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Patterns of tree species richness in relation to environment in southeastern New South Wales, Australia

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Abstract We present regression models of species richness for total tree species, two growth forms, rainforest trees (broadleaf evergreens) and eucalypts (sclerophylls), and two large subgenera of *Eucalyptus*. The correlative models are based on a data set of 166 tree species from 7208 plots in an area of southeastern New South Wales, Australia. Eight environmental variables are used to model the patterns of species richness, four continuous variables (mean annual temperature, rainfall, radiation and plot size), plus four categorical factors (topographic position, lithology, soil nutrient level and rainfall seasonality). Generalized linear modelling with curvilinear and interaction terms, is used to derive the models. Each model shows a significant and differing response to the environmental predictors. Maximum species richness of eucalypts occurs at high temperatures, and intermediate rainfall and radiation conditions on ridges with aseasonal rainfall and intermediate nutrient levels. Maximum richness of rainforest species occurs at high temperatures, intermediate rainfall and low radiation in gullies with summer rainfall and high nutrient levels. The eucalypt subgenera models differ in ways consistent with experimental studies of habitat preferences of the subgenera. Curvilinear and interaction terms are necessary for adequate modelling. Patterns of richness vary widely with taxonomic rank and growth form. Any theories of species diversity should be consistent with these correlative models. The models are consistent with an available energy hypothesis based on actual evapotranspiration. We conclude that studies of species richness patterns should include local (e.g. soil nutrients, topographic position) and regional (e.g. mean annual temperature, annual rainfall) environmental variables before invoking concepts such as niche saturation.

Key words: environmental gradients, *Eucalyptus*, generalized linear modelling, plant diversity, species richness.

INTRODUCTION

What aspects of the environment are correlated with variations in the number of species per unit area? Can causal explanations be found for the observed patterns of species richness in relation to environment? Theories regarding these questions have been reviewed elsewhere (Brown 1981; Giller 1984; Begon *et al.* 1990; Schluter & Ricklefs 1993; Huston 1994).

There are long-recognized patterns of plant species richness in relation to latitude, altitude and sea depth (Giller 1984; Stevens 1989, 1992; Begon *et al.* 1990; Currie 1991; Huston 1994). These patterns are assumed to reflect the differential capacity of the environment to support species. Ultimately, the carrying capacity reflected in such variables as latitude or altitude is determined by the physical environment (Brown 1981; Rohde 1992). The environment varies in terms of the availability of energy, nutrients, light and other variables that determine plant growth. Environmental variables often covary along latitudinal or altitudinal gradients: there is no direct causal relationship between latitude and species richness. Latitude and altitude have been termed indirect gradients by Austin (1980). Correlative studies with such multi-factor variables are unlikely to generate insight into biological processes controlling species richness.

Statistical methods used in published analyses of diversity have varied widely but in general have not examined curvilinear responses or interactions among resource and environmental gradients (*sensu* Austin 1980). There are few empirical studies with careful quantitative descriptions of species richness patterns in relation to a multi-factor description of environment for plants (e.g. Currie & Paquin 1987; Margules *et al.* 1987; Currie 1991; Pausas 1994).

Peet (1978) and Grubb (1987) suggested that the pattern of plant species richness is different for different structural groups. However, few studies consider more

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than one growth form or taxonomic category (e.g. Richerson & Lum 1980; Minchin 1989; Pausas 1994). Patterns in species richness and associated environmental variation need to be described as accurately and unambiguously as possible in order that observed patterns can be compared with those predicted by explanatory theories. Rival theories cannot easily be distinguished otherwise.

In this paper, we provide a detailed quantitative description of the species richness patterns of trees for a large region (approximately 40 000 km^2). We endeavour to present statistically rigorous models of the patterns of tree species richness in relation to a large number of environmental variables using generalized linear modelling (McCullagh & Nelder 1989). Any theory seeking to explain variations in species richness should generate predictions that are consistent with these observed patterns. We believe that environmental variables operating at a local and regional scale are primary predictors of species richness patterns and that variables associated with spatio-temporal heterogeneity and species dispersal (e.g. Cornell & Lawton 1992) are of secondary importance.

The aims of this paper are to determine: (i) the extent to which species richness patterns can be modelled solely on the basis of environmental variables; (ii) the relative importance of different variables in predicting species richness; and (iii) the different patterns of species richness for different life forms. We present models for total tree species, two growth forms, rainforest trees (i.e. broadleaf evergreens) and eucalypts *sensu lato* (i.e. sclerophyllous species), and two large subgenera of *Eucalyptus*.

DATA AND METHODS

A data set was compiled, consisting of 7208 plots from southeastern New South Wales (Australia) in which the presence or absence of tree species was recorded. The data were collected from extensive surveys done in the area by a range of individuals and organizations, who have kindly made the data available (see Acknowledgements in Austin *et al.* 1990). They used a variety of sampling strategies and plot sizes, and measured a wide variety of vegetation and environmental attributes for each plot. A minimum data set of presence/absence of tree species and location was compiled from the surveys and environmental variables were derived from site descriptions and/or maps. The study area covers approximately 40 000 km^2. The plot size varies from 0.04 to 0.25 ha, but 65% of the plots had a size of 0.10 ha. Climate and topography vary widely over the study area. The rainfall varies from an annual total of 480 mm to 2200 mm with markedly different seasonal patterns while mean annual temperature varies from 2.5 to 17°C. Altitudes in the area range from sea level to Australia's highest peak, Mt Kosciusko, 2228 m a.s.l. The study area is limited by the coast in the east and by the Victorian border to the south. The northern and western limits correspond to 35°S of latitude and 148° of longitude. Austin *et al.* (1990) provide location maps and a more detailed description of the study area and its environment. Their models of the environmental niche of selected eucalypt species are based on a subset of the data analysed here.

Four groups of species were studied: all tree species; rainforest species; eucalypt species *sensu lato* (i.e. including the genus *Angophora*); and others. Numbers of species in each group were calculated. The eucalypts were further subdivided into the genus *Angophora* and the three *Eucalyptus* subgenera, *Monocalyptus*, *Symphyomyrtus* and *Corymbia* (Table 1). The species number or richness for each group (excluding *Angophora* and *Corymbia*, which had too few species per group, and 'others', which was a heterogeneous group) was then used as the dependent variable in the regression models.

Eight predictors were used to define the environmental space, four continuous variables (Table 2) and four categorical factors. Mean annual temperature and mean annual rainfall were estimated using a Laplacian smoothing spline procedure based on records of weather stations in the area and their elevation, latitude and longitude (Adomiet *et al.* 1984; Hutchinson 1984). Values for the

Table 1. Characteristics of the samples used to fit the models

Species group	Plots (*n*)	Species (*n*)	Maximum no. species	Mean no. species Total	Mean no. species Presence
Trees	6831	166	23	3.36	3.55
Rainforest	929	48	20	0.49	3.80
Eucalyptus	6421	83	10	2.49	2.80
Monocalyptus	5879	30	6	1.42	1.74
Symphyomyrtus	4343	49	5	0.88	1.46
Corymbia	796	2	2	0.12	1.10
Angophora	507	2	2	0.07	1.00
Others	2105	35	6	0.38	1.30

For each species group, the number of plots = the number of plots sampled in which the group occurs; the number of species = number of species in the group; maximum number of species = maximum number of species found together on a single plot; mean number of species = mean number of species found together for all plots (total) and for plots where that group is present (presence).

Table 2. Range of values of the continuous variables used to fit the models of species richness

Variable	Minimum	Maximum
Annual rainfall (mm)	486.3	2125.5
Mean annual temperature (°C)	2.6	17.0
Mean daily radiation (Mj/m^2)	10.2	18.43
Plot size (ha)	0.04	0.25

radiation variable were estimated using a similar procedure modified to include mean annual rainfall as a surrogate for local cloudiness and then adjusted for the aspect and slope of the plots (Mackey *et al.* 1988). The fourth continuous variable was plot size.

The four categorical factors used to categorize each plot were soil nutrient index, rock type, topography and seasonality of rainfall. A nutrient index was calculated based on phosphorus content of the bedrock for each of 159 rock types. Geochemical data were used to give a mean phosphorus pentoxide content for each rock type (Cocks *et al.* 1995). The numbers of observations per rock type vary widely but significant differences exist between many rock types. These mean values provide the best available estimate of nutrient status. The soil nutrient index values were categorized from 1 (poorest) to 5 (richest). The rock types were clustered in five classes (volcanic, hard sediments, soft sediments, granites and others). There is only limited correlation between the five rock types and the five nutrient levels. Six topographic positions were distinguished: ridge, slope, lower slope, gully, flat, and others or unknown. Three seasonalities of rainfall were recognized: summer-dominated, aseasonal and winter-dominated; these are related to three geographical situations: coastal hills, tablelands, and western slopes and mountains, respectively (Austin & Yapp 1978).

Numerical analysis

Generalized linear models (GLM; McCullagh & Nelder 1989) of species richness were developed for each group of tree species. Austin *et al.* (1990; see also Austin *et al.* 1984) provide an explanation of the method, while Nicholls (1989, 1991) provides a detailed exposition of the use of the method in modelling plant species distribution. A Poisson error distribution for the number of species was assumed in all models. The response variable, species richness, was linked to the linear predictor (LP: the set of predictor variables) via a logarithmic link function. The linear predictor was therefore:

$$V_{LP} = f[\text{mean annual temperature, mean annual rainfall, mean monthly radiation, plot size, rock type (5), topography (6), seasonality (3), nutrient index (5)}]$$

where V refers to the species number (number of levels per categorical factor is indicated in parentheses).

A forward stepwise procedure was used to enter the variables into the model. Only variables that accounted for a significant change in deviance with probability less than 0.001 were included in the model. This conservative level of significance was chosen because, with the large number of degrees of freedom available, chance effects can appear significant at the conventional 5% level. Simple polynomial functions up to order three were tested for continuous variables. The possibility of an interaction between rainfall and temperature was investigated by fitting a trend surface (Gittins 1968; Margules *et al.* 1987). Plot size was log transformed because of the well-known logarithmic relationship between area and species richness. The goodness of fit was measured by the deviance statistic. The change in deviance after including a parameter in the model was tested by a Chi-squared test. When overdispersion was clearly observed (mean residual deviance >2.0), an *F*-ratio test was also performed to ensure the significance of the addition (McCullagh & Nelder 1989). As an example, full details of the equation and a summary of the forward selection of variables is given for total tree species richness (see Results).

The models obtained were tested using residual analysis. Three diagnostic measures (Pregibon 1981) were used: adjusted residuals, coefficient of sensitivity and potential leverage. The polynomial functions were displayed graphically as contour plots of species richness as a function of mean annual temperature and mean annual rainfall. Other predictors were set at selected values and plot size standardized at 0.1 ha for presentation. Those species groups with models that include seasonality of rainfall are shown for the reduced environmental space of climate variables appropriate for a single seasonality class.

RESULTS

Table 1 summarizes the statistics on species richness for each of the groups defined. The maximum number of species found on a plot was twenty-three. Not all plots contained trees. Some rock types frequently supported only heaths, and mountains in the study area extend above the tree line. Contrary to some theories (e.g. Pryor 1959), up to six species of a subgenus of *Eucalyptus* occurred on the same plot.

Total tree species richness

All environmental predictors were significant when tested separately (first step of the forward selection). Each variable was tested as either a linear, quadratic or cubic function, and the function that accounted for the maximum reduction in deviance was selected for inclusion. All remaining variables were then tested for significance as the second step and the process repeated until no more significant variables remain. The final model using this forward stepwise procedure contained in order of entry (Table 3): temperature (T), plot size (lsize), radiation (L), topography (topo), nutrients (nutr), rainfall (R) and rock type (lith). The first level in each categorical factor is set to zero, and the coefficients for the other levels indicate their relative difference from level 1. Seasonality of rainfall did not account for significant deviance when the other variables were in the model and so was not included in the final model. Having fitted a simple polynomial model, the possibility of an interaction between temperature and rainfall was examined by fitting a trend surface. This proved significant (Table 3). The final model and its coefficient values is given by

$$V = \exp(LP)$$

where,

$$\begin{aligned} LP = {} & 5.442 + 0.5945T - 0.9631T^2 + 0.003293T^3 \\ & + 0.2976\mathrm{lsize} \\ & - 0.3342L + 0.008664L^2 \\ & + [+0.04927\mathrm{topo}(2) + 0.1782\mathrm{topo}(3) + \\ & \quad 0.2468\mathrm{topo}(4) - 0.09958\mathrm{topo}(5) + \\ & \quad 0.06489\mathrm{topo}(6)] \\ & + [-0.01737\mathrm{nutr}(2) + 0.1840\mathrm{nutr}(3) + \\ & \quad 0.08164\mathrm{nutr}(4) + 0.1936\mathrm{nutr}(5)] \\ & - 0.01271R + 5.762\times10^{-6}R^2 - 6.214\times10^{-10}R^3 \\ & + [-0.03041\mathrm{lith}(2) - 0.1166\mathrm{lith}(3) - \\ & \quad 0.1194\mathrm{lith}(4) - 0.07476\mathrm{lith}(5)] \\ & + 0.001377RT - 4.001\times10^{-7}R^2T - 2.505\times \\ & \quad 10^{-5}RT^2. \end{aligned}$$

V is the number of species, the numbers in parentheses represent the factor level, and other symbols are as defined in the text previously.

Mean annual temperature was the most important predictor of tree species richness in the study area. A cubic response of this variable was found, with the maximum number of species at the highest temperature values. When the response surface is examined (Fig. 1a,b), the response to rainfall depends on temperature. At low (and intermediate) temperatures, the number of species is quite constant along the rainfall gradient, while at high temperatures a humped response is observed, with the maximum number occurring between 900 and 1200 mm. Species richness has a quadratic relationship with radiation, and topography is the first categorical factor to enter the model. Figure 1 illustrates two contrasted situations: gullies with low radiation and ridges with high radiation, both at the same nutrient level (intermediate) and on the same rock type (granites). The maximum species richness was found in gullies (category topo(4)) with volcanic bedrock (category lith(1)) and an intermediate or high nutrient index.

Eucalypt species richness

All variables were significant when tested independently in the forward stepwise regression procedure. When nutrients were included in the model, rock type was non-significant. Rainfall was significant only when expressed

Table 3. Summary of the forward selection of variables to build the model of total species richness

	Residual		Change		
Model	Deviance	d.f.	Deviance	d.f.	*P*
null	10 754.0	7207			
Step 1					
T	7 980.4	7206	2773.6	1	***
$+T^2$	7 934.4	7205	46.0	1	***
$+T^3$	7 857.7	7204	76.7	1	***
Step 2					
+lsize	7 046.9	7203	810.8	1	***
Step 3					
+L	6 790.6	7202	256.3	1	***
$+L^2$	6 775.4	7201	15.2	1	***
Step 4					
+topo	6 598.5	7196	176.9	5	***
Step 5					
+nutr	6 484.7	7192	113.8	4	***
Step 6					
+R	6 471.6	7191	13.2	1	***
$+R^2$	6 468.6	7190	2.9	1	NS
$+R^3$	6 445.3	7189	23.3	1	***
Step 7					
+lith	6 417.4	7185	27.9	4	***
Step 8					
$+RT+R^2T+RT^2$	6 350.1	7182	67.3	3	***

Residual mean deviance 0.885. R = rainfall; T = temperature; L = radiation; lsize = natural logarithm of plot size; topo = topographic position; lith = rock type; nutr = nutrient index; ***$P<0.001$.

as a cubic function (i.e. the linear and quadratic terms were not significant until the cubic term was added). An interaction between temperature and rainfall was significant. Examination of residuals in relation to radiation suggested that a skewed function was preferable to a quadratic function and a function of the form $x + \log x$ was fitted. The order of variables entered in the model was: temperature, plot size, topography, rainfall, radiation, seasonality of rainfall and nutrient index.

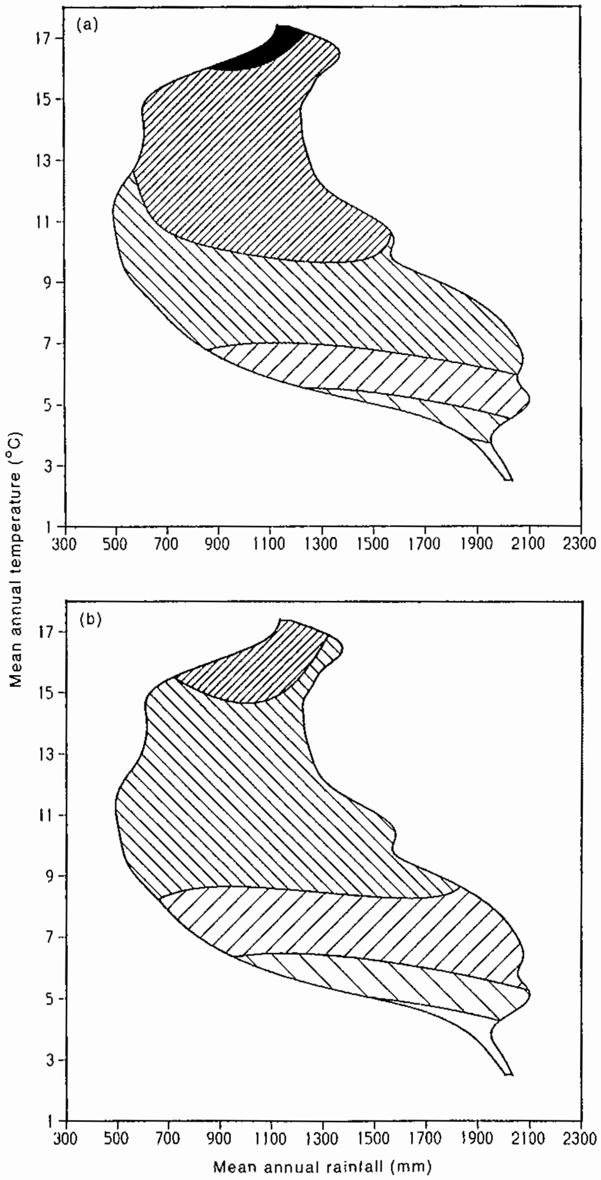

Fig. 1. Contour plots of the total number of tree species per 0.1 ha in the temperature and rainfall space, and in two topographic positions: (a) gullies with low radiation; and (b) ridges with high radiation. Both plots are displayed for granites with intermediate nutrient levels. The region outside the envelope represents unsampled rainfall and temperature combinations. (■) Above 8.0; (▨) 4.0–8.0; (▧) 2.0–4.0; (⧄) 1.0–2.0; (⧅) 0.5–1.0; (□) below 0.5.

The generalized form of the linear predictor (LP) was

$$V_{LP} = f(R^3 + T^3 + R \times T + L + \log(L) + \text{lsize} + \text{nutr} + \text{seas} + \text{topo})$$

where, V = number of species, R = rainfall, T = temperature, L = radiation, lsize = logarithm of plot size, nutr = soil nutrient factor, seas = seasonality of rainfall, topo = topographic position, R × T = interaction terms for cubic trend surface.

The maximum number of eucalypt species was found at high temperature and intermediate rainfall. The two-dimensional environmental space (Fig. 2) shows that at

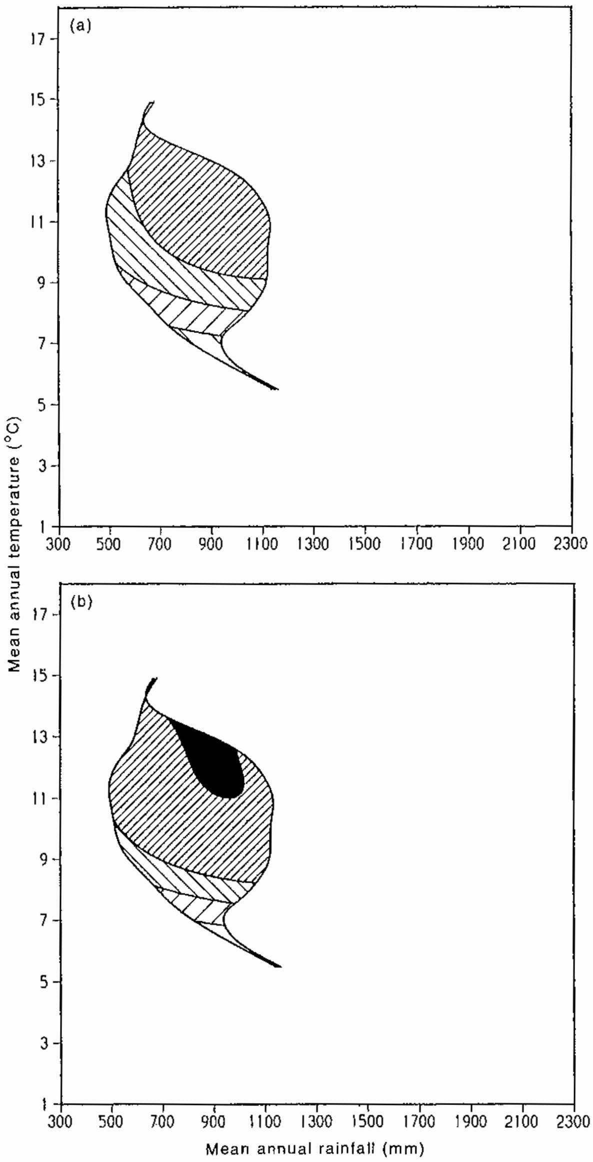

Fig. 2. Contour plots of the eucalypt species richness model on intermediate nutrient level and in aseasonal rainfall areas for (a) gullies with low radiation and (b) ridges with high radiation. (■) Above 3.0; (▨) 2.0–3.0; (▧) 1.5–2.0; (⧄) 1.0–1.5; (⧅) 0.5–1.0; (□) below 0.5.

low temperatures rainfall has only a small influence on the number of eucalypt species, while at intermediate and high temperatures, species richness depends on position along the rainfall gradient. Figure 2 shows predicted species richness at intermediate levels of nutrients and radiation in two contrasted topographic positions: gullies and ridges. Topographic position and radiation have a clearly different influence on eucalypt species richness than on total tree species richness (e.g. compare Figs 1 and 2). *Eucalyptus* species richness is highest on slopes and ridges (Fig. 2a) rather than gullies (Fig. 2b), and there is a positive relationship between number of *Eucalyptus* species and incoming radiation. The relative influence of the different levels of the categorical factors is shown in Table 4 (left column). Species richness of eucalypts is much reduced in gullies and on flats relative to ridges and slopes. It is also reduced at the highest nutrient level and under summer rainfall conditions.

Rainforest species richness

All variables were significant when tested separately. The order they entered into the model was temperature, topography, rainfall, radiation, nutrients, rainfall seasonality and plot size. Temperature and topography were of almost identical importance in explaining rainforest species richness at the first step of the forward selection. Topographic position and rainfall were more important in explaining rainforest species richness than in explaining *Eucalyptus* and total species richness.

Initially, cubic responses for temperature and rainfall were found. The shape of the response curve was a high temperature skewed response and a peaked rainfall response with the maximum at intermediate levels. Inspection of the contour plots produced from this model (not shown) indicated that use of a cubic polynomial

Table 4. Coefficients of the categorical factors for *Eucalyptus* species richness and for species richness of two subgenera of *Eucalyptus*: *Monocalyptus* and *Symphyomyrtus*

	Eucalyptus	*Monocalyptus*	*Symphyomyrtus*
Topographic position			
Ridge	0.0	0.0	0.0
Slope	−0.029	−0.030	0.183
Lower slope	−0.175	−0.276	0.094
Gully	−0.332	−0.505	0.096
Flat	−0.343	−0.549	0.029
Unknown	−0.117	−0.123	0.031
Nutrient Index			
1 (low)	0.0	0.0	0.0
2	−0.025	−0.237	0.264
3	0.017	−0.242	0.454
4	0.053	−0.318	0.567
5 (high)	−0.220	−0.123	0.015
Rock type			
Volcanics		0.0	0.0
Hard sediments		0.184	−0.226
Soft sediments		0.356	−0.206
Granites		0.340	−0.162
Other		−0.117	−0.072
Seasonality of rainfall			
Summer	0.0		0.0
Aseasonal	0.137		0.312
Winter	0.134		0.542

A blank space indicates the factor was not significant for the given species group.

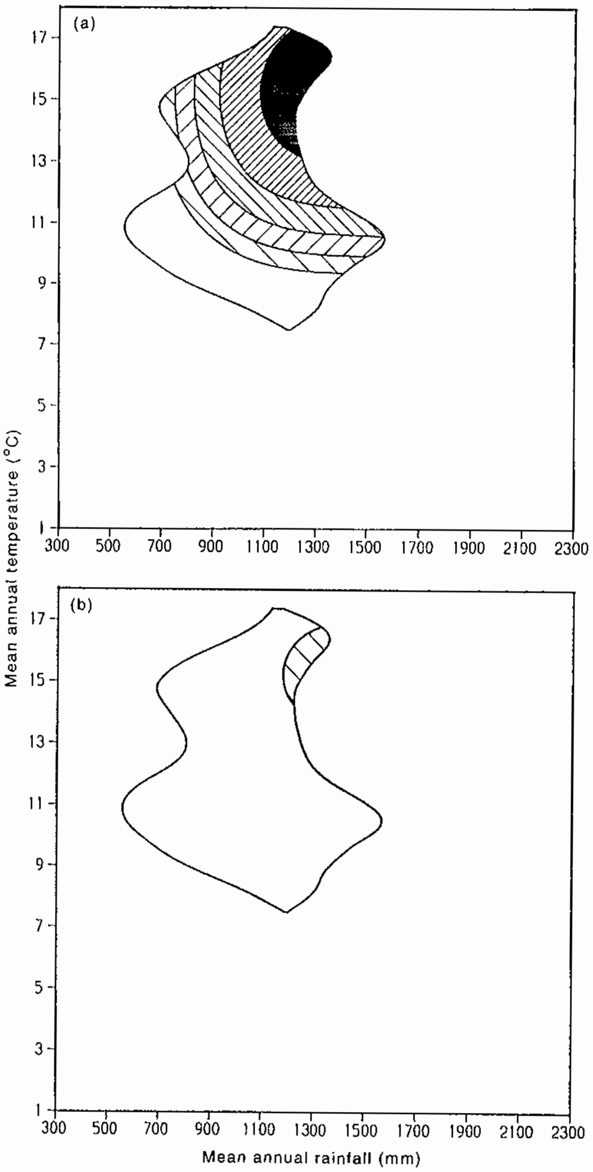

Fig. 3. Contour plots of the rainforest species richness model on intermediate nutrient level, soft sediments for (a) gullies with low radiation and (b) ridges with high radiation. Rainforest species only occur in areas with summer rainfall, so only this section of the environmental space is shown. (■) Above 8.0; (▨) 4.0–8.0; (▧) 2.0–4.0; (▨) 1.0–2.0; (▧) 0.5–1.0; (□) below 0.5.

response surface gave rise to unrealistic predictions at low temperatures. Cubic polynomial functions are well-known to be prone to predict odd values at the extremes of the data space. There were no sampled sites with mean annual temperature less than 8.4°C that had rainforest species. In a correlative analysis, a function is needed that gives a parsimonious description and is biologically rational. A logarithmic function ($x+\log x$) was therefore fitted to overcome the prediction failure at low temperature levels. This yielded a more biologically realistic model, which predicted maximum rainforest species at high temperature and at intermediate levels of rainfall.

The marked contrast in rainforest species richness between gullies and ridges is shown in Fig. 3. Rainforest species richness declines linearly with increasing radiation, in contrast to the model for *Eucalyptus* species where number of species increases with radiation to a maximum and then declines. Maximum numbers of rainforest species are found in gullies, unlike *Eucalyptus*. Rainforest species rarely occur on slopes or ridges (Fig. 3b). The preferred substrate for rainforest is a volcanic bedrock with rich nutrient content.

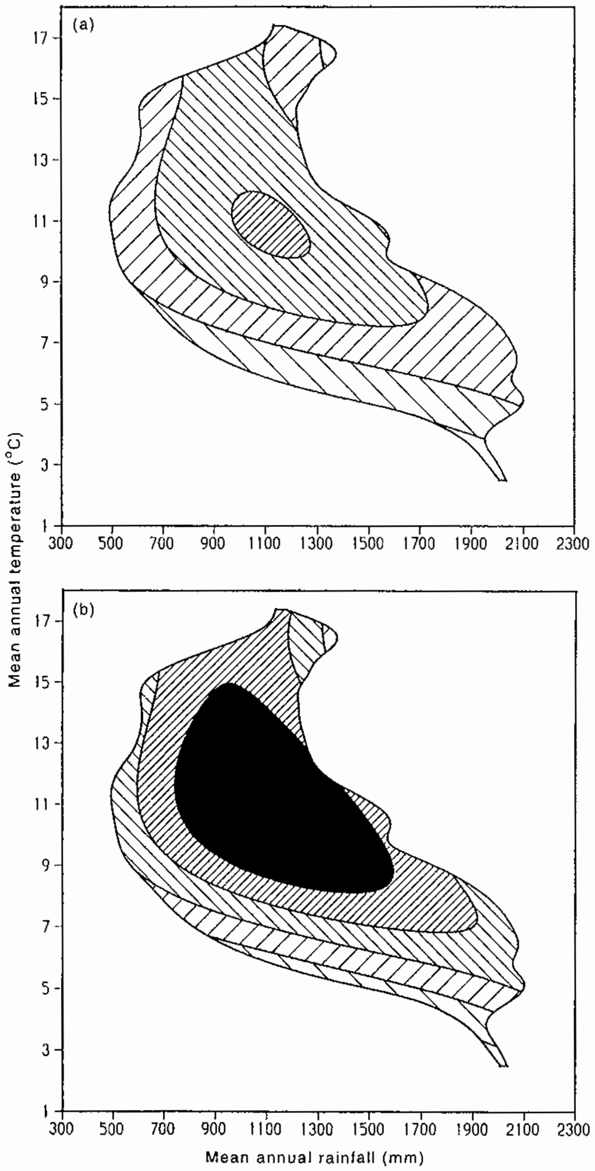

Fig. 4. Contour plots of the *Monocalyptus* species richness model on poor nutrient soft sediments for (a) in gullies with low radiation and on (b) ridges with high radiation. (■) Above 2.0; (▨) 1.6–2.0; (▧) 1.2–1.6; (▨) 0.8–1.2; (▧) 0.4–0.8; (□) below 0.4.

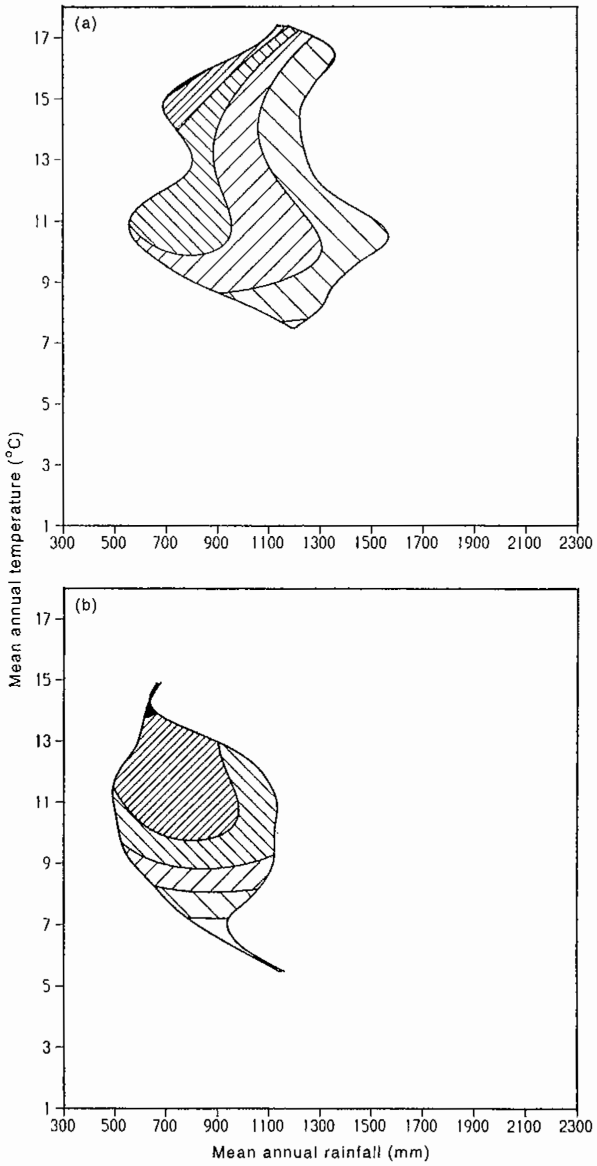

Fig. 5. Contour plots of the *Symphyomyrtus* species richness model on slopes on volcanic nutrient rich soils in (a) areas with summer rainfall and in (b) areas with aseasonal rainfall. (■) Above 3.0; (▨) 2.0–3.0; (▧) 1.5–2.0; (▨) 1.0–1.5; (▧) 0.5–1.0; (□) below 0.5.

Monocalyptus species richness

All environmental variables accounted for significant deviance when tested independently. The final model included, in order of entry: rainfall, topographic position, temperature, plot size, nutrients, rock type and radiation. Seasonality of rainfall did not account for significant deviance when other variables were in the model.

A cubic response surface for two variables, rainfall and temperature, and a quadratic response for radiation, were included in the final model for this subgenus. The maximum *Monocalyptus* richness is at intermediate levels of rainfall and temperature. The radiation response curve is skewed to high values, and the temperature response curve is clearly asymmetric (Fig. 4). High *Monocalyptus* species richness is found on ridges and on sediments and granites with low nutrient index.

Symphyomyrtus species richness

All environmental variables accounted for significant deviance when tested independently. The order of entry into the final model was: rainfall, temperature, seasonality of rainfall, plot size, nutrients, rock type and topography. Radiation was not significant. Significant shifts in behaviour occur between rainfall seasonality levels (Fig. 5).

Cubic functions were fitted for both rainfall and temperature. The response curve of rainfall is skewed, with high species richness at low rainfall. The response curve of temperature is also skewed, with high values at high temperatures (Fig. 5). High *Symphyomyrtus* species richness was found on volcanic slopes with intermediate and rich nutrient content in areas with winter rainfall. Topographic position had a relatively small influence on the species richness values (Table 4).

DISCUSSION

Total tree species richness

Trees occur in almost the entire environmental space of the study area. Trees are absent on some hard quartzose sediments where soils are very shallow and prone to drought, water-logging and fire. Trees are also absent in the coldest areas above 1600 m a.s.l. and in frost pockets. Areas with temperatures sufficiently low to be above the tree line are restricted to the high altitude Snowy Mountains. The maximum number of tree species is found in warm, mesic environments on protected sites with low radiation. These occur in coastal regions with summer rainfall, temperatures above 15°C, annual rainfall greater than 800 mm and low radiation levels. Protected south-facing gullies and lower slopes with moderate to high nutrient levels define the preferred environment. This maximum occurs in those environments that are optimal habitat for rainforest species particularly where protected from fire (Austin 1978; Helman 1983).

These results are consistent with those of Currie (1991) in that most predictors are associated with plant water balance (e.g. temperature, rainfall, radiation and topographic position) and hence to actual evapotranspiration. However, the inclusion of nutrient status suggests that variables other than evapotranspiration may be important. There are clearly constraints on the number of tree species that can occur under different environmental conditions. The temperature constraint is not solely a threshold effect (Woodward 1987), but a continuous influence over the range of temperatures studied. On the basis of these descriptive regression models, and given the evolutionary history of the Australian flora, it could be postulated that there are environmental influences on the number of tree species that a given environment can support. Alternatively, it could be argued that a previous environmental regime may have selectively reduced the number of species from some previous high. The actual causal mechanism remains to be determined.

There are two principal types of the tree life form growing in the study area: broadleaf rainforest trees casting a dense shade; and eucalypt trees with an open branching habit and pendulous, sclerophyllous leaves. The rainforest species are a taxonomically diverse group, although well-recognized as an ecological group in eastern Australia (Helman 1983; Floyd 1989), while the eucalypt (*sensu lato*) life form is a clear taxonomic entity. The two groups make the major contribution to total tree species richness yet comparison of their richness patterns (see Figs 2 and 3) indicates that the orderly pattern for total richness can be disaggregated into quite different types of environmental richness pattern for each group.

Eucalypt species richness

The species richness pattern for eucalypts corresponds quite closely to that described by Margules *et al.* (1987), despite differences in the data sets, the expression and number of environmental variables, and the technical details of the regression modelling. The most significant difference is the influence of topographic position on species richness, a factor not included in the Margules *et al.* (1987) analysis. Eucalypt species are characteristic of exposed positions on slopes and ridges (Fig. 2), rather than the protected gullies and lower slopes favoured by rainforest species (Fig. 3). Topographic position in fact accounts for more deviance than either rainfall or radiation, which were included in the original (Margules *et al.* 1987) analysis. The added factors, nutrient index and rainfall seasonality, also have predictive value but are less important than the variables tested by Margules *et al.* (1987). The coefficient values for the nutrient index indicate a preference for intermediate nutrient levels (Table 4). The coefficients also indicate a slight increase in species richness on the tablelands and western slopes compared with the coast with its summer rainfall conditions.

Margules *et al.* (1987) speculated that low eucalypt species richness under warm temperate, mesic conditions might be due to competition with the rainforest growth form. The different but complementary GLM models obtained for the two groups support this interpretation.

Rainforest species richness

The species richness pattern of rainforest trees contrasts strongly with that of eucalypts (compare Figs 2 and 3). Sites with the highest rainfall have temperatures too low to allow growth of rainforest species. Maximum species richness for rainforest species is found in gullies, as opposed to ridges and slopes for eucalypts. In the region of the environmental space where the higher values of the two groups overlap (upper parts of Figs 2 and 3) they are in fact segregated by topography. Thus, at high temperature with high or intermediate rainfall, high eucalypt and rainforest species richness is expected, but the former occurs on ridges and slopes while the rainforest occurs in gullies. Rainforest species apparently are not able to survive on ridges or slopes in the studied area (Fig. 3b). The extent to which the role of topographic position and radiation is due to direct evaporative demand or to protection from fire or another unmeasured factor is not known.

At low temperatures the number of rainforest species decreases sharply and below 8.4°C no rainforest species occur. Few cool temperate rainforest species occur in the study region. For example, *Nothofagus* species are absent, and the corresponding niche appears to be filled by *Eucryphia moorei* F. Muell., a local endemic. The only other members of the cool temperate element present are *Eleaocarpus holopetalus* F. Muell. and *Atherosperma moschatum* Labill (Helman 1983).

An influence of rock type and nutrients on species richness of rainforest trees was detected but was less important than climate, local radiation or topographic position. This is in accord with the work of Helman (1983).

Species richness of eucalypt subgenera

Three subgenera of *Eucalyptus* occur in the study area, *Monocalyptus*, *Symphyomyrtus* and *Corymbia*. The last has only two species in the study area. *Monocalyptus* species are found in the whole environmental space. The peak of richness is situated at intermediate values of temperature and rainfall, on ridges with low fertility soils on granites and sediments (Fig. 4, Table 4). Seasonality of rainfall is not a significant predictor of *Monocalyptus* richness. *Symphyomyrtus* species cover a narrower environmental space. Topographic position is a less important predictor of species richness for this subgenus than for *Monocalyptus*. The peak of *Symphyomyrtus* richness is on intermediate or high fertility soils and volcanic rock type with low rainfall and high temperature (Fig. 5, Table 4). Seasonality of rainfall has predictive value for species richness of this subgenus. There is a clear tendency for maximum numbers of *Symphyomyrtus* species to occur at a lower rainfall and higher temperature than *Monocalyptus*.

There has been considerable interest in the co-occurrence of species from these two subgenera since Pryor (1953, 1959) put forward his rule, 'In such mixed stands [of eucalypt forest] the two species concerned do not interbreed, and always each is derived from a different subgeneric group'. Several authors (Florence 1963, 1981; Burdon & Chilvers 1974; Burdon & Pryor 1975; Austin *et al.* 1983) have investigated this hypothesis with varying conclusions. In a review of relevant literature, Noble (1989) highlighted traits of the species in each subgenus that suggest the subgenera would occupy distinct ecological niches in the sclerophyll forests of eastern temperate Australia. However, there has been little quantitative analysis of the co-occurrence and the geographical distribution of the subgenera, with the exception of Austin *et al.* (1983). The experimental observations reviewed by Noble (1989) are for varied selections of species from the two subgenera, often with markedly different environmental niches. Consistent comparisons across all traits for a representative selection of species from each subgenus is not yet possible.

The models presented here are consistent with many of the suggestions of Noble (1989) and can be best summarized by a comparison of the factor coefficients from the predictive equations (Table 4). *Monocalyptus* has a clear preference for ridges over lower positions in the landscape; coefficients are increasingly negative. *Symphyomyrtus*, while having a maximum coefficient for the slope position, shows a positive tendency for higher species numbers on the lower parts of the landscape. This corresponds to the known sensitivity of *Monocalyptus* species to the fungal pathogen *Phytophora cinnamoni* as compared with *Symphyomyrtus* species (Burdon & Chilvers 1974). The water-borne infection is more prevalent in gullies and on lower slopes. The two subgenera show opposite tendencies with respect to the nutrient index. Higher numbers of *Monocalyptus* are predicted for low nutrient conditions while *Symphyomyrtus* is predicted to have higher numbers on intermediate nutrient levels, although not at the highest levels (Table 4). This preference for environments with high nutrients is consistent with Noble's (1989) conclusions. There are also differences in the response of the two subgenera to rock type and rainfall seasonality.

These correlative models provide circumstantial field evidence for differences between species from the two subgenera. They do not provide evidence for the co-occurrence rule proposed by Pryor (1953). They support instead the result of Austin *et al.* (1983) that patterns of co-occurrence of species from the subgenera are governed by differences between the subgenera in environmental preferences.

Hierarchical pattern of diversity

Two distinct types of species richness patterns have been illustrated, one based on tree life-forms and the other based on taxonomic status. Different species richness patterns predictable from environmental variables have been demonstrated in both cases, rainforest trees versus sclerophyll trees or *Monocalyptus* versus *Symphyomyrtus* subgenera. The models provide circumstantial evidence for several hypotheses; for example, that for each taxon or growth form there is a part of the environmental niche space within which maximal survival and/or speciation is possible. These descriptive models need to be tested for consistency in other areas and need to be expressed as testable hypotheses in terms of mechanisms.

Minchin (1989) provides an interesting series of patterns of species richness for different growth form groups (trees, shrubs, herbs, graminoids, ferns) in subalpine environments of Tasmania. The patterns relate to two-factor gradients of soil drainage and altitude. They support the general hypotheses presented previously, regarding the occurrence of distinct optimal environments for maximal speciation for different groups of organisms whether based on taxonomy or life form. Pausas (1994) also reports an example of different patterns of species richness for different life forms (woody species, herbs and mosses) in Pyrenean forests. This has implications for recognition of functional types and their use for modelling global change (Chapin *et al.* 1992). Some of the life-forms studied by Minchin (1989) and Pausas (1994) have an implicit taxonomic status (e.g. graminoids, ferns, mosses). Are higher taxonomic categories more or less useful than life form classifications? It would also be useful to know whether numbers of species per category show the same or different patterns as number of individuals (or biomass) per category.

CONCLUSIONS

These results provide conservative, quantitative descriptions of the patterns of species richness of different taxa and growth forms of trees. The description of species richness patterns requires the simultaneous use of several environmental variables, both local (e.g. soil nutrients, topographic position) and regional (e.g. mean annual rainfall). Generalized linear models provide a versatile method of modelling the correlative relationship between richness and environment. Any theory of species richness patterns should be consistent with the descriptive models presented here to justify the theory's generality.

The results do not immediately distinguish among alternative theories explaining species diversity, but they do demonstrate that local environment should not be ignored in any analysis of regional patterns of species richness. A concept such as niche saturation should not be invoked until environmental explanations have been sought and shown to be inadequate. The environmental model is consistent with the energy model based on actual evapotranspiration described by Currie (1991), although the variables used here are less causally related than those of Currie. Different patterns of richness for different growth forms have been known for a long time. The models here provide quantitative expression of those differences for rainforest trees and sclerophyllous trees.

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