

## CHAPTER FIVE

**The influence of management and environment variables on evenness and species richness of ground-storey vegetation**



**Valley near Wollomombi, east of Armidale**

## **5.1 INTRODUCTION**

Many abiotic and biotic factors influence the diversity and composition of ground-layer vegetation (Collins and Barber 1985). Much of the Northern Tablelands of NSW has been intensively developed for pastoralism and grazing is the dominant land use (Morgan and Terry 1990). Agricultural management has had major impacts on the vegetation (Lodge and Whalley 1989), land degradation (Morgan and Terry 1990) and wealth of the region (Nadolny 1998). Some 2.2 million ha of the region is used for agricultural production and the range of environmental and climatic characteristics help to determine the vegetation and nature of land use across the region.

The influence of agricultural management on vegetation has important ramifications for ground-storey vegetation, especially in regard to the conservation of natural heritage. Primary producers manage some 70% of the Australian continent (Australian State of the Environment Committee 2001) and at least a similar percentage of the study region. Landholders are responsible for this important resource (Wentworth Group 2003), and their management decisions have had both positive and negative influences on ground-storey vegetation. For example landholders' agricultural decisions have contributed to the disappearance of plant species (Leigh *et al.* 1984), while landholders also have a role in protecting diversity through setting aside land for conservation (Davidson and Davidson 1992).

Species diversity consists of evenness and richness components (Greig-Smith 1983; Noss 1990), although frequently evenness is neglected in favour of richness. Australian studies commonly measure native and exotic species richness (e.g. Hobbs and Atkins 1988; McIntyre *et al.* 1993) and their response to disturbance (e.g. McIntyre *et al.* 1993; McIntyre and Lavorel 1994a; Pettit *et al.* 1995; Prober and Thiele 1995; Lunt 1997; Lunt and Morgan 1999; Clarke 2003). In Australian landscapes, exotic species often behave differently to native species as exotic species as a group are often functionally different to most of the native flora. In general, as disturbance increases, exotic species richness increases as well. The studies above have set a standard and a basis to examine patterns in species richness in response to disturbance. Commonly the comparisons are between private and public land tenures as in McIntyre *et al.* (1993).

This chapter investigates the diversity of the ground-storey vegetation of the agriculturally managed lands of the Northern Tablelands in terms of both species richness and evenness. Species composition is discussed in Chapters 6 and 7.

This chapter aims to determine the impact of agricultural management (grazing, fertiliser and cultivation) and environmental (e.g. climate, geographical and soil) variables on the evenness and native and exotic species richness of ground-storey vegetation in grazing production systems on the Northern Tablelands of NSW. The management and environmental influences on evenness and native and exotic species richness were determined by:

1. identifying the management variables (e.g. grazing, fertiliser and cultivation) that significantly affect evenness and native and exotic species richness; and
2. identifying the environmental variables (e.g. climate, geographical, soil and sampling date) that significantly affect evenness and native and exotic species richness.

## **5.2 METHODS**

### **5.2.1 Sampling methods**

The sampling methods for the regional survey of ground-layer vegetation on the Northern Tablelands of NSW were presented in full in Chapter 4.

### **5.2.2 Determining evenness and species richness**

A community or vegetation sample can be characterised in various ways, one of these being a count of the species that are present. Species richness is defined as the number of species in a community (McIntosh 1967) or as the number of species per unit area. Evenness, the second component of species diversity (Krebs 1994), is defined by Greig-Smith (1983) as the variability in the proportion of each species in the community or vegetation sample.

Evenness indices provide a simple measure of structure (Mouillot and Wilson 2002). The appropriateness of different evenness indices has been the subject of much conflicting

review and discussion (Smith and Wilson 1996; Mouillot and Lepretre 1999; Ricotta and Avena 2000; Mouillot and Wilson 2002). In an excellent review, Krebs (1999) discussed the appropriateness of 14 indices reviewed by Smith and Wilson (1996). The fundamental premise of Krebs' review was that an evenness index must be independent of species richness, due to problems in measuring the species richness of communities. Krebs (1999) advocated the use of Smith and Wilson's evenness index ( $E_{\text{var}}$ , Equation 5.1). This recommendation was adopted in this study, with  $E_{\text{var}}$  calculated for each site, based on the projected foliage cover of each species (Krebs 1999). The index is defined as:

$$E_{\text{var}} = 1 - \left[ \frac{2}{\pi \arctan \left\{ \frac{\sum_{i=1}^s \left( \log_e(n_i) - \sum_{j=1}^s \log_e(n_j) / s \right)^2}{s} \right\}} \right] \quad (\text{Equation 5.1})$$

where the arctangent is measured as an angle in radians,  $n_i$  is projected foliage cover of species  $i$ ,  $n_j$  is the projected foliage cover of species  $j$ , and  $s$  is the number of species in the sample (Krebs 1999).

### 5.2.3 Data Analysis

Statistical modelling using generalised linear models (GLMs) (McCullagh and Nelder 1997; Venables and Ripley 1999) was used to investigate the relationships between evenness, species richness, and management and environmental variables. Species richness was the number of native or exotic species present at a site, while evenness varied between 0 and 1, with 1 representing maximum evenness (Equation 5.1).

Due to the large number of management and environmental variables described in Table 4.5, and the even larger number of variable combinations and higher order interactions that could have been generated and tested, it was not possible to model the data with all variables included despite starting with some 372 degrees of freedom. Therefore variables were grouped into 12 classes to reduce the number of variables that might be included (Table 5.1). Four stratification variables were used in the overall design of the

study (Section 4.2.1) and higher order interactions between these stratification variables (Table 5.2) were tested.

**Table 5.1 Groups of variables used in modelling ground-storey vegetation evenness and species richness.**

Variable groupings	Number of variables in group
Grazing variables (excluding stratification variables)	5
Cultivation variables (excluding stratification variables)	4
Fertiliser variables (excluding stratification variables)	7
Other management variables	4
Rainfall	15
Moisture Index	15
Minimum Temperature	15
Maximum Temperature	15
Radiation	15
Soil variables	7
Geographical variables (excluding lithology)	9
Sampling date	1

**Table 5.2 Stratification variables used in modelling ground-storey vegetation evenness and species richness.**

Stratification variables	Number of levels
Lithology	3
Grazing	4
Fertiliser	3
Cultivation	3

Two variables in each group were prioritised (Appendix 5.1) using two methods to judge their particular importance in explaining deviance in evenness and species richness. The first was based on trends noted in the literature (Tiver and Andrew 1997; Gibbs *et al.* 1999; Reseigh 1999; Sustainable Grazing Systems 2001; Waters 2001) and field observations, such as the changes observed in species incidence under tree canopies in grazed pastures. The second method was based on correlation analysis. Correlation analysis of the linear relationship between management and environmental variables and native and exotic species richness and evenness was undertaken using Statistix 7 (Analytical Software 2000). The two most highly correlated variables were prioritised for inclusion in each of the models.

Initially, the responses of species richness to management and environmental data were analysed using Spatial Analysis Mixed Models (SAMM) (Butler *et al.* 2002) in S-PLUS

(Lucent Technologies 2002) to determine the significance of the random effect (site nested within lithology [Site %in% Lithology] and fixed (all other variables: Tables 5.1 and 5.2) effects. SAMM is designed to fit general linear mixed models using Residual Maximum Likelihood (REML) estimation rather than maximum likelihood (ML), as parameters in the variance structure are estimated by maximising the marginal likelihood of the residuals from a least-squares fit of the linear model (Venables and Ripley 1999) and estimating the variance of the distribution of the random variable. A binomial error distribution with a probit link function (Venables and Ripley 1999) was used for evenness statistical models because the data were proportions. A Poisson error distribution with a log link function (Venables and Ripley 1999) was used for species richness models because the species richness data were counts. Determining the significance of the random component involves testing whether the corresponding variance component is significantly different from zero (Verbyla *et al.* 1999). Therefore the variance component divided by the standard error (the z-ratio) had to approach 2 to be significant. The random component was non-significant in all models for species richness and evenness, and therefore mixed models were not required to analyse the fixed components of the data. All further analysis was therefore undertaken using GLMs with no random component in S-PLUS (Lucent Technologies 2002) and R (Chambers 2002).

Generalised linear models (GLMs) are mathematical extensions of linear models that do not force data into unnatural scales, therefore allowing for non-linearity and non-constant variance (McCullagh and Nelder 1997; Venables and Ripley 1999). The relationship between response variable and the linear combination of explanatory variables forms the basis for GLMs (Guisan *et al.* 2002). Many different families of probability distributions can be used including Gaussian, binomial, gamma or Poisson, which may better fit the non-normal error structures of most ecological data (Venables and Ripley 1999; Guisan *et al.* 2002). GLMs are generally more suited to analysing ecological data. The class of model selected in analyses was Poisson with a log link function for species richness, and a binomial error distribution with a probit link function for evenness models, as used in the earlier mixed models.

Parsimonious models were generated using stepwise selection (Lucent Technologies 2002) with the significance of probability increased to 0.1 *a priori* (Quinn and Keough 2002), to prevent important management and environmental variables being removed from the

analysis in haste. The selection of each variable in forward selection was based on the Akaike Information Criterion (AIC), commonly described as penalised log likelihood, to test whether terms were needed in the minimum adequate model by using a trade-off between the goodness of fit and the number of parameters required by parsimony (Venables and Ripley 1999; Crawley 2002). Significance of the fixed effects was tested using the Wald statistic (Butler *et al.* 2002). The Wald statistic has a chi-square distribution on  $r$  degrees of freedom, where  $r$  = denominator.

Terms were removed from the equation if they were collinear<sup>1</sup> or non-significant. Removal of the distance to travelling stock route variable in the native species richness statistical model, which was non-significant, caused other parameters in the model to become non-significant, reflecting its collinearity with other terms in the model. The problem could not be overcome so distance to travelling stock route was retained, with the resulting model being considered the ‘best’ model for the native species richness data. Terms in final models were also checked for orthogonality, by rearranging the order of terms and confirming their significance. Calculation of predicted means was undertaken for the main effects only, as terms in both the native and exotic species richness statistical models had missing values for some sites (Chapter 4). Calculation of predicted means using the full model would result in rows (containing missing values) being omitted and predicted means based on a smaller than necessary and possibly biased sample. The significance between the predicted means was tested by calculating 95% confidence intervals for the difference between the means (Crawley 2002).

Sums of squares typically reported when testing variables using analysis of variance are sequential sums of squares, also referred to as Type I sums of squares. Fox (2002) stated that for non-orthogonal data such as that from field experiments, sequential sums of squares generally do not correspond to meaningful hypotheses about parameters in a model. He recommended that Type II sums of squares or incremental sums of squares be calculated. The *Anova* function in R (Chambers 2002) calculates a test for each of the terms in the model obeying the principle of marginality, and the denominator for the F-test is taken

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<sup>1</sup> Collinearity: correlation of the predictor variables and their impacts on the estimates of the parameter and hypothesis tests (Quinn and Keough 2002). Statistically this means there is little or no information about the corresponding variable, if the other terms remain in the model (McCullagh and Nelder 1997).

from the estimated error variance for the full model (Fox 2002). Aliasing<sup>2</sup> occurred with the main effect, cultivation nested within lithology, in modelling native species richness: the term was aliased with one or more of the other explanatory variables in the model and so was removed from the final model. All models were inspected for fit to the data and for outliers through the patterns in residual graphics (Quinn and Keough 2002). A summary of the sequence of statistical modelling used to analyse the ground-storey evenness and species richness data is shown in Figure 5.1. A non-significant result in the species richness or evenness models did not preclude inclusion of an explanatory variable from subsequent analysis of the compositional data in Chapters 6 and 7.

### **Evaluation of management impacts on species richness**

The effect of the management stratification variables on species richness could be interpreted in various ways: firstly, from the effect of each variable by itself on species richness; secondly, by comparing predicted values from statistical modelling, taking into account the influence of other variables in the statistical model; and finally, by controlling variation in confounding variables to minimise their influence on species richness when examining the impact of a particular management variable. Lithology has an important role in determining species richness (see McIntyre and Lavorel 1994a; Clarke 2003) and therefore this variable was taken into account when interpreting the influence of management variables on species richness. Two different analyses were undertaken. Firstly, the predicted means of native and exotic species richness and their response to grazing, fertiliser and cultivation management nested within lithology were modelled and the different level of each management variable compared while accounting for the variation due to other management main effects. Secondly, comparisons between the untransformed mean species richness of different levels of each management variable were made using one-way analysis of variance within a controlled set of comparisons (Table 5.3) using Tukey's test (Zar 1999) and diagnostics checked. The particular comparisons of native and exotic species richness are described in Table 5.3, where shaded areas and ticks indicate the

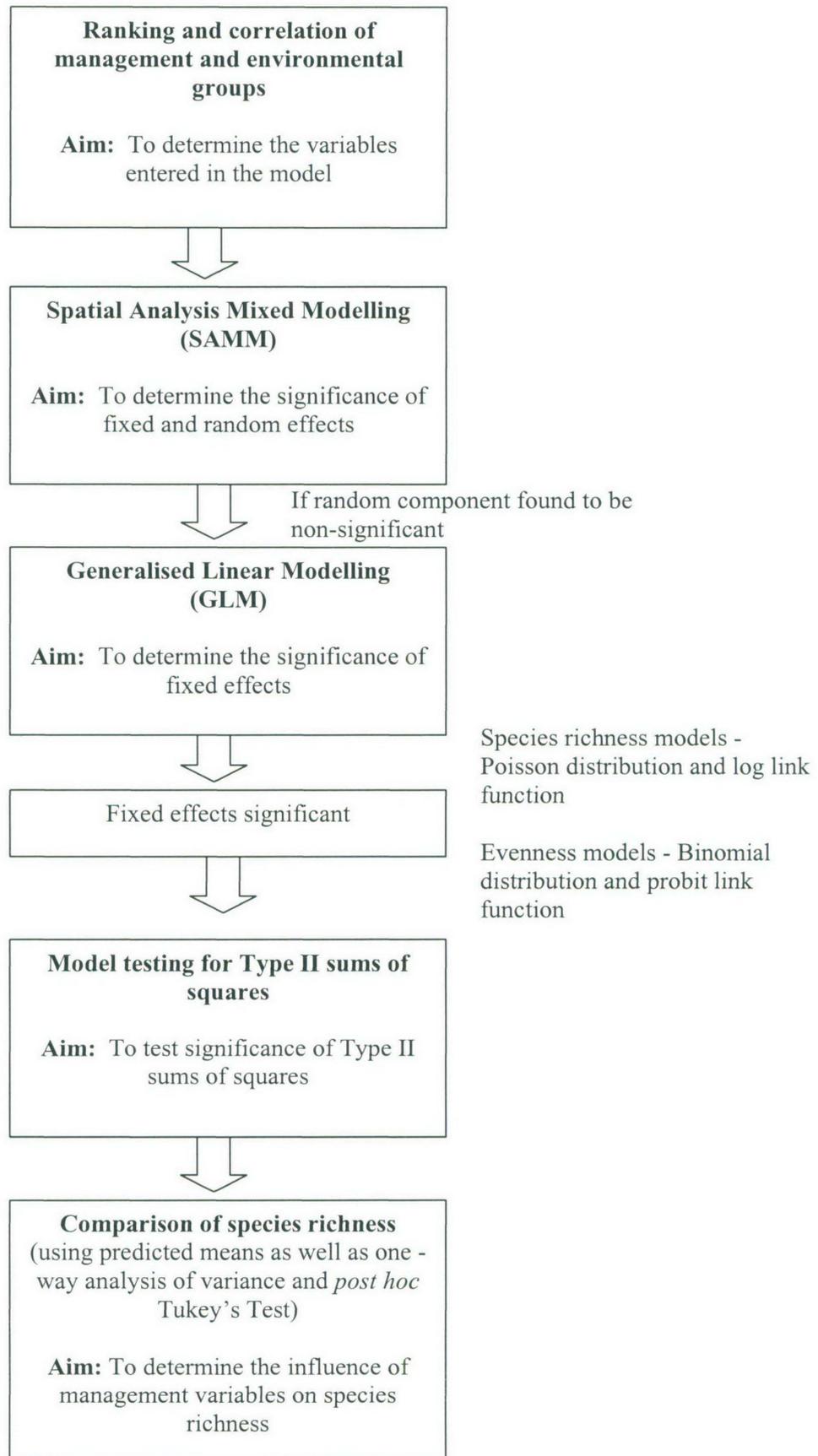
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<sup>2</sup> Aliasing: McCullagh and Nelder (1997) state "each term in a model formula describes a set of covariables to be included in a linear predictor. If such a set is denoted by  $x_1, \dots, x_p$ , the  $x$ 's being  $n$ -vectors, then the covariates can be thought of as defining  $p$  directions in  $n$ -dimensional Euclidean space. The maximum dimension is achieved if the  $x$ s are linearly independent. Losses of dimension occur when joint subspaces are covered by more than one term. This overlapping of terms in a generalised linear model is described as aliasing."

comparisons made within a management variable and the asterisks indicate management variables that were held constant (e.g. the first comparison in Table 5.3 is a comparison of never grazed, episodic, planned rest and continuous grazing in unfertilised uncultivated sites on granite).

**Table 5.3 Controlled comparisons of management variables (grazing, fertiliser and cultivation) within lithology (granite, basalt and metasediment). Ticks and shading illustrate the subset of the regional data set being compared and asterisks indicate the management variables held constant within the subset. Abbreviations: Epi – episodic; Plan rest – planned rest; Cont - continuous grazing; Low – low levels of fertiliser applied; High – high levels of fertiliser applied; > 20 ya – cultivated > 20 years ago; 10-20 ya – cultivated 10-20 years ago.**

Lithology	Grazing levels				Fertiliser levels			Cultivation levels			n
	Never	Epi	Plan rest	Cont	Never	Low	High	Never	>20 ya	10-20 ya	
Granite	✓	✓	✓	✓	*			*			49
Basalt	✓	✓		✓	*			*			34
Metasediment	✓	✓		✓	*			*			33
Granite			✓	✓			*			*	22
Basalt			✓	✓			*			*	27
Granite			✓	✓			*		*		24
Basalt			✓	✓			*		*		19
Granite			✓	✓		*		*			17
Basalt			✓	✓		*		*			19
Granite			*		✓	✓	✓	*			33
Basalt			*			✓	✓	*			19
Metasediment			*			✓	✓	*			20
Granite				*	✓	✓	✓	*			37
Basalt				*	✓	✓	✓	*			28
Metasediment				*	✓	✓	✓	*			24
Granite			*				*	✓	✓	✓	36
Basalt			*				*	✓	✓	✓	34
Granite				*			*	✓	✓	✓	31
Basalt				*			*	✓	✓	✓	32



**Figure 5.1** Flow diagram of statistics used in the analysis of evenness and species richness data, Northern Tablelands of NSW.

## 5.3 RESULTS

### 5.3.1 Native species richness

The most parsimonious model (Equation 5.2) of native species richness contained eight variables: three management variables (fertiliser nested within lithology, grazing nested within lithology and size of paddock), and five environmental variables (lithology, precipitation in May, slope, distance to travelling stock route and percentage of site under tree canopy).

Native species richness ~

$$\begin{aligned}
 & \text{lithology} & + \text{size of paddock} \\
 + \text{precipitation in May} & + \text{distance to travelling stock route} \\
 & + \text{slope} & + \text{percentage of site under tree canopy} \\
 + \text{fertiliser \%in\% lithology} & + \text{grazing \%in\% lithology} \\
 & (\text{aliasing of cultivation \%in\% lithology})
 \end{aligned}$$

(Equation 5.2)

where fertiliser %in% lithology = fertiliser nested within lithology; grazing %in% lithology = grazing nested within lithology; and cultivation %in% lithology = cultivation nested within lithology. Analysis of Equation 5.2 in SAMM showed that the random component, site nested within lithology, was non-significant (Table 5.4), as the z-ratio did not approach 2. Accordingly, the model was analysed further using GLM, without a random component.

**Table 5.4 Variance components for the random effects for Equation 5.2.**

Source	Variance component	Standard error	z-ratio <sup>3</sup>
Site %in% Lithology	8.41 x10 <sup>-7</sup>	7.88 x10 <sup>-7</sup>	1.06
Residual	1.43	0.11	13.17

In the resulting final equation, only seven of the eight variables were significant (Table 5.5). Distance to travelling stock route was retained in the equation although it was non-significant because its removal caused other variables to become non-significant, reflecting the collinearity between distance to travelling stock route and other variables in the equation (Section 5.2.3). Residual diagnostics for the final native species richness equation showed one outlier in the fitted values and residuals plot (Appendix 5.2). Thus the equation

<sup>3</sup> p < 0.05 if z-ratio ~ 2

was fitted twice, once with the outlier omitted and once with the outlier included. This resulted in little difference between the two analyses so the observation was not deemed influential.

Cultivation nested within lithology was not retained in the final equation for native species richness and was not reported in the analysis of variance table. Cultivation nested within lithology was aliased with one or more of the other variables in the equation and so was removed. Cultivation is nonetheless considered an important determinant of native species richness (see Section 1.2.6) and should not be disregarded, despite its absence from the final equation.

**Table 5.5 Analysis of variance table for the GLM from Equation 5.2. Results in the order as in the equation.**

Variable	df	Wald	p
Lithology	2	37.88	< 0.001
Size of paddock	1	11.74	< 0.001
Precipitation in May	1	26.65	< 0.001
Distance to travelling stock route	1	0.65	0.420
Slope	1	16.38	< 0.001
Percentage of site under tree canopy	1	29.71	< 0.001
Fertiliser %in% lithology	6	71.52	< 0.001
Grazing %in% lithology	9	16.09	0.065

The size of paddock in which sites were located significantly affected native species richness in the GLM (Table 5.5) and in linear regression (Table 5.6). The direct influence of size of paddock in the absence of other factors was positive, such that native species richness increased with paddock size. Of the three continuous environmental variables found to significantly influence native species richness, slope and percentage of site under tree canopy had positive influences on native species richness, as did the regression coefficients from the GLM (Table 5.7). In other words, as slope or the percentage of the site under a tree canopy increased, so too did native species richness. In contrast, May precipitation was negatively related to native species richness, as was the regression coefficient. Therefore sites with higher May precipitation had lower native species richness.

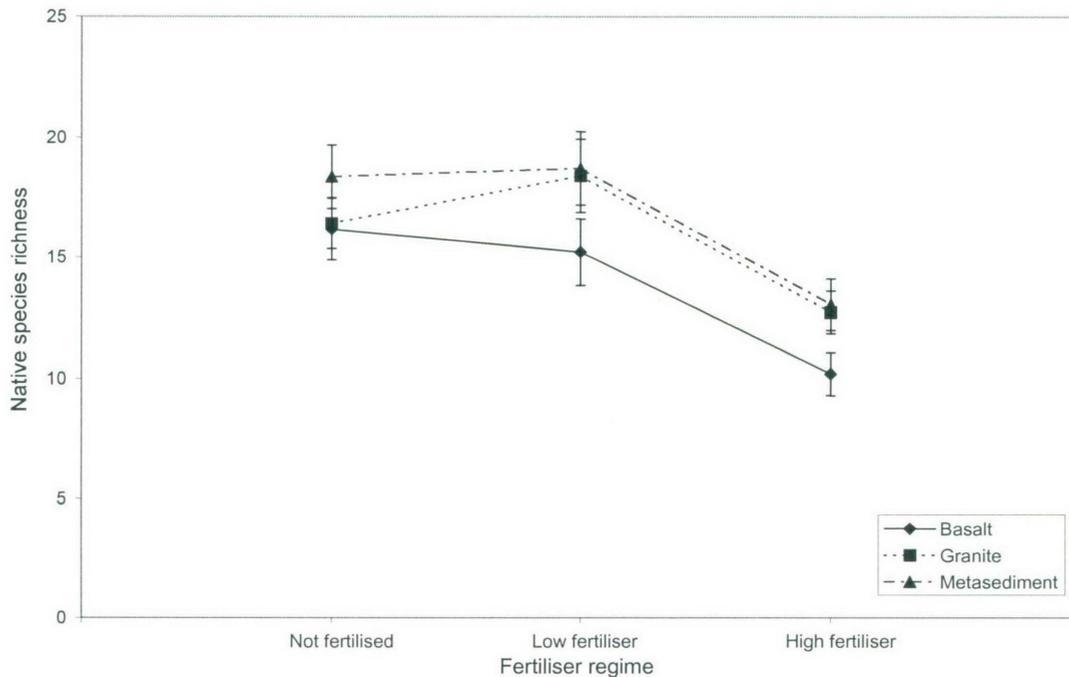
**Table 5.6 Linear regressions of native species richness on significant explanatory variables from Equation 5.2.**

Explanatory variable	Regression equation	n	R <sup>2</sup>	p
Precipitation in May	$y = -0.5229x + 36.234$	373	0.080	< 0.001
Slope	$y = 0.4432x + 12.152$	371	0.044	< 0.001
Percentage of site under tree canopy	$y = 0.0738x + 12.989$	373	0.103	< 0.001
Size of paddock	$y = 0.0326x + 12.150$	323	0.088	< 0.001

**Table 5.7 Regression coefficients and standard errors from GLM of Equation 5.2, native species richness of ground-storey vegetation.**

Variable	Coefficient	Standard error
Intercept	4.044	0.300
Lithology – granite	-0.222	0.155
Lithology – metasediment	0.117	0.121
Size of paddock	0.001	< 0.001
Precipitation in May	-0.037	0.007
Slope	0.024	0.006
Percentage of site under tree canopy	0.003	< 0.001
Distance to Travelling Stock Route	0.005	0.006
Basalt : Low fertiliser	-0.269	0.112
Granite : Low fertiliser	0.082	0.074
Metasediment : Low fertiliser	-0.017	0.099
Basalt : High fertiliser	-0.479	0.099
Granite : High fertiliser	-0.243	0.066
Metasediment : High fertiliser	-0.326	0.096
Basalt : Episodic grazing	0.009	0.126
Granite : Episodic grazing	0.450	0.188
Metasediment : Episodic grazing	0.057	0.123
Basalt : Planned rest grazing	0.02	0.134
Granite : Planned rest grazing	0.241	0.147
Metasediment : Planned rest grazing	-0.073	0.138
Basalt : Continuous grazing	0.099	0.105
Granite : Continuous grazing	0.127	0.141
Metasediment : Continuous grazing	0.088	0.116

Predicted means of native species richness were generated for each of the three levels of fertiliser nested within lithology from the GLM based on the main effects in Equation 5.2 (Figure 5.2). Predicted mean native species richness was lower on basalt and highest on metasediments, however no significant differences between the means in Figure 5.2 were established using conservative 95% confidence intervals for the difference between the predicted values.



**Figure 5.2 Predicted mean ( $\pm$  SEM) native species richness on basalt, metasediment and granite lithology in relation to fertiliser history. Predicted means take into account the main stratification variables, lithology and grazing ( $n = 373$ ). Significance between means discussed in text. Observed means in Table 5.8.**

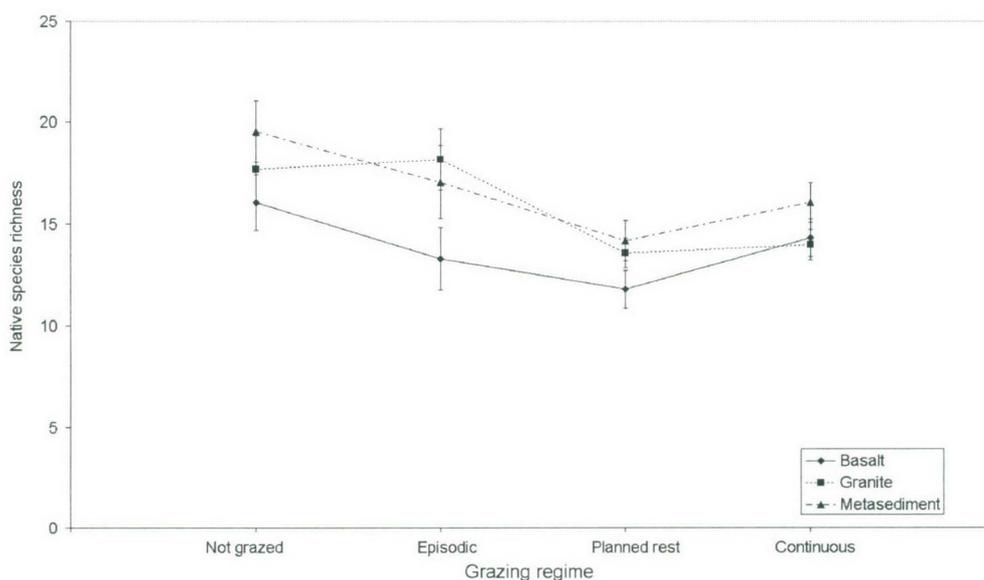
Fertiliser and grazing were the two management main effects found to significantly influence native species richness in the first model. The importance of cultivation to native species richness could only be determined by the appropriate controlled comparisons in the data set when other main management and environmental influences were held constant. In the controlled set of comparisons of the influence of fertiliser on native species richness, significant differences in native species richness due to fertiliser regime were only detected on basalt under continuous grazing with no history of cultivation (Table 5.8). Under these conditions, sites with a history of high fertiliser application had significantly fewer native species than sites never fertilised or fertilised at low level. This trend was consistent over all sites on all lithologies with various grazing regimes and cultivation histories. Heavily fertilised sites consistently had fewer native species than less fertilised or unfertilised sites, but these other relationships were not significant. Comparisons between unfertilised and less heavily fertilised sites were conditional on lithology. Low levels of fertiliser application on metasediment resulted in fewer native species compared to unfertilised sites but the converse was true on granites and basalt. These results were not significant but were consistent with those of the predicted means for metasediment, granite and basalt.

On all lithologies (basalt, metasediments and granite), sites with a history of high fertiliser application had significantly lower native species richness than sites that were not fertilised or had a history of low fertiliser application.

**Table 5.8 Results of one-way analysis of variance of native species richness, in relation to fertiliser levels on different lithologies while holding grazing and cultivation history constant. Superscript letters indicate significant differences between means. Data are mean ( $\pm$  SEM) of observed data.**

Lithology	Mean native species richness for fertiliser levels ( $\pm$ SEM)			Variables held constant		n	F	p
	Never	Low	High	Grazing	Cultivation			
Granite	13.6 (1.37)	16.6 (4.57)	13.5 (1.44)	Planned rest	Never	33	1.22	0.31
Basalt		10.3 (1.29)	9.8 (0.97)	Planned rest	Never	19	0.08	0.78
Metasediment		16.7 (1.59)	14.8 (1.26)	Planned rest	Never	20	0.85	0.37
Granite	14.4 (0.95)	16.3 (1.30)	12.5 (1.55)	Continuous	Never	37	1.78	0.18
Basalt	17.4 <sup>a</sup> (1.21)	19.1 <sup>a</sup> (0.92)	8.1 <sup>b</sup> (0.95)	Continuous	Never	28	31.67	< 0.001
Metasediment	20.0 (8.45)	19.6 (3.14)	16.4 (1.64)	Continuous	Never	24	0.55	0.58

The predicted means generated from the main effects in Equation 5.2 showed that mean native species richness on basalt sites was lower than for metasediments or granite with the exception of continuously grazed sites (Figure 5.3). No significant differences between the means in Figure 5.3 were established using conservative 95% confidence intervals for the difference between the predicted values.



**Figure 5.3 Predicted mean ( $\pm$  SEM) native species richness on basalt, metasediment and granite lithology in relation to grazing regime. Predicted means take into account the main stratification variables: lithology and fertiliser (n = 373). Significance between means discussed in text. Observed means in Table 5.9.**

Three comparisons of grazing regime on varying lithology while holding fertiliser and cultivation history constant were significant: two comparisons on basalt and one on granite (Table 5.9). The comparison of all four grazing regimes on granite sites that had never been cultivated or fertilised showed that episodic grazing resulted in significantly more native species than planned rest or continuous grazing. On basalt, planned rest resulted in fewer native species than continuous grazing at sites with a history of high fertiliser and cultivation more than 20 years ago, as well as at uncultivated sites with a low fertiliser history.

**Table 5.9 Results of one-way analysis of variance of native species richness, in relation to grazing levels on different lithologies while holding fertiliser and cultivation history constant. Superscript letters indicate significant differences between means. Data are mean ( $\pm$  SEM) values of observed data. Abbreviations: Cult – cultivation; Cont – Continuous; ya – years ago.**

Lithology	Mean native species richness for grazing levels ( $\pm$ SEM)				Variables held constant		n	F	p
	Not grazed	Episodic	Planned rest	Cont	Cult	Fertiliser			
Granite	18.3 <sup>a</sup> (1.88)	19.9 <sup>a</sup> (1.74)	13.6 <sup>b</sup> (1.37)	14.4 <sup>b</sup> (0.95)	Never	Never	49	4.31	0.009
Basalt	18.4 (1.50)	15.50 (1.15)		17.4 (1.21)	Never	Never	34	0.88	0.42
Metasediment	20.6 (1.06)	18.8 (2.16)		20.0 (2.99)	Never	Never	33	0.26	0.77
Granite			9.5 (0.78)	11.4 (1.42)	10-20 ya	High	22	1.40	0.25
Basalt			10.1 (1.05)	8.0 (0.80)	10-20 ya	High	27	2.61	0.12
Granite			10.0 (0.73)	10.3 (1.32)	> 20 ya	High	24	0.05	0.83
Basalt			9.4 <sup>c</sup> (0.72)	13.4 <sup>d</sup> (1.56)	> 20 ya	High	19	6.58	0.02
Granite			16.6 (1.6)	16.3 (1.3)	Never	Low	21	0.02	0.89
Basalt			10.3 <sup>e</sup> (1.29)	19.1 <sup>f</sup> (0.92)	Never	Low	19	32.26	<0.001

Predicted values for each level of cultivation regime variable nested within lithology could not be generated due to aliasing (Section 5.2.3). However, comparisons of native species richness in response to cultivation history were possible using controlled comparisons of the data, while holding lithology, grazing and fertiliser history constant (Table 5.10). Two such comparisons were significant, one on basalt, the other on granite. On granite under planned rest and continuous grazing with a history of high fertiliser, all cultivated sites had fewer native species than uncultivated sites. Least native species were found at sites

cultivated more recently under a planned rest grazing regime. Trends on basalt were not as straightforward. The high number of native species on sites cultivated more than 20 years ago generated a significant difference due to cultivation on basalt sites with high fertiliser use and continuous grazing. Sites not cultivated or cultivated more recently (10-20 years ago) had similarly low numbers of native species.

**Table 5.10 Results of one-way analysis of variance of native species richness, in relation to cultivation levels on different lithologies while holding fertiliser and grazing constant. Different superscript letters indicate significant differences between means. Data are the mean ( $\pm$  SEM) of observed data. Abbreviation: ya – years ago.**

Lithology	Mean native species richness for cultivation levels ( $\pm$ SEM)			Variables held constant		n	F	p
	Never	Cultivated > 20 ya	Cultivated 10-20 ya	Grazing	Fertiliser			
Granite	13.5 <sup>a</sup> (1.44)	10.0 <sup>b</sup> (0.73)	9.5 <sup>b</sup> (0.78)	Planned rest	High	36	4.17	0.02
Basalt	9.8 (0.97)	9.4 (0.71)	10.1 (1.05)	Planned rest	High	34	0.15	0.86
Granite	12.5 (1.55)	11.4 (1.42)	10.3 (1.32)	Continuous	High	31	0.55	0.59
Basalt	8.1 <sup>c</sup> (0.95)	13.4 <sup>d</sup> (1.56)	8.0 <sup>c</sup> (0.80)	Continuous	High	32	7.31	0.003

### 5.3.2 Exotic species richness

The most parsimonious model for exotic species richness contained seven variables: four management variables (number of rests from grazing per year, number of months grazed per year, fertiliser nested within lithology and grazing nested within lithology), and three environmental variables (lithology, average summer maximum temperature and altitude) (Equation 5.3):

$$\begin{aligned}
 \text{Exotic species richness} \sim & \text{lithology} + \text{number of rests from grazing per year} \\
 & + \text{average maximum temperature in summer months} + \text{number of months grazed per year} \\
 & + \text{altitude} + \text{fertiliser \%in\% lithology} \\
 & + \text{grazing \%in\% lithology}
 \end{aligned}
 \tag{Equation 5.3}$$

The random component, site nested within lithology, was not significant (Table 5.11), so the model was analysed as a GLM, without a random component.

**Table 5.11 Variance components for the random effects for Equation 5.3.**

Source	Variance component	Standard error	z-ratio
Site %in% Lithology	$2.73 \times 10^{-7}$	$3.54 \times 10^{-7}$	0.77
Residual	1.54	0.12	13.19

Three variables were only significant at the 10% level but were retained (Table 5.12).

Diagnostics for the final exotic species richness model illustrate an acceptable scatter of points with no obvious pattern of increasing or decreasing variance in the residuals (Appendix 5.3).

**Table 5.12 Analysis of variance table of the GLM of Equation 5.3. Results presented in the order as in the equation.**

Variables	df	Wald	p
Lithology	2	21.11	< 0.001
Number of rests from grazing per year	1	16.68	< 0.001
Average maximum temperature during summer	1	3.51	0.060
Period grazed per year (months)	1	7.60	0.005
Altitude	1	2.74	0.098
Fertiliser %in% lithology	6	17.68	0.007
Grazing %in% lithology	9	6.26	0.099

Two management variables associated with grazing significantly affected exotic species richness. The number of rests from grazing per year had a negative influence on exotic species richness in both the GLM (Table 5.12), regression coefficients (Table 5.13) and the linear regression (Table 5.14), so that as the number of rests increased, exotic species richness declined. The number of months grazed per year had a positive influence, so that as the number of grazing months increased, so too did exotic species numbers. The regression coefficient for number of months grazed per year was positive, in contrast to the modelled regression coefficient, which was negative, due to fitting terms higher in the table. Average maximum temperature during summer affected exotic species richness, but only marginally, with a significant negative influence in both the GLM and linear regression. Sites with a higher maximum summer temperature had fewer exotic species. Altitude did not significantly influence exotic species richness as the linear regression showed that altitude had a small but non-significant positive influence on exotic species richness.

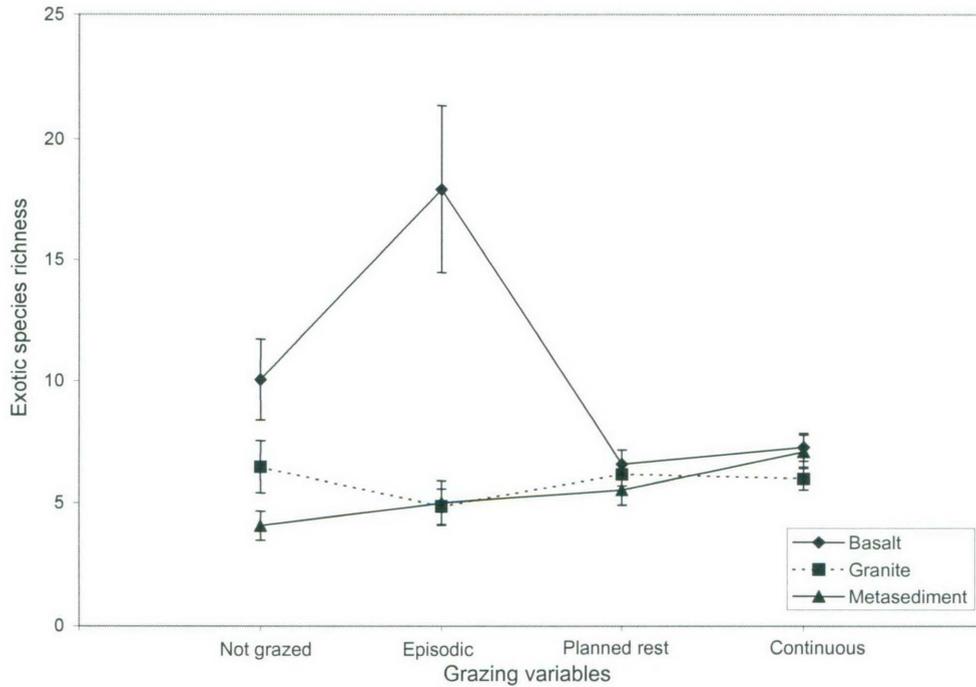
**Table 5.13 Regression coefficients and standard errors from GLM for Equation 5.3 of exotic species richness of ground-storey vegetation.**

Variable	Coefficient	Standard error
Intercept	5.400	1.998
Lithology – Granite	0.506	0.406
Lithology – Metasediment	0.629	0.421
Number of rests from grazing per year	-0.091	0.022
Average maximum temperature during summer months	-0.122	0.065
Number of months grazed per year	-0.041	0.015
Altitude	< 0.001	< 0.001
Basalt : Low fertiliser	0.807	0.399
Granite : Low fertiliser	0.254	0.160
Metasediment : Low fertiliser	-0.219	0.167
Basalt : High fertiliser	0.943	0.384
Granite : High fertiliser	0.318	0.110
Metasediment : High fertiliser	-0.117	0.142
Basalt : Grazing	0.092	0.160
Granite : Grazing	-0.021	0.115
Metasediment : Grazing	0.299	0.144

**Table 5.14 Linear regressions of exotic species richness on the significant explanatory variables from Equation 5.3.**

Explanatory variable	Regression equation	n	R <sup>2</sup>	p
Average maximum temperature in summer	$y = -0.71x + 23.14$	373	0.044	< 0.001
Altitude	$y = 0.01x + 0.98$	373	0.031	0.562
Number of rests from grazing per year	$y = -0.22x + 7.72$	245	0.023	< 0.001
Number of months grazed per year	$y = 0.06x + 6.26$	312	0.007	< 0.001

Use of the main effects in Equation 5.3 to predict mean exotic species richness for grazing regimes on each lithology established that means on basalt lithologies were highest (Figure 5.4). However, no predicted means were significantly different from one another, using conservative 95% confidence intervals for the difference between the predicted values.



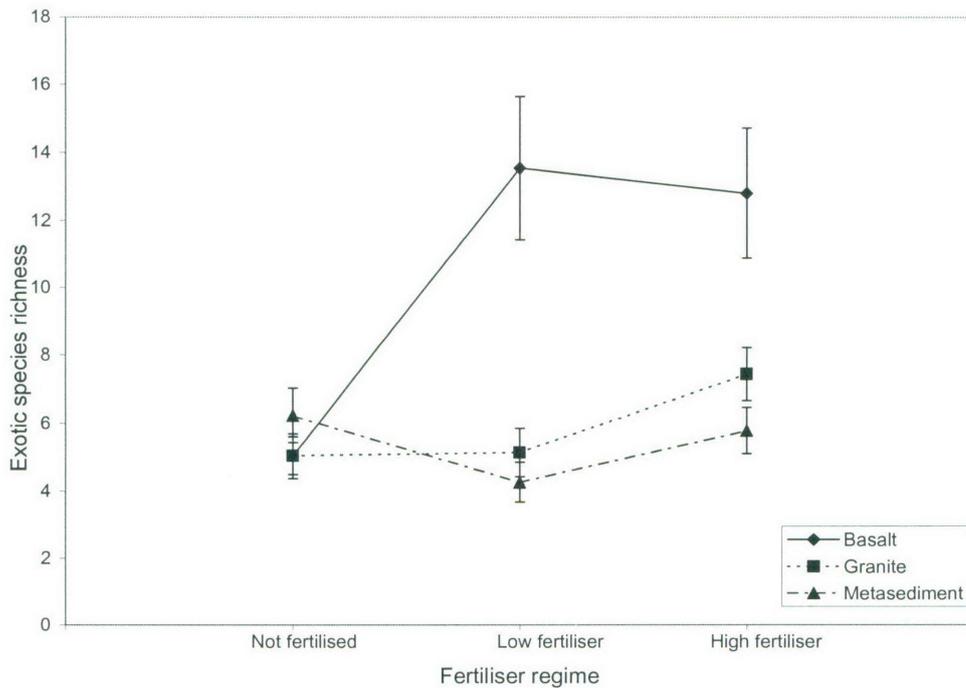
**Figure 5.4 Predicted mean ( $\pm$  SEM) exotic species richness on basalt, metasediment and granite lithology in relation to grazing regime. Predicted means take into account the main stratification variables: lithology and fertiliser ( $n = 373$ ). Significance between means discussed in text. Observed values in Table 5.15.**

Subsets of sites were compared to determine the effect of particular management variables and lithology on exotic species richness as for native species richness, while controlling for other management effects (Table 5.15). For basalt sites that had never been cultivated or fertilised, episodic grazing resulted in significantly more exotic species than with no or continuous grazing. Different results were seen on metasediments, where continuously grazed sites had more exotic species than episodically grazed or ungrazed sites. In the absence of cultivation but with a history of low fertiliser use, planned rest sites had lower exotic species richness than continuously grazed sites on both basalt and granite, although the difference was only significant on the latter ( $p < 0.001$ ).

**Table 5.15 Results of one-way analysis of variance of exotic species richness in relation to grazing levels on different lithologies while holding cultivation and fertiliser constant. Different superscript letters indicate significant differences between means. Data are the mean ( $\pm$  SEM) of the observed data. Abbreviations: Cont – Continuous; Cult – Cultivation.**

Lithology	Mean exotic species richness for grazing variables ( $\pm$ SEM)				Variables held constant		N	F	P
	Not grazed	Episodic	Planned Rest	Cont	Cult	Fertiliser			
Granite	5.6 (0.65)	5.5 (0.80)	5.2 (0.47)	4.7 (0.66)	Never	Never	49	0.37	0.780
Basalt	4.9 <sup>a</sup> (0.64)	8.6 <sup>b</sup> (1.22)		3.4 <sup>a</sup> (0.50)	Never	Never	34	8.45	0.001
Metasediment	4.7 <sup>c</sup> (0.72)	5.8 <sup>c</sup> (1.33)		8.6 <sup>d</sup> (1.22)	Never	Never	33	3.87	0.030
Granite			9.0 (1.18)	8.2 (0.97)	10-20 ya	High	22	0.29	0.600
Basalt			8.4 (0.69)	8.8 (0.78)	10-20 ya	High	27	0.12	0.730
Granite			8.5 (0.91)	7.5 (1.08)	> 20 ya	High	24	0.50	0.490
Basalt			8.8 (0.52)	8.9 (0.91)	> 20 ya	High	19	0.00	0.950
Granite			2.8 <sup>e</sup> (0.61)	7.4 <sup>f</sup> (0.80)	Never	Low	17	19.77	< 0.001
Basalt			7.6 (1.63)	10.3 (0.94)	Never	Low	19	2.37	0.140

Predicted means of exotic species richness were generated for each of the three levels of fertiliser nested within lithology. No significant differences between the means in Figure 5.5 were established using conservative 95% confidence intervals for the difference between the predicted values.



**Figure 5.5 Predicted mean ( $\pm$  SEM) exotic species richness on basalt, metasediment and granite lithology in relation to fertiliser history. Predicted means take into account the main stratification variables, lithology and grazing, in Equation 5.3 ( $n = 373$ ). Significance between means discussed in text. Observed means in Table 5.16.**

Four comparisons of exotic species richness in relation to fertiliser regime were significant (Table 5.16). Of the continuously grazed and never cultivated sites on metasediments, low fertiliser application corresponded to fewer exotic species than never fertilised and high levels of fertiliser application ( $p = 0.07$ ). Higher exotic species richness was also found at high fertiliser levels on granite sites under planned rest grazing that had never been cultivated. Granite and basalt sites that were continuously grazed and never cultivated had more exotic species under low levels of fertiliser than no fertiliser or high fertiliser sites. The impact of fertiliser use on exotic species on uncultivated basalt and metasediment sites under planned rest grazing was not significant. The predicted means were generally similar to the observed means for all lithologies and grazing regimes, with the exception of ungrazed and episodically grazed basalt sites where the predicted means were higher than the observed means. This is attributable to sample sizes, as the predicted means are based on 373 sites and the observed means based on  $< 50$  sites.

**Table 5.16 Results of one-way analysis of variance of exotic species richness, in relation to fertiliser levels on different lithologies while holding grazing and cultivation history constant. Different superscript letters indicate significant differences between means. Data are mean of observed data.**

Lithology	Mean exotic species richness for fertiliser variables ( $\pm$ SEM)			Variables held constant		n	F	p
	Never	Low	High	Grazing	Cultivation			
Granite	5.2 <sup>a</sup> (0.47)	2.9 <sup>a</sup> (0.61)	7.9 <sup>b</sup> (0.80)	Planned rest	Never	33	12.69	<0.001
Basalt		7.6 (1.63)	7.7 (0.66)	Planned rest	Never	19	0.00	0.950
Metasediment		4.3 (0.44)	4.5 (0.45)	Planned rest	Never	20	0.04	0.850
Granite	4.7 <sup>c</sup> (0.66)	7.4 <sup>d</sup> (0.80)	5.6 (0.50)	Continuous	Never	37	3.51	0.040
Basalt	3.4 <sup>e</sup> (0.50)	10.3 <sup>f</sup> (0.94)	8.4 <sup>f</sup> (1.08)	Continuous	Never	28	14.75	<0.001
Metasediment	8.6 (1.22)	4.8 (0.41)	8.4 (1.73)	Continuous	Never	24	3.02	0.070

### 5.3.3 Evenness

Despite many attempts to fit a significant model using the stepwise function in S-PLUS from the initial evenness model (Equation 5.4), no minimum adequate model could be generated, therefore the initial model containing 16 variables, nine management variables and seven environmental variables was used:

Evenness ~

$$\begin{aligned}
 & \text{lithology} & + \text{stocking rate} \\
 & + \text{number of times cultivated} & + \text{weight of fertiliser applied} \\
 & \quad + \text{radiation in May} & + \text{moisture index in July} \\
 + \text{percentage of site under tree canopy} & + \text{minimum temperature in May} \\
 & \quad + \text{precipitation in July} & + \text{pH}_{\text{H}_2\text{O}} \\
 & \quad + \text{fertiliser \%in\% lithology} & + \text{grazing \%in\% lithology} \\
 & \quad + \text{cultivation \%in\% lithology} & + \text{grazing : fertiliser \%in\% lithology} \\
 + \text{grazing : cultivation \%in\% lithology} & + \text{cultivation : fertiliser \%in\% lithology}
 \end{aligned}$$

(Equation 5.4)

Analysis of Equation 5.4 as a mixed model showed that the random component, site nested within lithology (Site %in% Lithology), was not significant (Table 5.17), as the z-ratio did not approach 2. Due to the non-significance of the random component, the model was analysed as a GLM without a random component.

**Table 5.17 Variance components for the random effects for Equation 5.4.**

Source	Variance component	Standard error	z-ratio
Site %in% Lithology	$1.17 \times 10^{-7}$	$1.69 \times 10^{-7}$	0.69
Residual	2.58	$2.04 \times 10^{-3}$	12.58

The model for evenness had no explanatory variables (Table 5.18) that significantly affected evenness.

**Table 5.18 Analysis of variance table of Equation 5.4 from GLM. Results are presented in the same order as entered in the model.**

Explanatory variable	df	Residual deviance	p
Lithology	2	0.03	0.980
Stocking rate	1	0.31	0.580
Number of times cultivated	1	0.03	0.870
Weight of fertiliser applied	1	0.05	0.840
Radiation in May	1	0.08	0.780
Moisture index in July	1	0.14	0.710
Percentage of site under tree canopy	1	0.01	0.910
Minimum temperature in May	1	< 0.01	0.990
Precipitation in July	1	< 0.01	0.930
pH <sub>(H2O)</sub>	1	< 0.01	0.980
Grazing %in% lithology	7	0.15	< 0.990
Fertiliser %in% lithology	5	0.16	< 0.990
Cultivation %in% lithology	6	0.18	< 0.990
Grazing : fertiliser %in% lithology <sup>4</sup>	1	< 0.01	0.950
Grazing : cultivation %in% lithology	3	0.03	< 0.990
Cultivation : fertiliser %in% lithology	0	< 0.01	

## 5.4 DISCUSSION

### 5.4.1 Species richness

#### Management variables significantly influencing species richness

##### Grazing

Generally investigations of the effect of grazing management on species richness simply compare grazed and ungrazed sites, both in Australia (McIntyre and Lavorel 1994a; Pettit

<sup>4</sup> Grazing : fertiliser %in% lithology refers to the interaction of grazing and fertiliser nested within lithology.

*et al.* 1995; Clarke 2003; Reseigh *et al.* 2003) and elsewhere (e.g. Puerto *et al.* 1990; Montalvo *et al.* 1993; Noy-Meir 1995; Bullock *et al.* 2001). Rarely are comparisons made between different grazing regimes and ungrazed areas. Kemp *et al.* (2003a) stated 'in biodiversity experiments ... data are rarely from grazed pasture systems, and so little is known of the relationships between productivity, stability and diversity in Australian pastures'.

#### *Native species richness*

Ungrazed sites had higher native species richness on all substrates than those grazed either by planned rest or continuously. The results are consistent with other Australian studies (Gilfedder and Kirkpatrick 1993; McIntyre and Lavorel 1994b; Prober and Thiele 1995; Waters 2001; Clarke 2003) that grazing generally reduces native species richness. Trémont and Whalley (1995) found that native species richness was markedly higher in grazed than ungrazed pastures on the Northern Tablelands of NSW, but this was an unreplicated comparison of two paddocks. Species richness responses observed in the present study can be best explained by the adaptations of the Northern Tablelands ground-storey vegetation to the conditions of pre-European settlement where grazing was by soft-footed marsupials and was generally light and intermittent (Lodge and Whalley 1989; Jones 2003). As ungulate livestock moved into the region in the late 1830s (Lodge and Whalley 1989), native plants experienced changes associated with grazing including selective removal, concentration of nutrients, and increased trampling and grazing pressure. Other changes were also associated with livestock, such as increased nutrients from fertilisers, clearing of woody vegetation and greater soil disturbance from cultivation. The changes in species composition and the associated decline in native species numbers associated with agricultural management were inevitable (Lodge and Whalley 1989) in the face of this new grazing regime.

Grazing studies outside Australia generally investigate total species richness, rather than separating native and exotic species as is typically done in Australian studies (e.g. McIntyre and Lavorel 1994a; Pettit *et al.* 1995; Clarke 2003; Reseigh *et al.* 2003) with some exceptions (e.g. Kemp *et al.* 2003a). The conclusions of comparative research between ungrazed and grazed grasslands overseas often differ with regard to the influence of grazing on species richness. Some overseas authors have concluded that grazing increases richness

(Puerto *et al.* 1990; Montalvo *et al.* 1993; Noy-Meir 1995; Stohlgren *et al.* 1999), others that grazing reduces species richness (Collins and Barber 1985; Collins 1987; Chaneton and Facelli 1991; Grace and Jutila 1999). Differences between studies can be attributed to differences in grazing pressure: at low grazing pressure less competitive species are favoured and therefore maximum richness can be reached (Puerto *et al.* 1990).

Comparisons between planned rest and continuous grazing found that native species richness did not differ significantly, with the exception of observed mean species richness on basalt with a history of cultivation > 20 years ago and high fertiliser application. These data represent some of the first data available that contrasts the influence of planned rest and continuous grazing regimes on native species richness in Australia. The similarities between grazing regimes with respect to their influence on native species richness may be attributable to a number of different factors: planned rest grazing regimes may not have been implemented for a sufficient period of time to allow changes in species richness to be observed; results may be correlated with other management variables; or perhaps there is simply no difference in native species richness between planned rest and continuous grazing regimes. This last factor needs to be regarded with caution as planned rest grazing regimes on the Northern Tablelands have only been implemented for a relatively short period of time and the landholders of the region are still making changes to their planned rest grazing regimes to enable better utilisation of pastures.

Comparable results come from the research undertaken as part of the Sustainable Grazing Systems (SGS) program. In that work, Kemp *et al.* (2003a) concluded that native species richness increased at sites where grazing was discontinuous (i.e. falling within the determination of planned rest described in Section 4.2.3), although the increases in native species only averaged 0-2 species. The present study sampled paddocks that had a consistent grazing management history for at least 7 years (Section 4.2.3), while the results of Kemp *et al.* (2003a) were from several experiments with grazing treatments imposed for only 3-4 years (Kemp *et al.* 2003a; Lodge *et al.* 2003a). Fluctuations in species richness between the studies may be attributed to recent changes in grazing management. In addition, past and current management practices including grazing, cultivation and fertiliser history vary between this study and those of the SGS experiments (Lodge *et al.* 2003a; Lodge *et al.* 2003b; Michalk *et al.* 2003).

Other factors associated with grazing (e.g. stocking rates, grazing intensity, number of rests from grazing) have been found to be important determinants of native species richness in studies in Australia and of total species richness elsewhere. The time of year grazed (Olf and Ritchie 1998; Bullock *et al.* 2001), heavy stocking rates (Gilfedder and Kirkpatrick 1993), percentage of year grazed (Waters 2001), number of rests from grazing (Waters 2001) and grazing intensity (Puerto *et al.* 1990; Waters 2001) have all been shown to be important. In the present study, heavy stocking rates, percentage of year grazed, and the number of rests from grazing did not significantly influence native species richness. The influence of the time of year grazed was not measured in this study as grazing of commercial paddocks usually occurs in every season each year, irrespective of grazing regime. Paddock size had a positive significant effect on native species richness, as was also found by Waters (2001). Small paddock size leads to a reduction in grazing heterogeneity (Scanlan *et al.* 1990) and is generally associated with smaller overall property size, higher inputs and higher stocking rates. Grazing in large paddocks tends to be less intensive and more selective and heterogeneous, with more species likely to survive the less intense defoliation.

#### *Exotic species richness*

The influence of grazing regime on exotic species richness varied with lithology, however basalt lithology generally had higher predicted exotic species richness than comparable sites on other lithologies. On never cultivated or fertilised metasediments, observed exotic species richness was significantly higher under continuous grazing than in ungrazed sites. On granite lithologies, uncultivated continuously grazed sites with a history of low fertiliser application had significantly higher exotic species richness than comparable sites grazed under planned rest.

The trend on basalt lithologies of fewer exotic species in grazed sites was consistent with the results of Clarke (2003), but differed from those of Stuwe and Parsons (1977), McIntyre and Lavorel (1994b) and Waters (2001). Their results did conform with the present study with regards to metasedimentary and granitic lithologies. Higher numbers of exotic species at ungrazed or episodically grazed sites may be explained by preceding land use, proximity of sites to agricultural land and the presence of environmental weeds. Sites such as the

Kilcoy Cemetery (Plate 5.1) are small and surrounded by production land used for sheep and cattle grazing. Small areas such as these may have been subject to seed and fertiliser drift from aerial applications on adjacent land. Similar effects are seen at the edges of reserves in Western Australia (Hester and Hobbs 1992) and at field boundaries in the Netherlands (Kleijn and Verbeek 2000). Other ungrazed sites were known to have been continuously grazed prior to the area being set aside for conservation purposes > 10 years ago. It is likely that some species associated with previous grazing continue to persist under the changed grazing regime.



**Plate 5.1 Site at Kilcoy Cemetery approximately 35 km east of Armidale, NSW.**

The relative magnitude of exotic species richness at planned rest and continuously grazed sites differed only slightly, but were significant on granite (observed means), with continuous grazing having a higher mean than comparable sites grazed under planned rest. This result cannot readily be explained. Waters (2001) concluded that exotic species richness was generally higher on planned rest sites, when compared with continuous grazing. This is inconsistent with the results observed in this study on granite but not on basalt or metasediments.

Other significant grazing management influences on exotic species richness were a negative influence of the number of rests from grazing per year and a positive relationship with the number of months grazed per year. The results are consistent with those of Waters (2001), who concluded that as the proportion of the year grazed increases, so too does the number of exotic species. Conversely, she found that as the number of rests increases, the number of exotic species declines, which is consistent with this study. In remnant vegetation in

Tasmania, Gilfedder and Kirkpatrick (1993) found that shorter rest periods were associated with fewer exotic species than sites spelled for longer periods. Trends of increasing exotic species numbers with increasing number of months grazed could be attributed to the creation of bare ground by overgrazing. Exotic species may be able to make use of such gaps, as exotic species' optimal growth period is before that of native species (Longmore 1991) and a greater proportion of exotic species have weedy characteristics.

Other factors associated with grazing (e.g. paddock size, stocking rates and season of rest) did not significantly influence exotic species richness. In contrast, Waters (2001) found that paddock size was related to exotic species richness.

## Fertiliser

### *Native species richness*

Native species richness was highest at sites with low levels of applied fertiliser on granite and unfertilised sites on basalt and metasediment lithologies. A number of studies have investigated the relationships between abundance and fertiliser application, but relatively few have looked at species richness and fertiliser application. As stated by Whalley and Lodge (1987), little had been done to determine the effects of fertiliser on the floristics of native pastures and it had long been assumed, possibly incorrectly, that fertiliser application results in a decline in native species richness (Whalley and Lodge 1987). McIntyre and Martin (2001) were unable to differentiate the effects of fertiliser and cultivation because the variables were confounded, but their joint occurrence resulted in low native species richness. Robinson (1976) determined positive responses of *Austrodanthonia* species and *Microlaena stipoides* to increased nutrients on the Northern Tablelands.

Internationally, Blomqvist *et al.* (2003) found that in reserve areas in the Netherlands, low levels of nutrients were required to increase level species diversity, and Henkin *et al.* (1996) found that botanical composition, particularly the legume component, changed as a result of fertiliser application to Mediterranean rangelands in Israel. Generally, Australian native plants evolved under soil nutrient conditions that are naturally low in nitrogen and phosphorus (Lodge and Whalley 1989), although basalt derived soils in the region are higher in nutrients (Sections 2.2 and 4.3.3). As a consequence, many plant species are

unable to cope with nutrient additions (Garden and Bolger 2001) and may be less competitive than introduced species at high nutrient levels (Groves *et al.* 2003). Some native grasses, such as *Austrodanthonia* species and *Microlaena stipoides*, are able to thrive under increased nutrients (Robinson 1976) (Section 7.3.1). In general, however, introduced grasses are better able to respond to increased fertility than native grasses (Garden *et al.* 2003; Groves *et al.* 2003). This ability to respond to high soil nutrients often leads to greater growth, the crowding or shading out of other species leading to changes in composition (Garden and Bolger 2001) and reduced species richness. Species such as *Austrodanthonia* on the Northern Tablelands can respond positively to increased nutrients but can be disadvantaged by competition from clover (Whalley *et al.* 1978). Alternative explanations for the decrease in native species richness with increasing fertiliser application, is that high fertiliser addition is associated with increasing stocking pressure, reducing the survival of native species that are intolerant of intense ungulate grazing pressure.

The numbers of native species seen at nil and low fertiliser levels are possibly explained by the most abundant species in this study (Section 4.3), namely *Bothriochloa macra*, *Sporobolus creber* and *Poa sieberiana*. These species are known to be able to cope with increased nutrients (Lodge and Whalley 1989), while other native species (see Section 7.4.2) are able to cope with low levels of fertiliser and competition from the above native grasses but not with high levels of fertiliser. The response of native species numbers to high levels of fertiliser application is confounded with the increased stocking pressure that generally accompanies such inputs of fertiliser, as a response to increased pasture growth and the costs associated with high inputs. The decline in native species richness under high fertiliser applications could also be due to competition from exotic grasses such as *Vulpia* and *Bromus* (similar to the findings of Garden *et al.* 2003) and the legume *Trifolium repens* (Whalley *et al.* 1978), since high levels of fertiliser results in greater numbers of exotic species (next section).

#### *Exotic species richness*

Higher observed numbers of exotic species were associated with high fertiliser application compared to nil or low levels of fertiliser on granite sites under planned rest grazing with

no history of cultivation. Lower exotic species richness was found on unfertilised sites compared to low and high levels of fertiliser application on continuously grazed and never cultivated basalt. Explanations for these observations are embedded in the philosophy of planned rest grazing whereby pastures are grazed at high stock density for a short period of time (McCosker 2000) and then rested to allow plants to recover from defoliation (Earl and Jones 1996). Sites with high levels of fertiliser application and planned rest grazing allow exotic species such as annual grasses, thistles and forbs to establish in short-term vegetation spaces created after periods of intense defoliation. Native species, particularly perennial grasses, are unlikely to respond as effectively as exotic annuals to the creation of short-term gaps. The additional nutrients provided by the high fertiliser regime are more likely to benefit exotic species than native species due to their evolution under such conditions (Groves *et al.* 2003). The dominance of exotic species over native species at high levels of fertiliser application under planned rest grazing is also relevant. Pastures dominated by exotics species such as phalaris (*Phalaris aquatica*) and fescue (*Festuca pratensis*) may crowd out native species due to the spreading habit of phalaris (FitzGerald and Lodge 1997) or tillering by fescue.

At continuously grazed sites with no history of cultivation, highest exotic species richness was associated with low fertiliser application on granite and basalt. Similar sites on metasediments had lowest exotic species richness with low fertiliser application. The higher stocking rates on basalt result in more gaps for exotic species to exploit. Similarly, on granite lithologies with lower stocking rates and fertility than comparable sites on basalt, livestock create gaps which are utilised by exotic species. Metasediments have the most vigorous native grasses at low fertilities and low stocking rates, resulting in few or no gaps that exotic species can exploit.

## Cultivation

### *Native species richness*

The influence of cultivation on native species richness was dependent on lithology, but recent cultivation (10-20 years ago) generally decreased native species richness. This result is not surprising, as cultivation to sow crops or improved pasture requires the disturbance of the natural cover of plant species. Many native plant species are unable to cope with the

disturbance, and the associated management that often includes herbicide and fertiliser application, therefore the species disappear from the disturbed area. Long (> 20 years) after a cultivation event, species richness levels were found to increase to levels similar to those before the disturbance event, with an increase in species that were able to tolerate the disturbance and associated management changes or recolonise the previously disturbed area.

These results are similar to other studies. Lavorel *et al.* (1991) found that species richness increased with time since cultivation in abandoned Mediterranean fields in France. In Australia, Waters (2001) concluded that the more recent the cultivation, the lower the native species richness, with never cultivated areas having highest native species richness. Similarly, McIvor (1998) found that pasture sowing and cultivation reduced densities of native species in north-east Queensland. The decline in native species richness with cultivation could be attributed to a number of factors. Firstly, Bean and Whalley (2001) suggested that on the Liverpool Plains, NSW, where there is a history of cultivation, the interstitial spaces between tussocks that were presumably dominated by native species prior to cultivation had been invaded by exotic annuals and perennials. Therefore, fewer native species occurred at locations with a history of cultivation. Secondly, sensitivities of native species to cultivation may explain reduced native species richness at cultivated sites. Munnich *et al.* (1991) and Scott and Whalley (1982) concluded that native tussock species such as *Austrodanthonia* species are sensitive to cultivation, while rhizomatous species such as *Microlaena stipoides* are less sensitive and can persist in cultivated pastures. Many native herbs have bulbs, tubers or fleshy roots (e.g. *Murdannia graminea*, *Microseris lanceolata* and *Thysanotus tuberosus*, Plate 5.2) for vegetative reproduction, and were seldom found at sites with a history of cultivation (pers. obs.), although they occurred in adjacent sites that had never been cultivated.



**Plate 5.2** *Thysanotus tuberosus* on the Northern Tablelands, NSW.

**Environmental variables significantly influencing native and exotic species richness**

As slope increased so, too, did native species richness. Steeper areas have generally not undergone as intensive development (Morgan and Terry 1990) in terms of tree clearing, sowing of introduced pasture species or ground spreading of fertiliser, and are therefore less likely to be favourable for most exotic species with less competitive exclusion of natives by exotic species. These areas may reflect the original species rich vegetation of the region which would have been mainly eucalypt open-forest and woodland (Benson and Ashby 2000). Another explanation concerns patterns of herbivore grazing as generally animals are unwilling to graze on steep slopes (Hester *et al.* 1999). This characteristic of herbivores may reduce the grazing pressure on steeper slopes resulting in fewer grazing-induced losses of native species. Steep slopes are associated with shallow erodible soil, but with greater heterogeneity and more fertile areas developing where litter is trapped (Hester *et al.* 1999). The heterogeneity may also explain increases in native species richness with increasing slope.

Slope did not significantly influence exotic species richness in this study. Gilfedder and Kirkpatrick (1993), however, found higher exotic species richness on moderately sloping sites (3-10°) in remnants in Tasmania. Increases in exotic species richness on moderate slopes were attributed to grazing influences, as livestock avoid grazing on steep slopes and flatter areas were protected from heavy grazing (Gilfedder and Kirkpatrick 1993).

Tree cover was positively related to native species richness, as found by other researchers (Waters 2001; Prober *et al.* 2002a; Clarke 2003). Higher native species richness under trees has been attributed to a number of factors (see Gibbs *et al.* 1999). One hypothesis is that trees release the herbaceous vegetation from competition from dominant grasses, creating gaps for other species (Prober *et al.* 2002a). No relationship was found between tree cover and exotic species richness in accord with Gilfedder and Kirkpatrick (1993), Waters (2001) and Clarke (2003). However, Gilfedder and Kirkpatrick (1993) and Waters (2001) found a negative relationship between exotic species richness and tree basal area. Clarke (2003) found most exotic species at sites with out tree cover, and suggested that trees suppress exotic species.

Native species richness was lower at sites with high precipitation in May. Precipitation in May was highly correlated ( $r > 0.6$ ) with precipitation in July, August, September, October, and mean annual and winter average precipitation (Appendix 5.4). Therefore any one of these precipitation variables is likely to have had a similar effect on native species richness in the GLM. Precipitation on the Northern Tablelands is closely related to a number of other variables including easting, altitude and local relief (Hobbs and Jackson 1977) (Chapter 4). The relationship involving precipitation and native species richness in this study may have a similar basis to the relationship observed by Waters (2001) between easting and native species richness. The reduction in native species with increasing winter rainfall may be due to the persistence of competitive exotic pasture species such as *Trifolium*, *Phalaris* and *Festuca* species which crowd out native species due to their spreading habit or tillering (FitzGerald and Lodge 1997). Gilfedder and Kirkpatrick (1993) found that precipitation only influenced exotic plant cover in Tasmanian remnants, with exotics declining with increasing rainfall in the driest month and the driest quarter. However, in this study, the significant positive relationship between exotic species richness and altitude may have subsumed the variance due to increased precipitation, as precipitation increases with altitude on the Northern Tablelands.

Exotic species richness was significantly reduced in areas with higher summer maximum temperatures. Harris and Lazenby (1974) and Fitzpatrick and Nix (1975) stated that summer temperatures on the Northern Tablelands are ideal for temperate grasses while also allowing tropical grasses to produce dry matter. Reduction in the numbers of exotic species with increasing summer maxima may be attributable to the active growth of native warm-seasonal perennial grasses such as *Bothriochloa macra*, *Eragrostis leptostachya* and *Sporobolus creber*. These species, particularly *B. macra*, form a dense mat or low tussocks crowding out other grasses and forbs (Lodge 1983), perhaps reducing the number of other species. Other explanations include that the temperate zone exotic species such as *Phalaris aquatica* and *Dactylis glomerata* do not do as well in drier areas and are therefore found in lower frequencies. Other species disadvantaged by summer warmth include *Trifolium repens* and winter annuals, which decline during summer if moisture is limited and temperature exceeds 20°C (FitzGerald and Lodge 1997).

#### **5.4.2 Lack of significant relationships between species richness and management and environmental variables**

No soil chemistry variables were found to have a significant relationship with native or exotic species richness, which differs from other research findings. Prober *et al.* (2002a) concluded that soil nutrient status, particularly phosphorus, has a direct influence on species composition and possibly richness in temperate grasslands in southern NSW (Section 7.4.2). In Tasmania, Gilfedder and Kirkpatrick (1993) found that pH, potassium and nitrogen/phosphorus ratio significantly influenced both native and exotic species richness, whereas available phosphorus only significantly affected exotic species richness. Similarly, Waters (2001) concluded that native species richness was related to pH, and exotic species richness was related to the carbon/nitrogen ratio. The absence of such relationships here may be partly explained by the overriding effects of lithology and applied fertiliser. Soil nutrient levels are related to parent materials and climate (Cumming and Elliott 1992), with phosphorus levels in granite and metasediments being generally low (0.05-0.1%) compared to basalts (0.2-0.5%) (Lockwood, P., pers. comm. May 2002). Results from multivariate analysis indicate that basalt soils and phosphorus levels were correlated in this study (Section 4.3.4).

The distance of sites to the nearest travelling stock route was not significant for either native or exotic species richness. This variable was included because of the potential role of travelling stock routes as important conservation areas (Austen 2002) and as a source of propagules. However, this lack of influence does not mean that travelling stock routes are not important in conservation or as seed sources. Significant relationships may be apparent at a finer scale than that (0-16 km) used in this study, as well as in terms of species composition.

Landscape morphology had no bearing on either native or exotic species richness. Various authors including Gilfedder and Kirkpatrick (1993) and Clarke (2003) have found significant relationships between landscape position (often in relation to slope) and species richness, while other authors (e.g. McIntyre and Lavorel 1994b; Waters 2001) have found no such relationships. The importance of slope for native species richness in this study may have subsumed any variance attributable to position in the landscape.

This study failed to find a significant relationship between aspect and native or exotic species richness. This is in contrast to the findings of Bean and Whalley (2001) but consistent with Gilfedder and Kirkpatrick (1993) who found that aspect had no relationship with exotic species richness. Discrepancies with the results observed by Bean and Whalley (2001) could be attributed to aspect not being as important a variable as others.

Geographical position east-west and north-south and position in the landscape (accumulating/shedding water) were not found to significantly influence native or exotic species richness. This may be explained by other relationships between species richness and variables such as altitude, rainfall and slope. The lack of influence of position in the landscape was contrary to the findings of McIntyre and Lavorel (1994b) where water enrichment from unnatural drainage resulted in fewer native species and more exotic species. The artificial water enrichment recorded by McIntyre and Lavorel (1994b) was very different to the natural drainage patterns in this study, and was associated with earthworks and soil disturbance. These perturbations were avoided here.

Radiation and moisture indices were not significantly related to either native or exotic species richness. This may be due to the overriding importance of related variables such as

precipitation, altitude and geographical position east-west. The moisture index used in this study was relatively crude and did not take into account the moisture stored in the root zone (Fitzpatrick and Nix 1975) or soil type at each location. Radiation is influenced by altitude and slope so its explanatory value may have been subsumed by these variables in the statistical models.

Julian time did not significantly influence native or exotic species richness, validating the comparisons of species richness over the 3-4 month sampling periods and the 2 years that vegetation was surveyed (Appendix 5.5). Julian time did have significant influences on composition (Section 7.3.2), reflecting changes in species composition rather than the number of species recorded.

### 5.4.3 Evenness

No significant relationships could be detected between the evenness of ground-storey vegetation plant cover and management or environmental variables. This may be explained by the fact that plant cover changes quickly in response to management and environmental factors, particularly rainfall and grazing management, over the space of days. Therefore the measurement of climatic and management factors may need to be on a finer scale of days or weeks rather than the periods of months and years captured by the environmental and management variables measured here. The result is perhaps not surprising given that Pettit *et al.* (1995) concluded that plant species evenness was not affected by grazing in southwestern Western Australia. Many studies of the determinants of ground-layer vegetation diversity in eastern Australia do not report evenness results (e.g. McIntyre *et al.* 1993; McIntyre and Lavorel 1994a; Pettit *et al.* 1995; Prober and Thiele 1995; Lunt 1997; Lunt and Morgan 1999; Clarke 2003). Reasons for not reporting evenness results are unclear, but may include uncertainty over which of the numerous measures of evenness to use: some 14 were reviewed by Smith and Wilson (1996). Sometimes, abundance data is not collected. Krebs (1999) also commented that 'For many decades field ecologists had known that most communities of plants contain a few dominant species and many species that are relatively uncommon'. This argument is further supported by the BOTANAL method of estimating pasture yield and composition (Tothill *et al.* 1978), where the three dominant species in natural or native pastures are ranked in order in terms of dry weight, their percentage

contributions being fixed at 70%, 21% and 9%, respectively. It follows that Australian grassland ecologists and pasture agronomists assume that herbaceous communities are uneven in abundance and that their structure is more or less inert in response to the environmental and management factors that affect composition and agronomic and ecological processes.

Outside Australia, grazing influences on evenness have been reported from south-western Oklahoma, USA (Collins and Barber 1985; Collins 1987), northern Israel (Noy-Meir 1995), and Spain (Puerto *et al.* 1990). Noy-Meir (1995) concluded that grazing had positive effects on plant species evenness in Israel. Similarly, Collins and Barber (1985) observed lower evenness at sites excluded from grazing for 20 years than at sites grazed by ungulates in Oklahoma. In contrast, Collins (1987) noted virtually no differences in evenness when comparing ungrazed and grazed sites in a similar study in Oklahoma.

#### **5.4.4 Conclusions**

Management and environmental variables were important determinants of native and exotic species richness. In general, increasing intensity of management reduced native species richness and increased exotic species richness. Ungrazed and episodically grazed sites had more native species than matched grazed areas, and, on basalt and metasediments, continuously grazed areas had more native species than areas grazed with a planned rest regime. These results present some of the first comparisons of species richness at planned rest and continuously grazed sites and contrast with those of Kemp *et al.* (2003a) who found small increases (0-2 species) in native species richness under planned rest grazing. High fertiliser use lowered native species richness in comparison to no fertiliser and low fertiliser use. Cultivation impacts were dependent on lithology. On infertile granite soils, the more recent the cultivation event, the lower the native species richness.

Increases in exotic species richness were normally observed as the intensity of agricultural management increased. Most exotic species occurred in grazed areas (episodic, planned rest or continuous grazing), and at fertilised sites, with one exception: continuously grazed sites that had never been cultivated or fertilised had lower exotic species richness than ungrazed areas on basalt and granite lithologies.

Native species richness was significantly influenced by a number of additional variables including tree cover, size of paddock, winter precipitation and slope. Several grazing variables were important determinants of exotic species richness as were summer temperature and altitude.

Evenness was not significantly affected by any of the environmental or management variables recorded in this study. Generally, Australian studies have not investigated the relationship between evenness and ecological determinants. Although some studies have failed to find a significant relationship between ground-storey vegetation evenness and grazing, as in this study, others have shown significant impacts of grazing on evenness. The utility of BOTANAL (a pasture biomass and composition estimation technique that assumes a constant evenness ratio in the three most abundant plants in grassy vegetation) under a wide range of environmental and management conditions in Australia would tend to suggest that the evenness of ground-storey plants is inert in relation to the ecological pressures that affect diversity and composition over the longer term.

In summary, native and exotic species richness were strongly affected by agricultural management so that with increasing intensity of management, native species richness declined and exotic species richness increased. Environmental variables including climate and site conditions were also important determinants of species richness.