

ENVIRONMENTAL CORRELATES OF SPECIES RICHNESS AT WAIPOUA FOREST SANCTUARY, NEW ZEALAND

Summary: Descriptions of 247 forest stands at Waipoua Forest, Northland, were used to explore relationships between species richness (alpha-diversity) of the vascular flora and stand environmental characteristics, both in terms of total flora and within a number of the component synusiae. The Waipoua forests, with an average of 52 species per forest stand, are comparatively species-rich compared to other New Zealand forests. An ordination score (interpreted as expressing variation in soil fertility related to soil catenary sequences), altitude, and canopy height correlated most strongly with indices of species richness and species diversity, although different synusiae showed different trends. Models using these factors predicted that greatest total species richness and tree species richness would occur in tall forest on moderately infertile sites, but at high altitude for total richness and low altitude for tree richness. Epiphyte richness was highly correlated with altitude, with greatest richness in tall forest on sites at high altitude. Observations of highest total and tree richness at intermediate positions on some environmental gradients are consistent with the intermediate stress/disturbance hypothesis.

Keywords: Alpha-diversity; Waipoua Forest Sanctuary; Northland; species richness; species diversity; forests; epiphytes.

Introduction

The preservation of biodiversity is now a major focus of world conservation strategies. One of the first steps identified as necessary to advance this focus is to characterise and understand patterns of biodiversity in relation to underlying environmental variables (Lubchenco *et al.*, 1991) with the ultimate goal of prediction (Wisheu and Keddy, 1989). The prediction of species diversity from environmental factors is also a goal of theoretical ecology (Peet, Glenn-Lewin and Walker Wolf, 1983; Baker, 1990; Hill and Keddy, 1992).

Many diversity indices have been developed to measure biodiversity, although the development of new measures continues (Cousins, 1991). A commonly used index is simply species richness or species density. This easily measured attribute of communities is thought to relate directly to underlying processes such as competition, speciation, and immigration (Peet, 1978), which in turn are influenced by environmental factors (Richerson and Lum, 1980). It therefore seems reasonable to expect predictable relationships between species richness and environmental factors, particularly those that limit biological processes, such as temperature or nutrient or water availability.

Some of the most interesting recent observations for understanding patterns of biodiversity have been

those of maximum species richness at intermediate levels of biomass in herbaceous communities (Al-Mufti *et al.*, 1977; Wilson and Keddy, 1988) or on moderately infertile soils in tropical forests (Huston, 1980). Such observations have led to the hypothesis that maximum species richness occurs at intermediate levels of stress (site favourability) or disturbance (Connell, 1978; Huston, 1979; Grime, 1979; Tilman, 1988). However, several authors have stressed that species richness responds in a multidimensional way to environmental gradients (Peet, 1978; Margules, Nicholls and Austin, 1987; Allen, Peet and Baker, 1991), so that analyses of changes in species richness with environment should consider a range of potential interactions. Also, studies of patterns of species richness suggest that richness varies both over environmental gradients, i.e. through space, and over successional gradients, i.e. through time (Auclair and Goff, 1971; Peet, 1974; Peet and Christensen, 1988).

The objectives of this paper are to describe patterns of vascular plant species richness (alpha-diversity *sensu* Whittaker, 1972), and to investigate the relationships between species richness and a range of stand environmental characteristics, at Waipoua Forest in Northland. The investigation was confined to mature forest or, occasionally, to that in the latter stages of secondary succession to avoid confounding effects of succession on species richness trends.

Methods

Study area

The Waipoua Forest Sanctuary and Waipoua Kauri Management and Research Area (henceforth 'Waipoua') form a large (12 851 ha), prestigious, and botanically valuable reserve complex on the west coast of Northland, New Zealand (Halkett and Sale, 1986; Burns and Leathwick, 1992, and *in press*). It occurs at 35°38'S latitude and 173°34'E longitude in the catchments of the Waipoua and Wairau Rivers, extends 19 km inland from the coast, and to 640 m altitude. The landscape is dominated by moderately dissected and gently sloping hill country with low-fertility clay soils of basaltic origin (Sutherland *et al.*, 1980; Gibbs, 1964). However, important landscape variation is provided by fertile, alluvial riparian terraces and extremely low fertility plateaux at mid- and high-altitudes.

The Waipoua region experiences a "warm temperate" climate (Meurk, 1984) with a moderately high annual rainfall (1651 mm yr⁻¹ at Waipoua Forest Headquarters, 88 m) evenly spread throughout the year, and a mean annual temperature of 14.1°C (New Zealand Meteorological Service, 1983). With increasing altitude, rainfall increases and temperature decreases. Using regression equations developed by Norton (1985), at the highest altitudes in the study area rainfall is approximately 2500 mm yr⁻¹, with a mean annual temperature estimated at 11.5 °C.

Forests at low altitude are dominated by taraire¹ (*Beilschmiedia tarairi*) and kohekohe (*Dysoxylum spectabile*) with many patches of the massive conifer kauri (*Agathis australis*). Higher-altitude forests have emergent rimu (*Dacrydium cupressinum*) over a canopy dominated by towai (*Weinmannia silvicola*), makamaka (*Ackama rosifolia*), and tawa (*Beilschmiedia tawa*). Four hundred and seventy-eight vascular plant species have been recorded from the study area (Burns and Leathwick, 1992), although only 263 species were found in the vegetation samples.

Collection of compositional data

Data were collected from 247 forest stands. Sampling sites were chosen by regular location along transects positioned to sample across the range of altitudes, aspects, and topographies represented in the study area (Austin and Heyligers, 1989). Sampling procedure followed the 'reconnaissance' method of Allen (1992). In this technique, each

sample records all vascular plant species in height tiers centred in a structurally uniform vegetation patch on a single landform unit. Sampling area or shape is not fixed. Rather, sampling effort is continued until new species are rarely encountered indicating that sample area is larger than the Braun-Blanquet concept of minimal area (Kershaw and Looney, 1985). This concept assumes that, with increasing sampling area, species number approaches an asymptote at an area within which all species characteristic of a habitat type will be found. In practice, the area of forest described by reconnaissance descriptions in this study was approximately 0.02–0.04 ha, which Allen (1992) records as typical for forest ecosystems.

Environmental variables and stand descriptors

At each site altitude, aspect, slope, topographic position, drainage, groundcover characteristics, mean canopy height (Allen, 1992), and canopy cover were recorded. Topographic position was described using the landsurface catena model of Conacher and Dalrymple (1977). This model recognises nine landsurface units at different positions on a soil catena with each unit defined by different soil characteristics responding to differences in soil-forming processes. Drainage was described using the six point soil drainage scale of Taylor and Pohlen (1979) which assesses the rate at which water is removed from the soil. Groundcover characteristics were described by separately assessing the area (%) covered by live vascular vegetation, bryophytes, litter, and surface rock. Canopy cover was estimated by summing the percentage cover for all tiers greater than 5 m high.

Two derived variables were also used: scores on an indirect ordination axis and an index of solar radiation. The first axis (DC1) of an ordination (DCA, detrended correspondence analysis) of weighted species cover data collected for the 247 sampled sites was highly interpretable, and indicated the most important variable in determining species compositional patterns (methods follow Burns and Leathwick, *in press*). There were significant differences ($F = 7.93$, $P < 0.001$) in DC1 scores between samples on different topographic units, with significantly higher scores for samples on upper slopes and ridges than those on middle and lower slopes. Although there are few data on the soils of Waipoua Forest, studies on soil catenae from elsewhere in New Zealand indicate that topography is associated with soil fertility differences that arise probably due to greater leaching in the upper slope positions, leading to lower pH, lower base saturation, and lower P than the less leached downslope positions (Campbell, 1973; Birkeland, 1984). DC1 is

¹ Botanical nomenclature follows Allan (1961), Connor and Edgar (1987) and Molloy (1995).

therefore interpreted as ordering samples by topographically linked variation in soil fertility, from infertile high-DC1 score sites on ridges and plateaux to low-DC1 score sites of high fertility in gullies.

This explanation is consistent with observations of the presence and abundance of the same species sampled here on soils of different fertilities from elsewhere in New Zealand. Species found to occur elsewhere on the most infertile soils (Wardle, 1991) had highest abundances in samples with the highest DC1 scores, e.g., *Halocarpus kirkii*, silver pine (*Manoao colensoi*), *Neomyrtus pedunculata*. Species which occur elsewhere on moderately infertile soils (Ecroyd, 1982; McGlone, 1985; Wardle, 1991) had highest abundances on samples with medium to high DC1 scores, e.g., kauri, hinau (*Elaeocarpus dentatus*), tawari (*Ixerba brexioides*), kanuka (*Kunzea ericoides*), tanekaha (*Phyllocladus trichomanoides*), Hall's totara (*Podocarpus hallii*), tawheowheo (*Quintinia serrata*). Finally, species found elsewhere on semi-fertile to fertile soils (Taylor and Pohlen, 1979; Wardle, 1991) had highest abundances in samples with low scores, e.g., titoki (*Alectryon excelsus*), karaka (*Corynocarpus laevigatus*), kahikatea (*Dacrycarpus dacrydioides*), kohekohe, pukatea (*Laurelia novae-zelandiae*), maire tawake (*Syzygium maire*), puriri (*Vitex lucens*). Also, an analysis of variation of sample soil fertility based on sample location on mapped soil types (Sutherland *et al.*, 1980) was broadly consistent with DC1 representing a soil fertility gradient. Samples on very low-fertility soil types possessed significantly higher DC1 scores than samples on soils with low, medium to low, and medium to high fertility ($F = 16.069$, $P < 0.0001$).

Aspect, slope, and latitude were combined to give an index of incident solar radiation (Revfeim, 1982) and used to replace the angular variable, aspect. However, slope was retained as another variable in data analysis.

Calculation of richness and diversity indices

For each site sampled, species richness (number of vascular species per sample) and two indices of species diversity, the exponentiated form of H' and the reciprocal of Simpson's index ($Simpsons^{-1}$), were calculated, as recommended by Peet (1974). To derive these latter indices, relative abundance of each species was assessed using % cover. Both $\exp(H')$ and $Simpsons^{-1}$ can be interpreted as the number of equally common species needed to produce the same heterogeneity as was observed in the sample (Peet, 1974). H' is most sensitive to changes in the importance of rare species, whilst $Simpsons^{-1}$ index is most sensitive to changes in common species (Peet, 1974).

The area sampled at each site was not identical so that the index of species richness used here can not be used as a measure of species density. However, it is used here on the assumptions that: (1) each sample measures the species richness characteristic of the 'minimal area' of that habitat type; (2) slight differences in sampling area will not substantially affect this index; and (3) it is comparable with other studies. Reconnaissance samples have been previously used to analyse variation in vegetation species richness and composition in New Zealand forests, e.g., Wardle *et al.* (1971), Wardle (1984), Reif and Allen (1988), and Allen *et al.* (1991).

Plant species diversity, particularly in forest ecosystems, is complicated by the huge range of size and life expectancy of different plant species. Several authors have suggested that a clearer understanding of patterns of species richness in forest communities requires that patterns be assessed in component synusiae (*sensu* Richards, 1952), or 'guilds', comprising species that utilise common resource pools (Peet, 1978; Colwell, 1979; Grubb, 1987; Peet and Christensen, 1988; Minchin, 1989). Wilson (1989) argues that splitting species between vertical strata in forest situations does allow synusiae to be defined that utilise different resources. I also recognised that epiphytes can be separated on the basis of different resource use. Therefore, the 263 species recorded in samples were divided into the following 5 synusiae and the species richness of each synusia on each site calculated:

- Trees (adult height > approximately 12 m, 27 species);
- Shrubs ('woody' but usually < 12 m adult height, 69 species);
- Herbs ('herbaceous' ground plants, 108 species);
- Lianes (climbers, 18 species); and
- Epiphytes (41 species).

Data analysis

Pearson's product moment correlations were calculated between species richness and diversity measures and continuous environmental variables. Also, analyses of variance were carried out between species richness and diversity measures on different topographic positions.

A selection of environmental variables were then used to predict total species richness and richness for each synusia using the non-parametric regression technique of Generalised Additive Models (Hastie and Tibshirani, 1990; Yee and Mitchell, 1991). Four variables were selected which most closely approximated measures of environment relevant to community development: mean canopy

height (a surrogate for biomass), or to plant growth - DC1 (approximating soil fertility), altitude (a surrogate for climatic moisture and temperature gradients), and solar radiation index (available light). These were not substantially intercorrelated.

Results

Total species richness ranged from 24 to 70 vascular plant species per sample, with a mean of 52 (Table 1). However, despite this large range, total species richness was surprisingly uniform between samples (i.e., low coefficient of variation). On average, each sample had approximately equivalent numbers of tree, shrub, herb, and epiphyte species but fewer liane species. There was most variation between samples in the number of herbaceous and epiphyte species, i.e., a high coefficient of variation (Table 1).

Total species richness and diversity measures were significantly correlated with species richness of all synusiae (Table 2). However, few synusiae were intercorrelated apart from epiphyte and liane richness, and shrub and tree richness (Table 2).

Total species richness was significantly correlated with altitude, canopy height, and DC1, and varied significantly between different topographic units (Table 2). Tree richness was positively correlated with DC1, drainage, canopy height, canopy cover, and % litter groundcover, and negatively correlated with altitude and % bryophyte groundcover (Table 2). Shrub richness was strongly correlated with DC1 and varied significantly between topographic units (Table 2). No environmental variable measured, other than the descriptive variables of groundcover condition, showed any relationship to herbaceous species richness (Table 2). Epiphyte richness was highly positively correlated with altitude, canopy height, canopy cover and bryophyte groundcover (Table 2).

Liane richness showed a weak relationship with altitude (Table 2). The diversity indices showed a positive correlation with DC1 and significant variation between topographic units (Table 2).

The most positive and most frequent correlations between species richness and environmental variables occurred with DC1 and altitude (though still only of moderate strength). These relationships were examined further by plotting richness and diversity trend surfaces on DC1 and altitude (Fig. 1). There is a small increase in total species richness and diversity on the leading diagonal of these trend surfaces, with the highest values occurring at high altitudes and high DC1 scores (interpreted as low fertility on ridges or plateaux) (Fig. 1a-c). However, this pattern is a consequence of adding together quite different trends occurring for some synusiae (Fig. 1d-h). Tree species richness increases most strongly with DC1 at low to middle altitudes but not at higher altitudes. Highest shrub species richness occurs at high DC1 values. Epiphyte species richness shows a strong increase with altitude and little response to DC1. In contrast, liane and herbaceous species richness show little variation of richness across these two axes.

The most significant multiple regression models developed to predict total richness and diversity indices and synusiae richnesses using different combinations of four selected variables still had R^2 values between 16.4% and 33.9% (Table 3). DC1 was the variable most commonly involved in the regression models, with the models often improved using a non-linear, mostly quadratic form of this variable. Altitude and canopy height were also commonly included in models, with epiphyte richness predicted most significantly using altitude in a non-linear form. From these models, highest total species richness is associated with tall-canopied, higher altitude forests scoring in the mid-range of DC1 (i.e., moderately infertile sites on upper slopes and ridges).

Table 1: Means, standard deviations, coefficients of variation, and ranges for vascular plant species richness and diversity indices calculated for 247 forest samples of the Waipoua study area.

Index	Mean	SD	Coeff. of variation (%)	Minimum	Maximum
Total species richness	51.8	8.2	15.8	24	70
Simpsons ⁻¹	21.7	4.2	19.6	10.0	34.4
Exp (H')	29.6	5.1	17.3	13.7	44.1
Tree-richness	10.1	2.4	23.8	4	16
Shrub-richness	13.8	3.2	22.8	6	23
Herb-richness	10.1	2.9	29.0	2	23
Liane-richness	6.4	1.9	28.9	0	13
Epiphyte-richness	11.3	4.1	36.5	0	21

Table 2: Significant Pearson product moment correlations between synusia and total species richness and diversity indices, and continuous environmental variables. Significant *F* values resulting from analyses of variance of species diversity indices between these indices and different topographic units are also presented. * = $P < 0.01$, ** = $P < 0.001$.

Variable	Trees	Shrubs	Herbs	Lianes	Epiphytes	Total richness	Simpsons ⁻¹	Exp (H')
<i>Correlation coefficients:</i>								
Shrubs	0.346**							
Herbs								
Lianes		0.175*						
Epiphytes			0.166*	0.340**				
Total richness	0.440**	0.594**	0.522**	0.551**	0.646**			
Simpsons ⁻¹	0.503**	0.687**	0.250**	0.389**	0.186*	0.688**		
Exp (H')	0.518**	0.740**	0.372**	0.442**	0.331**	0.842**	0.953**	
Altitude	-0.274**			0.254**	0.481**	0.295**		
Vegetation groundcover			0.309**					
Bryophyte groundcover	-0.235**				0.204**			
Litter groundcover	0.236**		-0.282**		-0.175*			
Mean canopy height	0.276**	0.176*		0.163*	0.238*	0.279**		
Canopy cover	0.217**				0.247**			
DC1	0.262**	0.469**				0.231**	0.343**	0.368**
Drainage	0.239**							
<i>Analyses of variance:</i>								
Topography		3.149*	3.335*			2.936*	4.875**	5.169**

Table 3: Summary of regression models for predicting total species richness and species richness in synusiae from DC1, altitude, canopy height, and incident solar radiation.

Predicted variable	Predictor variable	df	Coefficient	<i>P</i>	R ² (%)
Total richness	Constant	1	3.54	< 0.001	23.3
	DC1	1	0.00289	< 0.001	
	(DC1) ²	1	-0.0000078	< 0.001	
	Altitude	1	0.00022	0.001	
	Canopy height	1	0.00508	< 0.001	
Trees	Constant	1	2.19	< 0.001	33.9
	DC1	4	0.001041	< 0.001	
	Altitude	1	-0.000732	< 0.001	
	Canopy height	1	0.00693	< 0.05	
Shrubs	Constant	1	2.38	< 0.001	21.6
	DC1	1	0.00161	< 0.001	
Lianes	Constant	1	1.31	< 0.001	16.4
	DC1	1	0.00805	< 0.001	
	(DC1) ²	1	-0.0000247	< 0.001	
Epiphytes	Constant	1	1.44	< 0.001	31.9
	DC1	1	-0.00111	< 0.001	
	Altitude	4	0.001293	< 0.001	
	Canopy height	1	0.0129	< 0.001	
	Solar radiation	1	0.496	< 0.05	
Exp (H')	Constant	1	3.05	< 0.001	20.4
	DC1	1	0.00373	< 0.001	
	(DC1) ²	1	-0.00000217	< 0.001	
Simpsons ⁻¹	Constant	1	2.73	< 0.001	17.1
	DC1	1	0.00376	< 0.001	
	(DC1) ²	1	-0.00000832	< 0.01	

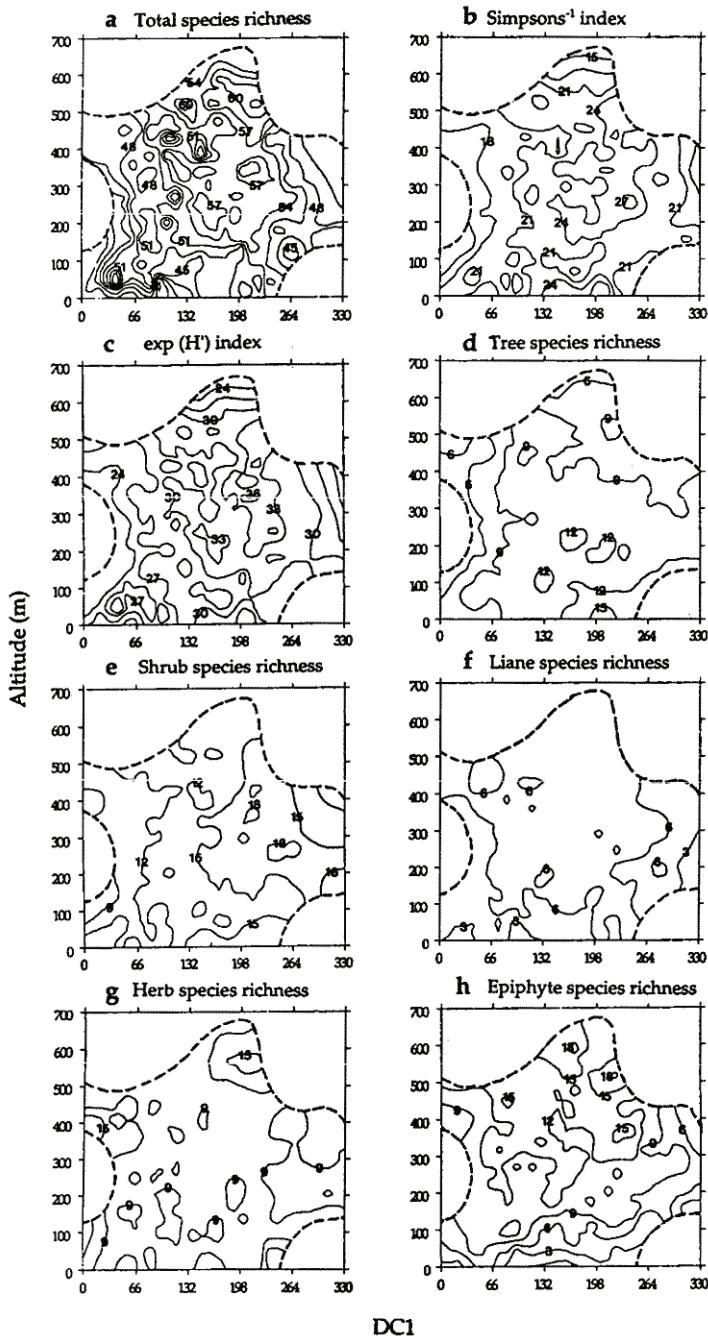


Figure 1: Contour plots of species richness and diversity indices (totals and for *synusiae*) on DC1 (an ordination axis interpreted as reflecting high to low soil fertility) and altitude for Waipoua forests: (a) total species richness, (b) $Simpsons^{-1}$ index, (c) $\exp(H')$, (d) tree species richness, (e) shrub species richness, (f) liane species richness, (g) herb species richness, and (h) epiphyte species richness. Contours were generated using the method of Lodwick and Whittle (1970) combined with linear interpolation. Dotted lines enclose the sampling envelope. Contour interval = 3.

Highest total diversity was also associated with moderately infertile sites. Each synusia's predicted location of maximum species richness differs somewhat from this. Tree richness is predicted to be highest in forests with tall-canopies on moderately infertile sites at lower altitude. Highest shrub species richness is predicted to occur on the most infertile sites on ridges and plateaux (high DC1 scores) and lianes on moderately infertile sites (moderate DC1 scores). Maximum epiphyte species richness is predicted to occur in tall forests on fertile (low DC1 scores), high altitude sites with high solar radiation (i.e., north-facing). No combination of the test variables provided a significant regression model for herb species richness.

Discussion

There have been surprisingly few studies of forest alpha-diversity in New Zealand. In podocarp/ hardwood forest in the central North Island, Leathwick (1987), Leathwick, Wallace and Williams (1988), and J.R. Leathwick (*pers. comm.*) found between 28 and 51 species per reconnaissance sample in different forest types. The most species-rich beech-dominant forests (*Nothofagus* spp.) of the lower North Island and South Island have between 30 and 40 species per sample (Wardle, 1984, p. 126). Similarly, Reif and Allen (1988) recorded between 24 and 37 species per sample in podocarp/ hardwood forest types in central Westland. Mixed podocarp/hardwood forests near Dunedin have about 24 vascular species per 0.01 ha plot (Wilson and Sykes, 1988), while Fiordland vegetation has between 20 and 40 species per 0.01 ha plot (Lee, Ward and Wilson, 1991). These figures suggest that the forests of Waipoua, at an average of 52 species per sample, have a comparatively high alpha-diversity. Northland forests are noted for their high diversity of vascular species, particularly woody species (McGlone, 1985). Internationally, the levels of richness at Waipoua may be considered medium to high for temperate forests but low in comparison to tropical rainforests (Rice and Westoby, 1983).

Environmental variables and stand descriptors that were most strongly correlated with species richness at Waipoua were DC1, altitude, and mean canopy height. DC1 is interpreted as a surrogate variable for soil fertility variation across catenary sequences and has been found to have a dominating influence in terms of site composition (Burns and Leathwick, 1992; *in press*). Altitude is an indirect gradient (*sensu* Austin, 1990) which can be partitioned into several direct factors such as temperature and rainfall (Austin, Cunningham and

Fleming, 1984). However, these may vary with altitude in different ways at different localities. At Waipoua precipitation is uniform through the year (New Zealand Meteorological Service, 1983) and, therefore, change with altitude probably reflects the influence of temperature more than rainfall. Canopy height is not an environmental variable but can perhaps be interpreted as representing forest site productivity (Hägglund, 1981).

Wardle (1984) reported that total species richness in beech forest increased to 300 m altitude then decreased to timberline at 1200 m. Reif and Allen (1988) found a significant decline in tall forest richness with altitude from sea level to 1100 m in central Westland. In this study, total species richness increased slightly with altitude over the range 0-640 m. These differences may be a result of changes in altitude reflecting different direct influences at different locations. For instance, at Waipoua temperatures experienced at 600 m are equivalent to those experienced at only 100 m in central Westland (Norton, 1985). However, alternatively, explanations of patterns of total vascular plant species richness may need to be sought in the simpler patterns of component synusiae. The altitudinal pattern of total species richness at Waipoua was the cumulative result of epiphyte richness increasing with altitude at a greater rate than tree richness declined. Other synusiae embodied less variation. Minchin (1989) also found that a complex pattern of total richness for Tasmanian forests was a consequence of the cumulative effect of different and simpler patterns occurring in different synusiae.

Canopy height was correlated with total, tree, and epiphyte richness. This may simply reflect the volume of habitat available to support species on any area. However, it may also reflect stand age (as the time available for species to colonise that site following stand-initiating disturbance), site biomass, or site productivity (Hägglund, 1981). Several studies of herbaceous vegetation indicate that species richness is related in a complex way to biomass (Al-Mufti *et al.*, 1977; Wheeler and Giller, 1982; Wisheu and Keddy, 1989).

Shrub richness increased with declining DC1 (soil fertility). Small trees and shrubs in the understorey probably experience a fertility gradient quite differently from dominant canopy species. Understorey plants mainly compete for the light remaining after most has been screened out by canopy trees (Givnish, 1982; Tilman, 1988). At the fertile end of this gradient, dominant tree species probably intercept most of the light (Peet and Christensen, 1988). However, lower-fertility sites generally have more open canopies, with light reaching to lower strata (Tilman, 1988). The

probable relationship of high shrub richness to low soil fertility on upper slopes and ridges suggests that, even though soil resources are diminished on infertile sites, increases in light availability allow a more diverse subcanopy to develop.

Epiphyte richness is strongly and positively correlated with altitude. The amount of trunk surface available for epiphytic colonisation and growth is probably dependent on the surface area that is regularly moist enough to support plant growth. Such surface area probably increases at higher altitudes with higher precipitation and mist cover. Therefore, the increase in epiphyte diversity with altitude may simply reflect increases in available habitat. Moreover, at sites with higher rainfall, different types of surface may become available, e.g., areas on the underside of branches, so that epiphyte habitat diversity may also be greater at higher altitudes. Epiphyte diversity was also highest on sites with tall canopies. Taller trees probably provide more sites for epiphytic colonisation and therefore more habitat area and diversity.

Synusia richnesses were generally not inter-correlated, whereas each synusia was correlated with total richness. This suggests that these synusiae generally function independently in determining species richness and somewhat supports the subdivisions undertaken in this study. Positive correlations between tree and shrub richness, and epiphyte and liane richness did occur perhaps indicating interactions within these group pairs.

Huston (1980) found that tree species richness was negatively correlated with soil nutrient availability in tropical forests of Costa Rica, although he noted that extremely infertile forests also showed reduced species richness. Assuming that DC1 does reflect soil fertility differences, I also found that tree and total species richness increased with decreasing fertility but decreased again on the least fertile sites. Such observations are consistent with the intermediate stress/disturbance hypothesis (Connell, 1978; Tilman, 1988; Grime, 1979; Huston, 1979). The two measures of species diversity used also followed this general pattern suggesting that evenness of species abundance also increases to a maximum on moderately infertile sites. However, Peet and Christensen (1988) report a strong positive correlation between total species richness and soil cation status in steady-state forests in North Carolina. This trend was attributable to the herb and shrub strata (equivalent to synusiae), which are numerically dominant in these predominantly deciduous forests; the tree species richness showed no trend with soil cations.

This study indicates that plant species diversity should be viewed as variation across several

interacting gradients (Peet, 1978). Also, groups of morphologically similar plants may experience considerably different resource levels and limitations than site conditions alone would suggest, owing partly to the influence of other synusiae with which they co-occur. For instance, shrub richness is probably determined by the availability of light not intercepted by trees, and epiphyte richness is probably determined by the availability of moist surface area. Therefore the availability of microhabitats within a synusia changes subtly across environmental gradients. Nevertheless, examination of species richness in plant synusiae partially based on vertical stratification of forest appears to have been a revealing approach in exploring patterns of total vascular plant species richness and diversity.

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