual rainfall ranges from *ca.* 800 $\text{mm}\cdot\text{yr}^{-1}$ along the west coast to 4500 $\text{mm}\cdot\text{yr}^{-1}$ along the central mountain chain, with a typical dry season from late August to December (METEO-FRANCE 2007).

The island is dominated by two main types of substrate: (1) substrates on ultramafic rocks (encompassing serpentinite and peridotite, UM hereafter) also known as *terrains miniers*, covering about 5600 km^2 (i.e. 32.7% of the main island) mostly in the south, and (2) volcano-sedimentary substrates (non-UM hereafter) covering about 9000 km^2 (i.e. 52.6% of the main island) mostly in the north (forests on calcareous substrates mainly present on the *Iles Loyauté* are not considered here, but see Morat et al. 2001). Both UM and non-UM substrates are very diverse. Overall, UM substrates (also known as serpentine soils, see Proctor & Woodell 1975) differ greatly from non-UM substrates in that they possess low levels of macronutrients such as phosphorus, calcium and potassium often combined with high levels of magnesium, which antagonizes plant calcium uptake. UM substrates also contain high levels of potentially phytotoxic metals such as nickel, chromium or manganese (see Jaffré 1980; Brooks 1987; Kazakou et al. 2008; L'Huillier et al. 2010). As a consequence, distinctive

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vegetation evolves in these stressful environments resulting in high levels of endemism (Kazakou et al. 2008; L'Huillier et al. 2010).

The NC-PIPPN

The New-Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN) was set up in 2005 and currently consists of 201 plots measuring 20 m × 20 m (0.4 ha) exclusively located on the main island (Fig. 1). The plots are located in homogeneous stands of mixed tropical rain forest with no apparent evidence of recent disturbance. The plots are not distributed in a homogeneous geographic manner across the main island but in the main forested massifs. In the north, along the central mountain chain, 33 plots are located on *Mont Aoupinié* (reaching 1006 m), 17 on *Mont Panié* (1628 m) and 12 on *Massif des Lèvres* (1091 m). In the south (*Grand Massif du Sud*), 40 plots are located in *Forêt Nord*, 21 near *Yaté* and 12 on *Montagne des Sources* (912 m). These plots are almost equally distributed between UM and non-UM substrates (114 and 87 plots, respectively). Plot elevation ranges from 5 m to 1292 m on UM and from 105 m to 1187 m on non-UM (Fig. 2). Few plots are located above 1000 m (six on UM and three on non-UM), which is consistent with the scarcity of high-elevation rain forest that covers only about 100 km^2 (i.e. 2.5% of the total rain forest found on the main island). Slopes are 1.3–33.8° on UM and 0.9–43.4° on non-UM, and rainfall is 1548–3516 $\mathrm{mm{\cdot}yr}^{-1}$ on UM and 1781–3409 $\mathrm{mm{\cdot}yr}^{-1}$ on non-UM.

All plants in the plots (including trees, tree ferns, palms and lianas) with diameter at breast height (i.e. at 1.3 m, DBH) $\geq$5 cm have been tagged with a permanent number. Most species were identified in the field, but in cases where identity was in doubt, samples were collected and identified by comparison with the collection of voucher specimens in the IRD herbarium in Nouméa (NOU). The DBH $\geq$ 5 cm threshold on 0.04-ha plots (as in Basset et al. 2007) was preferred to the more standard DBH $\geq$ 10 cm on 1-ha plots in order to maximize the floristic richness of the woody plants considered by including understorey shrubs. We nevertheless provide statistics for and between these two thresholds such that broader comparisons may be made.

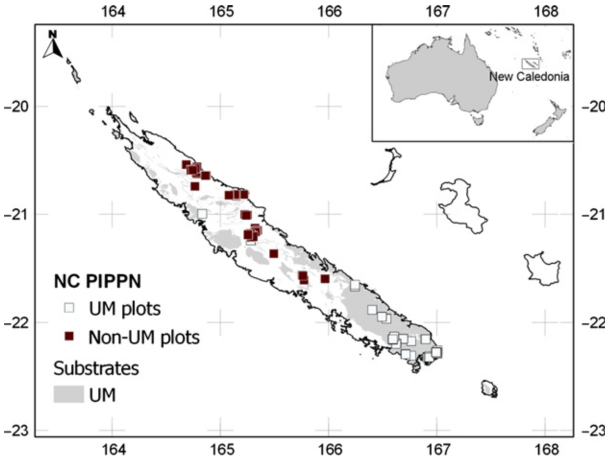

Fig. 1. The New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN). Location of plots on non-ultramafic (non-UM) and ultramafic (UM) substrates.

Data analysis

Different structural and floristic attributes were computed at the plot level to characterize the New Caledonian mixed rain forest. Structural attributes consisted of number of plants, distribution of their DBH and their total basal area. Floristic attributes consisted of species relative densities (i.e. number of stems of the species/total number of stems), their relative dominances (i.e. basal area of the species/total basal area), species richness and Shannon and Simpson diversity indices. The range of variation, together with the mean and SD were calculated for each statistic. We also tested the correlation between statistics calculated with a DBH threshold of 5 cm and 10 cm (Pearson's test). Since the number of plots differed on the two substrates, we used rarefaction curves to compare species richness on UM and non-UM.

We determined the effect of the geological substrate (i.e. UM or non-UM) and additional environmental factors (elevation, rainfall and slope) on variations in forest structure and composition by ANOVA. The difference between mean values on UM and non-UM was also analysed (Student's *t*-test). Elevation and slope were extracted from a 50-m grid digital elevation model and rainfall from a 1-km grid interpolation model using the mean annual rainfall recorded between 1990 and 2010 (AURELHY model, METEO-FRANCE).

Floristic composition was analysed to assess differences between plots. Here we used the standardized Morisita index (I_{mor}) to test the aggregation of the species present in at least two plots of the NC-PIPPN (UM and non-UM subsamples separately). The standardized I_{mor} ranges from -1 to 1; species with $I_{\mathrm{mor}} < -0.5$ are equally distributed across the plots, while species with $I_{\mathrm{mor}} > 0.5$ are aggregated in some plots (the distribution is random between -0.5 and 0.5).

Non-metric multidimensional scaling (NMDS) was used to spatially represent floristic similarities between plots. NMDS was applied at different taxonomic levels (family, genus and species) with the Bray–Curtis dissimilarity index (BC) as input (BC = 0 means that two plots have the same floristic composition, and BC = 1 means that two plots do

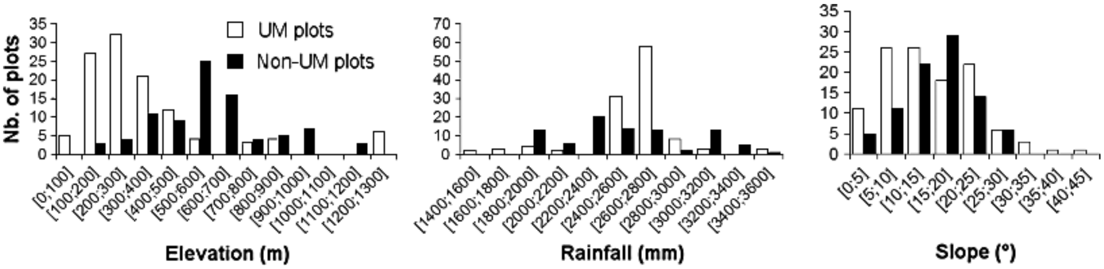

Fig. 2. Distribution of ultramafic (UM) and non-UM plots along environmental gradients.

not share any taxa). BC was calculated on relative density. The effect of substrate type on dissimilarities was assessed by permutational ANOVA.

We then assessed to what extent differences in elevation, rainfall, slope and geographic distance between plots (Euclidean distances) explained floristic dissimilarities (Bray–Curtis distances). Here we used the Mantel test to determine the correlation between distance matrices, and non-linear quantile regressions to analyse variations of the floristic dissimilarity with environmental (spatial) gradients. Geographic distance was log-transformed in accordance with the accepted relationship between distance and dissimilarity (Tuomisto et al. 2003; Soininen et al. 2007). All geographic processing was performed using Quantum GIS 1.8.0-Lisboa (Quantum GIS Development Team 2009; OSGeo.org) and all statistical analyses were performed using R 2.15.2 (R Foundation for Statistical Computing, Vienna, Austria) and the '*vegan*' and '*quantreg*' R packages.

Results

Structure

The structure of the mixed rain forest was broadly similar on both substrates (UM and non-UM), and the other environmental variables investigated did little to explain the observed variations (Table 1). Overall, the plots were characterized as having many small stems and high basal areas (all structural and floristic characteristics are shown by plot in Appendix S1).

Table 1. Percentage variance of the structural characteristics explained by environmental variables, as determined by ANOVA.

	Substrate	Elevation	Rainfall	Slope
Number of stems	**5.62*****	**15.71*****	**4.80*****	0.57
Basal area	**2.35***	**6.98*****	0.12	0.15
Mean DBH	0.98	0.68	**2.29***	0.33

Bold value denotes P value < 0.05.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

A total of 28,640 plants with DBH ≥ 5 cm were inventoried in the 201 0.04-ha plots. The number of stems per plot was slightly but significantly lower (*t*-test, $P < 0.001$) on UM (from 55 to 235; mean = 132.4 ± 44.0) than on non-UM (from 79 to 325; mean = 155.6 ± 51.3). This minor difference resulted from distinct stem density responses to elevation gradients. Stem density increased linearly up to the highest altitude plots on non-UM substrates, while on UM-substrates it increased up to 1000 m then decreased (Fig. 3). Basal area was also slightly lower (*t*-test, $P < 0.05$) on UM (from 0.96 to 5.89 m^2; mean = 2.42 ± 0.79 m^2) than on non-UM (from 1.21 to 5.79 m^2; mean = 2.69 ± 0.92 m^2) and was strongly correlated with the DBH of the largest tree ($r = 0.72$, $P < 0.001$). Number of stems and basal areas estimated with DBH thresholds of 5 cm and 10 cm were strongly correlated ($r = 0.64$ and 0.78 respectively, $P < 0.001$ in both cases).

Plot mean DBH (from 7.84 cm to 19.45 cm; mean = 12.17 ± 2.12 cm) did not differ significantly between substrates (*t*-test, $P > 0.05$). The lower diameter

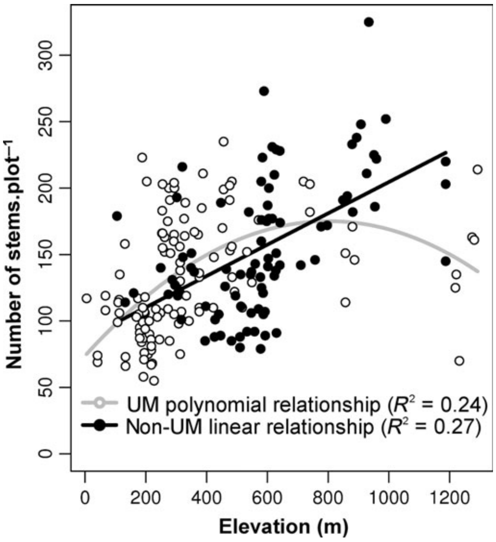

Fig. 3. Relationship between number of stems per plot and elevation on UM and non-UM substrates ($P < 0.05$).

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class (DBH = 5–10 cm) accounted for 60% of all stems (Fig. 4), while almost a quarter of the species (23.6%) never occurred in a higher class. Three quarter of all the species never exceeded the 36 cm DBH threshold (Fig. 4).

Floristic composition and dissimilarity

Most of the plants were identified at the specific or infraspecific level (88.2%) and almost all at the family level (99.8%). A total of 749 species, belonging to 240 genera and 92 families, were inventoried. Many species were scarce in the NC-PIPPN as 19.6% were recorded in only one plot (uniques) and 14.0% in only two plots (duplicates). Also, 15% of the species were represented by a single individual (singletons) and 6.5% by two individuals (doubletons). Overall, more than one-third of the species (33.8%) may be considered as rare in the NC-PIPPN (i.e. singletons, doubletons, uniques or duplicates). Most of the species occurring on UM or non-UM substrates (91.2% and 89.8%, respectively) were significantly aggregated ($I_{\mathrm{mor}} > 0.5$), while the remainder was randomly distributed between the plots.

Environmental variables did little to explain the variations noted in species richness and diversity (Table 2). Generally, species richness was slightly lower (Student's *t*-test, $P < 0.05$) on UM (from 12 to 68 species per plot^{-1}; mean = 37 ± 12 species per plot^{-1}) than on non-UM (from 20 to 73 species per plot^{-1}; mean = 40 ± 10 species per plot^{-1}) and overall, species rarefaction was slightly faster on UM (Fig. 5a). The optimal range for species richness corresponded to intermediate rainfall and altitude (about 2500–3000 mm·yr^{-1} and 600–800 m, Fig. 5b,c, respectively) and was independent of the substrate. Shannon and Simpson diversity indexes, ranging from 0.82 to 1.71 (mean = 1.33 ± 0.18) and from 0.02 to 0.33 (mean = 0.07 ± 0.05), were not significantly different between the two substrates. Species richness, Shannon and Simpson diversity indexes computed for the 5 cm and 10 cm DBH thresholds were strongly correlated (r = 0.88, 0.86 and 0.67, respectively, $P < 0.001$).

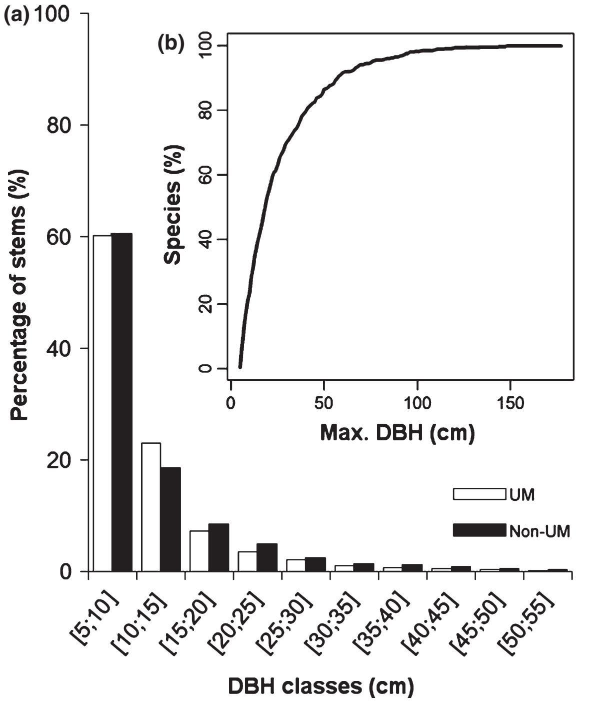

Fig. 4. (**a**) Distribution of stems by DBH class on the two different substrates, and (**b**) cumulated fraction of species in relation to maximum DBH.

Floristic composition at a family level was strongly determined by substrate type (i.e. UM or non-UM). Plots on UM substrate were dominated by Myrtaceae, Cunoniaceae, Clusiaceae, Sapotaceae and Rubiaceae, while non-UM plots were dominated by Arecaceae (Palms), Sapindaceae, Meliaceae, Monimiaceae and Lauraceae in decreasing order of abundance (Fig. 6). More than 75% of all species were recorded on a single substrate (38.1% on UM and 37.8% on non-UM). The same floristic segregation was observed at the genus level (20.8% on UM and 17.5% on non-UM) and at the family level (10.8% on UM and 12.9% on non-UM). The Bray–Curtis (BC) index of floristic dissimilarity computed at the species level between the two substrate types was therefore very high and ranged from 0.73 to 1.00 (mean = 0.97 ± 0.03).

Substrate explained 12.3, 12.6 and 12.9% of the variance observed in plot floristic composition at the species, genus and family levels (ANOVA, $P < 0.001$), respectively. But the difference in floristic composition between UM and non-UM substrates varied with elevation, as illustrated by the ordination of plots on a NMDS (Fig. 7). Floristic dissimilarity decreased at high elevation such that the UM plots were closer to the non-UM plots irrespective of the taxonomic resolution.

Bray–Curtis floristic dissimilarities within substrate types were weakly correlated with differences in elevation

Table 2. Percentage variance of species richness and diversity explained by environmental variables, as determined by ANOVA.

	Substrate	Elevation	Rainfall	Slope
Species richness	**2.26***	0.01	**4.88 ****	0.06
Shannon diversity	0.41	0.80	**5.73*****	0.05
Simpson diversity	0.01	1.18	**4.51 ****	0.26

Bold values denotes P value < 0.05.
*P < 0.05.
**P < 0.01.
***P < 0.001.

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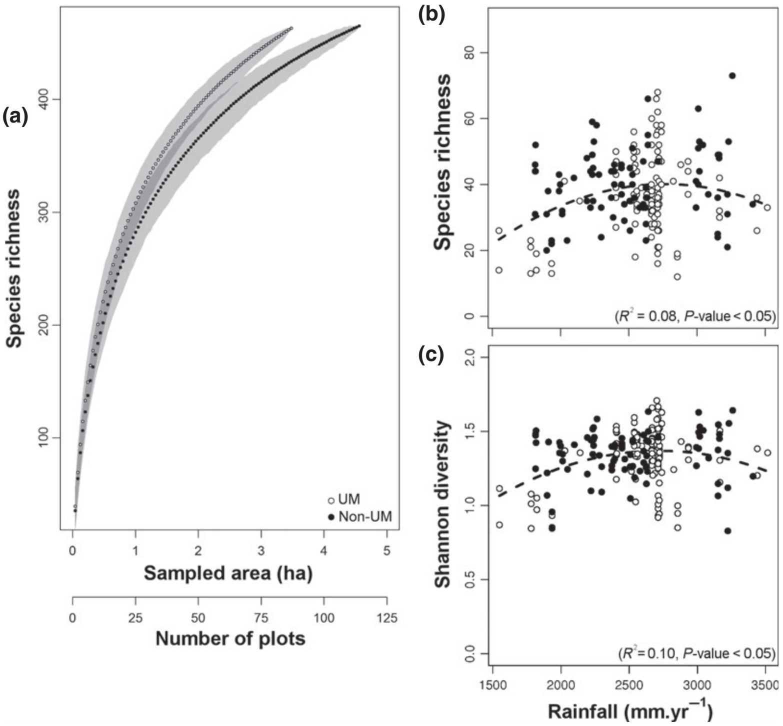

Fig. 5. (**a**) Relationships between sampled area and species richness on UM and non-UM substrates (points represent the average of 1000 random re-samplings and grey areas 95% confidence intervals). Relationship between rainfall and (**b**) species richness (i.e. number of species per plot) and (**c**) Shannon diversity (dashed lines represent the second-order polynomial relationship for the whole data set).

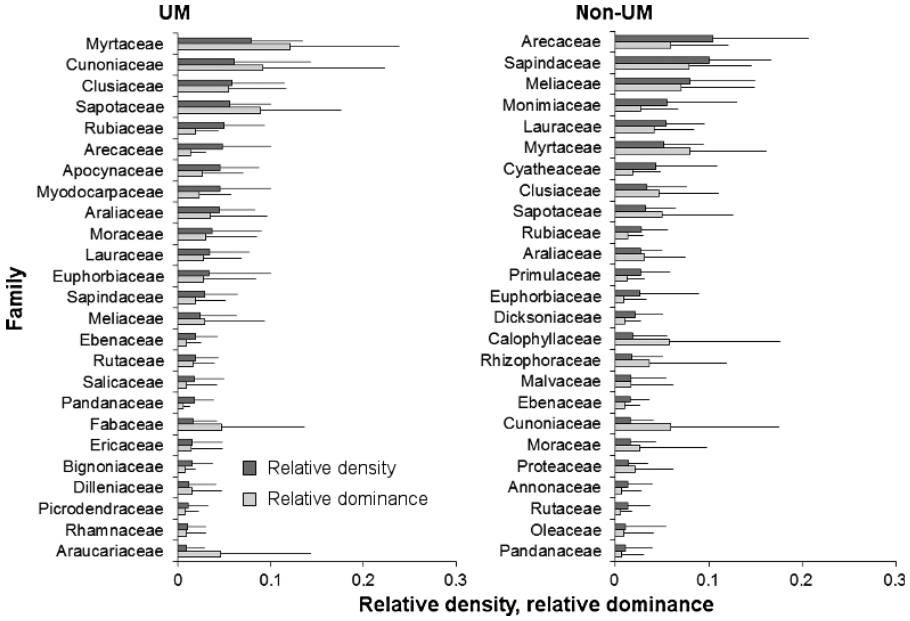

Fig. 6. Dominant families on UM and non-UM (only the first 25 in a decreasing order of relative density are represented). The height of the bars represents mean relative density (black stripes) and relative dominance (grey) ± 1 SD.

and rainfall, and even with logarithm of geographic distances (Fig. 8). Most of the variance in the BC remains unexplained. Although marked noise was observed in BC variations with environmental gradients and geographic distance, these factors were nonetheless rather efficient predictors of the range of BC variations (Fig. 8).

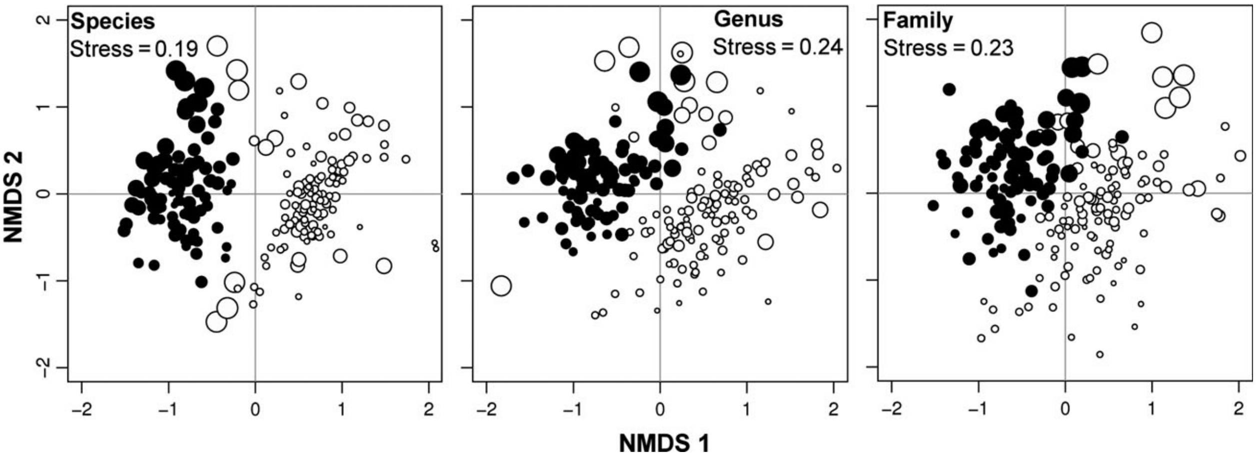

Fig. 7. Ordination of plots with NMDS according to Bray–Curtis dissimilarities computed at three taxonomic levels (species, genus and family) for UM (white) and non-UM (black) substrates. Point size is relative to plot elevation. The stress value indicates the quality of the representation (stress ranges from 0 to 1: the smaller the stress, the better the representation).

Discussion

New Caledonian mixed rain forest

The New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN) offered the first opportunity to investigate and describe variations in mixed tropical rain forest structure and composition across New Caledonia. Overall, New Caledonian mixed rain forests are dense and composed of many small stems. They have a high basal area, a low canopy (about 15–20 m, J. Munzinger, unpublished data), and high species richness and diversity. When extrapolated to international standards (1 ha with a 10-cm DBH threshold), average stem densities (1318 stems per ha^{-1} on UM and 1526 stems per ha^{-1} on non-UM) and basal areas (53.4 m^{2}·ha^{-1} on UM and 56.7 m^{2}·ha^{-1} on non-UM) were in agreement with previous studies published on New Caledonian mixed rain forest (Jaffré & Veillon 1991, 1995; Read et al. 2000).

Our results also support the idea that New Caledonian mixed rain forest has a higher stem density and basal area than similar ecosystems in the South Pacific. High stem density (>1000 stems·ha^{-1}) and basal area (>50 m^{2}·ha^{-1}) are also encountered in other tropical island forests, e.g. in La Réunion and Mauritus (Strasberg 1996), and in Indonesia (Slik et al. 2003). By contrast, the values obtained in New Caledonia for these structural characteristics are only about half those noted in continental tropical forest, e.g. in Amazonia (Malhi et al. 2002), India (Ayyappan & Parthasarathy 1999) or Central Africa (Eilu et al. 2004). However, such an extrapolation from small plots (0.04 ha) to international standards (1 ha) must be carefully interpreted, given that stem density and basal area in New Caledonia showed marked variability that was poorly explained by environmental gradients, and extrapolation is therefore likely to be overestimated by both small plot size and the low disturbance level of the selected forest that prevented us from including the structural heterogeneity observed at larger scales. Basal area is particularly difficult to estimate from small plots such as those in the NC-PIPPN since its magnitude is correlated to the diameter of the largest tree (Busing & White 1993). Basal area averaged over a plot network is nevertheless robust given that the average stabilizes with the increasing number of plots (see Busing & White 1993; Clark & Clark 2000).

Drivers of floristic diversity

With 749 species inventoried since 2005, NC-PIPPN harbours about 46% of the 1631 species of vascular plants (excluding herbaceous species) known to grow in New Caledonian rain forest (after Morat et al. 2012). This highlights to what extent the NC-PIPPN is an effective tool for investigating the species richness of New Caledonian mixed rain forest and determining species abundance and aggregation patterns. The fraction of inventoried species would obviously be higher if we had considered only the flora able to reach the 5 cm DBH threshold. For example, although most of the 68 *Psychotria* and 74 *Phyllanthus* are considered as forest species in Morat et al. 2012, they rarely reach 5 cm DBH. More generally, the 5 cm DBH threshold encompasses many understorey species, and thus their rarity is due more to a low probability of reaching high DBH classes rather than to limited geographic distribution. More than half (51.4%) of the species considered as rare in NC-PIPPN did not reach 10 cm DBH, but on the whole, rarity may also be attributed to the small plot size.

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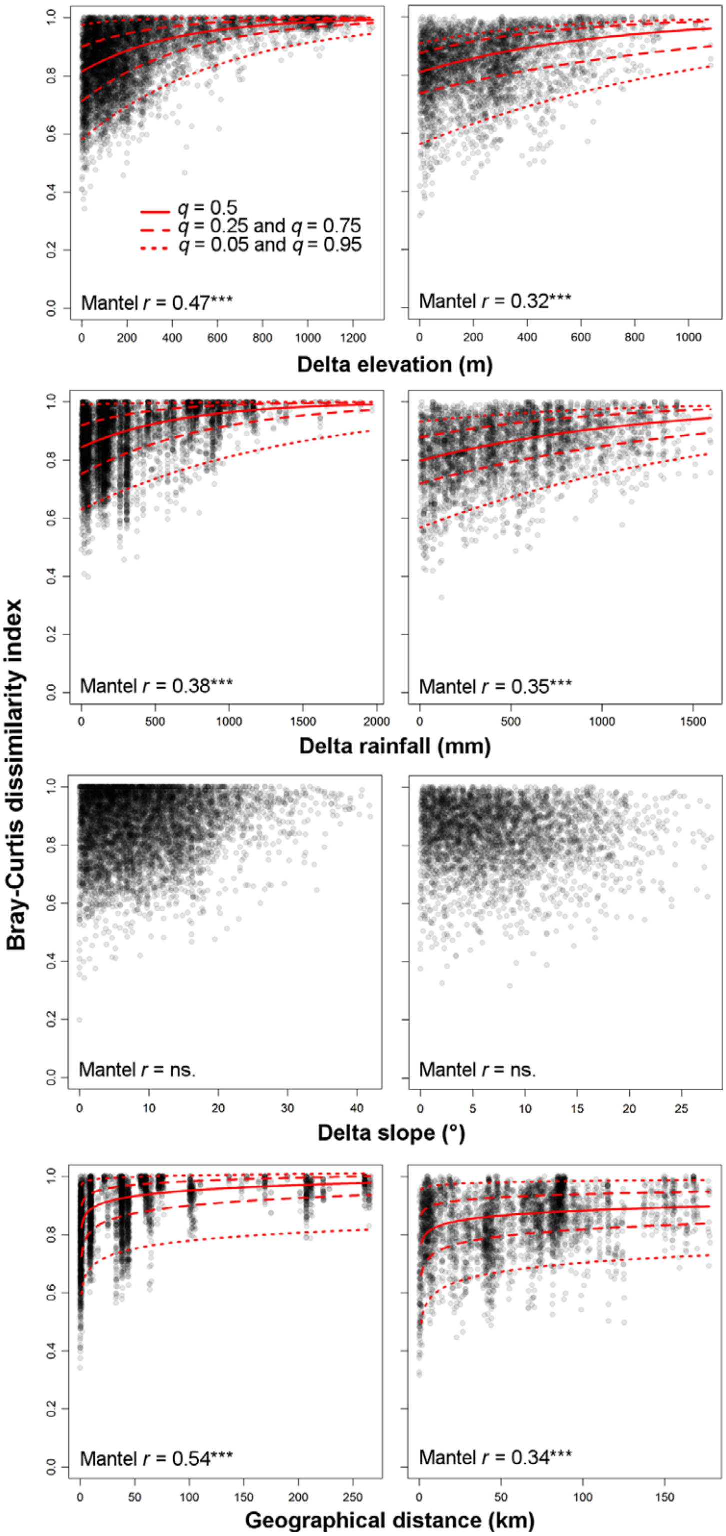

Fig. 8. Relationship between the Bray–Curtis dissimilarity index (BC) and differences in elevation, rainfall, slope and geographic distance, on UM and non-UM substrates. The Mantel *r* statistic describes the strengths of the correlations between the distance matrices (*** for $P < 0.001$, ns. for $P > 0.05$). Lines represent non-linear quantile (*q*) regressions for $q = 0.05$, 0.25, 0.50, 0.75 and 0.95. Models used are $BC = a + (1-a) \times (1-e^{-b \times x})$ for differences in elevation and rainfall and $BC = a \times \ln(x) + b$ for geographic distance (all represented fits are significant at $P < 0.05$).

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The high species richness recorded in NC-PIPPN plots (alpha diversity, mean = 38 ± 11 species per plot^{-1}) combined with the high floristic dissimilarities between plots (beta diversity, mean BC = 0.91 ± 0.10) confirm that New Caledonian mixed rain forest is exceptionally diverse, as described on the territory scale (Mittermeier et al. 2004; Morat et al. 2012). Although elevated small-scale beta diversity is typical of tropical forests (Condit et al. 2002; Soininen et al. 2007), the marked floristic dissimilarity observed is not easily explained. It could be due to marked local environmental gradients (mainly substrate, elevation and rainfall), but more likely results from an overestimation due to small plot size and the large fraction of rare species (more than one-third of all inventoried species) in NC-PIPPN (Nekola & White 1999; Plotkin & Muller-Landau 2002; Tuomisto et al. 2003; Chao et al. 2005).

Geographic distance between sites is widely accepted as the main driver of floristic dissimilarity, with floristic dissimilarity increasing with geographic distance. This reflects species turnover in space due to increasing dissimilarities in environmental conditions, dispersal limitation and speciation processes (Condit et al. 2002; Cadenasso et al. 2003; Tuomisto et al. 2003; Soininen et al. 2007). However, the strength of this relationship is expected to be dependent upon the extent (i.e. geographic scale) and the grain (i.e. plot sizes) of the study (Nekola & White 1999; Soininen et al. 2007; Steinbauer et al. 2012). As a result, the floristic dissimilarity observed in our study was poorly explained by geographic distance within NC-PIPPN. The same situation is encountered in other networks based on relatively small plots (e.g. Potts et al. 2002) compared to larger-scale networks using larger plots (e.g. Slik et al. 2003; Coronado et al. 2009; Keppel et al. 2010). By way of a comparison, Keppel et al. (2010) investigated floristic dissimilarity in lowland tropical forests at 12 sites using larger plots (1 ha or more) in the South Pacific (excluding New Caledonia) and found comparable dissimilarity (BC = 0.90) between sites at least 1000 km apart.

Rain forest on UM and non-UM differs in floristic composition but not in structure

Consistent with Jaffré & Veillon (1995), NC-PIPPN confirms that mixed rain forest on UM and non-UM differs in floristic composition but not in structure. But outside the rain forest plots, vegetation resulting from the degradation of rain forest (e.g. by fire, see McCoy et al. 1999; Ibanez et al. 2013) differs markedly both in structure and composition. On UM substrates the anthropogenic secondary vegetation mainly consists of maquis (sclerophyllous shrubland) while it mainly consists of savannas on non-UM substrates (see Jaffré 1980).

Three quarter of the inventoried species occurred on a single substrate type, and this specialization was also found at higher taxonomic levels. The dominant families on UM and non-UM were consistent with the observations of Jaffré & Veillon (1995) even though some family circumscriptions had changed. Unfortunately, the diversity of the UM substrates and a paucity of data on non-UM substrates prevented us from determining which edaphic factors were driving this floristic dissimilarity. Contrary to Malaysia (Proctor et al. 1988), New Caledonian UM substrates constitute a clear ecological limitation for many species, since 40% of the native flora is considered to be endemic to this substrate (Jaffré et al. 1987) and sympatric speciation due to UM substrate adaptation has been described for different groups of species, such as palms (Pintaud & Jaffré 2001) and Cunoniaceae (Pillon et al. 2009b). Such a level of endemism is even likely to be under-evaluated as some species growing on both UM and non-UM substrates could actually be different cryptic species (Pillon et al. 2009a).

Our results suggest that floristic dissimilarity is likely to be lower at high elevations, with some common species such as *Metrosideros brevistylis* (Myrtaceae), *Paracryphia alticola* (Paracryphiaceae), *Retrophyllum comptonii* (Podocarpaceae) and *Weinmannia dichotoma* (Cunoniaceae) being found on both substrates. This could be driven by different factors, and we hypothesize that UM and non-UM substrates may be more similar following high leaching due to high rainfall. Another hypothesis is that stressful conditions at high altitude (low temperatures during the cold season or high solar radiation) may restrict the pool of species to a limited number of stress-tolerant species on both UM and non-UM substrates (see Nasi et al. 2002). These results differ radically from those obtained in Borneo by Aiba & Kitayama (1999), whose study showed that rain forest on UM and non-UM does not differ in floristic composition at 700 m, while dissimilarity in both structure and composition increases at higher elevations.

Conclusion

In comparison to standard plot networks (1 ha, 10 cm DBH threshold), small plots with a low DBH threshold maximize the alpha diversity assessment by increasing the number of plots, the number of individuals per plot, and the biological types inventoried (not only trees but also small trees and vines). On the other hand, this design makes beta diversity and structural characteristics more difficult to interpret and compare with other networks, but average structural metrics remain robust and reliable for comparison. In the future, we will continue to use these small plots (0.04 ha) to investigate alpha diversity along environmental gradients but will add standard plots (1 ha) to the network in order to improve our knowledge of the beta diversity and structure of New Caledonian mixed rain forest.

Our study supports the findings of previous studies that highlighted the exceptional diversity of New Caledonian mixed rain forest. As shown in Jaffré et al. (1998), it is now crucial to extend the current system of protected area that today is mainly restricted to the south part of the main island. Middle elevation rain forests, shown here to be the richest in vegetation, are inadequately protected, even though they are threatened by fire and by mining on UM substrates. No areas on UM substrates are currently protected in the north of New Caledonia while mining activities are booming. Data collected across NC-PIPPN, combined with occurrence data from the Nouméa herbarium (NOU), provide essential tools that can be used to assess diversity distribution and identify priority areas for conservation.

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Supporting Information

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

Appendix S1. Table of the location and characteristics of the 201 plots of the New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN).

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