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Structural and floristic characteristics of some monodominant and adjacent mixed rainforests in New Caledonia

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Abstract

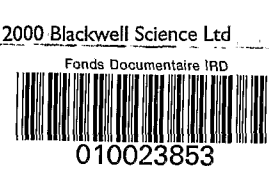
Nothofagus spp. dominate the upper canopy of some rainforests on ultramafic soils in New Caledonia. These monodominant forests typically occur within, or contiguous with, larger areas of mixed-canopy rainforest. In this study the structure, diversity and composition of six *Nothofagus*-dominated plots were investigated, and comparisons were made with three adjacent mixed rainforest plots. Stand density and basal area (all stems ≥ 1.3 m high) in the *Nothofagus* plots were in the range 16,056–27,550 stems/ha and 43.1–69.9 m^2/ha, respectively. There was no significant difference ($P \geq 0.05$) in total stand density or basal area between the paired *Nothofagus* and mixed rainforests, but there were consistently fewer trees and less basal area of trees ≥ 40 cm d.b.h. in the *Nothofagus* forests. Species richness, species diversity (Shannon-Wiener, based on basal area) and equitability (based on basal area) of trees ≥ 20 cm d.b.h. on 0.1 ha *Nothofagus* plots were in the range 4–17, 0.96–3.76 and 0.45–0.87, respectively. No significant differences ($P \geq 0.05$) were recorded in these three parameters between the paired *Nothofagus* and mixed rainforests, although species diversity was consistently lower in the paired *Nothofagus* forests. Comparison of dominance by density and basal area indicated that although the uppermost canopy of the *Nothofagus* forests was dominated by *Nothofagus* (70–95%), the basal area and density contribution was ≤ 55% except at Col de Yaté (≈ 85%). Analysis of similarity indicated no significant difference in stand composition of trees ≥ 20 cm d.b.h. (following removal of *Nothofagus* from the data set) between *Nothofagus* and mixed rainforests using basal area, density or presence-absence data. It is concluded that the *Nothofagus*-dominated forests differ from the adjacent mixed rainforests mainly by (1) dominance of the uppermost canopy, without necessarily dominance of the stand by basal area or density, and (2) the smaller basal area contributed by large trees (all species).

Keywords

Monodominance, New Caledonia, Nothofagus, species diversity, tropical rainforest.

Résumé

La voûte des forêts sur sols issus de roches ultramafiques de Nouvelle-Calédonie, peut être localement dominée par différentes espèces du genre *Nothofagus*. La structure, la diversité et la composition floristique de six parcelles de forêts ainsi dominées, sont analysées et comparées à celles de trois parcelles adjacentes de forêts, à strate supérieure plus diversifiée. La densité et la surface terrière des tiges d'une hauteur ≥ à 1.3 m, des forêts à *Nothofagus*, s'échelonnent respectivement, de 16,056 à 27,550 tiges/ha et de 43.1 à 69.9 m^2/ha. Ces valeurs ne sont pas significativement différentes ($P \geq 0.05$) de celles obtenues pour les forêts adjacentes. Cependant le nombre des arbres d'un d.b.h. ≥ à



40 cm, ainsi que la surface terrière correspondante sont nettement moins élevés dans le cas des forêts dominées par *Nothofagus*. La richesse spécifique de ces dernières, établie pour les arbres d'un d.b.h. ≥ 20 cm, sur des parcelles de 0.1 ha, varie de 4 à 17 espèces. La diversité spécifique (exprimée selon l'indice de Shannon-Wiener, à partir de la surface terrière des arbres de d.b.h. ≥ 20 cm sur 0.1 ha), s'échelonne de 0.96 à 3.76 et l'équitabilité calculée sur les mêmes bases, de 0.45 à 0.87. Aucune différence significative ($P \geq 0.05$) n'est enregistrée pour ces trois paramètres entre les couples forêt à *Nothofagus* et forêt adjacente, et ceci, bien que la diversité spécifique soit, pour chaque couple de forêt étudié, inférieure dans le cas de la forêt dominée par *Nothofagus*. En dépit d'une nette dominance de *Nothofagus* dans la voûte de la forêt (70 à 95%) cette espèce intervient, à une seule exception près, pour ≤ 55% dans la constitution de la densité et de la surface terrière. Les analyses de similarité portant sur les arbres d'un d.b.h. ≥ 20 cm, après suppression des données relatives à *Nothofagus*, ne montrent pas de différences significatives de surface terrière, de densité des arbres et de présence-absence des espèces, entre les deux catégories de forêts. Il ressort en conclusion que les forêts à strate supérieure dominée par *Nothofagus* diffèrent des forêts adjacentes à strate supérieure plus variée par (1) une dominance de *Nothofagus* dans la voûte qui ne s'accompagne pas nécessairement d'une dominance de cette espèce dans la contribution à la surface terrière ou à la densité des tiges, et par (2) une surface terrière inférieure à celle des forêts adjacentes, pour l'ensemble des grands arbres d'un d.b.h. ≥ 40 cm.

INTRODUCTION

Nothofagus commonly forms almost pure upper canopies in the cool temperate forests of southern South America, New Zealand and Australia (e.g. Donoso, 1996; Ogden *et al.*, 1996; Read & Brown, 1996; Veblen *et al.*, 1996). Even through its range in tropical New Guinea and New Caledonia *Nothofagus* is gregarious, usually dominating the upper canopy (e.g. Dawson, 1966; van Steenis, 1971; Hynes, 1974; Read & Hope, 1996). Within-stand species richness and diversity of tropical rainforests is more usually high (e.g. Richards, 1952; Gentry, 1982, 1988; Whitmore, 1984). For example, it is not unusual for more than 200 species, including more than 100 tree species, to coexist within 1 ha of tropical rainforest (Whitmore, 1984; Gentry, 1988). However, not all tropical rainforests are characterized by high species richness and diversity, and secondly, even in very species-rich rainforests, high richness and diversity do not necessarily extend to all strata (e.g. Richards, 1952; Whitmore, 1984). The first group of forests includes those occurring on suboptimal sites where features such as low nutrients, poor drainage, low rainfall or high altitude effects (e.g. low temperatures, low irradiance, acid soils) are accompanied by a loss of richness throughout the strata of higher plants, and sometimes by a canopy dominated by a single species (monodominance) (Connell & Lowman, 1989; Hart, 1990). The second group of forests comprises those in which the upper canopy may be monodominant or dominated by several closely related species, but which otherwise retain a high richness and diversity of species in lower strata (Connell & Lowman, 1989; Hart, 1990).

Monodominance in tropical rainforests occurring in relatively favourable environments has been principally attributed to soil differences, or to successional phases, either to early successional dominance by a species with well-dispersed and numerous seeds, tolerant seedlings and rapid growth rates, or to late successional dominance by slow-growing but shade-tolerant species with long lifespans, with the intermediate phases being more species-rich (Connell & Lowman, 1989; Hart *et al.*, 1989; Hart, 1990). Other suggested influences include herbivory, with reduced seed predation and herbivory maintaining the dominant species (Hart *et al.*, 1989) and mycorrhizae, for example via effects on successional change in tree composition (e.g. Connell & Lowman, 1989) or by effects on below-ground competition (Malloch *et al.*, 1980).

The factors leading to monodominance in the *Nothofagus* forests of New Guinea and New Caledonia are uncertain. Studies in New Guinea (Ash, 1988; Read *et al.*, 1990) and New Caledonia (Read *et al.*, 1995), suggest that some stands dominated by *Nothofagus* are an early successional stage, with potential replacement by mixed-canopy forest in the further absence of disturbance. This conclusion is based on two sets of observations. First, in those stands studied to date, population size structures of *Nothofagus* suggest a major episode of regeneration has occurred with commonly little subsequent regeneration, other than in those stands where the canopy is more open, for example, on ridges or at high altitudes. Second, seedlings and saplings of other canopy trees occur in the understorey, suggesting that the canopy

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will progress towards greater diversity in the hypothetical absence of disturbance. In New Guinea, *Nothofagus* forms mondominant stands under suboptimal conditions, such as on low nutrient or poorly drained soils, on ridge crests, or at high altitudes (Hynes, 1974; Ash, 1982). However, it also occurs under more favourable conditions as patches within a matrix of mixed rainforest (Kalkman & Vink, 1970; Hynes, 1974; Ash, 1982). In New Caledonia *Nothofagus* appears restricted to ultramafic soils. Even on these suboptimal soils, it typically occurs as patches within or adjacent to larger areas of mixed rainforest (also on ultramafic soils). Although there appears to be a role of disturbance in the establishment and persistance of *Nothofagus* in New Caledonia (Read & Hope, 1996), it is not clear what other factors influence its distribution with respect to the adjacent mixed rainforest. There is little information on the structure, composition and dynamics of these forests, and it is not clear whether these monodominant forests have a lower species richness and diversity than the adjacent mixed rainforests.

The aims of this paper are (1) to describe the structural (density and basal area) and floristic (species richness, species diversity and composition) characteristics of some monodominant *Nothofagus* forests, and (2) to compare these with adjacent mixed rainforest on ultramafic soils. Where possible, comparisons will also be made with rainforests elsewhere in New Caledonia and elsewhere in the tropics. Analysis of floristic composition is restricted in this paper to trees ≥ 20 cm diameter at breast height (d.b.h.).

Study region

Rainforest in New Caledonia occurs discontinuously along the central mountain chain and east coast of the main island (La Grande Terre) and the Loyalty Islands, covering about 22% of the territory (Jaffré 1993). The rainforest flora is diverse, with 1575 species of flowering plants and 88% endemism (Morat, 1993). Jaffré (1980) classified the *Nothofagus*-dominated forests as a facies of the dense evergreen rainforest formation. The five species of *Nothofagus* occur only on the main island, extending from 160 m to 1350 m asl. *Nothofagus* is most common along the central mountain chain, often above 500 m, but is not uncommon at low altitudes in the south of the island where the lowlands receive relatively high and reliable rainfall. Within the southern region rainforest patches can be extensive, or small and surrounded by maquis (shrub-dominated vegetation), often restricted to moist or topographically protected sites.

New Caledonia experiences a tropical climate modified by the prevailing easterly airflow (Anonymous, 1981). The rainfall can be irregular from year to year and month to month and prolonged dry periods can be experienced in any year. The driest months are September to November with a variable duration and severity of the dry season. The annual rainfall at the study sites is projected from rainfall maps to be 1700–3500 mm, depending on site location. The mean annual temperatures at the nearest lowland stations are 22 °C to 24 °C (Cherrier, 1984). At Ouenarou (170 m asl) in the south of the main island, with a mean annual temperature of 21.7 °C, the mean monthly maxima range from 22.1 °C (August) to 28.8 °C (February), with minima ranging from 14.8 °C (August) to 21.6 °C (February) (Jaffré, 1980). Calculations from lapse rates suggest mean annual temperatures as low as ≈ 15 °C in the highest altitude *Nothofagus* forests (Read & Hope, 1996), and minima may approach 0 °C above 1000 m asl (Jaffré, 1980). Tropical depressions forming to the north during the summer wet season sometimes develop into cyclones that pass through or near the territory (Anonymous, 1981).

Apart from a few isolated records, *Nothofagus* occurs only on ferrallitic soils (syn. oxisols or ferrasols) overlying ultramafic rocks, primarily peridotite. The ferrallitic soils are typically of the ferritic type (deficient in aluminium clays) (Jaffré, 1980): well-drained dark reddish-brown to brown-yellow silt clays, often of considerable depth, depending on topographic location (Latham, 1980). These soils have high contents of nickel, chromium, manganese and iron, very low contents of plant nutrients such as phosphorus, calcium and potassium, and sometimes high contents of magnesium relative to calcium and potassium (Latham *et al.*, 1978; Latham, 1980; Jaffré, 1992).

METHODS

Study sites

Six study sites were selected in the south-east of the main island (Fig. 1) to include *Nothofagus* across a variety of altitudes and topographies, forest structures and degrees of dominance and a range of *Nothofagus* species (four of the five New Caledonian species) (Table 1). *N. baumanniae* (Baumann-Bodenheim) Steenis[1], has a very restricted distribution, confined to three mountain tops, and is not included in this study. The study also includes a comparison of adjacent mixed-species rainforest at three low altitude sites (Col de Yaté, Col de Mouirange Haut and Pic du Grand Kaori; Table 1). Although plots were planned to be 0.5–1.0 ha, this was not always possible because of the small size of some forest patches. Some sites contain evidence of infrequent early selective logging, particularly of *Agathis*, but not more than 1–3% of tree density. All soils are ferrallitic, developed over peridotite (ferrallitic-ferritic soils) or in the case of Col de Mouirange, including intruded gabbro. Soil depth varies with topographic position, as does soil profile and physicochemical characteristics, particularly with respect to modification by erosion or colluvial deposition. Detailed analysis of soils will be given in a later paper.

[1] Nomenclatural authorities are taken from the Flora of New Caledonia vols 1–22 (under the direction of Ph. Morat; Muséum National d'Histoire Naturelle, Paris) where possible, or otherwise from 'Fichier Nomenclatural et Ecologique de Nouvelle-Calédonie' (Laboratoire de Botanique et d'Ecologie appliquée, IRD (ORSTOM), Nouméa).

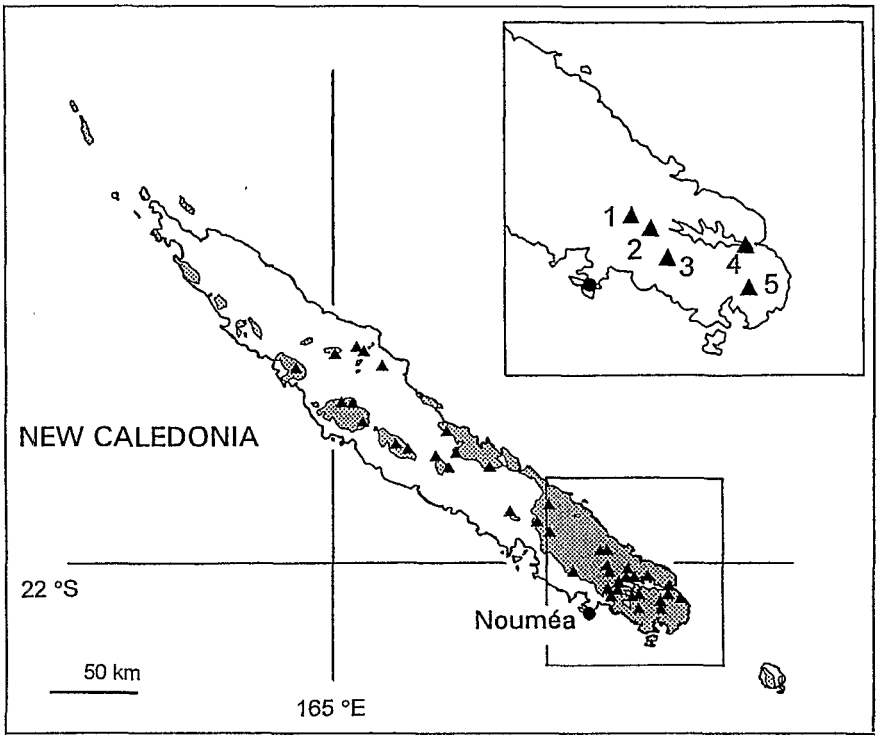

Figure 1 Map showing location of study sites. The stippled area indicates the distribution of peridotite (after Paris, 1981). Triangles indicate records of *Nothofagus*. 1, Dzumac; 2, Montagne des Sources; 3, Col de Mouirange; 4, Col de Yaté; 5, Pic du Grand Kaori.

Table 1 Summary of study site characteristics.

Site	Altitude (m asl)	Size (ha)	Canopy	Proportion of *Nothofagus* in upper canopy (%)
Col de Mouirange Haut				
Lower site	300	0.5	Mixed species	0
Upper site	320	0.5	Dominated by *N. aequilateralis*	75
Col de Mouirange Bas	250	1.0	Dominated by *N. discoidea* and *N. aequilateralis*	70
Col de Yaté				
Lower site	330	0.1	Dominated by *N. aequilateralis*	95
Upper site	340	0.3	Mixed species, including *N. balansae*	20
Dzumac	940	0.2	Dominated by *N. codonandra*	80
Montagne des Sources	600	1.0	Dominated by *N. aequilateralis* and *N. balansae*	70
Pic du Grand Kaori				
Lower site	240	0.5	Dominated by *N. aequilateralis*	80
Upper site	240	0.5	Mixed species	0

Col de Mouirange Haut

This site lies on a south-west facing slope within a large area of *Nothofagus aequilateralis* (Baumann-Bodenheim) Steenis forest that lies contiguous with both maquis and mixed rainforest (Fig. 2a). The *Nothofagus* forest in this area is often patchy, commonly restricted to hill crests and slopes with mixed rainforest occupying the base of the gullies. The study plot was located so that the upper half (≈ 50 m × 100 m) comprised *N. aequilateralis*-dominated rainforest, and the lower half comprised mixed rainforest. It lies near the forest edge (a fire boundary) that grades into burnt forest and maquis. The upper part of the plot is transected by a permanent creek. Selective logging occurred in this area until ≈ 50 years ago, first around 1900 and again around 1950 (M. Boulet,

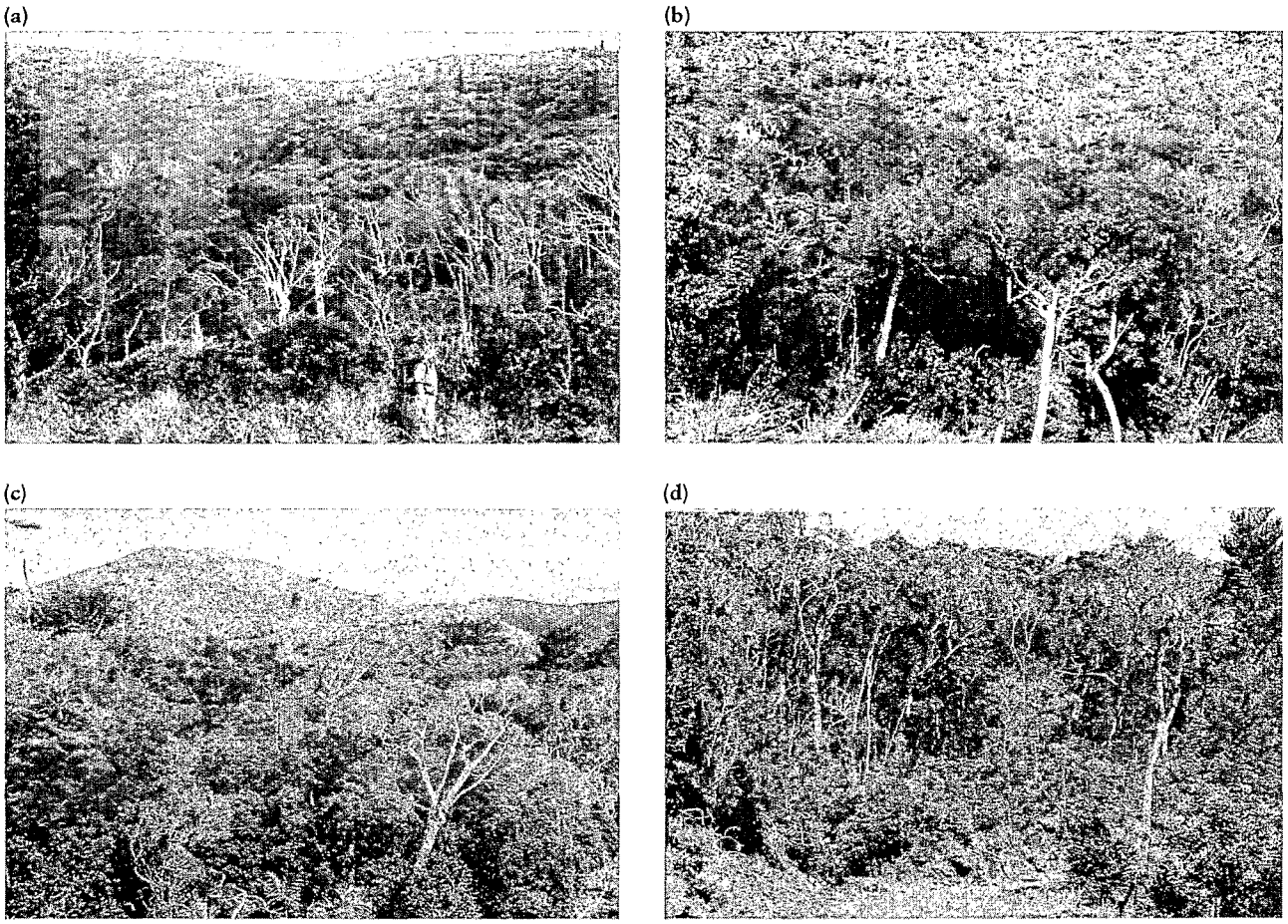

Figure 2 Study sites. (a) Col de Mouirange Haut. The *Nothofagus* forest is the smooth-crowned canopy. The dead trees in the foreground are predominantly *Arillastrum gummiferum*, evidence of previous fires. (b) Col de Yaté *Nothofagus*-dominated forest. (c) Col de Yaté mixed rainforest. (d) Dzumac.

pers. comm.). There are a few very large old cut stumps on the plot (≈ 1% of the density of live trees ≥ 20 cm d.b.h.), probably from selective logging around 1900.

Col de Mouirange Bas

This site is 1 km east of Col de Mouirange Haut, on the south-east slope of a dividing ridge, transected by a creek. The forest extent is smaller on this side of the ridge, giving way to a rainforest-maquis ecotone and subsequently to maquis ≈ 30–100 m east of the study site. *N. aequilateralis* and *N. discoidea* (Baumann-Bodenheim) Steenis codominate the upper canopy. Some old sawn stumps occur through the plot (≈ 2% of the density of live trees ≥ 20 cm d.b.h.).

Col de Yaté

A plot was established in each of two forest remnants at Col de Yaté. The lower forest (Fig. 2b) (studied by Read *et al.*, 1995) is a small stand dominated by *N. aequilateralis* bounded to the south by a small patch of mixed rainforest, to the east by maquis and to the west and north by road-works. The upper forest (Fig. 2c) occurs ≈ 50–80 m to the east in a small basin and has a mixed canopy including *N. balansae* (Baillon) Steenis. It is bounded by maquis to the west, maquis and fire-regrowth forest to the south, and to the east by a lateritic outcrop occupied by rainforest and maquis species (probably established after fire), with emergent *Agathis ovata* (Moore) Warburg. The north side is formed by road works. Drainage from the road during rainstorms commonly leads to minor flooding in the floor of the basin. Despite this disturbance, this stand is of interest because it provides the only known mixed rainforest containing *Nothofagus* in the region. There was no other evidence of human disturbance in either stand.

Dzumac

This study site, with an upper canopy dominated by *N. codonandra* (Baillon) Steenis, occurs in a small forest remnant (≈ 0.3 ha) on a north-west facing slope dissected by two shallow drainage lines (Fig. 2d). The forest grades fairly abruptly into maquis on the ridge to the south-west and upslope to the south-east, into a rainforest-maquis fire-regrowth ecotone to the east, and clearing due to roadworks

occurs near the north-west edge. The plot was located in the central part of the forest, the perimeter ≈ 5–10 m from the forest edge. There was no evidence of human disturbance.

Montagne des Sources

This site lies on a gentle south-east facing slope, cut by several drainage lines, with an upper canopy dominated by *N. balansae* and *N. aequilateralis*. An old forestry track cuts through the south-east corner of the plot. The only evidence of past logging on the plot was two old cut stumps (< 1% of the density of living trees ≥ 20 cm d.b.h.). The north and east boundaries of the plot are continuous with tall *Nothofagus*-dominated forest. To the south the forest grades into shorter *Nothofagus*-dominated forest (≈ 8 m high) and the forest grades into fire-regrowth beyond the west boundary.

Pic du Grand Kaori

This study site occurs in a region that was logged from 1867 to 1880 (M. Boulet, pers. comm.). Forest occurs up the west side of the Pic du Grand Kaori, with mixed-species forest on most of the slope and *N. aequilateralis*-dominated forest on colluvial soil at the base. The forest at the base of the slope is bounded by forest-maquis ecotone (probably fire-influenced) and *Gymnostoma* woodland grading into maquis. Two 70 × 70 m plots were located on each side of an old logging track. The upper canopy of the lower forest is dominated by *N. aequilateralis*. The upper plot, on a gentle slope, is mixed in composition. There was no evidence of human activities in the *Nothofagus*-dominated stand, but some small trees have recently been felled to the west, outside the plot. In the upper, mixed-species plot, there is topographic evidence of an old logging track near the upper (east) boundary, but this old track is vegetated and otherwise indistinguishable from the remainder of the stand. Only two old cut stumps were recorded within the forest (< 1% of the total density of trees ≥ 20 cm d.b.h.). However, the upper plot is dissected by isolated 2–4 m deep channels, probably formed by surface and subsurface erosion around dead (now absent, possibly logged) large trees.

Survey methods

A permanent plot was established at each site with plot boundaries surveyed using a Sokkia Set 6 Total Electronic Station™. All trees of ≥ 20 cm d.b.h. (1.3 m above ground) were surveyed, identified, tagged and d.b.h. measured. The height of each tree was recorded as 25, 50, 75 or 100% of the height of the canopy above and immediately adjacent (within ≈ 20 m of the tree). Smaller plants were sampled by a grid of quadrats. Although randomly placed quadrats are preferable for statistical reasons, surveying of vegetation gradients was achieved more easily using a regular grid. The arrangement comprised a 2 m × 4 m quadrat in which all postcotyledonary seedlings 0.03–1.29 m high were identified, tagged and counted (2–7% of the total plot area). A 4 m × 4 m quadrat was placed on each of two opposite sides of the seedling quadrats, and all woody plants ≥ 1.30 m high were identified, tagged and d.b.h. measured in these and the seedling quadrats (10–35% of the total plot area). The proportion of plot sampled varied to allow sufficient sampling of rare species on the smaller plots for later studies of rates of establishment, growth and mortality. The proportion of *Nothofagus* foliage in the upper canopy was estimated by identifying the tree (*Nothofagus* or 'non-*Nothofagus*') in the uppermost canopy closest to each of twenty (sites < 1 ha) or thirty (1 ha sites) random points located on the ground by random number tables and projected upwards by sight.

Data analysis

Analyses of composition and density follow those of Jaffré & Veillon (1991, 1995), where possible, to allow direct comparisons with these New Caledonian studies. Stems less than 20 cm d.b.h. have not been included in analyses of floristic composition, richness and diversity because some irregularly flowering species have not yet been identified.

The Shannon-Wiener function, H, was used as an index of species diversity (Peet, 1974) for comparison among sites. $H = -\sum_{i=1}^{S}(p_i)(\log_2 p_i)$ where S = number of species and p_i = proportion of total sample belonging to the i th species. Equitability (E) or evenness of allotment of individuals among species was calculated as H/H_{max}, where H_{max} (maximum species diversity) = $\log_2 S$ (Peet, 1974). To allow comparison among plots of different sizes, each plot greater than 0.1 ha was divided into 0.1 ha subplots. Species richness, H and E were determined in each of two or three subplots (randomly selected on all sites except Dzumac).

Randomized-block ANOVA was used to compare density, basal area, species richness, H and E of *Nothofagus* and mixed rainforest plots using SYSTAT v.7.01 (Wilkinson, 1996). Tests of species richness, H and E were undertaken on means of the 0.1 ha subplots. Data were transformed where necessary prior to analysis. If outliers remained after transformation, data were re-analysed without the outliers. In each case conclusions were not altered. The critical α-level for hypothesis testing was 0.05.

Non-metric multidimensional scaling (NMDS) was used to reduce compositional variation among sites to two main axes, following computation of a Bray-Curtis similarity matrix. Analysis of similarity (ANOSIM) (Clarke, 1993) was used to test the hypothesis of different species composition between the paired *Nothofagus* and mixed rainforests. Col de Mouirange Bas (lowland *Nothofagus*-dominated forest in the same region as the paired sites) was included in the comparison to increase power, increasing the number of permutations from ten to thirty-five. Similarity percentage breakdown (SIMPER) (Clarke, 1993) was used to determine average (dis)similarity within and between groups and the order of species contribution. ANOSIM and SIMPER were undertaken with PRIMER vs. 4 (Clarke & Warwick, 1994). Because study sites varied in size,

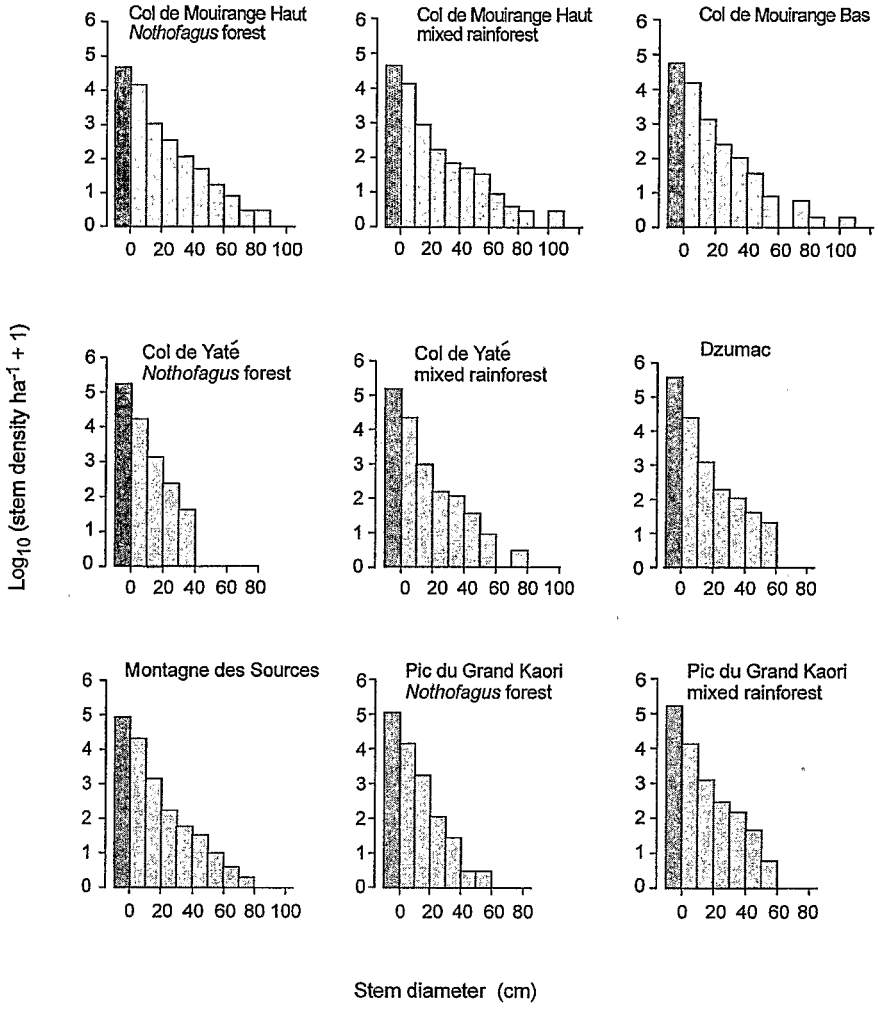

Figure 3 Stem density with respect to diameter size classes. The first category (dark shading) comprises plants less than 1.3 m high.

ANOSIMs were repeated using data from the 0.1 ha subplots, with three random selections of subplots, except for the Yaté *Nothofagus* forest where the full study site was only 0.1 ha.

RESULTS

Canopy characteristics

Nothofagus dominates the upper canopy at the upper site of Col de Mouirange Haut, Col de Mouirange Bas, Dzumac, Montagne des Sources, the lower site at Yaté and the lower site at Pic du Grand Kaori and is infrequent or absent from the upper canopies of the other sites (Table 1). The average height above ground of the upper canopy is variable, ranging from a low of ≈ 15 m at Yaté to ≈ 25–30 m at Col de Mouirange.

Stem density

Highest stem densities occur in the smallest size class, density decreasing with increasing diameter (Fig. 3). There are no statistically significant differences in densities between the paired *Nothofagus* and mixed rainforests in any size classes, although higher densities of stems ≥ 40 cm d.b.h. are consistently recorded in mixed rainforests than adjacent *Nothofagus* forests (Table 2). Dzumac has the highest total stem density (Table 2), with ≈ 3,500–5000 stems per ha more than at other high density stands, and ≈ 10,000 stems per ha. more than at the low density stands, predominantly due to the high density of stems < 10 cm d.b.h. Stem densities of trees ≥ 40 cm and ≥ 60 cm in mixed stands overlap values recorded by Jaffré & Veillon (1995) in mixed rainforests at Riviere Bleue, but not the high densities of stems ≥ 60 cm d.b.h. recorded at the nonultramafic forest at Col d'Amieu (Table 2). The densities of stems ≥ 10 cm d.b.h. in all stands are high compared with studies cited in Table 2 of tropical rainforests elsewhere, with the exception of a site in Sabah on ultramafic soil (Proctor *et al.*, 1988) (Table 2). However, densities of stems ≥ 60 cm d.b.h. are lower than cited in Table 2 from other regions.

Basal area

Highest basal areas are recorded in the smallest or second

Table 2 Density of stems on each study site, compared with other tropical rainforests. Stems included are ≥ 1.3 m high. The results of randomized block ANOVA of the paired *Nothofagus* and mixed rainforest plots are included (*F*-ratios and *P*-values). Asterisks indicate where data were too skewed for analysis. Total density was arcsine-transformed, the remainder were $\log_{10}$-transformed prior to analysis.

Localities	Sample area (ha)	Number of stems per hectare					
		d.b.h. < 10 cm	d.b.h. ≥ 10 cm	d.b.h. ≥ 20 cm	d.b.h. ≥ 40 cm	d.b.h. ≥ 60 cm	Total
New Caledonia, this study							
Col de Mouirange Haut:							
Nothofagus-dominated	0.5	14,597	1609	535	76	11	16,206
Mixed	0.5	13,796	1239	334	96	15	15,035
Col de Mouirange Bas	1	14,811	1687	394	49	7	16,498
Col de Yaté:							
Nothofagus-dominated	0.1	17,050	1351	286	0	0	18,401
Mixed	0.3	22,533	1312	318	53	3	23,845
Dzumac	0.2	25,975	1575	355	60	0	27,550
Montagne des Sources	1	20,809	1708	277	45	4	22,517
Pic du Grand Kaori							
Nothofagus-dominated	0.5	14,208	1848	140	4	0	16,056
Mixed	0.5	13,458	1741	491	49	0	15,199
Locality $F_{2,2}$, p		4.06, 0.20	6.27, 0.14	0.31, 0.76	1.80, 0.36	*	3.04, 0.25
Forest-type $F_{1,2}$, p		0.25, 0.67	2.57, 0.25	0.34, 0.62	4.00, 0.18	*	0.23, 0.68
New Caledonia, other studies							
Col d'Amieu (schist)[1]	3		1256		88	26	
Riviere Bleue (ultramafic slope)[2]	2.8		1533		65	8	
Riviere Bleue (ultramafic alluvium)[2]	2.7		1183		74	16	
Rainforests of the tropical Far East							
Java[3]	8		521		95	38	
Kalimantan[4]	1.6		399–541				
New Guinea[5]	0.8		435–700				
Sarawak[6]	1		615–778				
Sarawak[7]	1		356–407			23–36	
Sabah[8]	0.04–0.4		513–1596				
Sabah[9]	4		484–455		61–65		
Sulawesi[10]	1		408		44		
Sumatra[4]	1.6		460				

[1] Jaffré & Veillon (1995)
[2] Jaffré & Veillon (1991)
[3] Rollet (1979)
[4] Kartawinata *et al.* (1981)
[5] Paijmans (1970)
[6] Proctor *et al.* (1983)
[7] Chin & Chua (1984)
[8] Proctor *et al.* (1988)
[9] Newbery *et al.* (1992)
[10] Whitmore & Sidiyasa (1986)

smallest size class at all sites except in the Nothofagus forest at Col de Mouirange Haut (Fig. 4). The highest basal area of trees ≥ 10 cm d.b.h. occurs at Col de Mouirange Haut and Pic du Grand Kaori mixed rainforest, with similar values to those recorded in other New Caledonia studies, both on ultramafic and nonultramafic soils (Table 3). The basal areas of the other study sites are in the range 30.7–44.8 m^2 ha^{-1}, lower than those of other New Caledonian rainforests, but comparable to those recorded in some other tropical forests (Table 3). Yaté and Pic du Grand Kaori *Nothofagus* forests have the lowest basal area of trees ≥ 10 cm d.b.h. (Table 3), and low percentage basal areas in each of the large size classes

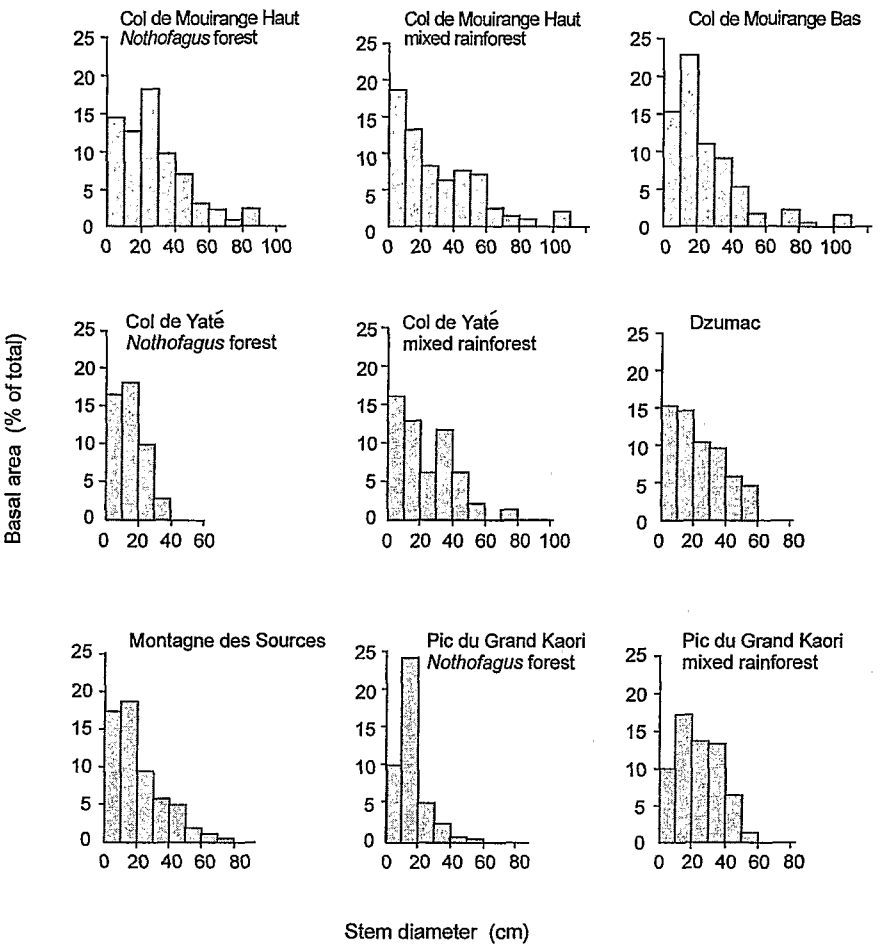

Figure 4 Basal area with respect to diameter size classes. Only plants ≥ 1.3 m high are included.

(Fig. 4), with 73–80% of stems less than 20 cm d.b.h. (Table 3). Significant differences in basal area between paired *Nothofagus* and mixed rainforests only occur in the ≥ 40 cm d.b.h. class, with a significant difference also among localities (Table 3).

Floristic richness and species diversity

The 106 species of trees ≥ 20 cm d.b.h. recorded in this study belong to thirty-nine families and seventy-seven genera. Eighty-nine species from thirty-seven families and sixty-seven genera occur on the six *Nothofagus*-dominated plots (3.3 ha over an altitudinal range of 690 m). Sixty-six species from thirty-one families and fifty-five genera occur on the three mixed rainforest plots (1.3 ha over an altitudinal range of 100 m) with forty-seven species from twenty-six families and forty-two genera on the paired *Nothofagus* plots (1.1 ha). Fifty species (47%), forty-four genera (57%) and twenty-nine families (74%) are shared between the full set of *Nothofagus* plots and the mixed rainforest plots.

The number of species of trees ≥ 20 cm d.b.h. ranges from only four in the Yaté *Nothofagus* forest to forty-eight at Montagne des Sources, with a range of four to forty-three genera and four to twenty-six families (Table 4). Highest species richness occurs on the two largest plots (Col de Mouirange Bas and Montagne des Sources) and lowest species richness on the two smallest plots (Yaté *Nothofagus* forest and Dzumac) (Table 4). Species richness declines sharply in the larger stem size classes (Fig. 5). The number of species per family ranges from 1.0 to 1.1 on plots of low species richness (Yaté *Nothofagus* forest and Dzumac) to 1.8 on plots with high species richness (Montagne des Sources and Col de Mouirange Bas) (Table 4). It is difficult to make meaningful comparisons with other studies because of the confounding influence of sample area. Jaffré & Veillon (1991) cite twenty-four to forty species ≥ 20 cm d.b.h. on 0.25 ha plots of mixed rainforest at Riviere Bleue, comparable to the species richness on the Yaté mixed rainforest plot (0.3 ha), but higher than that on the Dzumac (0.2 ha) and even the Pic du Grand Kaori (0.5 ha) *Nothofagus* plots.

Table 3 Basal area of each study site, compared with other tropical rainforests. Stems included are ≥ 1.3 m high. The results of randomized block ANOVA of the paired *Nothofagus* and mixed rainforest plots are included (*F*-ratios and *P*-values). Asterisks indicate where data were too skewed for analysis.

Localities	Sample area (ha)	Basal area (m^2 ha^{-1})						% basal area < 20 cm d.b.h.
		d.b.h. < 10 cm	d.b.h. ≥ 10 cm	d.b.h. ≥ 20 cm	d.b.h. ≥ 40 cm	d.b.h. ≥ 60 cm	Total	
New Caledonia, this study								
Col de Mouirange Haut:								
Nothofagus-dominated	0.5	14.3	55.6	43.1	15.5	5.5	69.9	39
Mixed	0.5	18.8	50.0	36.7	22.0	8.6	68.8	47
Col de Mouirange Bas	1	15.4	38.6	31.4	11.4	4.4	54.0	42
Col de Yaté:								
Nothofagus-dominated	0.1	16.5	30.7	12.6	0	0	47.2	73
Mixed	0.3	16.1	40.4	27.5	9.6	1.4	56.5	51
Dzumac	0.2	15.3	44.8	30.3	10.4	0	60.1	50
Montagne des Sources	1	17.2	42.3	23.8	8.5	1.7	59.6	60
Pic du Grand Kaori								
Nothofagus-dominated	0.5	10.2	33.0	8.8	1.2	0	43.1	80
Mixed	0.5	9.9	51.5	34.4	7.7	0	61.4	44
Locality $F_{2,2}$, p		7.02, 0.12	2.02, 0.33	1.83, 0.35	81.92, 0.01	*	4.24, 0.19	0.94, 0.52
Forest-type $F_{1,2}$, p		0.63, 0.51	0.33, 0.40	1.46, 0.35	52.61, 0.02	*	2.45, 0.26	1.68, 0.32
New Caledonia, other studies								
Col d'Amieu (schist)[1]	3		55.5	42.8				
Riviere Bleue (ultramafic slope)[2]	2.8		49.5	32.9				
Riviere Bleue (ultramafic alluvium)[2]	2.7		47.0	35.1				
Rainforests of the tropical Far East								
India[3]	0.44–1		31.1–47.3	21.1–44.1	9.3–33.7	4.6–17.0		
Java[4]	8		50.1					
Malaya[5]	—		33.41					
New Guinea[6]	0.8		29.2–56.7					
Sarawak[7]	1		28–57					
Sarawak[8]	1		32.1–36.0					
Sabah[9]	0.04–0.4		32.9–46.2					
Sabah[10]	4		26.4–26.8		17.3–18.6			
Rainforests of tropical South America								
French Guyana[11]	1–1.8			17.6–32.8				
Venezuela[12]	—		23.1		6.9	3.7		
Rainforests of tropical Africa								
Côte d'Ivoire[13]	5		30–34					
Nigeria[12]	—			11.6–24.1		4.4–12.8		

[1] Jaffré & Veillon (1995)
[2] Jaffré & Veillon (1991)
[3] Rai & Proctor (1986)
[4] Rollet (1979)
[5] Barnard (1954) in Jaffré & Veillon (1991)
[6] Paijmans (1970)
[7] Proctor *et al.* (1983)
[8] Chin & Chua (1984)
[9] Proctor *et al.* (1988)
[10] Newbery *et al.* (1992)
[11] Lescure & Boulet (1985)
[12] Rollet (1974) in Jaffré & Veillon (1991)
[13] Huttel (1975) in Jaffré & Veillon (1991) for d.b.h. ≥ 13 cm

Table 4 Taxonomic richness of the canopy. The data include only trees with d.b.h. ≥ 20 cm. The number of unidentified trees is given in brackets with the number of species.

Localities	No. of species	Genera	Families	Species/family
Col de Mouirange Haut:				
Nothofagus-dominated	40	37	25	1.6
Mixed	42	38	26	1.6
Col de Mouirange Bas	46	42	25	1.8
Col de Yaté:				
Nothofagus-dominated	4	4	4	1.0
Mixed	26	26	18	1.4
Dzumac	15	15	14	1.1
Montagne des Sources	48	43	26	1.8
Pic du Grand Kaori:				
Nothofagus-dominated	18 (1)	16[1]	13[1]	1.4
Mixed	31	30	19	1.6

[1] The unknown tree may belong to an additional genus or family.

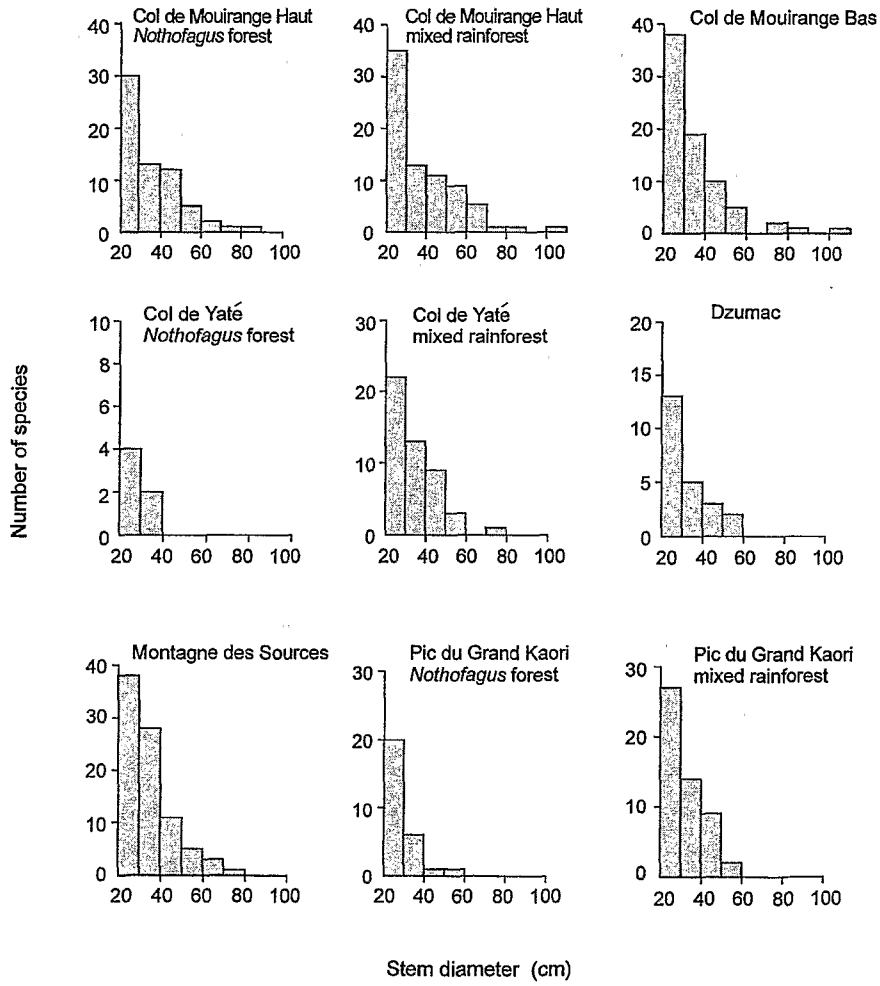

Figure 5 Number of species with respect to diameter size classes.

Table 5 Species richness and diversity of the canopy. The calculated values are the mean (± sem) species richness, the Shannon-Wiener index of diversity, *H*, and equitability, *E*, from 1 to 3 (*n*) 0.1 ha subplots. Only trees ≥ 20 cm d.b.h. are included. The results of randomized block ANOVA of the paired *Nothofagus* and mixed rainforest plots are included (species richness and *H* untransformed, *E* arcsine-transformed prior to analysis).

Localities	*n*	Species richness	Diversity (*H*)		Equitability (*E*)	
			density	basal area	density	basal area
Col de Mouirange Haut:						
Nothofagus-dominated	3	14 ± 1	2.48 ± 0.26	2.54 ± 0.11	0.65 ± 0.05	0.66 ± 0.02
Mixed	3	15 ± 1	3.29 ± 0.16	2.96 ± 0.06	0.84 ± 0.04	0.76 ± 0.01
Col de Mouirange Bas	3	14 ± 3	2.73 ± 0.59	2.77 ± 0.46	0.71 ± 0.09	0.73 ± 0.05
Col de Yaté:						
Nothofagus-dominated	1	4	0.90	0.96	0.48	0.45
Mixed	3	16 ± 1	3.58 ± 0.17	3.44 ± 0.19	0.90 ± 0.01	0.87 ± 0.02
Dzumac	2	9 ± 3	1.90 ± 0.84	1.69 ± 0.85	0.60 ± 0.19	0.53 ± 0.20
Montagne des Sources	3	17 ± 5	3.66 ± 0.39	3.76 ± 0.39	0.92 ± 0.01	0.87 ± 0.01
Pic du Grand Kaori:						
Nothofagus-dominated	3	6 ± 1	2.30 ± 0.22	2.17 ± 0.23	0.87 ± 0.08	0.82 ± 0.08
Mixed	3	12 ± 1	2.83 ± 0.22	2.75 ± 0.22	0.80 ± 0.01	0.78 ± 0.02
Locality $F_{2,2}$, *p*		1.13, 0.47	0.30, 0.77	0.23, 0.81	0.28, 0.78	0.30, 0.77
Forest-type $F_{1,2}$, *p*		3.97, 0.19	3.94, 0.19	3.07, 0.22	1.48, 0.35	1.33, 0.37

Lower species richness is still recorded in the Yaté *Nothofagus* plot using data from 0.1 ha subplots, as well as low *H* and *E* (Table 5). Highest species richness, *H* and *E* occur in the Yaté mixed rainforest and at Montagne des Sources (Table 5). The *Nothofagus* forests at Yaté, Pic du Grand Kaori and Col de Mouirange Haut have lower species richness and *H* than adjacent mixed rainforests, and except for Pic du Grand Kaori, also a lower *E* (Table 5). The differences are particularly pronounced at Yaté with two-to four-fold variation in richness, *H* and *E*. However, there is no significant difference between forest type in species richness, *H* or *E* for the paired sites (Table 5).

Floristic composition

Basal area and stem density per family

Nineteen families contribute at least 5% of the basal area at one or more study sites (Table 6). Apart from Fagaceae, the families with greatest abundance at any site are Myrtaceae, forming up to 40% of the basal area, and Cunoniaceae at Pic du Grand Kaori forming 40–45% of the basal area of both study sites (Table 6). The other families typically contribute small proportions of the basal area, of less than 20%. Similar patterns are recorded in stem density (Table 6). The families forming ≥ 5% basal area that form < 5% stem density typically comprise a small number of very large individuals.

With respect to trees ≥ 20 cm d.b.h., only Myrtaceae is present on all sites. Araucariaceae and Cunoniaceae are present on all sites other than the floristically depauperate Yaté *Nothofagus* forest, and Icacinaceae, Araliaceae, Clusiaceae, Rhamnaceae and Sapotaceae occur on all except two sites.

Basal area and stem density per species

Of the trees ≥ 20 cm d.b.h., no species other than *Nothofagus* spp. contribute more than 50% of total basal area or stem density, and even *Nothofagus* spp. account for more than 50% only at Dzumac, Col de Mouirange Bas and Yaté (Table 7). *Nothofagus* spp. account for a much smaller proportion of basal area (15–83%) and stem density (16–84%) in the *Nothofagus*-dominated forests (Tables 6 and 7) than is estimated in terms of foliar cover of the upper canopy on the same sites (70–95%, Table 1). Recalculation of basal area based only on trees ≥ 40 cm d.b.h. generally leads to similar or reduced rather than increased contribution by *Nothofagus* (Table 6). Other than *Nothofagus* spp., only five species, *Arillastrum gummiferum* Pancher ex Baillon (Myrtaceae), *Cerberiopsis candelabra* Vieillard ex Pancher & Sebert (Apocynaceae), *Codia discolor* (Brongniart & Gris) Guillaumin (Cunoniaceae), *Codia* sp. McKee 19050 and *Pancheria sebertii* Guillaumin (Cunoniaceae), contribute ≥ 20% of the total basal area or stem density at any site (Table 7). Of these, *C. candelabra*, *C. discolor* and *P. sebertii*, at least, are common pioneer species. Fifteen species contribute ≥ 10% to total basal area or density, with twenty-seven species contributing at least 5% (Table 7). No species occur at all sites, but three species (*Myodocarpus fraxinifolius* Brongniart & Gris (Araliaceae), *Calophyllum caledonicum* Vieillard (Clusiaceae) and *Gastrolepis austrocaledonica* (Baillon) Howard (Icacinaceae)) occur at seven of the nine sites.

Ordination of site canopy composition

The NMDS plot of the full data set using basal area suggests

Table 6 Major plant families on each study site by basal area and stem density. The data are from trees ≥ 20 cm d.b.h. and comprise only those families contributing ≥ 5% of the total basal area or stem density. The figures in brackets are percentage basal area contributed by *Nothofagus* to trees ≥ 40 cm d.b.h.

Localities	Family	Basal area %	Stem density %	No. of genera/species
Col de Mouirange Haut:				
Nothofagus-dominated	Fagaceae	33 (4)	46	1/1
	Myrtaceae	31	18	7/8
	Clusiaceae	6	6	2/2
	Apocynaceae	6	4	1/1
	Araucariaceae	5	4	2/2
Mixed	Myrtaceae	40	29	5/7
	Apocynaceae	19	21	2/2
	Icacinaceae	14	14	1/1
Col de Mouirange Bas	Fagaceae	45 (23)	55	1/2
	Euphorbiaceae	9	4	3/3
	Burseraceae	8	2	1/1
	Sterculiaceae	7	6	1/1
	Araliaceae	6	8	3/3
	Icacinaceae	6	4	1/1
Col de Yaté:				
Nothofagus-dominated	Fagaceae	83	84	1/1
	Casuarinaceae	8	10	1/1
	Myrtaceae	7	6	1/1
Mixed	Myrtaceae	22	26	4/4
	Clusiaceae	19	19	3/3
	Icacinaceae	14	11	1/1
	Fagaceae	12	13	1/1
	Sapotaceae	8	8	3/3
	Casuarinaceae	7	7	1/1
	Euphorbiaceae	6	4	2/2
Dzumac	Fagaceae	53 (38)	53	1/1
	Araucariaceae	16	10	1/1
	Casuarinaceae	11	19	1/1
	Strasburgeriaceae	10	6	1/1
Montagne des Sources	Fagaceae	26 (26)	25	1/2
	Araucariaceae	14	11	2/3
	Sapotaceae	11	8	5/7
	Clusiaceae	11	14	3/3
	Icacinaceae	7	8	1/1
	Cunoniaceae	6	5	4/4
	Casuarinaceae	5	3	1/1
Pic du Grand Kaori:				
Nothofagus-dominated	Cunoniaceae	40	41	2/3
	Fagaceae	15 (31[1])	16	1/1
	Rhamnaceae	11	13	1/2
	Araucariaceae	7	4	1/1
	Casuarinaceae	5	7	1/1
	Flindersiaceae	5	6	1/1
	Icacinaceae	5	1	1/1
Mixed	Cunoniaceae	45	46	4/4
	Dilleniaceae	13	13	1/1
	Mimosaceae	9	9	1/1
	Proteaceae	8	7	2/2

[1] Only three trees ≥ 40 cm d.b.h.

Table 7 Major plant species on each study site by basal area and stem density. The data are from trees ≥ 20 cm d.b.h. and comprise only those species contributing ≥ 5% of the total basal area or stem density.

Localities	Species	Basal area %	Stem density %
Col de Mouirange Haut:			
Nothofagus-dominated	*Nothofagus aequilateralis* (Baumann-Bodenheim) Steenis (Fagaceae)	33	46
	Arillastrum gummiferum Pancher ex Baillon (Myrtaceae)	22	12
	Cerberiopsis candelabra Vieillard ex Pancher & Sebert (Apocynaceae)	6	4
	Calophyllum caledonicum Vieillard (Clusiaceae)	5	5
Mixed	*A. gummiferum*	33	22
	C. candelabra	19	21
	Gastrolepis austrocaledonica (Baillon) Howard (Icacinaceae)	14	14
Col de Mouirange Bas	*N. aequilateralis*	25	31
	Nothofagus discoidea (Baumann-Bodenheim) Steenis	20	25
	Neoguillauminia cleopatra (Baillon) Croizat (Euphorbiaceae)	8	3
	Canarium oleiferum Engler (Burseraceae)	8	2
	Acropogon dzumacensis (Guillaumin) Morat (Sterculiaceae)	7	6
	G. austrocaledonica	6	4
	Schefflera gabriellae Baillon (Araliaceae)	6	6
Col de Yaté:			
Nothofagus-dominated	*N. aequilateralis*	83	84
	Gymnostoma deplancheanum (Miq.) Johnson (Casuarinaceae)	8	10
	Melaleuca pancheri (Brongniart & Gris) Craven & Dawson (Myrtaceae)	7	6
Mixed	*G. austrocaledonica*	14	11
	Montrouziera gabriellae Baillon (Clusiaceae)	13	10
	Nothofagus balansae (Baillon) Steenis	12	13
	Xanthostemon ruber (Brongniart & Gris) Pancher & Sebert (Myrtaceae)	10	12
	Syzygium nitidum (Brongniart & Gris) Dawson (Myrtaceae)	10	10
	Gymnostoma intermedium (Poiss.) L. Johnson	7	7
	Bureavella wakere (Pancher & Sébert) Aubréville (Sapotaceae)	6	4
	N. cleopatra	6	4
	C. caledonicum	5	7
Dzumac	*Nothofagus codonandra* (Baillon) Steenis	53	53
	Agathis ovata (Moore) Warburg (Araucariaceae)	16	10
	G. intermedium	11	19
	Strasburgeria robusta (Vieillard ex Pancher & Sébert) Guillaumin (Strasburgeriaceae)	10	6
Montagne des Sources	*N. aequilateralis*	16	16
	N. balansae	9	9
	Agathis lanceolata Lindley ex Warburg	9	7
	A. ovata	5	4
	C. caledonicum	7	8
	G. austrocaledonica	7	8
	B. wakere	5	3
Pic du Grand Kaori:			
Nothofagus-dominated	*Codia discolor* (Brongniart & Gris) Guillaumin (Cunoniaceae)	25	26
	N. aequilateralis	15	16
	Alphitonia neocaledonica Guillaumin (Rhamnaceae)	11	10
	Pancheria sebertii Guillaumin (Cunoniaceae)	10	10
	A. lanceolata	7	4
	G. deplancheanum	5	7
	Flindersia fournieri Pancher & Sebert (Flindersiaceae)	5	6
	Codia sp. Hopkins 5046, 5047	5	4
	G. austrocaledonica	5	1
Mixed	*Codia* sp. McKee 19050	24	25
	P. sebertii	20	19
	Hibbertia lucens Brongniart & Gris ex Sebert & Pancher (Dilleniaceae)	13	13
	Archidendropsis granulosa (Labillardiere) Nielsen (Mimosaceae)	9	9
	Stenocarpus trinervis (Montrouzier) Guillaumin (Proteaceae)	8	7

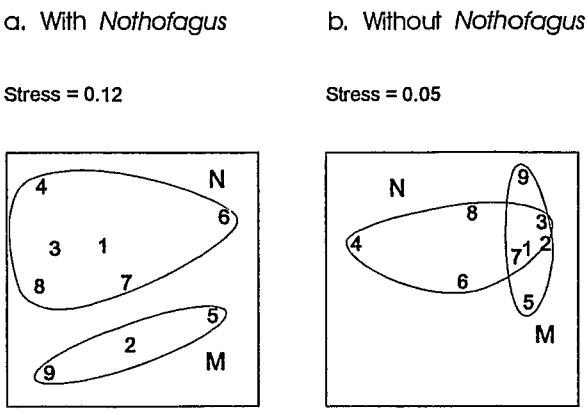

Figure 6 NMDS configuration plots using basal area data. N, *Nothofagus*-dominated forest; M, mixed rainforest. 1, Col de Mouirange Haut *Nothofagus* forest; 2, Col de Mouirange Haut mixed rainforest; 3, Col de Mouirange Bas; 4, Col de Yaté *Nothofagus* forest; 5, Col de Yaté mixed rainforest; 6, Dzumac; 7, Montagne des Sources; 8, Pic du Grand Kaori *Nothofagus* forest; 9, Pic du Grand Kaori mixed rainforest.

some distinctiveness of the two forest types (Fig. 6a). Consistent with this pattern, ANOSIM of the paired *Nothofagus* and mixed forest plots (with Col de Mouirange Bas), indicates significant difference in species composition using either density or basal area (Table 8). However, there was no significant difference using presence-absence data, or most importantly, when the data were reanalysed without *Nothofagus* (Table 8, Fig. 6b). The analysis using data from 0.1 ha subplots (Table 8) is consistent with the results described above. *N. aequilateralis* contributes most to within-group similarity in the *Nothofagus* plots, and to between-group dissimilarity (Table 9). Similarity within both forest types is low, and decreases by 4–21% among the *Nothofagus* plots when *Nothofagus* is removed from the analysis (Table 8). *Calophyllum caledonicum*, *Gastrolepis austrocaledonica* and *Bureavella wakere* contribute most to within-group similarity of the mixed rainforest (Table 9). The former two species also make a relatively high contribution, with *Agathis lanceolata* and *Gymnostoma deplancheanum*, to within-group similarity of the *Nothofagus*-dominated forests after *Nothofagus* is removed from the data set.

Table 8 Results of similarity analysis between *Nothofagus*-dominated and paired mixed rainforest using analysis of similarity (ANOSIM) and similarity percentages (SIMPER). The Global *R* and *P*-values are derived from the full data set of the paired sites with Col de Mouirange Bas (*Nothofagus*-dominated) included to increase power. *N* is the number of ANOSIM tests (out of a total of 3) that were significant ($P < 0.05$) using random assortments of 0.1 ha subplots, i.e. correcting for plot size. SIMPER was undertaken on the full data set, i.e. uncorrected for plot size.

Comparison	*R*	*p*	*N*	*Nothofagus* forest similarity (%)	Mixed rainforest similarity (%)	Dissimilarity between groups (%)
Nothofagus included						
Density	0.648	0.029	2	34	13	88
Basal area	0.556	0.029	1	29	15	86
Presence-absence data	0.028	0.314	0	25	32	72
Nothofagus excluded						
Density	−0.083	0.629	0	13	13	83
Basal area	−0.102	0.686	0	11	16	81
Presence-absence data	−0.046	0.543	0	21	34	72

Table 9 Major species contributing to within-group similarity and between-group dissimilarity derived by SIMPER. The analysis was undertaken on the full data set, i.e. uncorrected for plot size, of the paired *Nothofagus* and mixed rainforests, with Col de Mouirange Bas. Species are listed only where they contribute ≥ 10% to the total similarity or dissimilarity.

Comparison similarity	*Nothofagus* forest similarity	Mixed rainforest similarity	Dissimilarity between groups
Density	*Nothofagus aequilateralis* 78%	*Calophyllum caledonicum* 12% *Gastrolepis austrocaledonica* 12%	*N. aequilateralis* 25%
Basal area	*N. aequilateralis* 74%	*G. austrocaledonica* 30% *Bureavella wakere* 10%	*N. aequilateralis* 22%
Presence-absence data	*N. aequilateralis* 24%	*B. wakere* 14% *C. caledonicum* 10%	
Density without *Nothofagus*	*Agathis lanceolata* 13% *Gymnostoma deplancheanum* 11%	*C. caledonicum* 12% *G. austrocaledonica* 10%	
Basal area without *Nothofagus*	*G. austrocaledonica* 25%	*G. austrocaledonica* 31% *B. wakere* 10%	
Presence-absence data	*G. austrocaledonica* 11% *C. caledonicum* 10%	*B. wakere* 14% *Calophyllum caledonicum* 10%	

DISCUSSION

There is little consistent or significant difference between the *Nothofagus* forests and adjacent mixed rainforests in terms of stand structure, species composition and species richness, *H* and *E* among trees ≥ 20 cm d.b.h. The main structural difference lies in the lower basal area of large trees in the *Nothofagus* forests than the mixed rainforests. *H* was consistently lower in the *Nothofagus* forests than the paired mixed rainforests, though not significantly different. The small number of replicate sites reduces the power of statistical power considerably, and therefore care should be exercised in interpretation. However, the highest *H* was recorded in *Nothofagus* forest (Montagne des Sources) and therefore it can at least be concluded that high species diversity of trees is not precluded by dominance by *Nothofagus*.

The stem densities of both forest types are relatively high compared with other tropical rainforests, though similar to other New Caledonian rainforests (Table 2). Jaffré & Veillon (1995) noted that forests studied to date in New Caledonia have high stem densities compared with rainforests in Malesia and Melanesia. They suggested this may be caused by the shorter stature of the New Caledonian forests and their less dense canopy, i.e. allowing greater light penetration to the understorey. In addition, stand basal area is not lower in the forests on the low nutrient and potentially toxic ultramafic soils than in those on nonultramafic soils. The primary influence of these soils on tree morphology appears to be stunted height, leading to a lower stand biomass, but there is insufficient information to allow detailed comparison.

Only the three stands at Col de Mouirange have stems greater than 80 cm d.b.h. It is not clear to what extent site factors are responsible, that is, better conditions leading to higher growth rates, rather than temporal factors, such as stand age. The absence of stems larger than 34 cm d.b.h. in the Yaté *Nothofagus* forest is probably related to stand youth. Read *et al.* (1995) noted the absence of rotting logs in the understorey, indicating that the forest has not reached the potential lifespan of the canopy trees and suggesting that it originated following a large-scale disturbance. Charcoal was recorded in the soil at 10–40 cm depth, suggesting a fire responsible for clearing the site and facilitating the episode of *Nothofagus* regeneration. It is uncertain to what extent the low species richness, *H* and *E* of this study site are caused by features such as poor survival of the fire and/or low propagule availability, or simply to stand youth. Although there is little forest within this region, particularly uphill of the forest, the mixed rainforest study site is only ≈ 50 m away, uphill and upwind, providing a potential seed source of at least thirty additional canopy species.

Although the upper canopy of the *Nothofagus* forests comprises 70–95% of *Nothofagus* spp. in terms of foliar cover, the density and basal area of the same forests is not dominated to the same degree (≤ 55%), other than the Yaté forest (85%). This disparity could occur for two main reasons. First, the *Nothofagus* are taller than many other canopy species so that basal area and density does not reflect dominance of the uppermost canopy layer. When basal area is recalculated to include all trees with foliage in the upper 25 percentile of the forest height, irrespective of tree diameter, there is little change in proportion contributed by *Nothofagus* (1–2%) except at Col de Yaté (additional 13%), Col de Mouirange Haut (additional 18%) and Pic du Grand Kaori (additional 52%). However, not all trees in the upper height quartile are as tall as *Nothofagus* and more precise height measurements are required to clarify the importance of this factor. Second, the *Nothofagus* trees may have a higher canopy diameter to stem diameter ratio, i.e. being taller than most other canopy species may allow a greater spread of foliage than in species that are overtopped. Hart (1990) defines monodominance as ≥ 80% basal area. Only the Yaté forest can be defined as monodominant on this basis. It is not unusual in other tropical forests for the dominant canopy species to dominate the larger stem diameter classes more than the smaller diameter classes (e.g. Eggeling, 1947; Newbery *et al.*, 1992). However, on the New Caledonian study sites *Nothofagus* generally forms a similar or lesser proportion of the large stem diameter classes, despite its dominance of the upper canopy. Irrespective of the form of monodominance, similar ecological questions are raised in relation to controls of diversity.

Previous research has suggested that *Nothofagus*-dominated stands on some lowland sites in New Caledonia are early successional stages (Read *et al.*, 1995). In this study the least difference between forest types often occurs at Col de Mouirange, and most at Yaté, consistent with a successional pattern in which the *Nothofagus*-dominated stands become progressively species-rich, with higher *H*, over time. However, the reasons for early dominance by *Nothofagus* are uncertain. Many of the co-occurring canopy species on these study sites are capable of reaching similar, or greater, heights to those of *Nothofagus*. Whether the dominance of the upper canopy on these study sites is a function of early arrival on site, low mortality, rapid growth rate, or unusually tall stature (relative to co-occurring species) under these specific site conditions is uncertain.

The number of species of large tree in the *Nothofagus* forests is comparable to many other tropical rainforests, as far as can be judged from data sets using different diameter classes and sample areas. For example, Gentry (1982) cites 22–179 tree species (d.b.h. > 15 or > 25 cm) on 1 ha plots in the neotropics. Our results are consistent with those of Jaffré & Veillon (1991) indicating that New Caledonian rainforests on ultramafic soils are not unusually high or low in tree species richness compared with other tropical rainforests. In addition, they indicate that the monodominance of the uppermost canopy is not necessarily correlated with a low species richness of the whole canopy.

The lack of significant difference in species composition between the monodominant and adjacent mixed rainforests is consistent with reports from some other studies (Beard, 1946; Hart *et al.*, 1989), including some New Guinea *Nothofagus* forests (Walker, 1966; Kalkman & Vink, 1970). This result is also consistent with the New Caledonian *Nothofagus* forests being a successional phase, but does not refute the alternative hypothesis that differences in environment cause the differences in canopy dominance between the two forest types.

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