Subtropical rainforest turnover along an altitudinal gradient

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ABSTRACT

The rainforests of south-east Queensland and northern New South Wales are highly diverse and floristically and structurally complex. This diversity is due, in part, to regional variation in soil and parent geology, climate and topography. Patterns in regional species composition were investigated along an altitudinal transect from 300 to 1100 m elevation in Lamington National Park, south-east Queensland. This study also relates subtropical rainforest composition to soil variables and to the environmental correlates of altitude, namely temperature and moisture. Twenty-nine climatic and nine soil variables were correlated with floristic variation between altitudes. Twelve species groups were also identified from the 282 vascular plant species recorded along the transect. These baseline data will form the benchmark against which future changes in the forest can be monitored. The use of adjacent altitudes as surrogates for adjacent climates can also provide a useful insight into the potential impacts of a changing climate. ❑ *altitudinal gradient, climate change, compositional turnover, subtropical rainforest, surrogacy.*

The subtropical rainforests of south-east Queensland and northern New South Wales are a living link to our botanical past. They support subtropical through to cool temperate biota and have done so throughout the climatic fluctuations of the Late Tertiary and Quaternary (Adam 1987). This continuity of climate has allowed the persistence of primitive plant families (Winteraceae, Eupomatiaceae, Annonaceae, Trimeniaceae, Monimiaceae, Atherospermataceae and Lauraceae) which have undergone little evolutionary change since Gondwanan times (McDonald 2010; Floyd 1990a). These rainforests also host 42 genera of primitive angiosperms and gymnosperms (Floyd 2008), relictual and endemic species, as well as rare and threatened flora (McDonald 2010).

Subtropical rainforest is particularly well represented in Australia and extends from approximately 21°–35° latitude (based on the prominence of notophyll and microphyll canopy leaves) (Webb 1959). These forests have been described and classified under various schemes at both continental (Webb 1978, 1968, 1959) and state levels (Sattler & Williams 1999; Baur 1964). Lamington National Park supports several structural types of rainforest, three of which were examined in this study and described below. The approximate equivalents between classification schemes are also included below.

Araucarian Complex Notophyll Vine Forest (ANVF) (Webb 1978, 1968, 1959)/Qld Regional Ecosystem (RE) 12.8.4 (Sattler & Williams 1999)/Dry rainforest (Floyd 1990b; Baur 1964). This structural form occurs on basalt soils on the northern and western slopes of the Lamington Plateau and on shallow rocky soils on steep slopes. ANVF is a subtype of the more extensive complex notophyll vine forest (CNVF) dominant in the region. It differs from other forms of CNVF in supporting emergent hoop pine, *Araucaria cunninghamii*. This structural type is tolerant not only of a lower annual rainfall, but a marked dry season between spring and early summer (McDonald & Whiteman 1979).

Complex Notophyll Vine Forest (CNVF) (Webb 1978, 1968, 1959)/RE 12.8.3 and 12.8.5 (Sattler & Williams 1999)/Subtropical rainforest (Floyd 1990b; Baur 1964). CNVF occurs on basalt soils and Lamington National Park supports some of the most extensive and best developed stands of this rainforest type in the region. It is both floristically and structurally complex. There are two broad subtypes, the distributions of which are associated with altitude. Warm subtropical CNVF/RE 12.8.3, generally occurs below 600–700 m a.s.l., particularly in valleys. This forest type can grade into ANVF on steep slopes and on drier aspects (McDonald & Whiteman 1979). Cool subtropical CNVF/RE 12.8.5 generally occurs at altitudes above 600–700 m, although a broad ecotone of high floristic diversity between these two subtypes can occur (Laidlaw *et al.* 2000). All forms of CNVF support robust and woody lianes, a diverse community of vascular epiphytes, canopy species with plank buttresses and compound, entire leaves, as well as other life forms such as palms and climbing aroids (*Pothos longipes*) (Webb 1959).

Microphyll Fern Forest (MFF) (Webb 1978)/RE 12.8.6 (Sattler & Williams 1999)/Cool temperate rainforest (Floyd 1990b; Baur 1964). MFF occurs on the high plateaus and mountain tops at altitudes over 1000 m. Rainfall at this altitude is supplemented by the interception of water from clouds that occur frequently with onshore winds (Floyd 2008). This forest is typically dominated by *Nothofagus moorei* (Nothofagaceae), a species whose extent has contracted and moved south and upslope, along with cold and wet microclimates (Hopkins *et al.* 1976; Webb 1964). These forests are without plank buttress forming species or woody lianes. Instead, they support prolific mossy epiphytes, tree and ground ferns and tree species with simple, toothed leaves (McDonald & Whiteman 1979).

The distribution of these three structural types of rainforest at Lamington National Park are known to be correlated with the environmental features of topography (particularly aspect), climate, soil nutrient status, soil depth and moisture content (Adam 1987; Hopkins *et al.* 1976; Webb 1969, 1968). The response of species groups to these environmental variables is complex and interactions between them are likely (Adam 1987). It can be very difficult to attribute rainforest distribution to any one factor, however, general trends can be identified. Broadly speaking, CNVF (and subtypes) occur in a mesothermal environment with annual mean maximum temperatures of 18–22°C and an annual mean minimum of 5°C. By comparison, MFF is found in a microthermal environment with an optimum annual mean maximum temperature of 10-12°C and an annual mean minimum of 0°C (Floyd 1990a; Adam 1987). Such microthermal conditions in the study region are restricted to altitudes over 1000 m and to elevated gullies, where cold air drainage allows the downslope extension of these conditions. The downslope extension of MFF, under appropriate moisture regimes, is likely restricted by either intolerance of higher temperatures (Fraser & Vickery 1939), or by the superior competitive ability of CNVF species (Dolman 1982). The upslope extension of CNVF is restricted by its susceptibility to frost events tolerated by species such as *Nothofagus moorei* (Adam 1987; Dolman 1982).

The moisture regime is a result of the complex interaction between precipitation, aspect, slope, soil parent material and soil depth (Adam 1987). ANVF occurs where annual rainfall ranges between 660–1100 mm, CNVF is found where it exceeds 1300 mm, while MFF is found where annual rainfall is over 1750 mm, with the input of up to an additional 50% of this annual rainfall from fog drip (Floyd 2008, 1990; Hutley *et al*. 1997; King 1980; Fisher & Timms 1978). Rainfall seasonality is also important. ANVF is able to withstand a pronounced dry season. CNVF requires a largely uniformly distributed rainfall with a summer peak when evaporative potential is highest and MFF requires consistently moist conditions from both rainfall and regular contact with cloud and fog (Floyd 2008, 1990). The availability of these moisture inputs to rainforest species also depends quite strongly on the geological history of the region.

The volcanic strata underlying Lamington National Park were laid down in three major series of eruptions emanating from Mt Warning to the south. The Beechmont Basalt is overlain by the Binna Burra Rhyolite and scattered pyroclastic vents, which was then capped by the later Hobwee Basalt (Stevens 1976). The current erosion caldera is a result of the differential weathering of these strata for 20 million years (Willmott 1992). Basalts generally weather to red krasnozem soils which are fine textured with a high water holding capacity, acidic and low in soil nutrients, except for those stored in the surface horizons (Beckmann & Thompson 1976). Subtle differences in basalt chemical composition, differential weathering characters and age of weathering surfaces, in conjunction with varied topography and the resulting microclimate has resulted in a wide variety of soil types even on this one geology (Beckmann & Thompson 1976). The multiple basalt flows and their subsequent weathering has also resulted in step and bench sequences down the slopes (Turner 1976) and associated variations in soil depth.

According to Webb (1959), edaphic factors can be just as important in determining community composition and distribution as climatic variables. However, this is a complex interaction and equally for some structural types, edaphic factors are dominated by climate. A forest type which is highly competitive on poor soils under favourable climatic conditions, may be able to tolerate sub-optimal rainfall only on richer soils (Adam 1987). Similarly, CNVF may be able to tolerate poorer soils if rainfall is sufficient and there is no dry season (Adam 1987). High rainfall may also be able to compensate for poorer soils in some cases such as in sheltered, fire protected sites (edaphic compensation) (Floyd 1990a; Webb 1969, 1959).

Subtropical rainforest distribution is greatly impacted by topography (Adam 1987). Aspect is more important at this latitude than in tropical rainforests where the sunlight received annually is similar between northerly and southerly aspects. On the shortest day in winter at Lamington National Park, the sun shines for 10.25 hours (flat plane) and reaches a maximum altitude of 38.42° (Cornwall *et al*. 2009). This low altitude means that much of the forest on southerly slopes and enclosed gullies receives far less than 10 hours of sunlight per day. The forests tucked below the inner rim of the caldera may receive no direct sunlight at all for extended periods through winter. The southern and eastern aspects are also protected from drying northerly and westerly winds in late winter and spring and from direct solar radiation in the heat of summer, where the midday sun sits almost directly over the forest at an altitude of 85° (Cornwall *et al.* 2009; Floyd 2008). Erosion gullies shelter rainforest from fire, frost and damaging winds, as well as being sites of higher soil nutrients and moisture (Floyd 2008, 1990). Soils also vary significantly between ridges and valleys, generally becoming deeper and higher in soil nutrients and moisture downslope (McKenzie *et al.* 2004). However, on steep slopes, erosion and leaching of soil nutrients may be pronounced (Floyd 2008).

This study seeks to identify current patterns in species composition in the subtropical rainforest communities of south-east Queensland and to relate these patterns to current climatic conditions through the establishment of an altitudinal transect. This baseline will allow changes in floristic composition and their environmental correlates to be tracked over time and will serve as the essential benchmark against which resurveys of the forest will be compared. In addition, we use the current climatic envelopes of adjacent altitudes as a surrogate for climatic variation over time and identify species and groups for which predicted future climatic changes may prove challenging. This transect samples the response of vegetation along two major environmental axes along which human influenced climate is predicted to shift, temperature and moisture.

MATERIALS AND METHODS

Twenty permanently marked 20 m x 20 m vegetation survey plots were established in August 2006 in the Canungra Creek catchment of Lamington National Park, south-east Queensland, Australia. These plots sample several structural types of subtropical rainforest vegetation at five altitudes: 300, 500, 700, 900 and 1100 m a.s.l. Four plots were established at each of these altitudes, with a minimum distance of 400 m along the contour between replicates, and the data for each altitude were pooled. This was done in place of establishing large plots at each altitude, which previous studies (Laidlaw *et al.* 2000) have shown must be at least 80 x 80 m in size before an asymptote is achieved in the species accumulation curve. The plots were located ≥ 50 m from permanent water and away from recent disturbance, however, this was more difficult at 300 and 500 m a.s.l. due to the steep terrain lower in the catchment. All plots were positioned on basic Cainozoic volcanic rocks (Beechmont and Hobwee basalts). Soil samples were collected from each plot, air-dried and analysed for pH, conductivity and nutrient status. Soil analysis techniques are described in Strong *et al.* (2011).

The transect traverses a steep moisture and temperature gradient, where lower altitudes generally experience hotter and drier conditions, while upland sites generally experience colder and moister conditions. These trends can be strongly influenced by aspect. The establishment of all survey plots within a single catchment and, as far as possible, maintaining a common north-north-westerly aspect, attempted to reduce this variation. All established trees ≥ 5 cm diameter at breast height (dbh: measured at 1.3 m height or directly above buttresses or below bole deformities) were numbered and measured for diameter and height and were identified to species by the Queensland Herbarium (see Bostock & Holland (2007) for species authorities). Multi-stemmed species were treated as separate individuals wherever stems were ≥ 5 cm dbh. Where vines and epiphytes obstructed the bole, these were gently lifted to allow accurate dbh measurement. All other vascular species on each plot were identified and given a cover score.

Multivariate analyses were conducted on data pooled across four 20 m x 20 m plots per altitude.

The pattern analysis software WinPATN (Belbin *et al.* 2003) was used to examine the association between altitude and floristic composition along the transect. The Bray-Curtis dissimilarity metric (Bray & Curtis 1957) was applied to presence/absence data and used to determine the floristic dissimilarity between altitudes. A two-step procedure, based on the Bray-Curtis dissimilarity metric (Belbin *et al.* 2003), was used to examine the relationships between species based on the altitudes at which they were recorded. The groups resulting from both associations are displayed in a two-way table. The data were classified using unweighted pair group arithmetic averaging (UPGMA) (β value = -0.1). Semi-strong hybrid multidimensional scaling ordination (SSH MDS) was used to depict the association between altitudes based on their floristic composition in two-dimensional space (Belbin *et al.* 2003) using a dissimilarity cutoff value of 0.9. Minimum spanning trees are used to display the floristic links between pairs of altitudes surveyed along the transect.

Principal axis correlation (PCC) (Belbin *et al.* 2003) was used to calculate the correlation between sampled altitudes in ordination space and selected intrinsic (species) and extrinsic (climatic, edaphic and topographic) variables for the transect. Thirty-five climatic variables were modelled using the Bioclim climate modelling package (Houlder *et al.* 2000), applied to an 80 m digital elevation model. A Monte-Carlo permutation test (Belbin *et al.* 2003), MCAO (1000 permutations) was used to test the significance of the relationship between altitudinal groups, their constituent species and extrinsic variables. Biplots of these significant extrinsic variables were overlaid on the ordination.

RESULTS

Recorded from the 20 plots along the transect were a total of 282 species, including 1218 tree stems (≥5 cm dbh) of 115 species, 90 genera and 37 families (including one species of tree fern and one species of tree palm). The study also recorded 10 species of shrub, 59 species of vine, 18 species of herb, 13 species of ground fern, 13 species of orchid, 17 species of 'epiphyte' (15 ferns, one climber and one true epiphyte). The remaining 37 species recorded were understorey tree species (<5 cm cutoff) and seedlings of tree species not recorded in the canopy.

The association between the sites at five different altitudes along the transect based on the plant communities recorded was examined using Bray-Curtis dissimilarity (Fig. 1). The high altitude sites (900 and 1100 m) were found to be dissimilar from the mid-low altitude sites (700-300 m) (BC = 0.77). The 900 m and 1100 m sites had a Bray-Curtis dissimilarity of 0.53. The two most closely related altitudes were 500 m and 700 m (BC = 0.27) and these were then joined with the 300 m altitude sites with a BC dissimilarity of 0.43. These results of the classification suggest that the altitudinal transect, and the large amount of environmental variation captured, contained four distinct rainforest communities, with the 500 m and 700 m sites representing the same community.

The 282 species were classified according to their occurrence at different altitudes using a two-step procedure (Belbin 2003). Twelve species groups were identified from the resulting dendrogram and are presented along with the four altitudinal groups in a two-way table (Table 1). A MCAO significance test on a principal components correlation for the transect showed that 72 species (25 tree species, 17 species of climber, three species of herb, five species of ground fern, one tree fern, five species of epiphytic orchid, five species of epiphytic fern and 11 species of tree seedling) were significantly (MCAO ≤ 1%) correlated with altitude. These species are highlighted as significant in Table 1.

A MCAO significance test of a principal components correlation for the transect showed that 29 climate variables were significantly (MCAO ≤1%) correlated with floristic composition. Of these climate variables, 11 were temperature-based, three precipitation, seven radiation and eight moisture-based. Figure 2 shows 10 of the 29 climate variables indicative of the trends. Higher temperatures, radiation and pronounced moisture seasonality were associated with the lower altitude sites, whilst higher precipitation (particularly during the winter dry season) was strongly associated with the high altitude sites. Radiation seasonality was highest at the 1100 m sites.

A MCAO significance test of a principal components correlation for the transect showed that nine soil variables were significantly (MCAO ≤1%) correlated with the altitudinal groupings. PH decreased with increasing altitude (Strong *et al.* 2011) and was found to be significantly correlated with the altitudinal groupings of plant communities (Fig. 3). Soil magnesium, potassium, sodium, chloride and sulphur content were found to be significantly correlated with plant community composition (Fig. 3). Sulphur and chloride content increased with altitude, while all other soil variables decreased with altitude (Strong *et al.* 2011). Sodium base saturation percentage (BSP) was found to be significantly correlated with vegetation communities at different altitudes (Fig. 2) and was highest at high altitude.

DISCUSSION

This study recorded approximately half of the 320 rainforest tree species recorded in the region (Floyd 1990a; W.J.F. McDonald personal observation). Four identifiable rainforest structural types were surveyed along the transect and these correspond to the structural types previously identified by Webb (1978, 1968, 1959), Sattler & Williams (1999) and Baur (1964). Twelve species groups were also identified from the 20 plots, each responding to the environmental conditions at the altitudes at which they occur.

Species group (a) is composed of ANVF specialists, recorded only from the 300 m sites. This forest type has been extensively cleared within the region for agriculture and species such as *Toona cilata* and *Araucaria cunninghamii* targeted for logging. These low altitude species are able to withstand extended dry periods and associated high evapotranspiration rates. This group of species could be expected to expand its distribution upslope should predicted climate warming and regional drying occur (Cai *et al.* 2005).

Species group (b) comprises those species occurring in both the warm and cool subtypes of CNVF, where evapotranspiration is lower due to increased moisture inputs and lower temperatures than in ANVF. Species group (c) is a mixed group which consists of a number of smaller species groups lumped together here due to the arbitrary splitting of the dendrogram at 12 groups. Some species in this group are distributed along all or much of the length of the altitudinal transect and are largely generalists in that they are able to persist under a variety of conditions. Some occurred in all structural forest types on the transect, others in all types except ANVF or MFF. Some species in group (c) were found to have disjunct distributions. This is a sampling artefact, however, as these species have previously been recorded at intermediate altitudes. Five species in this group (*Eupomatia laurina, Helicia glabriflora, Melodinus australis, Solanum inaequilaterum* and *Geitonoplesium cymosum*) were found only in the cooler types above 700 m and would form their own group at a finer scale of analysis. The two-way table lets us, however, identify that the five species in this finer group are perhaps more sensitive to drier conditions at lower altitudes and may be good indicators of increasing moisture stress in these forests.

Species group (d) are species found in all types of notophyll vine forest, but are absent from MFF. All of the species in this group, many of them tree species, were found to be significant in the MCAO. These species may not be able to tolerate the low levels of solar radiation, periodic soil waterlogging, higher acidity or colder soil temperatures at the highest altitude. This group includes three of the dominant species in these subtropical rainforests, *Argyrodendron actinophyllum*, *A. trifoliolatum* and *Pseudoweinmannia lachnocarpa*.

Species in group (e) are restricted to the warm CNVF forest at 500 m and 700 m. Forests at these two altitudes were found to be more similar than any other. The nominal altitude for distinguishing between warm and cool CNVF is 600 m, however, in this catchment, warm CNVF appears to extend higher with a broad ecotone into cool CNVF. This may be due to the generally northern aspect of the study transect.

Species group (f) includes ten species recorded only at 700 m. These ten species were found to be significantly correlated with altitude. The sites established at 700 m were located midslope with a mean slope of 11.25° (± SE 1.1). Steep slopes often have shallower, less mature soils with a reduced ability to hold moisture and soil nutrients (Turner 1976). These ten species could experience increasing stress under predicted climate change scenarios. Alternatively, their tolerance for difficult conditions may pre-adapt them for expansion.

Species group (g) consists of species recorded only from 300 m and 500 m, many of which are trees or tree seedlings. Sites at both of these altitudes were necessarily located approximately 50 m from a creek line. Soils along the creek at 300 m and 500 m were grey-brown and possibly impacted by alluvial processes during flood events (Strong *et al.* 2011). These species may be utilising the higher clay content and nutrients in the alluvial soils at these sites.

Species group (h) are species recorded solely at the 500 m sites. Only 3 species in this group are tree species and almost half are climbers. This, along with the location of these sites low in the valley close to a creek line and on steep slopes, may indicate a higher return rate of disturbance than at other altitudes.

Species recorded only from 900 m and 1100 m form species group (i). These species may have higher moisture requirements than those at lower altitudes and be tolerant of low solar radiation and lower temperatures. Species in group (j) were recorded only at 900 m. Species such as *Acradenia euodiiformis*, may be an indicator of a severe storm which passed through this area in 1983 (Olsen & Lamb 1984), although this study intentionally avoided the worst of this disturbance. This altitude also sits at the level of the current cloud base on moderately humid days and may be sensitive to moisture stress in the event that the cloud base rises along with increasing atmospheric temperatures. Species in this group may serve as sentinel species to identify future impacts of a drying climate (Laidlaw *et al.* 2011). For example, *Tasmannia insipida* has been shown to be a good indicator of the presence of cloud in the Mackay area (W.J.F. McDonald personal observation).

Species group (k) are those species found only at mid to low altitudes (≤ 700m a.s.l.). Species such as *Lophostemon confertus* (Myrtaceae) were recorded in the canopy and tell the tale of when these forests were more open than they are currently as this species cannot persist under a closed canopy. These forests may be younger than those upslope and resemble a forest type extensive during drier times as recent as 500 years ago (Turner 1976). This and the other species groups of mid to low altitudes (h, g, f, e and a) are likely to be more tolerant of higher temperatures, lower moisture inputs and higher evapotranspiration than those at 900 m and above.

Species group (l) are all MFF specialists, all significantly correlated with altitude and occur nowhere else along the transect. These species are tolerant of the low solar radiation, high soil acidity, soil water logging, low temperatures and occasional frosts and snow found at altitudes

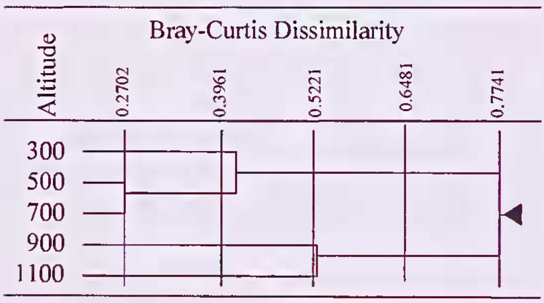

FIG. 1. Bray-Curtis dissimilarity dendrogram of altitudinal groups (300, 500, 700, 900 and 1100 m a.s.l.) based on floristic composition.

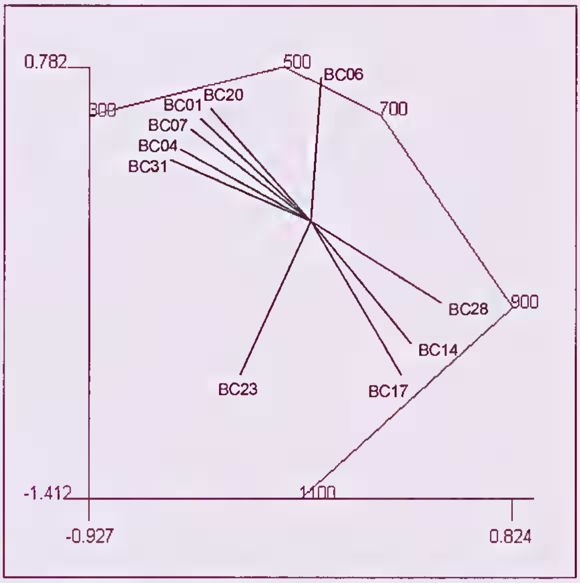

FIG. 2. Semi-strong hybrid multidimensional scaling ordination (stress = 0.08) of altitudes based on floristic composition with minimal spanning tree, and biplot of selected correlated climatic variables identified by the MCAO significance test. BC01, annual mean temperature; BC04, temperature seasonality; BC06, minimum temperature of the coldest period; BC07, temperature annual range; BC14, precipitation of the coldest period; BC17, precipitation of the driest quarter; BC20, annual mean radiation; BC23, radiation seasonality; BC28, annual mean moisture index; BC31, moisture index seasonality.

above 1000 m. Species such as *Nothofagus moorei*, *Quintinia sieberi* and *Callicoma serratifolia* are components of relictual Gondwanan rainforest (Webb *et al.* 1986). These forests support many high altitude endemic species which are at the highest risk of extinction from a warming climate. As such, these species will be important indicators of change in this forest type and may require intervention for their continued survival.

Soil variables, in conjunction with their climatic and topographic drivers, were found to be significantly correlated with floristic differences between altitudes. All twelve species groups were found on acidic soils (pH < 6.5). Acidity increased with altitude (Strong *et al.* 2011) in response to increased rainfall and subsequent leaching (McKenzie *et al.* 2004). Soil pH is known to impact on soil structure, weathering and humification (Larcher 1980). It is also known to impair the uptake of some soil nutrients such as calcium, magnesium and potassium (McKenzie *et al.* 2004), all three of which were found to be significantly correlated with altitudinal groupings and were found at higher concentrations at lower altitudes. Aluminium is preferentially liberated in acidic soils (Larcher 1980) and was found to increase with altitude (Strong *et al.* 2011). Aluminium can reduce the availability of calcium to plants (Graham 2001) and species which prefer calcareous soils, such as those of CNVF (Floyd 2008), are also often sensitive to aluminium (Larcher 1980). It is possible that the CNVF communities found at mid to low altitudes in this study are in part excluded from higher altitudes by this lowering of calcium availability.

Base saturation percentage (BSP) is the portion of soil cation exchange capacity (CEC) accounted for by exchangeable bases and is an indicator of soil fertility (Rayment & Higginson 1992). Bases such as sodium can be depleted from soil through leaching, particularly under the warm and moist conditions often found

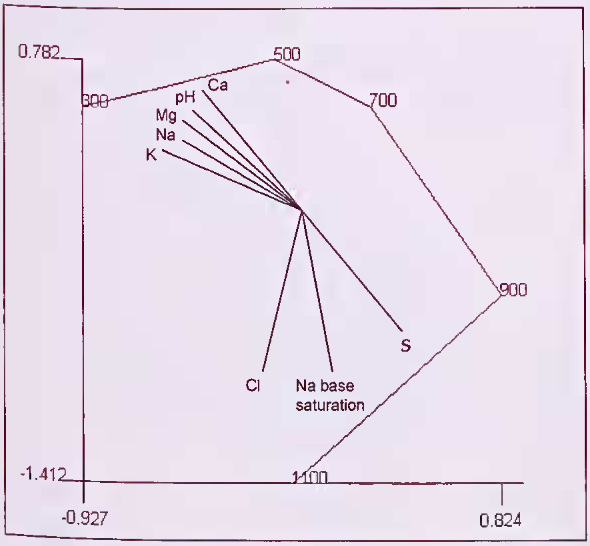

FIG. 3. Semi-strong hybrid multidimensional scaling ordination (stress = 0.08) of altitudes based on species composition with minimal spanning tree, and biplot of selected correlated soil variables identified by the MCAO significance test. (Ca, Calcium; Mg, Magnesium; Na, Sodium; K, Potassium; Cl, Chloride; S, Sulphur).

in rainforests (Rayment & Higginson 1992). This process is accentuated at higher, wetter altitudes. The higher altitude forests were also significantly associated with higher chloride and sulphur levels.

The identification of climatic variables significant in determining current species groups and distributions can be complicated by the long generation times of rainforest species, particularly trees. The conditions under which an individual germinated and established may be quite different from current climatic conditions. This may become increasingly difficult as the climate these forests will face in the near future will be both hotter and drier than those the forest is currently experiencing (Cai *et al*. 2005). For some species and communities, edaphic variables may be able to compensate to a degree, as will dispersal into cooler and moister altitudes and aspects. This study, along with continued monitoring along the altitudinal transect, will assist with change detection and management of these important forests.

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TABLE 1. Two-way table of twelve vascular plant species assemblages recorded for each of four altitudinal groups (300, 500 & 700, 900, 1100 m a.s.l.). * indicates species significant in driving altitudinal groups (MCAO ≤ 1%). # indicates non-native or naturalised species. Abbreviations for life forms are as follows: *t*, tree; *ts*, tree seedling/understorey tree; *tf*, tree fern; *p*, palm; *sh*, shrub; *h*, herb; *f*, fern; *c*, climber; *e*, epiphyte; *o*, orchid; *ec*, epiphytic climber; *ef*, epiphytic fern; *eo*, epiphytic orchid.

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres) 300	500	700	900	1100
a		*Abutilon oxycarpum*	Malvaceae	*sh*	*				
36 species		*Toona ciliata*	Meliaceae	*ts*	*				
		Syzygium francisii	Myrtaceae	*t*	*				
		Alchornea ilicifolia	Euphorbiaceae	*t*	*				
		Adiantum hispidulum	Adiantaceae	*f*	*				
		Asplenium attenuatum	Aspleniaceae	*ef*	*				
		Aneilema acuminatum	Commelinaceae	*h*	*				
		Castanospermum australe	Fabaceae	*t*	*				
		Carissa ovata	Apocynaceae	*sh*	*				
		Carex sp.	Cyperaceae	*h*	*				
		Capparis sarmentosa	Capparaceae	*c*	*				
		Calamus muelleri	Arecaceae	*c*	*				
		Deeringia amaranthoides	Amaranthaceae	*h*	*				
		Daphnandra apatela	Atherospermaceae	*t*	*				
		Dendrocnide excelsa	Urticaceae	*t*	*				
		Elaeocarpus obovatus	Elaeocarpaceae	*ts*	*				
		Ficus obliqua	Moraceae	*t*	*				
		Ficus macrophylla forma macrophylla	Moraceae	*t*	*				
		Ficus fraseri	Moraceae	*t*	*				
		Excoecaria dallachyana	Euphorbiaceae	*t*	*				
		Jasminum simplicifolium subsp. *australiense*	Oleaceae	*c*	*				
		Ixora beckleri	Rubiaceae	*t*	*				
		Hippocratea barbata	Celastraceae	*c*	*				
		Guilfoylia monostylis	Surianaceae	*t*	*				
		Mallotus discolor	Euphorbiaceae	*ts*	*				
		Mallotus claoxyloides	Euphorbiaceae	*t*	*				
		Morinda canthoides	Rubiaceae	*c*	*				
		Mischocarpus anodontus	Sapindaceae	*t*	*				
		Marsdenia pleiadenia	Apocynaceae	*c*	*				
		Oplismenus aemulus	Poaceae	*h*	*				

TABLE 1. continued…

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
a cont…		*Olea paniculata*	Oleaceae	*ts*	*				
		Pavetta australiensis	Rubiaceae	*ts*	*				
		Psydrax lamprophylla forma *lamprophylla*	Rubiaceae	*ts*	*				
		Podocarpus elatus	Podocarpaceae	*ts*	*				
		Sterculia quadrifida	Sterculiaceae	*ts*	*				
		Siphonodon australis	Celastraceae	*t*	*				
b 23 species	*	*Acmena ingens*	Myrtaceae	*ts*		*	*	*	
	*	*Dendrobium gracilicaule*	Orchidaceae	*eo*		*	*	*	
	*	*Dictymia brownii*	Polypodiaceae	*ef*		*	*	*	
	*	*Elattostachys xylocarpa*	Sapindaceae	*t*		*	*	*	
	*	*Guioa semiglauca*	Sapindaceae	*ts*		*	*	*	
	*	*Neolitsea australiensis*	Lauraceae	*t*		*	*	*	
	*	*Neolitsea dealbata*	Lauraceae	*ts*		*	*	*	
	*	*Morinda jasminoides*	Rubiaceae	*c*		*	*	*	
	*	*Mischocarpus australis*	Sapindaceae	*ts*		*	*	*	
	*	*Piper hederaceum* var. *hederaceum*	Piperaceae	*c*		*	*	*	
	*	*Phaleria chermsideana*	Thymelaeaceae	*t*		*	*	*	
	*	*Ripogonum elseyanum*	Ripogonaceae	*c*		*	*	*	
	*	*Dockrillia teretifolia*	Orchidaceae	*eo*		*		*	
	*	*Harpullia alata*	Sapindaceae	*ts*		*		*	
	*	*Litsea reticulata*	Lauraceae	*t*		*		*	
		Acronychia baeuerlenii	Rutaceae	*ts*			*	*	
		Zanthoxylum brachyacanthum	Rutaceae	*t*			*	*	
		Cinnamomum virens	Lauraceae	*t*			*	*	
		Clerodendrum floribundum	Vitaceae	*ts*			*	*	
		Decaspermum humile	Myrtaceae	*t*			*	*	
		Endiandra muelleri subsp. *muelleri*	Lauraceae	*ts*			*	*	
		Emmenosperma alphitonioides	Rhamnaceae	*t*			*	*	
		Platycerium bifurcatum	Polypodiaceae	*ef*			*	*	
c 38 species		*Alangium villosum* subsp. *polyosmoides*	Cornaceae	*t*	*			*	*
		Asplenium polyodon	Aspleniaceae	*ef*	*		*	*	*
		Melicope micrococca	Rutaceae	*t*	*		*	*	*

TABLE 1. continued…

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
c cont…		*Smilax australis*	Smilacaceae	*c*	*		*	*	*
		Archontophoenix cunninghamiana	Arecaceae	*p*	*	*	*		*
		Dianella caerulea var. *vannata*	Hemerocallidaceae	*h*	*	*	*		*
		Lastreopsis decomposita	Dryopteridaceae	*f*	*	*	*		*
		Pellaea falcata	Adiantaceae	*f*	*	*	*		*
		Pyrrosia confluens var. *confluens*	Polypodiaceae	*ef*	*	*	*		*
		Asplenium australasicum	Aspleniaceae	*ef*	*	*	*	*	*
		Derris involuta	Fabaceae	*c*	*	*	*	*	*
		Diploglottis australis	Sapindaceae	*t*	*	*	*	*	*
		Dysoxylum fraserianum	Meliaceae	*t*	*	*	*	*	*
		Lomandra spicata	Laxmanniaceae	*h*	*	*	*	*	*
		Pyrrosia rupestris	Polypodiaceae	*ef*	*	*	*	*	*
		Archidendron grandiflorum	Mimosaceae	*t*	*	*		*	
		Pentaceras australe	Rutaceae	*t*	*	*		*	
		Dianella caerulea var. *assera*	Hemerocallidaceae	*h*	*		*	*	
		Rhinerrhiza divitiflora	Orchidaceae	*eo*	*		*	*	
		Citronella moorei	Leptaulaceae	*t*	*			*	
		Austrosteenisia glabristyla	Fabaceae	*c*		*	*	*	*
		Wilkiea huegeliana	Monimiaceae	*t*		*	*	*	*
		Cephalaralia cephalobotrys	Araliaceae	*c*		*	*	*	*
		Cordyline rubra	Laxmanniaceae	*sh*		*	*	*	*
		Denhamia celastroides	Celastraceae	*t*		*	*	*	*
		Linospadix monostachya	Arecaceae	*p*		*	*	*	*
		Psychotria simmondsiana	Rubiaceae	*t*		*	*	*	*
		Pothos longipes	Araceae	*ec*		*	*	*	*
		Sarcopteryx stipata	Sapindaceae	*t*		*	*	*	*
		Cryptocarya erythroxylon	Lauraceae	*t*		*		*	*
		Wilkiea austroqueenslandica	Monimiaceae	*t*		*		*	*
		Microsorum scandens	Polypodiaceae	*ef*		*		*	*
		Eupomatia laurina	Eupomatiaceae	*t*			*	*	*
		Helicia glabriflora	Proteaceae	*t*			*	*	*
		Melodinus australis	Apocynaceae	*c*			*	*	*
		Solanum inaequilaterum	Solanaceae	*sh*			*	*	*
		Geitonoplesium cymosum	Hemerocallidaceae	*c*			*		*

TABLE 1. continued…

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
c cont…		*Pandorea floribunda*	Bignoniaceae	*c*		*	*		*
d	*	*Anthocarapa nitidula*	Meliaceae	*t*	*	*	*	*	
19 species	*	*Trophis scandens* subsp. *scandens*	Moraceae	*c*	*	*	*	*	
	*	*Arthropteris tenella*	Nephrolepidaceae	*ef*	*	*	*	*	
	*	*Argyrodendron trifoliolatum*	Sterculiaceae	*t*	*	*	*	*	
	*	*Argyrodendron actinophyllum* subsp. *actinophyllum*	Sterculiaceae	*t*	*	*	*	*	
	*	*Araucaria cunninghamii* var. *cunninghamii*	Araucariaceae	*t*	*	*	*	*	
	*	*Brachychiton acerifolius*	Sterculiaceae	*t*	*	*	*	*	
	*	*Baloghia inophylla*	Euphorbiaceae	*t*	*	*	*	*	
	*	*Atractocarpus chartaceus*	Rubiaceae	*t*	*	*	*	*	
	*	*Caesalpinia subtropica*	Caesalpiniaceae	*c*	*	*	*	*	
	*	*Cryptocarya obovata*	Lauraceae	*t*	*	*	*	*	
	*	*Diospyros pentamera*	Ebenaceae	*t*	*	*	*	*	
	*	*Embelia australiana*	Myrsinaceae	*c*	*	*	*	*	
	*	*Elaeodendron australe* var. *australe*	Celastraceae	*t*	*	*	*	*	
	*	*Doodia aspera*	Blechnaceae	*f*	*	*	*	*	
	*	*Ficus watkinsiana*	Moraceae	*t*	*	*	*	*	
	*	*Notelaea johnsonii*	Oleaceae	*t*	*	*	*	*	
	*	*Pseudoweinmannia lachnocarpa*	Cunoniaceae	*t*	*	*	*	*	
	*	*Sarcomelicope simplicifolia* subsp. *simplicifolia*	Rutaceae	*t*	*	*	*	*	
e		*Akania bidwillii*	Akaniaceae	*t*		*	*		
14 species		*Tylophora paniculata*	Apocynaceae	*c*		*	*		
		Alocasia brisbanensis	Araceae	*h*		*	*		
		Calanthe triplicata	Orchidaceae	*o*		*	*		
		Daphnandra tenuipes	Atherospermaceae	*t*		*	*		
		Dysoxylum rufum	Meliaceae	*t*		*	*		
		Lastreopsis microsora subsp. *microsora*	Dryopteridaceae	*f*		*	*		
		Parsonsia straminea	Apocynaceae	*c*		*	*		
		Parsonsia longipetiolata	Apocynaceae	*c*		*	*		
		Pseuderanthemum variabile	Acanthaceae	*h*		*	*		
		Pollia crispata	Commelinaceae	*h*		*	*		
		Scolopia braunii	Flacourtiaceae	*t*		*	*		

TABLE 1. continued…

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres) 300	500	700	900	1100
e cont…		*Sarcochilus olivaceus*	Orchidaceae	*eo*		*	*		
		Stenocarpus sinuatus	Proteaceae	*ts*		*	*		
f 16 species		*Austrosteenisia blackii*	Fabaceae	*c*	*		*		
		Cordyline congesta	Laxmanniaceae	*sh*	*		*		
		Cryptocarya bidwillii	Lauraceae	*ts*	*		*		
		Gossia bidwillii	Myrtaceae	*t*	*		*		
		Hodgkinsonia ovatiflora	Rubiaceae	*t*	*		*		
		Myrsine subsessilis subsp. *subsessilis*	Myrsinaceae	*ts*	*		*		
	*	*Cinnamomum oliveri*	Lauraceae	*ts*			*		
	*	*Clematis glycinoides*	Ranunculaceae	*c*			*		
	*	*Claoxylon australe*	Euphorbiaceae	*ts*			*		
	*	*Marsdenia flavescens*	Apocynaceae	*c*			*		
	*	*Pararchidendron pruinosum*	Mimosaceae	*ts*			*		
	*	*Plectorrhiza tridentata*	Orchidaceae	*eo*			*		
	*	*#Passiflora edulis*	Passifloraceae	*c*			*		
	*	*Parsonsia rotata*	Apocynaceae	*c*			*		
	*	*Rhysotoechia bifoliolata* subsp. *bifoliolata*	Sapindaceae	*ts*			*		
	*	*Symplocos thwaitesii*	Symplocaceae	*ts*			*		
g 16 species		*Acronychia pauciflora*	Rutaceae	*t*	*	*			
		Alpinia caerulea	Zingiberaceae	*h*	*	*			
		Aphananthe philippinensis	Ulmaceae	*t*	*	*			
		Bouchardatia neurococca	Rutaceae	*t*	*	*			
		Beilschmiedia obtusifolia	Lauraceae	*t*	*	*			
		Callerya megasperma	Fabaceae	*c*	*	*			
		Davallia pyxidata	Davalliaceae	*ef*	*	*			
		Dockrillia bowmanii	Orchidaceae	*eo*	*	*			
		Elattostachys bidwillii	Sapindaceae	*t*	*	*			
		Gossia hillii	Myrtaceae	*t*	*	*			
		Flindersia australis	Rutaceae	*t*	*	*			
		Jagera pseudorhus var. *pseudorhus*	Sapindaceae	*ts*	*	*			
		Mallotus philippensis	Euphorbiaceae	*t*	*	*			
		Psychotria loniceroides	Rubiaceae	*ts*	*	*			
		Polyscias elegans	Araliaceae	*t*	*	*			

TABLE 1. continued...

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
g cont...		*Rhodosphaera rhodanthema*	Anacardiaceae	*t*	*	*			
h 19 species		*Beilschmiedia elliptica*	Lauraceae	*t*		*			
		Neoachmandra cunninghamii	Cucurbitaceae	*c*		*			
		Cassia marksiana	Caesalpiniaceae	*ts*		*			
		Cayratia eurynema	Vitaceae	*c*		*			
		Urtica incisa	Urticaceae	*h*		*			
		Cordyline petiolaris	Laxmanniaceae	*sh*		*			
		Dockrillia schoenina	Orchidaceae	*eo*		*			
		Gossia acmenoides	Myrtaceae	*t*		*			
		Gmelina leichhardtii	Lamiaceae	*t*		*			
		Euroschinus falcatus	Anacardiaceae	*ts*		*			
		Homalanthus nutans	Euphorbiaceae	*ts*		*			
		Maclura cochinchinensis	Moraceae	*c*		*			
		Legnephora moorei	Menispermaceae	*c*		*			
		Parsonsia ventricosa	Apocynaceae	*c*		*			
		Parsonsia velutina	Apocynaceae	*c*		*			
		Pteris umbrosa	Pteridaceae	*f*		*			
		Syzygium australe	Myrtaceae	*ts*		*			
		Stephania japonica var. *discolor*	Menispermaceae	*c*		*			
		Sicyos australis	Cucurbitaceae	*c*		*			
i 19 species		*Acmena smithii*	Myrtaceae	*t*				*	*
		Atractocarpus benthamianus subsp. *glaber*	Rubiaceae	*t*				*	*
		Caldcluvia paniculosa	Cunoniaceae	*t*				*	*
		Cyathea leichhardtiana	Cyatheaceae	*tf*				*	*
		Cupaniopsis flagelliformis var. *australis*	Sapindaceae	*t*				*	*
		Endiandra crassiflora	Lauraceae	*t*				*	*
		Doryphora sassafras	Atherospermaceae	*t*				*	*
		Geissois benthamii	Cunoniaceae	*t*				*	*
		Fieldia australis	Gesneriaceae	*e*				*	*
		Lenwebbia prominens	Myrtaceae	*t*				*	*
		Parsonsia fulva	Apocynaceae	*c*				*	*
		Pararistolochia laheyana	Aristolochiaceae	*c*				*	*
		Pandorea baileyana	Bignoniaceae	*c*				*	*

TABLE 1. continued…

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
i cont…		*Palmeria scandens*	Monimiaceae	*c*				*	*
		Pilidiostigma glabrum	Myrtaceae	*sh*				*	*
		Orites excelsus	Proteaceae	*t*				*	*
		Rubus nebulosus	Rosaceae	*c*				*	*
		Quintinia verdonii	Quintiniaceae	*t*				*	*
		Syzygium crebrinerve	Myrtaceae	*t*				*	*
j 16 species		*Acradenia euodiiformis*	Rutaceae	*t*				*	
		Tasmannia insipida	Winteraceae	*sh*				*	
		Acronychia suberosa	Rutaceae	*t*				*	
		Acronychia pubescens	Rutaceae	*t*				*	
		Cephalomanes caudatum	Hymenophyllaceae	*ef*				*	
		Cupaniopsis baileyana	Sapindaceae	*ts*				*	
		Dianella caerulea	Hemerocallidaceae	*h*				*	
		Duboisia myoporoides	Solanaceae	*ts*				*	
		Halfordia kendack	Rutaceae	*t*				*	
		Lastreopsis sp. 1	Dryopteridaceae	*f*				*	
		Pittosporum undulatum	Pittosporaceae	*ts*				*	
		Sarcopetalum harveyanum	Menispermaceae	*c*				*	
		Sarcochilus falcatus	Orchidaceae	*eo*				*	
		Synoum glandulosum subsp. *glandulosum*	Meliaceae	*t*				*	
		Streptothamnus moorei	Berberidopsidaceae	*c*				*	
		Stenocarpus salignus	Proteaceae	*ts*				*	
k 38 species		*Actephila lindleyi*	Phyllanthaceae	*t*	*	*	*		
		Vitex lignum-vitae	Lamiaceae	*t*	*	*	*		
		Trichosanthes subvelutina	Cucurbitaceae	*c*	*	*	*		
		Tetrastigma nitens	Vitaceae	*c*	*	*	*		
		Alectryon subcinereus	Sapindaceae	*t*	*	*	*		
		Adiantum formosum	Adiantaceae	*f*	*	*	*		
		Arytera divaricata	Sapindaceae	*t*	*	*	*		
		Arytera distylis	Sapindaceae	*t*	*	*	*		
		Brachychiton discolor	Sterculiaceae	*t*	*	*	*		
		Atalaya multiflora	Sapindaceae	*t*	*	*	*		
		Casearia multinervosa	Flacourtiaceae	*t*	*	*	*		

TABLE 1. continued…

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres) 300	500	700	900	1100
k cont…		*Capparis arborea*	Capparaceae	*t*	*	*	*		
		Croton verreauxii	Euphorbiaceae	*t*	*	*	*		
		Clematis fawcettii	Ranunculaceae	*c*	*	*	*		
		Cleistanthus cunninghamii	Euphorbiaceae	*t*	*	*	*		
		Citrus australasica	Rutaceae	*t*	*	*	*		
		Cissus antarctica	Vitaceae	*c*	*	*	*		
		Cyperus tetraphyllus	Cyperaceae	*h*	*	*	*		
		Cryptocarya triplinervis var. *pubens*	Lauraceae	*t*	*	*	*		
		Dioscorea transversa	Dioscoreaceae	*c*	*	*	*		
		Dendrobium tetragonum	Orchidaceae	*eo*	*	*	*		
		Dendrobium speciosum	Orchidaceae	*eo*	*	*	*		
		Dendrocnide photinophylla	Urticaceae	*t*	*	*	*		
		Drypetes deplanchei	Putranjivaceae	*t*	*	*	*		
		Harpullia hillii	Sapindaceae	*t*	*	*	*		
		Lophostemon confertus	Myrtaceae	*t*	*	*	*		
		Lastreopsis munita	Dryopteridaceae	*f*	*	*	*		
		Melodorum leichhardtii	Annonaceae	*c*	*	*	*		
		Melodinus acutiflorus	Apocynaceae	*c*	*	*	*		
		Pandorea jasminoides	Bignoniaceae	*c*	*	*	*		
		Oplismenus imbecillis	Poaceae	*h*	*	*	*		
		Platycerium superbum	Polypodiaceae	*ef*	*	*	*		
		Planchonella myrsinifolia	Sapotaceae	*t*	*	*	*		
		Planchonella australis	Sapotaceae	*t*	*	*	*		
		Ripogonum brevifolium	Ripogonaceae	*c*	*	*	*		
		Streblus brunonianus	Moraceae	*t*	*	*	*		
		Solanum shirleyanum	Solanaceae	*sh*	*	*	*		
		Solanum serpens	Solanaceae	*sh*	*	*	*		
l 28 species	*	*Acronychia octandra*	Rutaceae	*t*					*
	*	*Arthropteris beckleri*	Nephrolepidaceae	*ef*					*
	*	*Blechnum wattsii*	Blechnaceae	*f*					*
	*	*Blechnum patersonii*	Blechnaceae	*f*					*
	*	*Berberidopsis beckleri*	Berberidopsidaceae	*c*					*
	*	*Callicoma serratifolia*	Cunoniaceae	*t*					*

TABLE 1. continued...

Species group	Sign. species (MCAO ≤1%)	Species	Family	Life Form	Altitudinal group (metres)				
					300	500	700	900	1100
1 cont...	*	*Dendrobium falcorostrum*	Orchidaceae	*eo*					*
	*	*Cyperus disjunctus*	Cyperaceae	*h*					*
	*	*Cyathea australis*	Cyatheaceae	*tf*					*
	*	*Cryptocarya foveolata*	Lauraceae	*t*					*
	*	*Dockrillia pugioniformis*	Orchidaceae	*eo*					*
	*	*Drymophila moorei*	Luzuriagaceae	*h*					*
	*	*Grammitis* sp.	Grammitidaceae	*ef*					*
	*	*Lastreopsis* sp.3	Dryopteridaceae	*f*					*
	*	*Hymenophyllum* sp.	Hymenophyllaceae	*ef*					*
	*	*Hibbertia scandens*	Dilleniaceae	*c*					*
	*	*Helmholtzia glaberrima*	Philydraceae	*h*					*
	*	*Marsdenia rostrata*	Apocynaceae	*c*					*
	*	*Lastreopsis* sp.2	Dryopteridaceae	*f*					*
	*	*Melicope hayesii*	Rutaceae	*ts*					*
	*	*Parsonsia induplicata*	Apocynaceae	*c*					*
	*	*Nothofagus moorei*	Nothofagaceae	*t*					*
	*	*Pennantia cunninghamii*	Pennantiaceae	*t*					*
	*	*Parsonsia tenuis*	Apocynaceae	*c*					*
	*	*Polyosma cunninghamii*	Escalloniaceae	*t*					*
	*	*Ripogonum fawcettianum*	Ripogonaceae	*c*					*
	*	*Ripogonum discolor*	Ripogonaceae	*c*					*
	*	*Quintinia sieberi*	Quintiniaceae	*t*					*
		Species richness			135	147	138	108	80

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