

**Studies on the Arboreal Marsupial Fauna of Eucalypt Forests being Harvested for Woodpulp at Eden, N.S.W.
II. Relationship between the Fauna Density, Richness and Diversity, and Measured Variables of the Habitat**

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Abstract

The relationships were examined between measurements of forest habitat (10 explanatory variables: X) and densities of three species of arboreal marsupials (greater glider, feathertail glider and sugar glider); the sum of these three and an additional five species that occurred; species richness and diversity of all eight species present in the area (six response variables: Y). The habitat variables were: landform profile; elapsed time since a severe fire; degree of forest maturity (total basal area of wood); an index of den tree density; ratio of number of regeneration size trees to den trees; floristic diversity; basal area of peppermints; basal area of gums; basal area of eucalypts with a low level of nutrients in their foliage; and an index of potassium concentration in the foliage.

The principal component transformation of the X set of variables (PCA) was used as an aid to interpret the individual response of Y to joint intercorrelated explanatory variables X . The regressions of Y on PCA-transformed X explained 76.2% of variation in density for the greater glider, 50.4% for the feathertail glider, 21.1% for the sugar glider, 68.3% for all arboreal marsupials, 49.7% for species richness and 30.1% for species diversity. The weak regressions obtained for densities for the sugar glider were attributed to probable non-measurement of important understorey habitat variables for this species, and those for species richness and diversity, to the presence of a curvilinear rather than linear relationship to foliage nutrients.

The gradient in foliage nutrient concentration appears to be the major determinant of the density and species richness and diversity of arboreal marsupials in the Eden forests. Exceptions to the trend seem to occur where the forests include certain xeromorphic eucalypt species that are high in foliage nutrients yet poor in fauna, and, for the feathertail and sugar glider, in those sections of the Eden forests exhibiting fire successional stages and that are usually composed of eucalypts with low nutrient levels in their foliage.

Introduction

The concession district for the harvesting of pulpwood from eucalypt forests at Eden, N.S.W., is currently about 405 000 ha in area. Some 5000-6000 ha of forests are clear-cut annually to supply this industry.

Within the forests of this district there is a marked discontinuity in the distribution and density of arboreal marsupials. It has been estimated (Braithwaite 1983) that, about 63% of the individuals of all species occurring in the forest are concentrated in about 9% of the area. In the study reported above, the density of each of the species of arboreal marsupials was maximal in the same general areas of forest. The question thus arises, as to the reasons for the clumping. An answer would provide understanding of the environmental requirements of the species involved and would be of relevance in setting fauna-related objectives for forest management.

There are practical difficulties in obtaining information about a nocturnal arboreal fauna in forest hard of access to the human observer. During this study, as in the one

reported above (Braithwaite 1983), the primary source of data on the animals was the logging crews, engaged in clear-felling of the forest. They reported on the location and on the species and numbers of animals they displaced from trees. The felling of the forests also facilitated the collection of information on habitat. Data on landform were available from management plans prepared by the Forestry Commission. Species identification of the eucalypts was facilitated by the ready availability of leaves, buds and fruit.

This paper presents analyses of these data and explains variations in animal density, faunal richness and diversity, in relation to the measured variables of the habitat.

The study lasted from May 1980 to September 1981.

Methods

Data on animals and on their habitat were collected from 'clear-cut' forest coupes each between 5 and 30 ha in area and dispersed over the 405 000-ha concession district. The location of the forest areas felled or 'clear-cut' was determined according to a plan of management (Forestry Commission of New South Wales 1975) and according to the time to time requirements of the pulpwood and also the sawlog industries.

Information available on the geology and botany of the concession district has been collated and summarized by Recher *et al.* (1980). Over 40 eucalypt species are known to occur in the forests of the district. About 30 species are considered common, and these have been grouped into different numbers of major forest types by different authors. In Recher *et al.* (1980) and literature cited by these authors, between 6 and 18 forest types or communities were recognized. In analyses of data collected for this study (Braithwaite 1983), 22 vegetation communities were recognized. The eucalypt species, and therefore forest type, vary with soil type, altitude and latitude. Of the common forest types in the district all were examined in the present study, with the exception of those forests dominated by spotted gum, *E. maculata*, which is more characteristic of forest areas to the north of the Eden concession area (see Austin 1978). Procedures for the collection of data on the species and numbers of animals have been previously outlined (Braithwaite 1983).

The analyses of animal densities presented in this paper are based on data for 898 animals of eight species (including some relating to unconfirmed reports of the squirrel glider *Petaurus norfolcensis*). The animals were reported by 36 logging crews from 337 coupes in which data on the predominant vegetation was collected, making up a total felled area of 5010 ha. The numbers of animals found and coupes and area felled are fewer than those reported in Braithwaite (1983), since data sets on habitat measurements were incomplete for 42 coupes. All data for these coupes have been omitted from this paper. The species and numbers of each reported were: the greater glider *Petauroides volans* (353 animals); feathertail glider *Acrobates pygmaeus* (328); sugar glider *Petaurus breviceps* (120); yellow-bellied glider *Petaurus australis* (33); brushtail possum *Trichosurus vulpecula* (30); ringtail possum *Pseudocheirus peregrinus* (28); pygmy possum *Cercartetus nanus* (2); squirrel glider (five reports of animals not positively identified).

Vegetation sampling plots of 0.25-ha area (a circle of 28.21 m radius) provided data on the size and species of trees in the 337 coupes. In the less diverse associations and where the tree species tended to be uniformly distributed, the area was reduced to one half of the circle and the resultant data multiplied by two to provide an 0.25-ha sampling equivalent. The diameter of trees was recorded in eight size classes based on their diameter at 80 cm above ground, the usual height of the saw-cut; these were (in centimetres): 1-9, 10-19, 20-29, 30-39, 40-59, 60-79, 80-99 and 100+.

A stratified-random system was adopted in setting out vegetation sampling plots. This ensured the collection of a representative set of data on the species composition and size range of trees in each coupe. In addition to these plots (random plots), other plots (animal plots) were set out at sites at which animals had been displaced from trees by the logging operations. In all there were 437 random plots and 276 animal plots. The majority of the tree species occurring on the random plots are listed in Table 1. Further information on the occurrence and associations of trees is given in Braithwaite (1983).

The X Variables

The measured variables of habitat (*X* variables) were obtained or derived from various sources. Information on past fires, logging activities and landform features were available from Forestry

Commission records, maps or observable features of the landscape. Others, such as basal area measurements, numbers of den trees and indices of foliage nutrients, were computed from the base data collected on the vegetation plots together with, for example, data on the species and size of trees used as dens and nutrient concentrations in the foliage of individual species of trees.

From a total of 30 variables either obtained by direct measurement of habitat or generated from the plot data and listed in Appendix 1, a final set of 10 variables was derived as outlined under 'Statistical Analyses'. The 10 variables and their mnemonic codes and definitions were as follows.

Landform profile (LP). A measure of the steepness of the landform was readily obtained from contour maps at a scale of 1:10 000, used by the Forestry Commission in planning forest management. The measure was derived by dividing the map distance (in millimetres) between the boundaries of each coupe at its highest and lowest elevations by the number of 10-m contours between these points. The values thus derived decreased with increasing steepness of terrain.

Fire (F). Wildfires sufficiently severe to burn the crowns of the trees occur somewhere in the Eden forests each year. Depending on the location, severe fires have an expected frequency of from about once in every 3 years to once in every 15 years (Walker 1979). For each coupe the elapsed time since a severe fire was determined, if possible, from records of the Forestry Commission of New South Wales or from the knowledge of local forestry workers. When this information was not available, estimates were made on field evidence of burns, scars, and the size of regrowth trees and understorey shrubs presumed to have germinated soon after a severe fire. A timespan of 40 years was accepted as the maximum within which records or estimates could generally be accepted as reliable. Where the last severe fire was thought to have been earlier than this, an arbitrary figure of 40 years was accepted.

Basal area (BA). The basal area of standing timber at 80 cm height, the usual height of the stumps, was readily calculated from the 0.25-ha sample plots.

Density of den trees (DT). During the study data were collected on the species and diameter at stump height (i.e. at 80 cm) of trees with holes that were used by animals for refuge. These trees were therefore referred to as den trees (Braithwaite, unpublished). In general, the minimum size of trees that were used was 80 cm for *E. cypellocarpa*, *E. obliqua* and *E. fastigata* and 60 cm for all other species. There was only marginal variation in the mean size of trees used by the different animal species. These criteria were used to calculate the density of trees per 0.25 ha over the minimum base diameter for den trees. The assumption was that this value would provide an index of the density of trees actually suitable.

Ratio of numbers of trees of regeneration size to numbers of den trees (RDT). This measure was obtained from the plot data by calculating the natural logarithm of 10 times the quotient of 1 plus the number of trees of less than 20 cm base diameter divided by 1 plus the number of den trees.

Floristic diversity (FD). The tendency for forest eucalypts to occur in a patchwork of species associations is well known. To obtain some measure of this complexity the distribution of the vegetation sampling plots was set out on Forestry Commission logging plans. This revealed that the minimum sampling intensity within felled areas was four plots within a 1-km radius of each coupe. Where there were more than four plots, a list of the plot numbers was prepared. Data for the four plots or, where there were more than this within the 1-km radius, four plots taken at random from the prepared list were then used to derive an index for floristic diversity as given by Shannon and Weaver (1963). The analysis used the basal area (measured to tenths of square metres) contributed by each tree species to the total basal area of the four plots.

Basal area of peppermints (BAP). Wherever animals were found by felling crews, the presence of one or more species of a group of eucalypts known as peppermints (*E. dives*, *E. radiata* and *E. elata*) was frequently noted (see Braithwaite 1983). To evaluate the usefulness of this observation in predicting the occurrence of animals, the basal area (in square decametres) contributed by these tree species was calculated and included in analyses.

Basal area of gums (BAG). Similarly, wherever animals were found, gums (eucalypts of the species *E. cypellocarpa*, *E. viminalis*, *E. maidenii*, *E. dalrympleana*, *E. ovata* and *E. rubida*) were the tree species most commonly found to be used as den trees. The basal area contributed by these species (in square decametres) was calculated.

Low foliage nutrient eucalypts (LFN). The initial observation during the study was that animals tended to be absent or very sparsely distributed in forest areas characterized by the presence of vegetation elements often referred to as 'dry sclerophyll' (see Seddon 1974; Hillis and Brown 1978). The understorey vegetation tended to a predominance of woody shrubs rather than of bracken, which is considered more characteristic of 'moist sclerophyll'. Basal area measurements of the eucalypt species that typically predominate in such forests were calculated and examined singly and in various combinations for the contribution to the variation in *Y* variables (see 'Statistical Analyses' and Appendix 1). Best fit was obtained by accepting the following species: *E. gummifera*, *E. muellerana*, *E. agglomerata*, *E. globoidea*, *E. sieberi* and *E. consideniana*. As indicated in Table 1, all are characterized by low concentrations of nutrients in their foliage.

Foliage potassium (K). The regular coincidence of the presence of animals with certain eucalypts, particularly the peppermints, when also taken together with the high nutrient levels of the foliage of those eucalypts (see Table 1), seemed indicative of some causal relationship. As the mass of foliage of a tree is correlated with its basal area (see, e.g., Feller 1980), indices of the concentration of nutrient potassium (and also of nitrogen and phosphorus) in the foliage could be derived from the proportionate contribution of the basal area of each eucalypt species to the total basal area of the plots in each coupe and the tree species' specific foliage nutrients. The methods of chemical analysis were those described by Lambert (1976). The sample numbers given in Table 1 refer to the number of trees of each species for which the foliage was analysed. A single bulk sample of approximately 40 freshly mature leaves was collected from each tree; the collections being made from usually 15–20 points randomly dispersed in the tree crown.

The Y Variables

The mnemonic codes used for descriptions of *Y* variables, the animal densities, species richness and species diversity, were as follows.

Density of greater gliders (DGG), feathertail gliders (DFG), sugar gliders (DSG) and of total arboreal marsupials (DAM). As outlined below, data for coupes of similar floristic composition were aggregated to obtain sample areas of forest of 100 ha. The number (i.e. density) of animals found was then readily expressed as numbers per 100 ha.

Animal species richness (SPR) and species diversity (SPD). These values were calculated for each series of coupes of similar floristic composition selected as outlined below, and making up a minimum area of 100 ha. Species richness (SPR) was defined as the number of species, and species diversity (SPD) as the diversity of species calculated according to Shannon and Weaver (1963).

Statistical Analyses

For many of the coupes cleared, the number of animals found was nil. When statistical analysis of the data was contemplated this fact created substantial difficulties. Clearly, the sampling unit (the coupe) for obtaining values of the response variables, *Y*, was impracticably small, yet this area was governed by conditions outside those of sampling control. An objective method was thus sought to cumulate data for coupes to obtain fewer sampling 'units' of larger area than the single coupe. Similarity in floristic composition was chosen as the most logical criterion for cumulation of coupe data. Various methods were examined, including the classification of vegetation data according to communities, as outlined in Braithwaite (1983). This procedure would have resulted in a relatively small number (22) of sample units of widely varying size; for example, the classification given in Braithwaite (1983) would have given communities with areas ranging from 24 to 1193 ha. An area of 100 ha was arbitrarily taken as a minimum size for a sample unit. Data for the 337 coupes were then reduced to 46 sample units, each comprising 4–7 coupes. This was done by adapting the technique of Hill (1973) to sort the coupes into order according to similarities in tree species and basal areas. In computing similarities between coupes the measurements of basal area for each tree species were standardized and ranked.

This ensured that equal value was given to each tree species, irrespective of the characteristic maximum size of trees or predominance of that species in species associations. Values for both explanatory, X , and response, Y , variables were then computed for each set of coupes making up a sample unit. Values for X were the means calculated for the X variables for all plots in each sample unit. Values for Y were obtained by correcting animal numbers for the coupes in each unit to a density per 100 ha. Animal species diversity for each sample unit was calculated according to the methods of Shannon and Weaver (1963), from data on numbers of each species found in the coupes making up the unit.

Table 1. Levels of nitrogen, phosphorus and potassium in foliage of forest trees in the Eden woodpulp concession area

Values are expressed as percentages of oven-dry weight, \pm standard deviations

Species	N	Nitrogen	Nutrient Phosphorus	Potassium
<i>Angophora floribunda</i> , rough-barked apple	6	1.04 \pm 0.11	0.057 \pm 0.010	0.96 \pm 0.35
<i>Eucalyptus agglomerata</i> , blue-leaved stringybark	16	0.78 \pm 0.10	0.043 \pm 0.007	0.33 \pm 0.05
<i>E. angophoroides</i> , apple-topped box	5	1.48 \pm 0.20	0.059 \pm 0.009	0.61 \pm 0.17
<i>E. badjensis</i> , badja gum	1	1.85 —	0.088 —	1.16 —
<i>E. bosistoana</i> , coastal grey box	3	1.44 \pm 0.19	0.110 \pm 0.080	1.29 \pm 0.41
<i>E. botryoides</i> , bangalay	4	0.81 \pm 0.17	0.057 \pm 0.020	0.51 \pm 0.16
<i>E. bridgesiana</i> , apple box	4	1.00 \pm 0.03	0.059 \pm 0.006	0.70 \pm 0.30
<i>E. considiana</i> , yertchuk	17	0.81 \pm 0.12	0.041 \pm 0.006	0.31 \pm 0.06
<i>E. cypellocarpa</i> , monkey gum	10	0.90 \pm 0.09	0.056 \pm 0.007	0.59 \pm 0.16
<i>E. dalrympleana</i> , mountain gum	5	1.46 \pm 0.12	0.089 \pm 0.020	0.70 \pm 0.20
<i>E. dives</i> , broad-leaved peppermint	4	0.99 \pm 0.18	0.053 \pm 0.006	0.49 \pm 0.10
<i>E. elata</i> , river peppermint	6	1.63 \pm 0.04	0.092 \pm 0.010	0.66 \pm 0.10
<i>E. fastigata</i> , brown barrel	5	0.89 \pm 0.11	0.065 \pm 0.020	0.55 \pm 0.21
<i>E. fraxinoides</i> , white ash	6	1.38 \pm 0.15	0.086 \pm 0.012	0.76 \pm 0.13
<i>E. globoidea</i> , white stringybark	14	0.79 \pm 0.16	0.044 \pm 0.008	0.34 \pm 0.05
<i>E. gummifera</i> , red bloodwood	6	0.69 \pm 0.11	0.033 \pm 0.010	0.24 \pm 0.09
<i>E. longifolia</i> , woollybutt	9	1.04 \pm 0.26	0.064 \pm 0.022	0.53 \pm 0.26
<i>E. maculata</i> , spotted gum	4	1.43 \pm 0.07	0.110 \pm 0.020	0.88 \pm 0.10
<i>E. macrorhyncha</i> , red stringybark	3	0.90 \pm 0.19	0.070 \pm 0.020	0.51 —
<i>E. maidenii</i> , Maidens gum	1	1.14 —	0.103 —	0.85 —
<i>E. muellerana</i> , yellow stringybark	22	0.82 \pm 0.13	0.052 \pm 0.008	0.39 \pm 0.06
<i>E. nitens</i> , shining gum	6	1.35 \pm 0.15	0.089 \pm 0.020	0.75 \pm 0.11
<i>E. obliqua</i> , messmate	12	0.97 \pm 0.15	0.061 \pm 0.016	0.44 \pm 0.07
<i>E. ovata</i> , swamp gum	6	1.34 \pm 0.32	0.076 \pm 0.018	0.55 \pm 0.03
<i>E. pauciflora</i> , snow gum	3	1.27 \pm 0.03	0.067 \pm 0.022	0.58 \pm 0.08
<i>E. polyanthemos</i> , red box	1	0.94 —	0.046 —	0.50 —
<i>E. radiata</i> , narrow-leaved peppermint	12	1.54 \pm 0.17	0.069 \pm 0.009	0.73 \pm 0.18
<i>E. rubida</i> , candlebark	2	1.48 —	0.070 —	0.77 —
<i>E. sideroxylon</i> , red ironbark	4	0.99 \pm 0.24	0.070 \pm 0.020	0.88 \pm 0.19
<i>E. sieberi</i> , silvertop ash	15	0.79 \pm 0.11	0.042 \pm 0.013	0.41 \pm 0.13
<i>E. smithii</i> , gully gum	4	1.73 \pm 0.11	0.084 \pm 0.006	0.54 \pm 0.35
<i>E. stellulata</i> , black sallee	4	1.42 \pm 0.23	0.113 \pm 0.024	0.53 \pm 0.04
<i>E. viminalis</i> , manna gum	5	1.33 \pm 0.24	0.076 \pm 0.011	0.62 \pm 0.09

Since nitrogen, phosphorus and potassium in foliage were highly intercorrelated, similar in response to Y (Table 2; see also Appendix 3), nitrogen and phosphorus were arbitrarily removed from the potential explanatory variables. The analysis strategy was then to examine the variation in Y variables in relation to the X variables. This was done by multiple regression, by means of the GENSTAT 'MINI' routine which eliminates X variables not contributing towards the relation. Thus from the original 30 variables a reduced set of 10 X variables was obtained, each member of X contributing significantly to the variation in one or more Y variables. The set of 10 X variables was then transformed by

principal components analysis (PCA) into $Z_1 \dots Z_{12}$ (including two quadratic functions: see below) explanatory variables, and again related in regression analysis to the Y variables.

There is an extensive literature on the use of PCA (e.g. Dudzinski 1973; Seber 1977; and literature cited by these authors). This technique is especially valuable in the likely circumstance that the human perception of the environment fails to coincide with that of the animals under study. The principal components are linear combinations of the original correlated variables but are not correlated with themselves. Where each component (Z value) is composed of X variables with loadings of all like

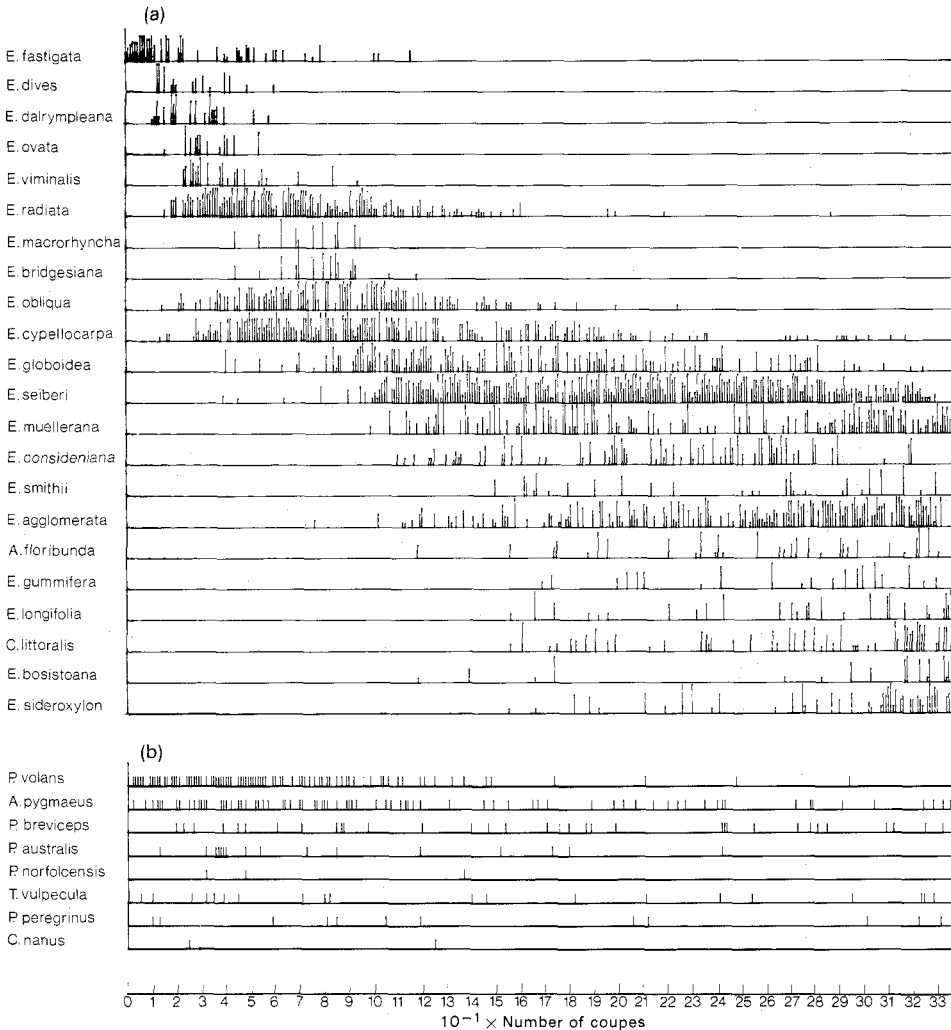


Fig. 1. (a) Eucalypt associations of 337 clear-felled forest coupes ranked by correspondence analysis (Hill 1973) according to tree species composition. The data used for the analysis were floristics and measurements of the basal area of each tree species, in square decametres per 0.25 ha. (b) Occurrence of animal species in each coupe.

sign (unipolar), the component merely indicates that the Y value varies with the X variables in various proportions. In the circumstance, as found in the present study, that the vectors of the X variables were bipolar, this is taken as evidence, of the animal(s) perhaps making a 'choice' between opposing sets of variables. The PCA was used here to summarize the basic definite relations (Table 2), which it did by means of first component. However, with the usual variability of ecological data any evidence from other components should be treated with care: perhaps as hypothesis-generating suggestions rather than firm inference.

Results

The ordination analysis of floristic information for the 337 coupes is presented in Fig. 1, together with corresponding data on the occurrences of animal species in each coupe. Also shown are data for animal densities (greater, feathertail and sugar gliders and all arboreals) and species diversity for sets of coupes aggregated to form the 100-ha sample units of forest of similar floristic compositions. Clearly demonstrated is a trend for maximum densities of animals to occur within forest communities that include, in various associations, *E. fastigata*, *E. dives*, *E. dalrympleana*, *E. ovata*, *E. viminalis*, *E. radiata*, *E. obliqua* and *E. cypellocarpa*. Species diversity is shown to be much more variable. Though it tends to be consistently high in these communities, other communities also often supported a similarly diverse fauna. There is, as a consequence, a moderate to high degree of intercorrelation between animal densities, species richness and species diversity, and the series of measured habitat variables. A correlation matrix for these data is presented in Table 2, which also includes correlation coefficients calculated for nitrogen and phosphorus.

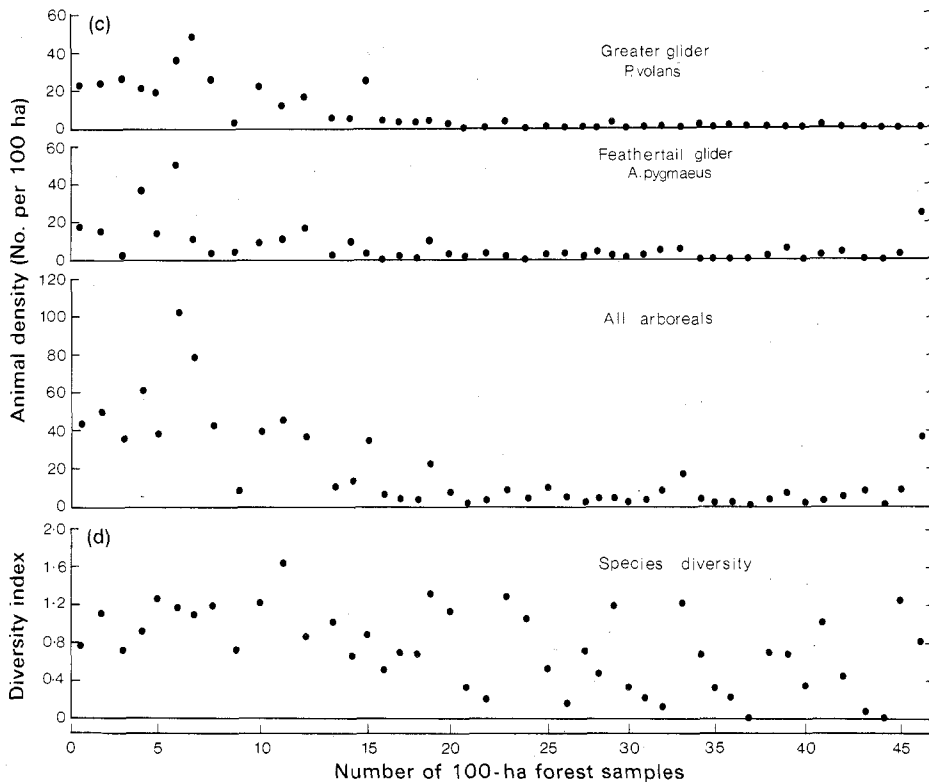


Fig. 1. (c) Densities of the greater and feathertail gliders and of all arboreal mammals for 100-ha samples of forest ranked according to species composition, as in Figs 1a and 1b. (d) Animal species diversity in the same samples.

PCA regressions of each of the six Y variables on the set of X variables were made after the following adjustment. Plots of Y variables for animal densities ($Y_1 \dots Y_4$) on F and LFN (see Appendix Fig. 1) displayed a curvilinear relationship. To approximate this to a linear relationship, quadratic functions of F and LFN, F^2 and LFN^2 were added to provide a total set of 12 X variables. Since the quadratics add nothing to interpretation, no reference is made to them in discussion.

Table 2. Correlation matrix for measured habitat variables and the densities, species and diversity of arboreal marsupials

Degrees of freedom, 44. Significance levels: $r = \pm 0.291$, $P < 0.05$; $r = \pm 0.376$, $P < 0.01$; $r = \pm 0.470$, $P < 0.001$. For explanation of abbreviations, see pp. 233–4

	LP	F	BA	DT	RDT	FD	BAP	BAG	LFN	N	P	K
F	0.592											
BA	0.730	0.509										
DT	0.013	-0.220	0.283									
RDT	-0.247	-0.326	-0.444	-0.428								
FD	0.445	0.657	0.317	-0.433	-0.056							
BAP	0.694	0.641	0.603	-0.273	-0.220	0.603						
BAG	0.782	0.594	0.681	-0.175	-0.159	0.429	0.883					
LFN	-0.604	-0.766	-0.526	0.496	0.156	-0.803	-0.850	-0.755				
N	0.705	0.716	0.538	-0.351	-0.149	0.709	0.934	0.868	-0.901			
P	0.634	0.775	0.547	-0.383	-0.163	0.806	0.842	0.758	-0.952	0.948		
K	0.674	0.755	0.570	-0.371	-0.173	0.763	0.911	0.835	-0.950	0.969	0.975	
Explanatory X variables												
Response Y variables												
DGG	0.613	0.660	0.675	-0.135	-0.363	0.574	0.815	0.724	-0.775	0.734	0.723	0.757
DFG	0.542	0.512	0.390	-0.234	0.001	0.480	0.616	0.620	-0.586	0.648	0.605	0.643
DSG	0.249	0.270	0.273	-0.065	-0.026	0.253	0.348	0.415	-0.339	0.369	0.321	0.383
DAM	0.629	0.656	0.598	-0.212	-0.198	0.595	0.803	0.766	-0.771	0.775	0.741	0.794
SPR	0.444	0.600	0.432	-0.277	-0.176	0.520	0.564	0.613	-0.654	0.608	0.614	0.656
SPD	0.354	0.477	0.328	-0.245	-0.128	0.385	0.419	0.482	-0.492	0.432	0.434	0.489

Table 2. (Continued)

	Densities, species richness and diversity of animals <i>Y</i>				
	DFG	DSG	DAM	SPR	SPD
DGG	0.593	0.347	0.896	0.656	0.452
DFG		0.253	0.852	0.530	0.412
DSG			0.495	0.474	0.356
DAM				0.732	0.549
SPR					0.927

The total variance accounted for by all components was: for density of the greater glider, 76.2%; feathertail glider, 50.4%; sugar glider, 21.2%; all arboreals, 68.3%; species richness, 49.7%; species diversity, 30.1%. Component Z1 accounted for most of the variation between *X* variables (62% of variation accounted) and was the major contributor to variation in all *Y* variables: density of the greater glider, 66.6%; feathertail glider, 40.1%; sugar glider, 11.1%; all arboreals, 67.0%; species richness, 45.0%; species diversity, 25.5%. Component Z1 suitably summarizes the set of basic correlations from Table 2, viz. the positive correlation of $Y_1 \dots Y_6$ with K (and thus with P and N), BAP, F, BAG, FD and negative correlations with LFN). Therefore, component Z1 can be regarded as a contrast of the group of variables K, BAP, F, BAG and FD with LFN. In other words, as displayed in Fig. 2, values for densities of the three species individually and of all arboreals, and species richness and diversity, are higher with high foliage potassium and other closely related variables and lower with high basal area of those eucalypts of low foliage nutrient content.

Components other than Z1 contributing to variation in *Y* variables differed according to the *Y* variable. Those contributing significantly were Z10 and Z2 for density of greater gliders, Z12 for density of feathertail gliders, and Z9 for species richness.

Component Z10, which contributed 4.4% of variation to greater glider density, contrasts BAP with K. The relationship thus differs from that shown to component Z1. As displayed in Fig. 2, higher densities of gliders coincide with a high basal area of peppermints, but lower densities with high values for foliage potassium. Component Z2, which contributed 2.3% of variation to the density of greater gliders, contrasts DT and BA with RDT. Thus the relationship (Fig. 2) is: high density of animals with high density of potential den trees and high basal area (i.e. forest of maximum maturity); low density of animals with a high incidence of regeneration-class trees (i.e. with numerous trees of less than 20 cm base diameter).

Component Z12 contributed 8.0% of variation in density of feathertail gliders. This component (Fig. 2) contrasts F and LFN: high density of animals with high basal area of eucalypts of low foliage nutrients and reduced time after fire; low density of animals with low basal area of eucalypts of low foliage nutrients and increased time post fire.

Component Z9 contributed 4.7% to variation in species richness. This contrasts BAG, FD, LFN and BAP (Fig. 2). Thus species richness is high with high basal area of gums, and decreases with increasing basal area of peppermints.

The accountable variation in density of sugar gliders, species richness and species diversity was thus rather small. Probably, as discussed below, the most important elements of habitat for this species were either not measured or inadequately reflected by the variables measured. For values of species richness and diversity, inspection of plots of first principal component scores (Fig. 2) reveals a curvilinear rather than linear relationship. Alternatively, this may reflect a threshold rather than linear relationship of the response variables to increasing concentrations of foliage nutrients (see Appendix 3). Although species richness and diversity are shown to vary widely at low concentrations of foliage nutrients, at nutrient levels over 0.9 (N), 0.05 (P) and 0.45 (K) grams percent dry weight, both richness and diversity of animals are maintained.

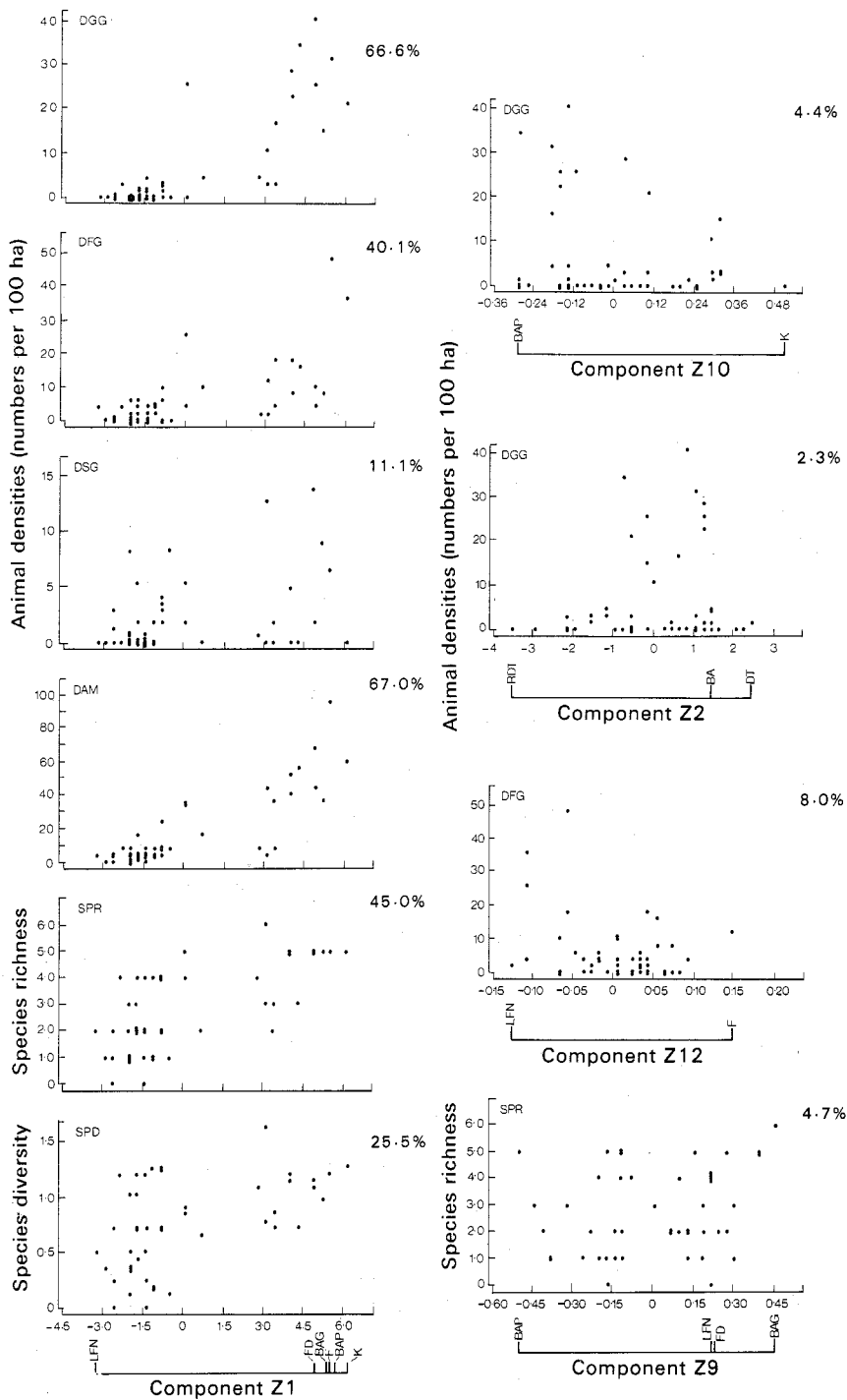


Fig. 2. Relation to principal component variables of response variables; density of the greater glider (DGG), feathertail glider (DFG), sugar glider (DSG) and all arboreals (DAM), species richness (SPR) and species diversity of animals (SPD). Percentages within graphs are the variance accounted for.

Discussion

The aim of this study has been to examine the relationships between the occurrence of arboreal marsupials in eucalypt forest and a range of measured variables of the forest as habitat. The existence of a highly intercorrelated system was demonstrated, and PCA was used to investigate the interrelations between variables.

The first component (Z1, Fig. 2) summarized correlations evident in Table 2. Namely, that forests with foliage of high nutrient concentration, large basal areas of certain groups of eucalypts (gums and peppermints), further in time from fire and with higher floristic diversity, favour high densities and diversity of arboreal marsupials. On the other hand, high basal areas of the species of trees described as LFN, do not. In terms of species richness and diversity the relationship to foliage nutrient concentrations could be either curvilinear or a threshold response. More work is required to gain certainty. The interpretation that the fauna is responding to concentration of foliage nutrients seems logical. As indicated by research elsewhere on species such as moose (Belovsky 1981), deer (Klein 1970), or grouse (Watson and Moss 1970), an animal species might be expected to occur at higher densities in richer and more productive habitats than in more marginal or less productive ones. Certainly nutrient (nitrogen) concentrations seem an important factor determining damage by grazing insects to *Eucalyptus* forests and woodlands (Fox and Macauley 1977). Such damage appears to occur irrespective of quantities of toxic compounds (tannins and phenols) in the foliage. It has also been noted (Ullrey *et al.* 1981) that the koala prefers to browse eucalypt foliage high in a number of factors, including protein and potassium. The possibility can, nonetheless, not be excluded that secondary compounds, perhaps toxic to vertebrate animals as suggested by Janzen (1974, 1978), may be related to nutrient levels and in turn reduce the ability of animals to maintain themselves in certain eucalypt associations.

Similarly, the conclusion that a nutrient gradient accounts for a significant part of the variation in density and richness of the fauna does not necessarily imply the existence of a direct relationship between the habitat variables measured and the fauna. Other factors, for example abundance of invertebrates, which could well be expected to be related to levels of foliage nutrients (see e.g. Fox and Macauley 1977; Carne and Taylor 1978; Schowalter *et al.* 1981; literature cited by these authors), may prove to be the most direct link in the relationship. Also, the variables of habitat measured were generally those that at the inception of the study seemed likely both to be most meaningful to the animals, and, of necessity, given the difficulties of gaining information about this fauna, to be adequate for statistical analysis. No measurements were thus made of the significant understorey flora. In the case of the sugar glider, two species of *Acacia*, *A. longifolia* and *A. terminalis*, were often noted from general observation as abundant in localities in which this animal was reported. The importance of *Acacia* species to the sugar glider is well documented (Smith 1980, 1982; Suckling 1980). Hence the lack of measurements of the understorey may well account for the weak regressions for sugar glider densities.

The relationship of all *Y* variables to component Z1 can be interpreted as that the arboreal fauna in general, and as a first choice, respond to the combination of factors, but in particular nutritive requirements, that they depend on most. For example, the greater glider, a folivore, might well be expected to be highly dependent on nutrient levels in the foliage for an adequate diet. High floristic diversity might similarly be seen as important for the diet of a folivore. High diversity would presumably ensure, depending on the phenology of eucalypts in the community, maximum choice of foods such that at any one time the most nutritive may be selected. High basal area reflects the maturity of the stand of eucalypts, and therefore the presence of den sites in old trees. And, again, the more mature forests might well be expected to be those least frequently devastated by fire. Species such as the feathertail, sugar and yellow-bellied gliders might equally be expected to respond to all these factors, but in particular to abundance of invertebrates, in turn dependent for

their food on the foliage. The interesting question remains the interpretation of other minor components which, with the present 'state of the art' and given the variability of the data, must remain in the realm of speculation rather than firm inference. For instance, the greater glider densities were significantly related to component Z10. The relationship of X variables making up this component seems the paradox of that evident in component Z1. Inspection of Fig. 1, however, shows that, often associated with the eucalypts included within the variable LFN, that are of low foliage potassium and that usually predominate in the associations in which they occur, are also the species *A. floribunda*, *E. bosistoana* and *E. sideroxylon*. These species show high to very high foliage potassium (Table 1), yet rarely occur in associations that include any of the peppermints, though one peppermint, *E. radiata*, also often occurs dispersed as a subdominant species in associations of the LFN group of eucalypts. Thus one paradox is explained only to create a second. The response of the greater glider to the first component Z1 was interpreted as a positive response to increasing foliage nutrients. The response to the second component Z10 thus now suggests that the response is negative, and that LFN communities of eucalypts that include the above-mentioned species with high foliage potassium are the least preferred communities of all. Any explanation is speculative but, since the greater glider is a folivore, possibly the combination of a tougher, often waxy foliage, or perhaps the presence of toxins in *A. floribunda*, *E. bosistoana* and *E. sideroxylon* compared to the more delicate foliage of the peppermints, may provide the answer.

The response of the greater glider to component Z2, the evident preference of the species for the most mature forest, may be readily interpreted as a selection for forest that provides maximum numbers of dens or refugia.

Component Z12 contributed to the variation in densities of the feathertail glider. The inference here could be as follows. Eucalypt associations of the LFN group are characteristic of a fire-prone environment. The occurrence of the feathertail glider in forests of this type tends to coincide with the phase of vigorous regrowth that prevails for 15–20 years after severe fire and after which the *Acacia* component is markedly reduced or dies out. Hence the successional habitat conditions following fire may be favoured over those of more senescent forest; a pattern of response that may parallel that known for a number of ground vertebrates occurring in forest of similar type nearby (Catling and Newsome 1981; and literature cited).

Species richness was significantly related to component Z9, animal richness increasing with increasing basal area of gums but decreasing with increasing basal area of peppermints. The gums were generally noted for the high frequency with which they contained hollows, i.e. potential refuge or den sites for animals. The inference is that they may be important for the provision of homesites in forest which are often dominated by fibrous-barked eucalypts, including peppermints, less well noted for the prevalence of holes.

If the existence of a relationship is accepted between the occurrence of animals and the concentration of foliage nutrients, then other relationships may be examined for light on the more physical constraints on the distribution of fauna. From the PCA regression analyses and the correlation matrix in Table 2, two physical attributes, landform profile and the estimated time since severe fire, are shown as highly correlated with foliage nutrients. The relationship to landform profile is readily understandable, but that to elapsed time since a major fire is less obvious, given the recognized lack of knowledge of the effects of severe fire on forest nutrient budgets (e.g. Raison 1980; Humphreys and Craig 1981).

Eucalypt species and the nutrient levels of the foliage of individual species are known to reflect concentrations of soil nutrients (Turner *et al.* 1978; Turner, unpublished). These in turn, as a consequence of run-off and leaching following rains, can be expected to decrease with increasing steepness of terrain; a relationship reflected in the correlation between the habitat variables LFN and LP (Table 2). With increasing 'flatness', LFN decreases. The relationship may have some practical relevance. It would seem that the frequent practice of setting aside as National Parks forests on the most rugged and mountainous terrain,

and therefore forests comprising a particular range of vegetation communities, may not be of substantial benefit to arboreal marsupials.

With regard to the relationship of foliage nutrients to time since a major fire, not only is much of the Eden forest area sited on poor soils derived from parent rocks constituted of low nutrient material (Kelly and Turner 1978), but the climate of the area is also characterized by hot dry summers highly conducive to wildfire (see Walker 1979). The eucalypts typical of the zone, those of the LFN category and one species in particular, *E. sieberi*, exhibit seemingly paradoxical attributes: high sensitivity to fire together with a requirement for periodic fire to ensure regeneration (Newman, unpublished data; cf. also Ashton 1981). The result is the setting up of a self-reinforcing cycle with a rotation of eucalypts adapted to fire and to soils poor in nutrients perpetuating their existence, if not predominance, in an environment prone to fire and of low soil fertility. In terms of providing an arboreal fauna with habitat this seems the equivalent of perpetuating 'desert conditions' suitable for supporting a sparse fauna at best. The exception here may be the sugar glider, with its known preference (Suckling 1980; Smith 1982) for habitat that includes *Acacia* and thus a flora that characteristically responds vigorously to form a successional community following fire (see, e.g. Christensen *et al.* 1981; literature cited). Certainly data presented here (see Appendix 2) on the relationship of densities of sugar gliders to the age of forests post fire suggest that the sugar glider may be more dependent on a successional community, or at least an earlier successional post-fire community, than either the greater or feathertail gliders. The exception may be, as noted above, that the feathertail glider also makes use of forest of eucalypts with low contents of foliage nutrients to a minor extent, under the successional conditions that follow severe fire. Densities of the sugar glider are shown to achieve an asymptote at about 30 years post fire and thereafter decline. By comparison, densities of both feathertail and greater gliders, in all forests, tend to be still increasing 35 years post fire (Appendix 2), close to the maximum timespan records or estimates which were considered reliable.

In summary, the interpretation of these data and analyses is that the arboreal marsupial fauna responds to a gradient in foliage nutrients, and that maximum densities and diversity of fauna occur in those sections of the Eden forests characterized by eucalypt species with a high concentration of foliage nutrients. This is with the exception of forest associations that include certain tough-leaved eucalypts. For two animals, the feathertail glider and more particularly the sugar glider, there seems to be some evidence to suggest that severe fire is beneficial, by providing more favoured successional conditions in forests of more fire-prone areas and characterized by eucalypt species of low levels of foliage nutrients.

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Appendix 1. Independent X variables Derived from Habitat Measurement or Generated from Vegetation Plot Data

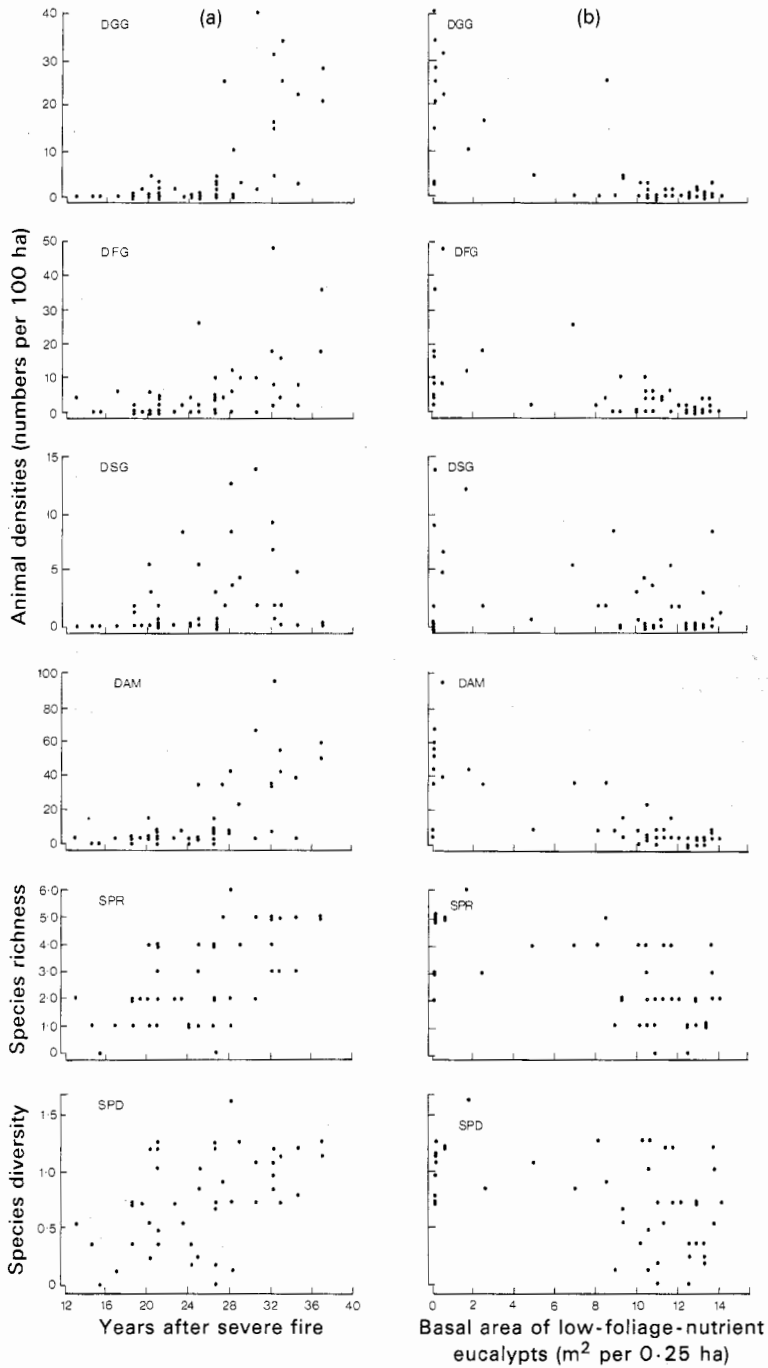
The 10 variables selected for regression analysis are indicated by asterisks

- | | |
|------------------------------------------------|-----------------------------------------|
| * 1. Landform profile | * 6. Numbers of den trees |
| 2. Aspect | * 7. Regeneration growth-den tree ratio |
| * 3. Age post fire | * 8. Floristic diversity |
| 4. Numbers of trees of size class <20 cm base | 9. Foliage nitrogen |
| 5. Numbers of trees of size class >100 cm base | 10. Foliage phosphorous |
| | *11. Foliage potassium |

A series of variables derived from basal area measurements were then as follows:

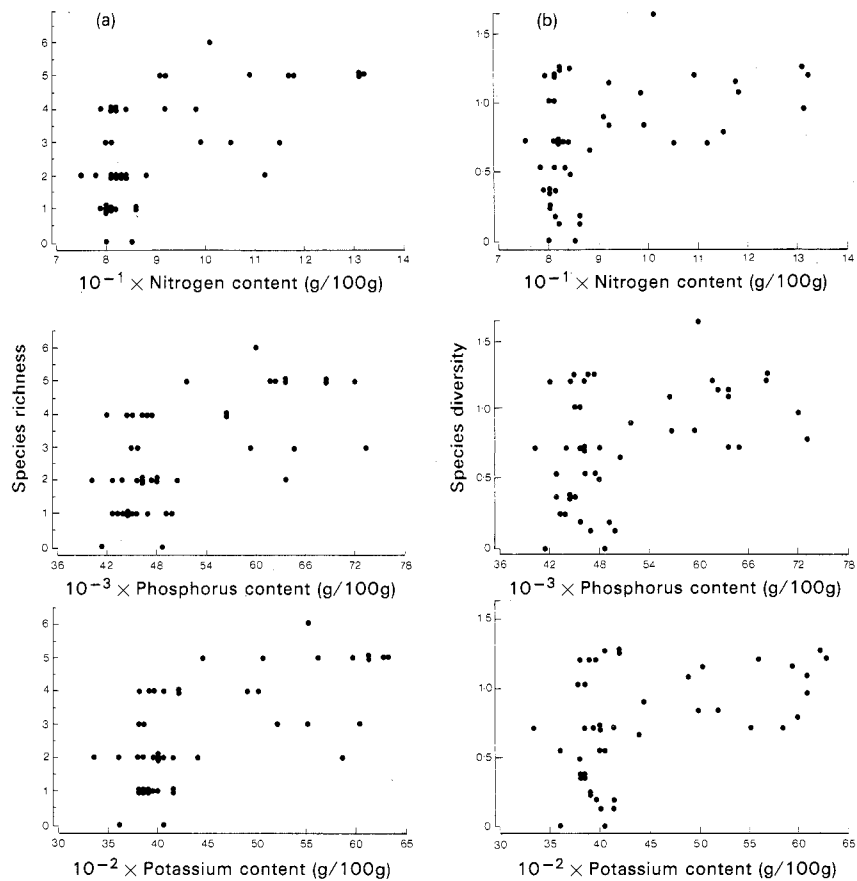
- | | |
|--------------------------------------|--------------------------------------|
| *12. Total basal area | 22. (21) plus <i>E. gummifera</i> |
| *13. Basal area of peppermints | 23. (20) less <i>E. sieberi</i> |
| *14. Basal area of gums | 24. (21) less <i>E. sieberi</i> |
| 15. Basal area of <i>E. sieberi</i> | 25. (22) less <i>E. sieberi</i> |
| 16. (15) plus <i>E. agglomerata</i> | 26. (23) plus <i>E. muellerana</i> |
| 17. (15) plus <i>E. globoidea</i> | 27. (24) plus <i>E. muellerana</i> |
| 18. (15) plus <i>E. consideniana</i> | 28. (25) plus <i>E. muellerana</i> |
| 19. (15) plus <i>E. gummifera</i> | 29. (28) less <i>E. consideniana</i> |
| 20. (16) plus <i>E. globoidea</i> | *30. (22) plus <i>E. muellerana</i> |
| 21. (20) plus <i>E. consideniana</i> | |

Appendix 2



Plots of variables for age post severe fire (a) and low-foliage-nutrient eucalypts (b) against densities of the greater glider (DGG), feathertail glider (DFG), sugar glider (DSG) and all arboreals (DAB), animal species richness (SPR) and species diversity (SPD). Data plotted are the 46 values calculated for 100-ha sample units of coupes of similar floristic composition.

Appendix 3



Plots of foliage nitrogen (N), foliage phosphorous (P) and foliage potassium (K) against animal species richness (SPR) and diversity (SPD). Nutrient values expressed in grams percent of oven-dry weight.

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