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Landscape scale measurement and monitoring of
biodiversity in the Australian rangelands

Thesis presented for the degree of

Doctorate of Philosophy

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B. Env. Mgt. (Hons), University of Adelaide

November 2008

Faculty of Sciences, Discipline of Soil and Land Systems

Chapter 4: Additive partitioning of rarefaction curves: removing the influence of sampling on species-diversity in vegetation surveys

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Key words: *species richness, rarefaction curve, sampling effort, species diversity, scale.*

4.1 Introduction

Increased interest in biodiversity conservation has resulted in government Natural Resource Management (NRM) bodies needing improved reporting on biodiversity condition in Australia's rangelands (Smyth *et al.* 2004). Hence, there is a clear need for an indicator of biodiversity suitable for these extensive regions. Such an indicator would allow monitoring of temporal change in biodiversity values and therefore inform the prioritisation of conservation goals and assist in sustainable pastoral management.

However the term biodiversity is complex and has come to encompass a great many variables which can be associated with ecosystem health and thus identifying what to monitor is a difficult task. To a great extent the aspect of biodiversity chosen for monitoring will determine what is conserved, or conversely the specific conservation goal will determine which aspect of biodiversity should be monitored.

Since it is impossible to measure biodiversity directly it is necessary to measure other factors which vary with biodiversity, indicators or surrogates. In this paper we use the language of Sarkar (2002) to differentiate between true-surrogates and estimator-surrogates: a true surrogate represents biodiversity directly; an estimator-surrogate represents a true-surrogate, which in turn represents biodiversity.

Sarkar (2002) argued that species-richness is one of the few suitable true-surrogates for biodiversity because 1) species are a well defined and understood category, and 2) species-richness is measurable. Thus total species-richness is a true-surrogate for biodiversity. However total species-richness is difficult and impractical to measure and we therefore seek to develop a surrogate of total species-richness, or an estimator-surrogate for biodiversity.

Thus the estimator-surrogate we seek must co-vary with total species-richness. At broad scales the species-richness of many phylogenetic groups is determined by climatic variables: trees (Currie and Paquin 1987; O'Brien 1993; O'Brien 1998; O'Brien *et al.* 2000); vascular plants (Venevsky and Venevskaya 2005); mammals (Badgley and Fox 2000); butterflies (Hawkins and Porter 2003; Hawkins and Porter 2003); and bird species (Hawkins *et al.* 2003). Thus the species-richness of each of these groups varies in response to similar environmental variables.

We propose to use the species-richness of one of these groups, woody plants, as an estimator-surrogate for biodiversity. Indeed, the use of cross-taxon biodiversity surrogates is supported by the meta-analysis of 27 biodiversity studies by Rodrigues and Brooks (2007). However some woody plants have ephemeral growth styles in our study area, an arid region of South Australia. The study area also receives localised heavy rainfall which can cause very spatially variable growth of ephemeral species. To remove the potentially confounding effect of variable ephemeral species occurrence we further refine our surrogate group to woody-perennial vegetation species-richness.

Two vegetation quadrat surveys in the study area have collected vegetation data which could potentially be used to create a measure of woody-perennial species-richness. However, previous work by us demonstrated frequent non-detection errors within the data collected by both surveys (Chapter 3). Therefore, raw species counts are not a valid measure of species-richness for these datasets (Gotelli and Colwell 2001).

At this point we will clarify our use of species-richness terminology. We have proposed measurement of the species-richness of regions, which is more accurately referred to as γ -diversity (Whittaker 1972). In addition to examining the species within a region (γ -diversity), we will also examine the species-richness of sites within regions (α -diversity),

and the difference in species composition between these sites (β -diversity). It is of particular note that these diversity measures are closely related. Whittaker (1972) notes that the γ -diversity of a region is a function the average number of species at each site (α -diversity) and the difference in species composition of those sites (β -diversity).

The goal of this study is to extract from the survey data an estimate of woody-perennial α -, β - and γ -diversity which accounts for the influences of sampling effort. To this end we turn to additive partitioning of species-diversity and rarefaction.

4.1.1 The influence of sample-grain and sampling effort

To examine variation in species-diversity across regions we must account for the influences of site size (sample-grain) and sampling effort (Fleishman *et al.* 2006). The combination of additive partitioning of species-diversity and rarefaction offers a theoretical framework for understanding and accounting for variation in both sample-grain and sampling effort.

Firstly, the theory of additive partitioning of species diversity provides a useful framework for understanding the interdependent nature of α -, β - and γ -diversity, and the influence of sample-grain and sampling effort on these forms of diversity (see Veech *et al.* 2002 for a review of additive partitioning). Additionally, additive partitioning allows the expression of α and β diversity in the same units of species richness, thus allowing direct comparison of the two (Veech *et al.* 2002; Crist and Veech 2006).

As described by Crist and Veech (2006), site size, or sample-grain, will affect measured α -diversity, as larger sites will contain more species. Spatial distribution of sites, and the number of sites surveyed (sampling effort) will affect measured β -diversity. According to the theory of additive partitioning of species diversity, α - and β -diversity together determine γ -diversity by their sum, as described in Equation 1. Thus, both sample-grain and sampling effort will determine the γ -diversity of a region.

$$\gamma = \alpha + \beta \tag{1}$$

Secondly, the process of rarefaction is commonly used to control for variation in sampling effort. Rarefaction is a process which calculates the average number of species represented

by 1, 2, 3, ...N samples. This is done either through Monte Carlo techniques, as we have done, or analytically with the expressions derived by either Ugland *et al.* (2003) or Mao *et al.* (2005) and Colwell *et al.* (2004). Thus rarefaction allows calculation of the expected species-richness of a region at any level up to the maximum sampling effort in that region.

Finally, work by Crist and Veech (2006) has demonstrated a sound link between additive partitioning of species diversity and rarefaction. The additive partitioning of species diversity allows the extraction of α -, β - and γ -diversity from sample-based rarefaction curves. Hence, by rarefying a group of regions to a common sampling effort and employing the theory of additive partitioning of species diversity we can compare α -, β - and γ -diversity at equivalent sampling efforts.

However, one final caveat needs to be made. The inherent properties of diversity are not the only variables which affect the shape of the rarefaction curve. Different sampling methods can favour the detection of certain species more or less, while observer ability can have a strong influence on the number of species recorded (Boulinier *et al.* 1998). Therefore, species-diversity derived from differing sampling methods should be compared with caution.

4.1.2 Research aims

To summarise, we aim to develop a biodiversity metric free from the influence of sampling effort, and we have argued that γ -diversity of woody-perennial vegetation is an estimator-surrogate for biodiversity. We hypothesise that rarefaction to a common sampling effort and extraction of α -, β - and γ -diversity through additive partitioning of species diversity will remove the influence of sampling effort. Hence we extract α -, β - and γ -diversity from the survey data through the use of additive partitioning of rarefaction curves. We then test each aspect of diversity for independence from sampling effort, and develop correction methods where necessary.

4.2 Methods

4.2.1 Study area

The study was conducted in central Australia in an area that stretches from the top of the Spencer Gulf in South Australia to the Northern Territory border (Figure 17). Specifically the study included the entire Stony Plains region, as defined in the Interim Biogeographic Regionalisation of Australia (IBRA) 6.1 as well as other adjacent IBRA sub-regions. Average annual rainfall across the area ranges from approximately 300 mm per annum in the south to 100 mm per annum in the north. While the study area is very large (approximately 210,000 km²) it contains little geographic variation, and the majority of the area is flat or gently sloping plains with few shallow ephemeral watercourses. The majority of vegetation cover is chenopod shrubland, although there are significant areas of tall shrubland and low open woodland with grass or chenopod understorey (Laut *et al.* 1977).

Throughout the area the dominant land use is pastoral grazing of sheep in the south and cattle in the north. However, the low rainfall of the region provides few natural watering points for livestock. To increase the proportion of the landscape usable by livestock and to increase stocking levels many artificial water points have been established.

4.2.2 Survey data

The plant species data were derived from two conventional vegetation surveys: the Department for Environment and Heritage's Biological Survey of South Australia (BSSA); and the Department of Water Land and Biodiversity Conservation's South Australian Pastoral Lease Assessment (SAPLA). The majority of the data were collected over fourteen years, from 1990 to 2003. Any data collected outside this period was excluded to ensure both surveys covered the same time span. The two surveys have different goals and therefore different data collection methodologies and site selection biases.

The aim of the Biological Survey of South Australia (BSSA) is to create an inventory of native species and therefore sites are generally chosen in areas less disturbed by grazing. A botanical expert is involved in all surveys, and voucher specimens are collected for species not identified on site. The plant inventory is conducted in square quadrats of one

hectare, or an equivalent rectangular area if placed in elongated vegetation communities (Heard and Channon 1997). Vegetation surveys are usually conducted only once per site, although several sites were resurveyed twice yearly for approximately eight years¹. There were 892 BSSA sites within the study area.

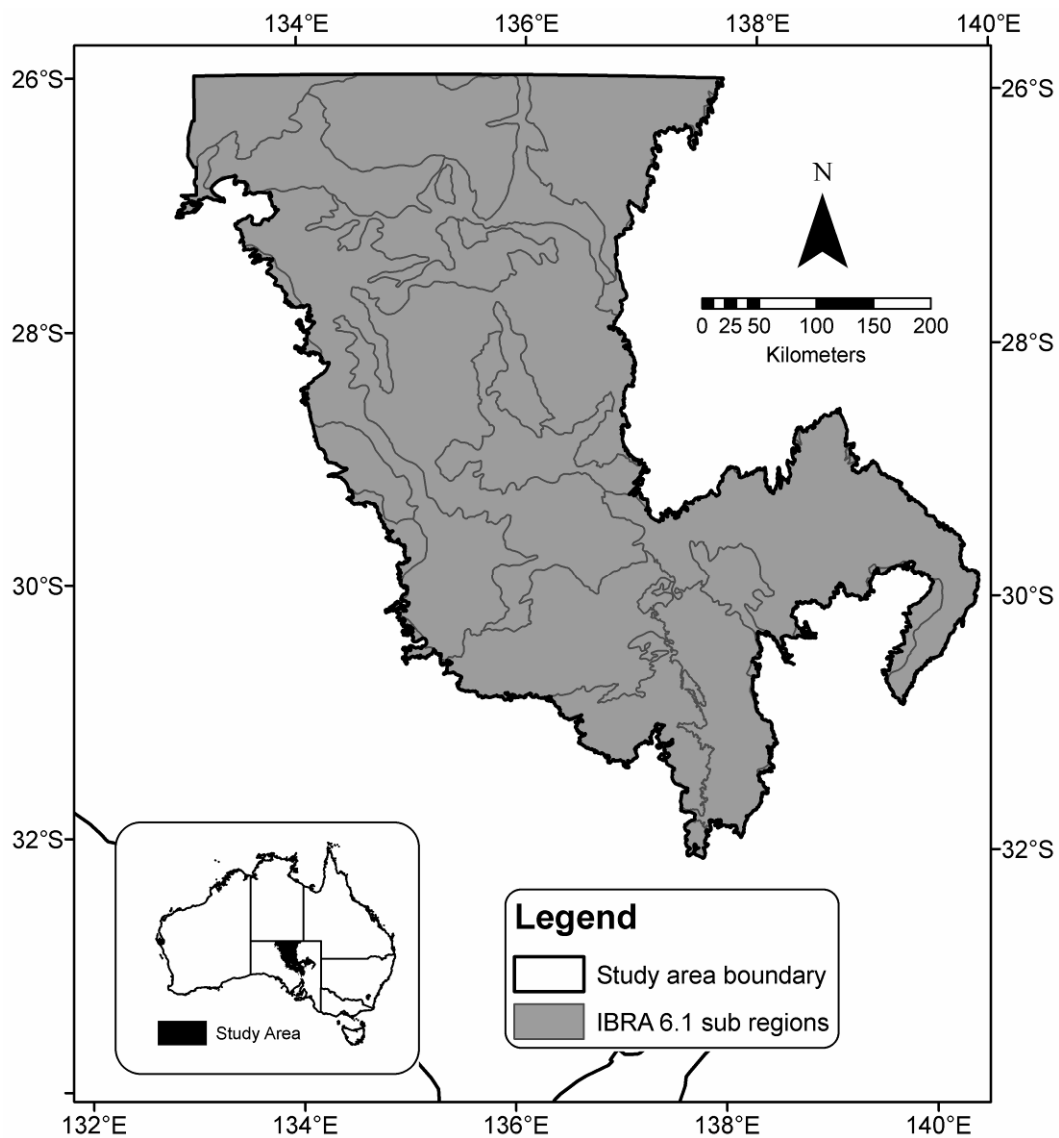


Figure 17. Study area; Interim Biogeographic Regionalisation of Australia (IBRA) sub-regions displayed within study area.

¹ Four BSSA sites were visited twice yearly for 8 years as part of a small-mammal monitoring program. Fauna and flora surveys were conducted on each visit.

The South Australian Pastoral Lease Assessment (SAPLA) is designed to monitor the effect of livestock grazing on land condition. Hence sample sites are placed within the piosphere but not in the immediate vicinity of the water point (Department of Water, Land and Biodiversity Conservation, 2002). In the sheep grazing properties of the southern study area, SAPLA monitoring points are located 1.5 km from watering points. In the cattle grazing properties in the north of the study area SAPLA monitoring points are located 3 km from watering points. Because SAPLA sites are located within stock piospheres they are more likely to be degraded than BSSA sites. Unlike the BSSA, no botanical expert is involved with SAPLA surveys in the field. SAPLA staff conduct the surveys and attempt to identify all vegetation species, while voucher specimens of any unknown species are collected for later identification. An area of 100 to 200 metres radius is surveyed at each site. Because the SAPLA is designed to monitor change in range condition, sites are revisited at regular intervals. There were 1185 SAPLA sites within the study area.

Prior to analysis, all species names in the survey data were checked for currency and consistency and updated where necessary. With the aid of advice from the South Australian Herbarium, species were classified as either perennial or ephemeral, where perennials were defined as plants with an expected lifespan of three or more years in the study area. All ephemeral plant species and perennial grasses were excluded from the analysis for two reasons. Firstly, most ephemeral species are physically small and perennial grasses may be grazed down to vestigial stubs, making them easily overlooked even when present at a site. Secondly, ephemeral plant populations vary greatly with preceding rain and were likely to confound the generation of species richness estimates.

Consistency of sample-grain

The sample-grain of one of the vegetation ground surveys was consistent, while the other varied within a small range. The sample-grain of the BSSA was consistent; a 100 m square quadrat was surveyed at each site visit. If a square quadrat would not fit within the surveyed vegetation community an equivalent non-square area was surveyed. The SAPLA methodology requires that ideally a 200 m radius around sites is surveyed, although concedes that if not possible a minimum 100m radius is acceptable. We would expect the variation in SAPLA sample-grain will cause a similar variation in measured α -diversity.

Therefore, we would expect the α -diversity measured by the SAPLA to vary more than the α -diversity measured by the BSSA for the same region.

Units of aggregation and sampling effort

The vegetation data used in this study contains widely distributed quadrats surveyed at different times. While the majority of quadrats were only surveyed once, a few quadrat-locations were visited and surveyed on two or more occasions. We have previously demonstrated that subsequent surveys at one quadrat-location detect previously unrecorded species (Chapter 3, Clarke *et al.* submitted). Therefore, to avoid pseudo-replication we only utilised the first quadrat-visit for each location in our analyses. Thus our unit of sampling effort is quadrat-surveys.

This dataset was stratified by IBRA 6.1 sub-regions (Figure 17). The IBRA regions and sub-regions have been defined based on regional and continental scale climate, geomorphology, landform, lithology and characteristic flora and fauna-data. Rarefaction curves were generated for each IBRA sub-region.

4.2.3 Rarefaction

We developed custom written software to calculate all rarefaction curves in this study. Our software generates the rarefaction curve by Monte Carlo sampling sites without replacement, rather than either of the analytical expressions derived by either Ugland *et al.* (2003) or Mao *et al.* (2005) and Colwell *et al.* (2004). Our software produces rarefaction curves identical to those produced by the analytical expression of Mao *et al.* (2005) and Colwell *et al.* (2004) in the software package EstimateS.

Previous work has demonstrated that one of the best methods of describing rarefaction curves is the semi-log relationship (Palmer 1990). This relationship is non-asymptotic, as are many species and higher taxon accumulation curves (Gotelli and Colwell 2001). As none of our rarefaction curves reach an asymptote this form of relationship is justified.

The semi-log relationship takes the form:

$$y = a \ln(x) + b \quad (2)$$

Where y is the number of woody-perennial species found for given sampling effort; x is the sampling effort; a is the log multiplier; and b is the offset.

Rarefaction curves were generated for both vegetation surveys for all IBRA sub-regions which contained six or more quadrats. Six quadrats was an arbitrarily determined threshold value, below which we had little confidence in generating a meaningful rarefaction relationship.

Additive partitioning of rarefaction curves

Work by Crist and Veech (2006) has demonstrated the extraction of α -, β - and γ -diversity from rarefaction curves through the use of additive partitioning. To illustrate with a hypothetical region, shown in Figure 18, the α -diversity equates to the average number of species per patch, which is mathematically identical to the first point on the rarefaction curve. The final point on the rarefaction curve is the total number of species recorded, or the γ -diversity. The β -diversity determines the shape of the rarefaction curve after this first point: if sites are similar, relatively few species will be added with each additional unit of sampling effort, producing a slowly climbing curve; if sites differ greatly in species composite on, then the opposite is true, and the curve climbs steeply. Thus, from diversity partitioning, the difference in species richness between the first and last points is the total β -diversity (Crist and Veech 2006).

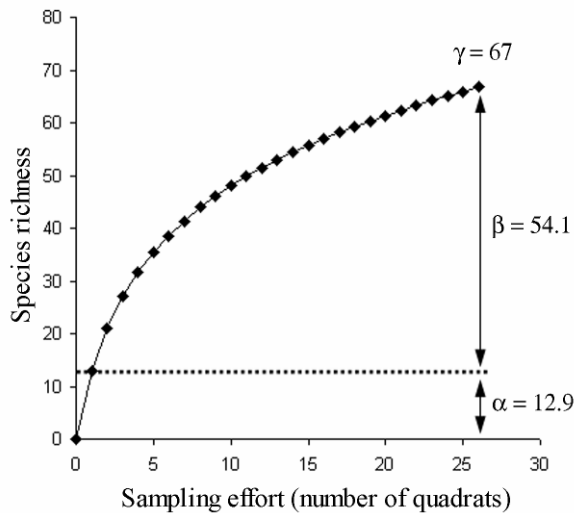


Figure 18. The relationship between rarefaction and additive partitioning. The first point on the rarefaction curve equates to the regional average α -diversity, the final point is the γ -diversity and the difference between the two is the β -diversity.

Rarefaction as a control for differences in sampling effort

In our introduction we hypothesised that rarefaction to a common sampling effort, and extraction of α -, β - and γ -diversity through additive partitioning of species diversity would remove the influence of sampling effort.

To test this hypothesis, we rarefied all IBRA sub-regions to a common sampling effort by solving the derived semi-log functions for gamma-diversity at a sampling effort of 50 quadrats. The figure of 50 was arbitrarily chosen to be in the middle of the range of maximum sampling efforts for sub-regions, necessitating extrapolation of some rarefaction relationships and interpolation of others. A smaller number was not chosen because all rarefaction curves tend to converge at low sampling effort (Tipper 1979). We believe this extrapolation is justified in this case, because all relationships are extracted from similar landscapes for a narrow range of taxa.

Finally, through additive partitioning we extracted α -, β - and γ -diversity for each region. We then tested the correlation between each diversity measure and original sampling effort for all regions.

Removal of sampling effort-influence

Post rarefaction sampling effort was still found to have a strong and predictable logarithmic influence on γ -, and hence β -diversity, but no influence on α -diversity. To counteract the influence of sampling effort on γ -, and hence β -diversity several steps were taken.

Firstly the relationship between post-rarefaction γ -diversity at a sampling effort of 50 (γ_{50}) and actual sampling effort was characterised by natural log relationship. This relationship describes the expected post-rarefaction γ -diversity (γ_{exp}) for a given sampling effort, and takes the form:

$$\gamma_{\text{exp}} = a \times \ln(x) + b \quad (3)$$

Where a and b are constants which influence the slope and intercept of the log curve respectively, and x is sampling effort in number of quadrats surveyed.

Finally, a sampling effort corrected γ -diversity (γ_{sec}) was calculated by adding the residual of the relationship between γ_{50} and γ_{exp} to the expected γ -diversity for a sampling effort of 50 quadrats. This function took the following form:

$$\gamma_{\text{sec}} = r + \gamma_{\text{exp}}(50) \quad (4)$$

Where r is the residual difference between a regions γ_{50} and the γ_{exp} for at that regions actual sampling effort, and $\gamma_{\text{exp}}(50)$ the the γ_{exp} at a sampling effort of 50 quadrats.

Thus, all rarefied γ_{50} values were corrected to a common sampling effort of 50 quadrats by taking into account the influence of sampling effort on that survey in the study area.

Sampling-effort corrected β -diversity, or β_{sec} , was calculated according to additive partitioning theory by subtracting α , which is not influenced by sampling effort, from γ_{sec} .

4.3 Results

4.3.1 Rarefied diversity

A typical sample-based rarefaction curve for the Macumba IBRA sub-region is presented in Figure 19. All rarefaction relationships were described well by the fitted semi-log functions ($R^2 \geq 0.96$).

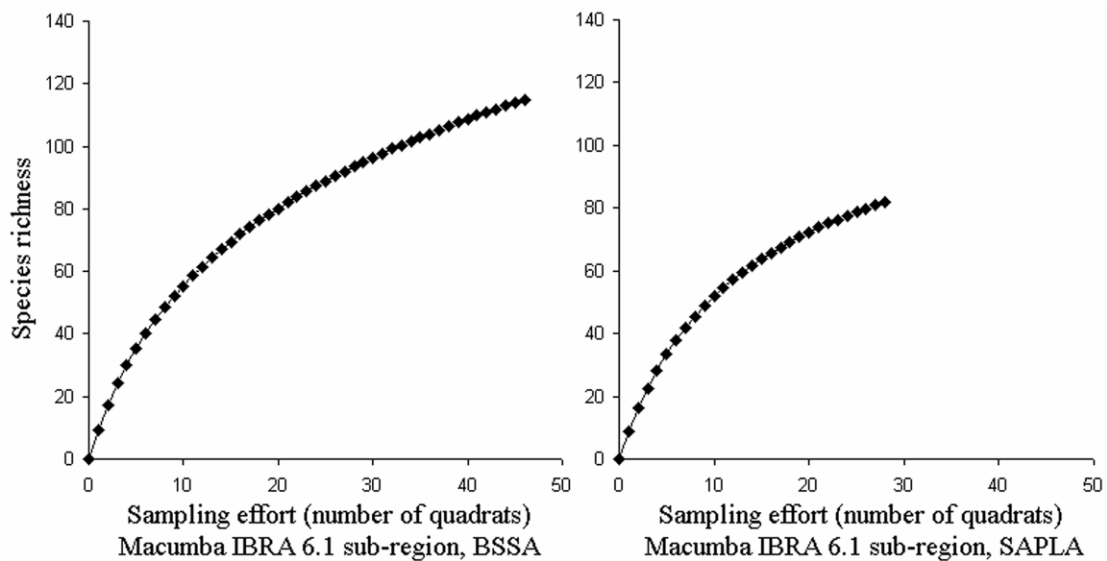


Figure 19. Sample-based rarefaction curves derived from BSSA and SAPLA data for the Macumba IBRA 6.1 sub-region, and typical of rarefaction curves for all sub-regions.

The α -, β - and γ -diversities derived from the rarefaction semi-log relationships are presented in Table 8. These figures are at maximum sampling effort for each region, before correction for sampling effort differences, and hence we use the terms α_{\max} , β_{\max} and γ_{\max} .

At this stage, prior to rarefaction to correct for differences in sampling effort, we examined the relationship of each diversity component to sampling effort. We would expect α_{\max} to be solely determined by sample grain and therefore independent of sampling effort, and conversely, we would expect γ_{\max} , and hence the derived β_{\max} , to be heavily influenced by sampling effort.

Table 8. Rarefaction derived α -, β - and γ -diversity at maximum sampling effort in each IBRA 6.1 sub-region.

IBRA 6.1 Sub-region	Biological Survey of South Australia				South Australian Pastoral Lease Assessment			
	sampling effort*	α_{\max}	β_{\max}	γ_{\max}	sampling effort*	α_{\max}	β_{\max}	γ_{\max}
Arcoona Plateau	43	13.34	96.66	110	113	9.35	91.65	101
Breakaway, Stony Plains	216	12.12	214.88	227	226	9.42	157.58	167
Dieri	7	12.23	38.77	51	<7			
Gawler Lakes	<7				59	11.48	93.52	105
Kingoonya	<7				243	8.93	125.07	134
Macumba	46	9.23	105.77	115	28	8.85	73.15	82
Murpeowie	192	10.98	179.03	190	239	9.59	149.41	159
Northern Flinders	51	12.32	98.68	111	57	9.39	75.61	85
Oodnadatta	230	10.65	177.35	188	151	8.25	115.75	124
Peake-Dennison Inlier	20	13.82	75.18	89	<7			
Pedirka	26	14.18	78.82	93	19	8.35	47.66	56
Simpson Desert	48	12.91	69.09	82	<7			
Tieyon, Finke	<7				36	8.28	66.72	75
Warriner	11	11.93	48.07	60	17	7.50	48.50	56

*Sampling effort in number of quadrats surveyed.

We tested this prediction by plotting the α_{\max} and γ_{\max} species-richness values for each sub-region against sampling effort and examining linear correlation. Our predictions are borne out, as demonstrated by Figures 20 and 21. The α_{\max} had almost no relationship to sampling effort (BSSA $R^2 = 0.18$; SAPLA $R^2 = 0.05$) and γ_{\max} was strongly influenced by sampling effort (BSSA $R^2 = 0.91$; SAPLA $R^2 = 0.89$). β_{\max} is derived from γ_{\max} and shares the same relationship with sampling effort (not shown; BSSA $R^2 = 0.91$; SAPLA $R^2 = 0.89$).

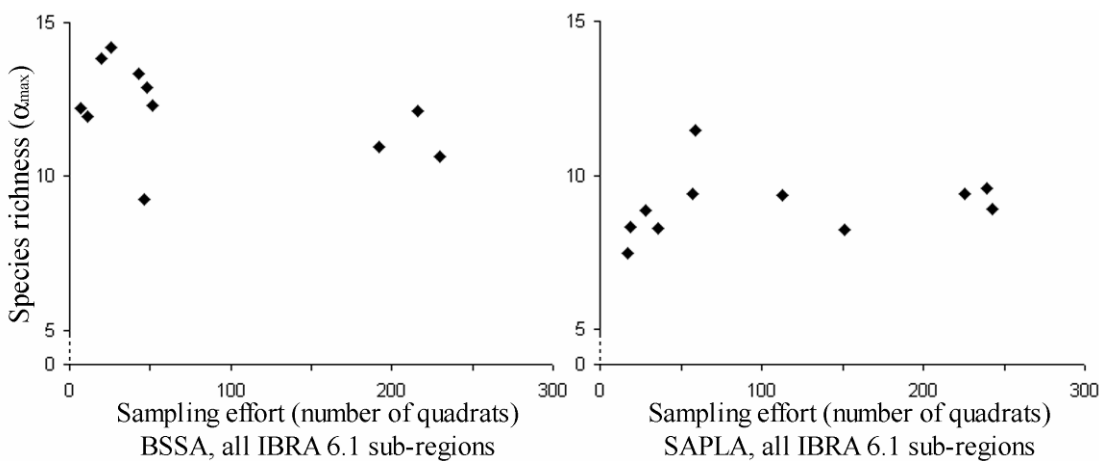


Figure 20. Relationship between α_{\max} and sampling effort (BSSA $R^2 = 0.18$; SAPLA $R^2 = 0.05$)

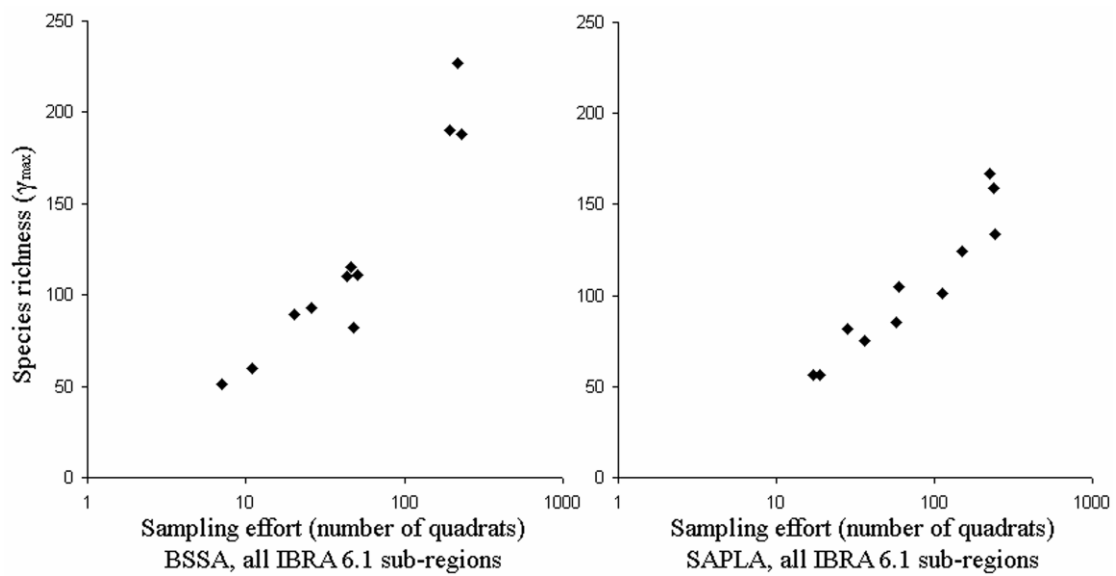


Figure 21. Relationship between γ_{\max} and sampling effort (BSSA $R^2 = 0.91$; SAPLA $R^2 = 0.89$)

4.3.2 Common sampling effort rarefaction

As the first step in correcting for differences in sampling effort, all IBRA sub-regions were rarefied to a common sampling effort. The rarefied β - and γ -diversities derived from the rarefaction semi-log relationships at a sampling effort of 50 are presented in Table 9. To distinguish the rarefied β - and γ -diversity from β_{\max} and γ_{\max} we use the terms β_{50} and γ_{50} .

We would expect that rarefaction would have removed any influence of sampling effort. A plot of γ_{50} species-richness values for each sub-region against sampling effort demonstrates that this is not the case (Figure 22). Fitted logarithmic functions demonstrate that the γ_{50} values of both surveys are influenced by sampling effort (BSSA $R^2 = 0.62$; SAPLA $R^2 = 0.44$).

Table 9. Rarefaction derived α -, β - and γ -diversity at maximum sampling effort in each IBRA sub-region.

IBRA 6.1 sub-region	Biological Survey of South Australia			South Australian Pastoral Lease Assessment		
	sampling effort*	β_{50}	γ_{50}	sampling effort*	β_{50}	γ_{50}
Arcoona Plateau	43	99.56	112.90	113	65.99	75.34
Breakaway, Stony Plains	216	139.52	151.65	226	98.18	107.60
Dieri	7	76.57	88.80	<7		
Gawler Lakes	<7			59	87.02	98.51
Kingoonya	<7			243	80.27	89.20
Macumba	46	102.70	111.93	28	84.75	93.60
Murpeowie	192	122.93	133.90	239	94.30	103.90
Northern Flinders	51	92.91	105.22	57	71.14	80.54
Oodnadatta	230	113.77	124.42	151	81.72	89.97
Peake-Dennison Inlier	20	94.99	108.81	<7		
Pedirka	26	93.50	107.67	19	61.76	70.11
Simpson Desert	48	67.04	79.95	<7		
Tieyon, Finke	<7			36	70.07	78.36
Warriner	11	77.22	89.15	17	64.74	72.23

*Sampling effort in number of quadrats surveyed.

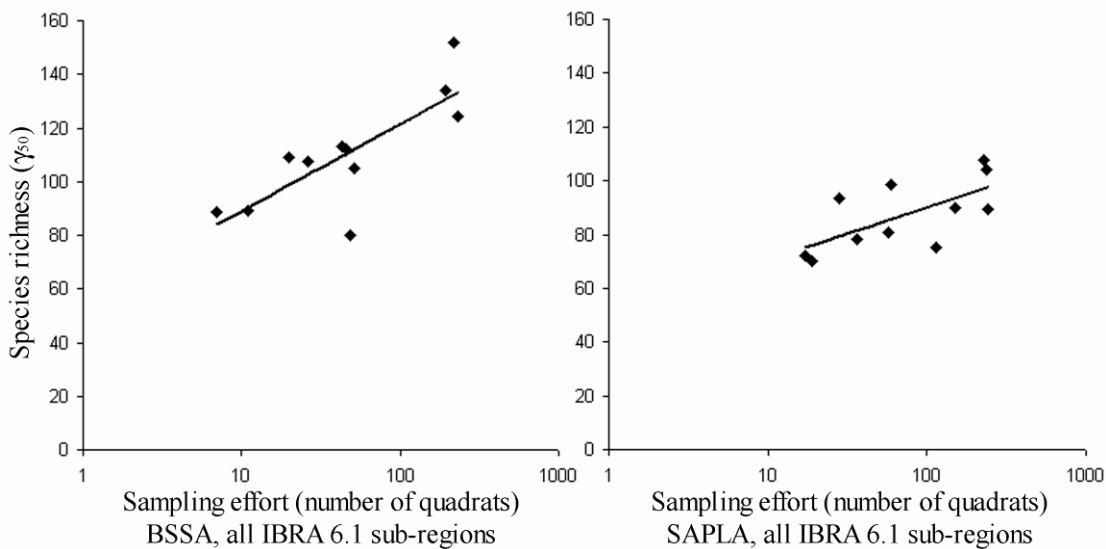


Figure 22. Relationship between γ_{50} and sampling effort (BSSA $R^2 = 0.62$; SAPLA $R^2 = 0.44$)

The fitted logarithmic functions describe the expected γ_{50} from that sub-region given the actual level of sampling effort. These functions are:

$$\text{BSSA} \quad \gamma_{50} = 14.06 \ln(x) + 56.65 \quad (5)$$

$$\text{SAPLA} \quad \gamma_{50} = 8.37 \ln(x) + 51.48 \quad (6)$$

Where x is sampling effort in number of quadrats surveyed.

4.3.3 Removal of sampling effort influence

The previous section demonstrated that the rarefied γ_{50} is predictably influenced by sampling effort. The residual influence of sampling effort was removed, and the sampling effort corrected β -diversity (β_{sec}) and γ -diversity (γ_{sec}), and α_{max} , which is not influenced by sampling effort, are presented in Table 10. A simple residual analysis detected no influence of sampling effort on either γ_{sec} or β_{sec} .

Table 10. α -diversity independent of sampling effort, α_{max} . β - and γ -diversity corrected for the influence of sampling effort, β_{sec} and γ_{sec} .

IBRA 6.1 sub-region	Biological Survey of South Australia			South Australian Pastoral Lease Assessment		
	α_{max}	β_{sec}	γ_{sec}	α_{max}	β_{sec}	γ_{sec}
Arcoona Plateau	13.34	101.68	115.02	9.35	59.17	68.51
Breakaway, Stony Plains	12.12	118.96	131.08	9.42	85.55	94.97
Dieri	12.23	104.20	116.43			
Gawler Lakes				11.48	85.64	97.12
Kingoonya				8.93	67.03	75.96
Macumba	9.23	103.87	113.10	8.85	89.60	98.46
Murnpeowie	10.98	104.02	114.99	9.59	81.20	90.80
Northern Flinders	12.32	92.63	104.94	9.39	70.05	79.44
Oodnadatta	10.65	92.32	102.97	8.25	72.47	80.72
Peake-Dennison Inlier	13.82	107.87	121.69			
Pedirka	14.18	102.69	116.86	8.35	69.87	78.21
Simpson Desert	12.91	67.61	80.52			
Teyon, Finke				8.28	72.82	81.11
Warriner	11.93	98.51	110.44	7.50	73.77	81.27

4.4 Discussion

In this study we set out to develop a biodiversity indicator free from the influence of sampling effort, using the γ -diversity of woody-perennial vegetation as an estimator surrogate for biodiversity. We hypothesised that rarefaction would remove the influence

of sampling effort, and that additive partitioning would allow the extraction of γ -diversity from the rarefaction curves.

Our analysis upheld our prediction that raw γ -diversity of each IBRA 6.1 sub-region would be strongly influenced by sampling effort, and that raw α -diversity would not. Our analysis also demonstrated that rarefaction did not remove the influence of sampling effort on γ -diversity, thus disproving our hypothesis. However, we demonstrated that the influence of sampling effort on γ -diversity was predictable, and therefore were able to correct for this influence.

It is interesting to compare the final measures of α -, β - and γ -diversity extracted from the BSSA and SAPLA. In all IBRA 6.1 sub-regions the BSSA records higher α -, β - and γ -diversity species richness than the SAPLA, despite the larger quadrat size of the SAPLA (Table 10). This was expected for two reasons, one methodological and one strategic. Firstly, the BSSA and SAPLA employ different methodologies: BSSA surveys include a botanical expert and SAPLA surveys do not. This difference alone could potentially explain the higher species richness recorded by the BSSA. However, there is another reason we expect the two surveys to record different species richness. The BSSA is an inventory survey and is specifically designed to record as much of South Australia's species richness with as little sampling effort as possible. BSSA sites are systematically located in less degraded areas of vegetation. In contrast, the SAPLA is designed to monitor the effects of grazing by stock, and recording species richness is part of that process, not its goal. The majority of SAPLA sites are located a moderate but regular distance from stock watering points, and as such would be expected to exhibit some impact of grazing pressure. We believe these two reasons adequately explain the difference in species richness values recorded by our revised index for the two vegetation surveys.

The relationships we described between rarefied γ -diversity of woody-perennial vegetation and sampling effort was derived empirically, and is specific to the study area, the taxon studied, and the vegetation survey methods. Therefore, these relationships should not be applied outside of our study area, to different taxa within our study area, or to data collected by other vegetation surveys within our study area.

An additional caveat is that our measure does not directly model and account for low detectability plants. However, the methods presented herein should minimise the potential impact of non-detection errors. By excluding ephemeral vegetation species, and limiting the study to woody perennial vegetation species we removed a large source of potential for non-detection errors. However, we have previously demonstrated significant non-detection errors in the vegetation surveys used in this analysis (Chapter 3, Clarke *et al.* submitted), even after limiting analysis to perennial species. By aggregating many sites in a region, the rarefaction method used in our analyses should have further reduced the influence of non-detection errors on γ -diversity: a low detectability species must only be recorded at one site in a region to contribute to γ -diversity. However, non-detection errors have probably artificially reduced α - and hence β -diversity in all sub-regions, although these errors will be lower at higher sampling efforts.

Our research supports the findings by others that semi-log relationships describe rarefaction curves well (Palmer 1990; Ugland *et al.* 2003). Additionally, our work answers the call by Fleishman *et al.* (2006) to standardize measures of species richness for differences in survey effort. However we have demonstrated that rarefaction alone does not adequately control for the influence of sampling effort, a finding not previously reported in the literature. If this relationship exists in other areas, interpolation or extrapolation of rarefaction relationships without a sound understanding of the influence of sampling effort will produce erroneous results.

These findings raise important questions for future research. Firstly, we need to ask whether the relationship between rarefied β - and γ -diversity and sampling effort exists in other areas. We have not sought a cause for the influence of sampling effort, but the search for that cause is a logical next step. We consider it possible that the previously mentioned non-detection errors are a partial cause of the relationship between rarefied diversity and sampling effort. Heavily sampled regions not only detect more species due to the expected influence of additional sampling on β - and γ -diversity, but also have more opportunities to record species with low detectability than less sampled regions.

While the α -, β - and γ -diversity values reported in this paper are specific to the taxa studied, vegetation quadrat survey methods and study area, the method we describe is

transferable. The method outlined in this paper provides a theoretically sound framework for deriving an indicator of α -, β - and γ -diversity which is comparable between regions of different sampling effort. Our final sampling effort corrected measure of γ -diversity, γ_{sec} , can conceivably be generated from any vegetation quadrat survey data obtained within a prescribed methodology. Through the use of additive partitioning, γ_{sec} is expressed in the same units as, and directly comparable to, our sampling effort corrected measure of β -diversity, β_{sec} , and our sampling effort independent measure of α -diversity, α_{max} . Application of our method will allow the extraction and comparison of α -, β - and γ -diversity from previously under-utilised vegetation-quadrat survey data collected by government agencies and non-government environmental organizations.

Lastly, we have argued that γ -diversity of woody-perennial vegetation is a theoretically sound estimator-surrogate for biodiversity at broad scales. Therefore, by removing the influence of sampling effort, our index allows examination of the real spatial variation of biodiversity across the study area. However, due to the need to aggregate site data to produce this index, the examination of variation in biodiversity is limited to a relatively coarse spatial scale. The method presented here also facilitates examination of other important components of biodiversity, namely the within sample (α), and between sample (β) diversity.

4.5 Acknowledgements

This work was supported by funding from the Australian Desert Knowledge Cooperative Research Centre (DKCRC) and the University of Adelaide. In addition, two DKCRC partners provided the data that made this analysis possible, the South Australian Department for Environment and Heritage and the South Australian Department of Water, Land and Biodiversity Conservation. Finally, special thanks to Helen Vonow of the South Australian State Herbarium for help in classifying and updating vegetation species lists.

4.6 References

- Badgley, C. and D. L. Fox (2000) Ecological biogeography of North America mammals: species density and ecological structure in relation to environmental gradients. *Journal of Biogeography* **27**: 1437-1467.
- Boulinier, T., J. D. Nichols, J. R. Sauer, J. E. Hines and K. H. Pollock (1998) Estimating species richness: the importance of heterogeneity in species detectability. *Ecology* **79**(3): 1018-1028.
- Clarke, K. D., M. M. Lewis and B. Ostendorf (submitted) False negative errors in vegetation surveys. *Biodiversity and Conservation*?(?): ??-??
- Colwell, R. K., C. X. Mao and J. Chang (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* **85**(10): 2717-2727.
- Crist, T. O. and J. A. Veech (2006) Additive partitioning of rarefaction curves and species-area relationships: unifying alpha-, beta- and gamma-diversity with sample size and habitat area. *Ecology Letters* **9**: 923-932.
- Currie, D. J. and V. Paquin (1987) Large-scale biogeographical patterns of species richness of trees. *Nature* **329**: 326-331.
- DWLBC (2002) Pastoral lease assessment, technical manual for assessing land condition on pastoral leases in South Australia, 1990–2000. Adelaide, Department of Water, Land and Biodiversity Conservation, Pastoral Program, Sustainable Resources.
- Fleishman, E., R. F. Noss and B. R. Noon (2006) Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators* **6**(3): 543-553.
- Gotelli, N. J. and R. K. Colwell (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**(4): 379-391.
- Hawkins, B. A. and E. E. Porter (2003) Does herbivore diversity depend on plant diversity? The case of California butterflies. *American Naturalist* **161**(1): 40-49.
- Hawkins, B. A. and E. E. Porter (2003) Water-energy balance and the geographic pattern of species richness of western Palearctic butterflies. *Ecological Entomology* **28**: 678-686.
- Hawkins, B. A., E. E. Porter and J. A. F. Diniz-Filho (2003) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology* **84**(6): 1608-1623.
- Heard, L. and B. Channon (1997) Guide to a native vegetation survey: Using the Biological Survey of South Australia. Adelaide, SA, Department of Environment and Natural Resources.
- Laut, P., G. Keig, M. Lazarides, E. Loffler, C. Margules, R. M. Scott and M. E. Sullivan (1977) Environments of South Australia: Province 8, Northern Arid. Canberra, Division of Land Use Research, CSIRO: 116-168.
- Mao, C. X., R. K. Colwell and J. Chang (2005) Estimating the species accumulation curve using mixtures. *Biometrics* **61**: 433-441.
- O'Brien, E. M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of Southern Africa's woody flora. *Journal of Biogeography* **20**: 181-198.
- O'Brien, E. M. (1998) Water-energy dynamics, climate, and prediction of woody plants species richness: an interim general model. *Journal of Biogeography* **25**: 379-398.
- O'Brien, E. M., R. Field and R. J. Whittaker (2000) Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. *Oikos* **89**(3): 588-600.
- Palmer, M. W. (1990) The estimation of species richness by extrapolation. *Ecology* **71**(3): 1195-1198.
- Rodrigues, A. S. L. and T. M. Brooks (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics* **38**(1): 713-737.
- Sarkar, S. (2002) Defining "Biodiversity"; Assessing Biodiversity. *The Monist* **85**(1): 131-155.

Smyth, A. K., V. H. Chewings, G. N. Bastin, S. Ferrier, G. Manion and B. Clifford (2004) Integrating historical datasets to prioritise areas for biodiversity monitoring? Australian Rangelands Society 13th Biennial Conference: "Living in the outback", Alice Springs, Northern Territory.

Tipper, J. C. (1979) Rarefaction and Rarefaction-The Use and Abuse of a Method in Paleocology. *Paleobiology* **5**(4): 423-434.

Ugland, K. I., J. S. Gray and K. E. Ellingsen (2003) The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology* **72**: 888-897.

Veech, J. A., K. S. Summerville, T. O. Crist and J. C. Gering (2002) The additive partitioning of species diversity: recent revival of an old idea. *Oikos* **99**: 3-9.

Venevsky, S. and I. Venevskaia (2005) Heirarchical systematic conservation planning at the national level: Identifying national biodiversity hotspots using abiotic factors in Russia. *Biological Conservation* **124**: 235-251.

Whittaker, R. H. (1972) Evolution and measurement of species diversity. *Taxon* **21**(2/3): 213-251.

Chapter 5: Remotely sensed surrogates of biodiversity stress

5.1 Introduction

As we become more environmentally aware, and as economic values are placed on natural ecosystems (Costanza *et al.* 1997), managers have begun to appreciate the potential cost of allowing further degradation of our natural systems. In the Australian rangelands this has resulted in an increased desire to monitor and manage biodiversity for conservation (Smyth *et al.* 2004). But how can we best measure biodiversity?

The term biodiversity is so all-encompassing that direct measurement is not possible, and it is necessary to measure other features which vary with biodiversity: surrogates. Sarkar (2002) argued that species richness was one of the few suitable true-surrogates for biodiversity because firstly, species are a well defined and understood category, and secondly, species richness is measurable. However measuring total species richness at any reasonable scale is not feasible. We have previously argued that woody perennial vegetation γ -diversity is a surrogate for total species richness, and hence a suitable estimator-surrogate for biodiversity (Clarke *et al.* submitted).

A surrogate which is practically measurable at broad scales must be established for total species richness, as an indicator-surrogate for biodiversity (Sarkar 2002). To do this we need to understand, at broad scales, the causes of and pressures on biodiversity in the arid and semi-arid rangelands of South Australia.

We have previously argued that the most compelling explanation for the distribution of biodiversity at broad scales is the “species-energy hypothesis,” and the most significant pressure on biodiversity in the study area is grazing-induced degradation, or overgrazing (Chapter 2). In examining the causes of and pressures on biodiversity, we see two potential surrogates of pressure on biodiversity which may be practical at broad scales.

The first surrogate we propose is based on the differential effect of overgrazing on water-energy balance and net primary productivity. Firstly, water-energy balance is a function of climatic variables and the redistribution of rainfall by topography, and therefore

independent of grazing disturbance. Therefore we will treat water-energy balance as an index of potential, or expected primary productivity. Conversely, net primary productivity is reduced by high grazing pressure. Given the differential influence of disturbance, we hypothesise that the difference between expected and net primary production will provide a measure of biodiversity-reducing disturbance in the study area.

The second surrogate we propose is based on the convincing link between grazing induced degradation and the temporal variability of net primary productivity and rainfall use efficiency. We propose the measurement of average and variation in annual net primary productivity and rainfall use efficiency as a tool for monitoring grazing induced landscape degradation, and hence pressure on biodiversity.

In this study a measurement of net primary productivity is derived from satellite imagery, water-energy balance is derived from climatic data, and rainfall use efficiency is derived from the combination of satellite imagery and climatic data. The two surrogates of pressure on biodiversity are examined in relation to our index of woody perennial vegetation α -, β - and γ -diversity derived from conventional vegetation quadrat surveys (Chapter 4, or Clarke *et al.* submitted). We have previously argued that woody perennial vegetation γ -diversity is a surrogate for total species richness, and hence a suitable estimator-surrogate for biodiversity (Clarke *et al.* submitted). For this validation we are assuming that prolonged biodiversity stress will result in low α -, β - and γ -diversity, and hence that high values of our biodiversity-stress index will coincide with low α -, β - and γ -diversity, and vice versa.

5.2 Methods

5.2.1 Study area

A more detailed description of the study area can be found in Chapter 1. The surrogates of biodiversity stress were developed in, and are restricted to the study area. Woody perennial alpha, beta and gamma diversity derived from the Biological Survey of South Australia data (Chapter 4, or Clarke *et al.* submitted) is presented in Figure 23.

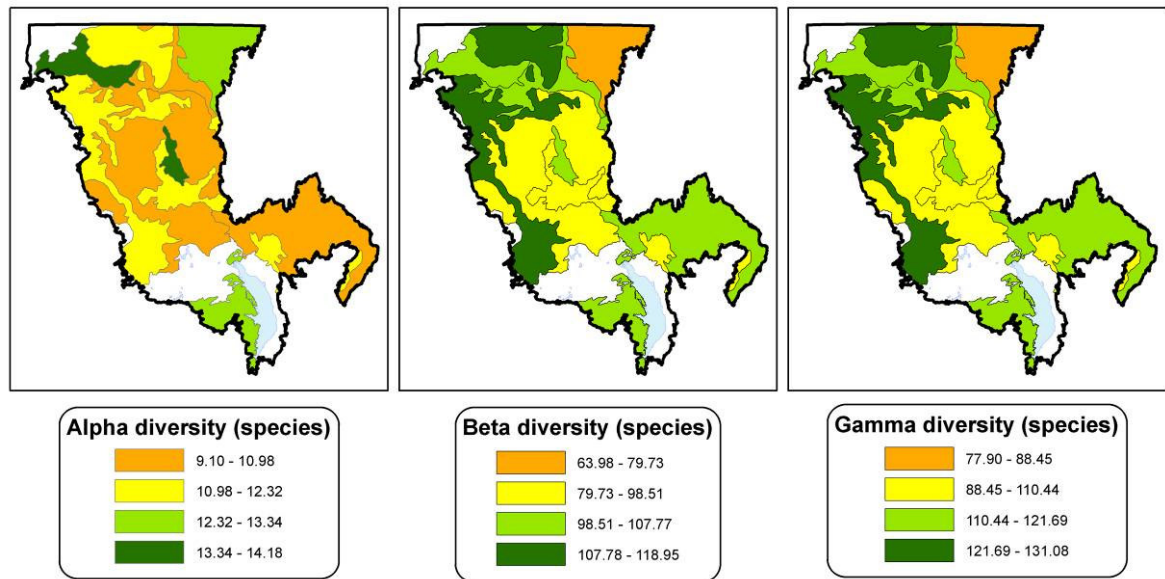


Figure 23. Alpha (α), beta (β) and gamma (γ) diversity derived by additive partitioning of rarefaction curves from data collected by the Biological Survey of South Australia.

5.2.2 Common components

The two biodiversity stress surrogates are composed of several components, two of which are common to both surrogates: an index of net primary production, and a topographic index of valley bottom flatness. Both surrogates were calculated from datasets which covered the same temporal period as the species diversity data used for evaluation, 1990 – 2003.

Net primary production (NPP)

Research has demonstrated that net primary production (NPP) is directly related to time integrated, or accumulated, normalised difference vegetation index (NDVI) (Tucker *et al.* 1981; Asrar *et al.* 1985; Tucker and Sellers 1986; Box *et al.* 1989). There are three commonly used cumulative vegetation indices: the sum of all NDVI images for a given period of time, integrated NDVI (Σ NDVI) (Tucker *et al.* 1981; Asrar *et al.* 1985; Tucker and Sellers 1986; Box *et al.* 1989); the first component of the power density spectrum (NDVI_S), produced through Fourier frequency analysis (Andres *et al.* 1994); and, the length of the vectorial representation of an annual time series of NDVI maximum value composite (MVC), |NDVII. (Lambin and Strahler 1994). However, Ricotta *et al.* (1999)

demonstrated that these three indices were statistically equivalent, and therefore we use the index which is easiest to implement, Σ NDVI.

It should be noted that some research has suggested amendments to the simple Σ NDVI to improve estimates of NPP. Reed *et al.* (1996) proposed the exclusion of non-growing season NDVI values from the integration process and the reduction of growing season NDVI values by the latent (non-growing season) NDVI values. However, neither of these modifications is appropriate for measuring primary production in Australia's arid rangelands due to the irregular nature of rainfall and hence vegetation growth.

Lastly, NDVI is known to perform inconsistently in areas with different soil brightness (Huete and Jackson 1987). Rasmussen (1998) counteracted this effect with a correction that utilised a map of average dry season albedo, generated from AVHRR channels 1 and 2 over several years. The implementation of this correction for this study would have been costly, and budgetary constraints prevented this. Consequently, soil colour has remained a potentially confounding factor.

National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) NDVI data were obtained from the National Aeronautics and Space Administration (NASA) Global Inventory Modelling and Mapping Studies (GIMMS) project. The GIMMS generates half-monthly maximum value composite (MVC) data by scanning each daily NDVI image in the half-month and retaining the highest value pixel for each cell. This procedure minimises problems common to single-date NDVI data such as cloud interference, atmospheric attenuation, look angle differences and illumination geometry (Holben 1986).

To address the specific requirements of the two surrogates, it was necessary to create two distinct NPP products. The first surrogate, based on the difference between expected and net primary production, required an index of total NPP (TNPP) over the 14 year study period, 1990 – 2003. This index of TNPP was calculated from the accumulated NDVI as the sum of all half-monthly MVC NDVI datasets (Σ NDVI) for the study period. The second surrogate, based on the average and variation in NPP and rainfall use efficiency, required an index of annual NPP (ANPP). Therefore, accumulated NDVI was calculated

for each of the 14 study years, 1990 – 2003, as the sum of all half-monthly MVC NDVI datasets (Σ NDVI) for that year

Topographic index: valley bottom flatness (VBF)

Both surrogates required a method for accounting for the redistribution of rainfall by terrain. To this end a topographic index titled multiple resolution valley bottom flatness (VBF) was calculated (Gallant and Dowling 2003). The VBF index classifies the landscape into valley bottom and non-valley bottom (slope and ridge) areas, which in the context of rainfall redistribution correspond to run-on and run-off areas respectively.

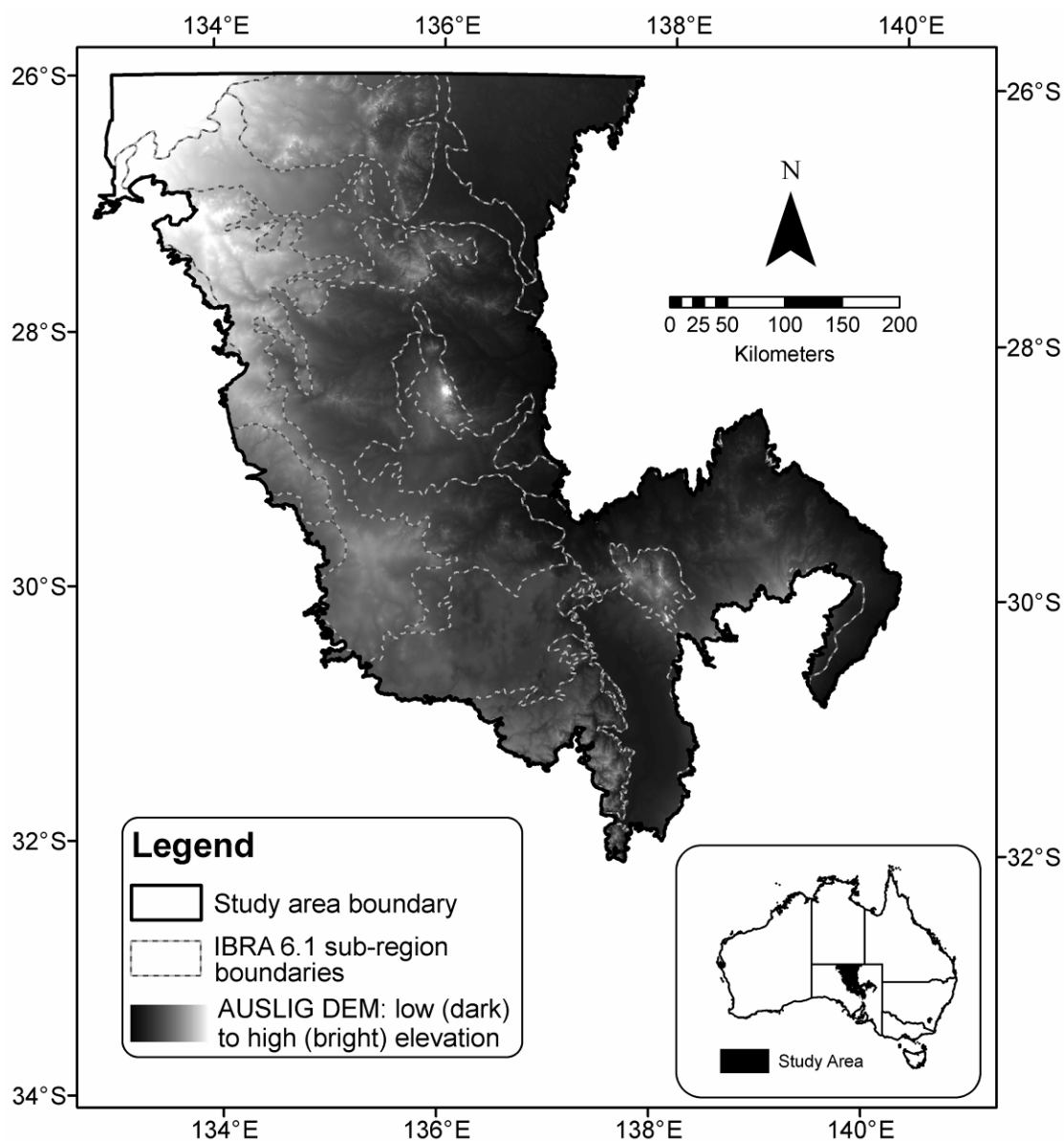


Figure 24. Elevation in the study area as recorded by the AUSLIG 9 second (~310 m) digital elevation model (DEM). IBRA 6.1 sub-region boundaries are overlain for interpretation; see Figure 25 for IBRA sub-region detail.

The VBF index was calculated from the AUSLIG 9 second (approximately 310 m) digital elevation model (DEM) (Figure 24). Due to software requirements, the DEM was resampled to 325 m prior to generation of the VBF index. The specific use of the VBF in each surrogate is discussed in the relevant sub-section: Surrogate 1, *Evapotranspiration and topographic redistribution of rainfall*; and Surrogate 2, *Topographically redistributed rainfall*.

5.2.3 Surrogate 1

In addition to the index of TNPP, Surrogate 1 requires one specific component, a measure of expected primary production derived from climatic data, actual evapotranspiration. The generation of this component is discussed below, followed by the details of the calculation of Surrogate 1 from the components.

Expected primary production (EPP)

Studies of water-energy balance in relation to variation in biodiversity have used several different measures of water-energy balance. One of the most widely used is actual evapotranspiration, a measure of the availability of water for transpiration in relation to ambient energy conditions (Currie and Paquin 1987; Currie 1991; O'Brien 1993; O'Brien 1998; Badgley and Fox 2000; Hawkins and Porter 2003; Hawkins and Porter 2003; Hawkins *et al.* 2003).

Actual evapotranspiration (hereafter AET) data were obtained from the Australian Bureau of Meteorology collaborative SILO project (Jeffrey *et al.* 2001). The SILO project employs Morton's complementary relationship areal evapotranspiration (CRAE) model (Morton 1983), a model which has performed well in extensive tests across different climatic regions (Hobbins *et al.* 2001). The SILO project calculates AET from climatic variables recorded at discrete climate stations, and a raster surface is then interpolated to create an Australia-wide AET surface with a resolution of 5 km.

Specifically, average monthly AET was obtained for the study period, 1990 to 2003.

However, the capacity for species richness is determined by the amount, and duration of

biological activity (O'Brien 2006). Therefore, the AET data were transformed to total accumulated AET, or AAET. This was accomplished by multiplying each month's average AET by the number of days in the month to produce monthly total, or accumulated, AET, in mm evapotranspiration. Within each year, monthly accumulated AET data were summed to produce yearly AET. Finally, yearly AET was summed to produce accumulated AET (AAET) for the 14 year study period, a theoretical index of expected primary production (EPP).

Topographically scaled EPP (TEPP)

Rainfall is a significant component of AET, but the SILO rainfall data are relatively coarse scale (see sub-section 0, *Rainfall*, for more detail). To account for the redistribution of rainfall by topography, the VBF index was scaled and combined with the AAET raster. This was done in such a way that evapotranspiration values on steep slopes remained unchanged, while values in valley bottoms were increased by up to 100%. Specifically, VBF was scaled from 1 – 2 and multiplied by AAET. This produced a topographically scaled index of expected primary production (TEPP). Finally, to facilitate comparison this index with the satellite derived index of actual primary production the TEPP was rescaled to 8 km resolution.

Calculation of Surrogate 1

The index of biodiversity-stress, Surrogate 1, was calculated as:

$$1 - (TNPP / TEPP) \quad (1)$$

Where TNPP is an index of total NPP over the 14 year study period and TEPP is an index of topographically scaled index of expected primary production. This method of calculation produced an intuitive index where low values of biodiversity-stress index would indicate that actual primary production is close to its climatic potential; and high values of biodiversity-stress index would indicate that actual primary production is falling short of climatic potential.

5.2.4 Surrogate 2

In addition to ANPP, Surrogate 2 requires an index of rainfall use efficiency (RUE). The calculation of RUE from rainfall and NPP data are discussed below, followed by the method used to calculate Surrogate 2.

Rainfall

There are 22 climate stations which measure rainfall within the study area. However, the rainfall surface is interpolated from all climate stations within 100 km, with a minimum requirement of 30 climate stations. If there are fewer than 30 climate stations within 100 km the radius is increased iteratively until this criterion is satisfied (Jeffrey *et al.* 2001). Due to the low density of climate stations in and around the study area, rainfall at any given point is interpolated from data collected at stations ranging from a few kilometres to several hundred kilometres away. Thus, the data supplied by the Australian Bureau of Meteorology collaborative SILO project (Jeffrey *et al.* 2001) makes no allowance for orographic influences on rainfall (uplift or rain-shadowing), or for the topographic re-distribution of rain by slopes (run-off areas) and valley flats and rivers (run-on areas).

Two rainfall indices were used in the analyses; climatically distributed rainfall as depicted by the SILO interpolation, and topographically re-distributed rainfall.

Climatically distributed rainfall use efficiency (CRUE)

The data obtained from the Australian Bureau of Meteorology collaborative SILO project (Jeffrey *et al.* 2001) makes no allowance for factors which cause meso-scale variation in rainfall, and is therefore treated as a measure of climatically distributed rainfall. Average monthly rainfall was obtained for the study period, 1990 to 2003 at 5 km resolution. From the average monthly rainfall, total annual rainfall (AR) was calculated for each of the 14 study years. Finally, the AR was resampled to 8 km resolution to facilitate comparison with the satellite derived index of net primary production (also at 8 km resolution).

Climatically distributed rainfall use efficiency (CRUE) was calculated for each of the 14 study years by dividing NPP for that year by the AR for the same 12 month period. This method is analogous to the method used by Holm *et al.* (2003), where RUE was calculated as total phytomass per mm of rainfall in the preceding 12 months.

Topographically redistributed rainfall use efficiency (TRUE)

To account for the redistribution of rainfall by topography, the VBF index was scaled and combined with the total annual rainfall rasters to produce a topographically scaled annual rainfall index (T-AR) for each of the 14 study years. This was done in such a way that rainfall values on steep slopes remained unchanged, while values in valley bottoms were increased by up to 100%. Specifically, VBF was scaled from 1 – 2 and multiplied by AR. Finally, the T-AR was resampled to 8 km resolution to facilitate comparison with the satellite derived index of net primary production (also at 8 km resolution).

Topographically redistributed rainfall use efficiency (TRUE) was very similar to the calculation of CRUE, with T-AR taking the place of AR.

Calculation of Surrogate 2

The average annual, and annual variation (standard deviation) were calculated for NPP, CRUE and TRUE. These were calculated as the average and standard deviation at each 8 km pixel location over the 14 annual RUE datasets. This resulted in six outputs, mean annual NPP (mean-NPP), annual variation in NPP (std-NPP), mean annual CRUE (mean-CRUE), annual variation in CRUE (std-CRUE), mean annual TRUE (mean-TRUE) and annual variation in TRUE (std-TRUE).

5.2.5 Evaluation method

High biodiversity-stress is expected to cause a reduction in woody perennial vegetation α -, β - and γ -diversity. Therefore, both surrogates of biodiversity-stress were compared to our measure of woody perennial vegetation α -, β - and γ -diversity values extracted from vegetation quadrat data collected by two surveys: the Biological Survey of South Australia (BSSA); and the South Australian Pastoral Lease Assessment (Chapter 4, or Clarke *et al.* submitted).

However, the α -, β - and γ -diversity values were generated from quadrat surveys at point locations and then aggregated by IBRA sub-region, while the biodiversity-stress index is a continuous surface. To ensure similar areas were compared, the value of the corresponding biodiversity-stress index pixel (8 km resolution) was extracted for each vegetation survey quadrat location and then averaged by IBRA sub-region (Figure 25).

Thus, α -, β - and γ -diversity value, and average surrogate values were calculated for each IBRA sub-region. Finally, correlation was examined between each type of diversity from both conventional vegetation surveys and all surrogates of biodiversity stress.

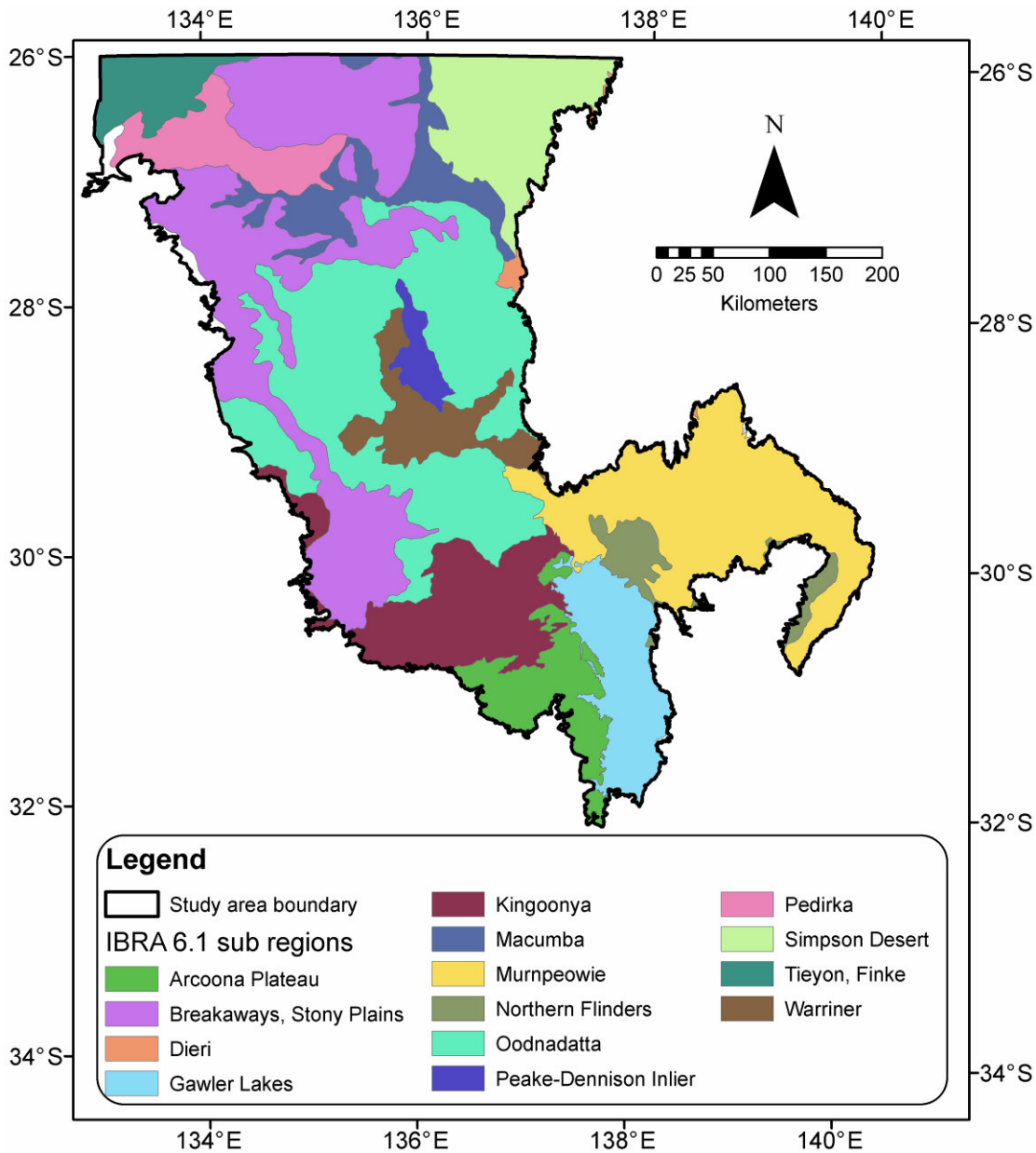


Figure 25. IBRA 6.1 sub-region name, location and extent.

5.3 Results

5.3.1 Common component: index of valley bottom flatness (VBF)

The topographic index, multiple resolution valley bottom flatness (VBF) is presented in Figure 26. Inspection of the VBF index in relation to the parent digital elevation model

(Figure 24) showed reasonably good agreement. The extensive flat areas in the north east and other parts of the study area correspond to dune filed and known valley bottoms, and the steep areas correspond to known ranges and other regions of high relief. However, the index sometimes struggled to distinguish ridge tops from valley bottoms, and in flat terrain sometimes failed to map valley bottoms.

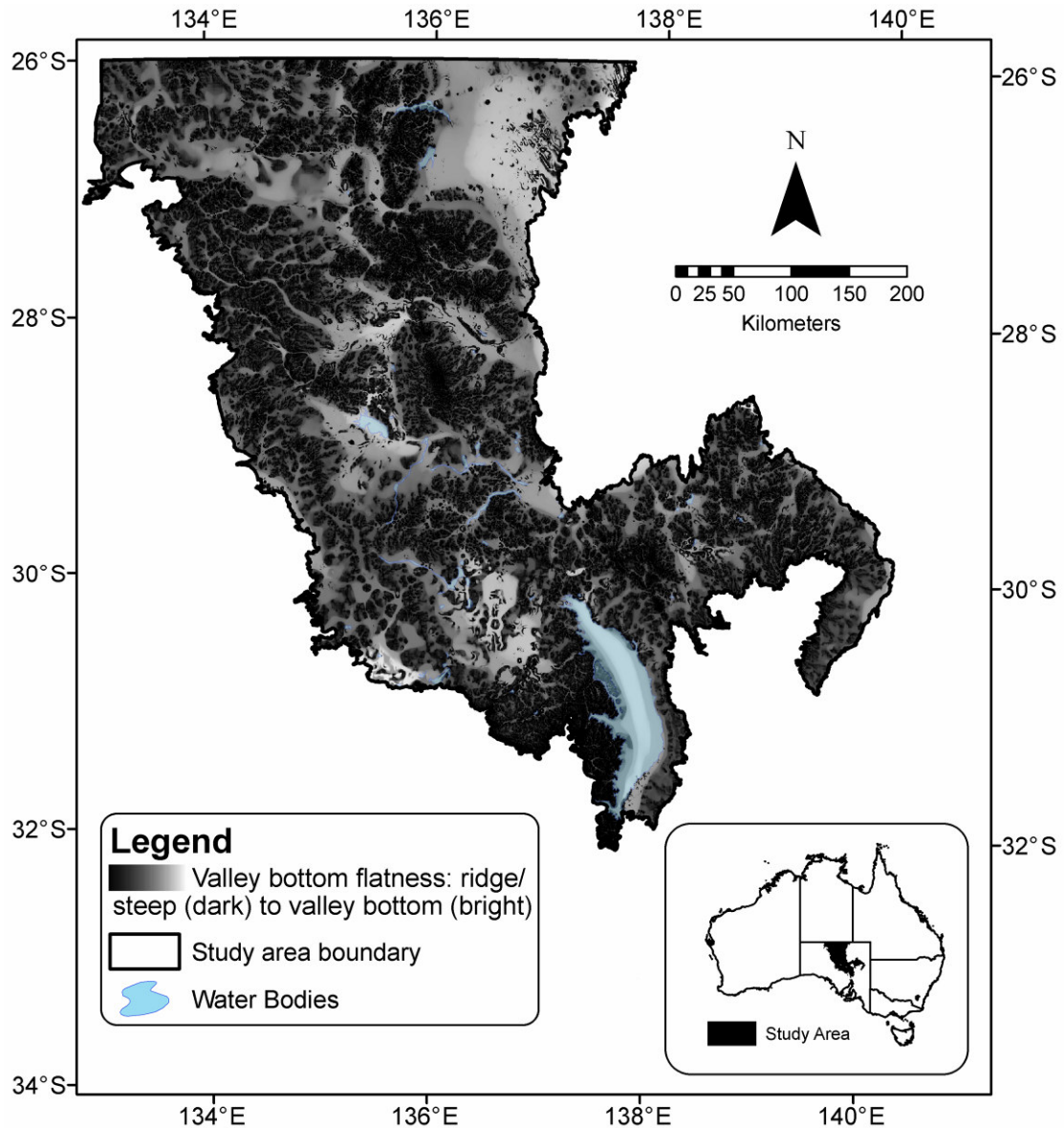


Figure 26. Multiple resolution valley bottom flatness (VBF) index, calculated from the AUSLIG 9 second digital elevation model (DEM). Resolution is 325 m.

5.3.2 Surrogate 1

Total net primary production (TNPP)

The index of net primary production used in Surrogate 1, total net primary production (TNPP), is presented in Figure 27. Two interesting features become apparent by comparing TNPP to IBRA sub-region boundaries (Figure 25); the tongue of high primary production in the north-west of the study area corresponds very closely to the Pedirka and Tieyon, Finke sub-regions. Additionally, a line of high TNPP is visible around about 28° S, following the edge of the Breakaways, Stony Plains and Oodnadatta sub-regions. These patches of high TNPP could either be the result of true variation in the spatial distribution of primary production as a result of soil type, rainfall and topography, or an error caused by the known influence of soil colour on NDVI.

Inspection of high-resolution QuickBird imagery (not shown) shows substantially greater vegetation cover in the Pedirka and Tieyon, Finke sub-regions than in surrounding areas. Likewise, two large tree-lined ephemeral rivers flow through the Oodnadatta and Peake-Dennison Inlier sub-region along 28° S, the Arckaringa Creek and the Neales (Nappamurra) River. Thus, this mapped variation in primary production corresponds to the on-ground variation in primary production, and not to artefacts related to soil colour.

Expected primary production (EPP)

The surrogate for expected primary production (EPP), accumulated Morton's actual evapotranspiration (AAET) is presented in Figure 28. The map has two main features of interest. Firstly, there is a pronounced gradient of EPP, ranging from low in the north to high in the south. Secondly, the map displays no local or regional deviation from this even gradient.

AAET, and hence EPP in the study area is primarily driven by rainfall; energy is not limiting in arid Australia. The direction of the gradient is a result of the location of the study area in relation to Australia's coast; less rain falls further inland. The southern end of the study area is relatively close to the Australian coast, specifically Spencer Gulf, receives more rainfall and has a higher EPP; the northern end of the study area is further away from the coast, receives less rainfall and has a lower EPP; the north-eastern corner of

the study area is the farthest from the coast, receives the least rainfall and has the lowest EPP.

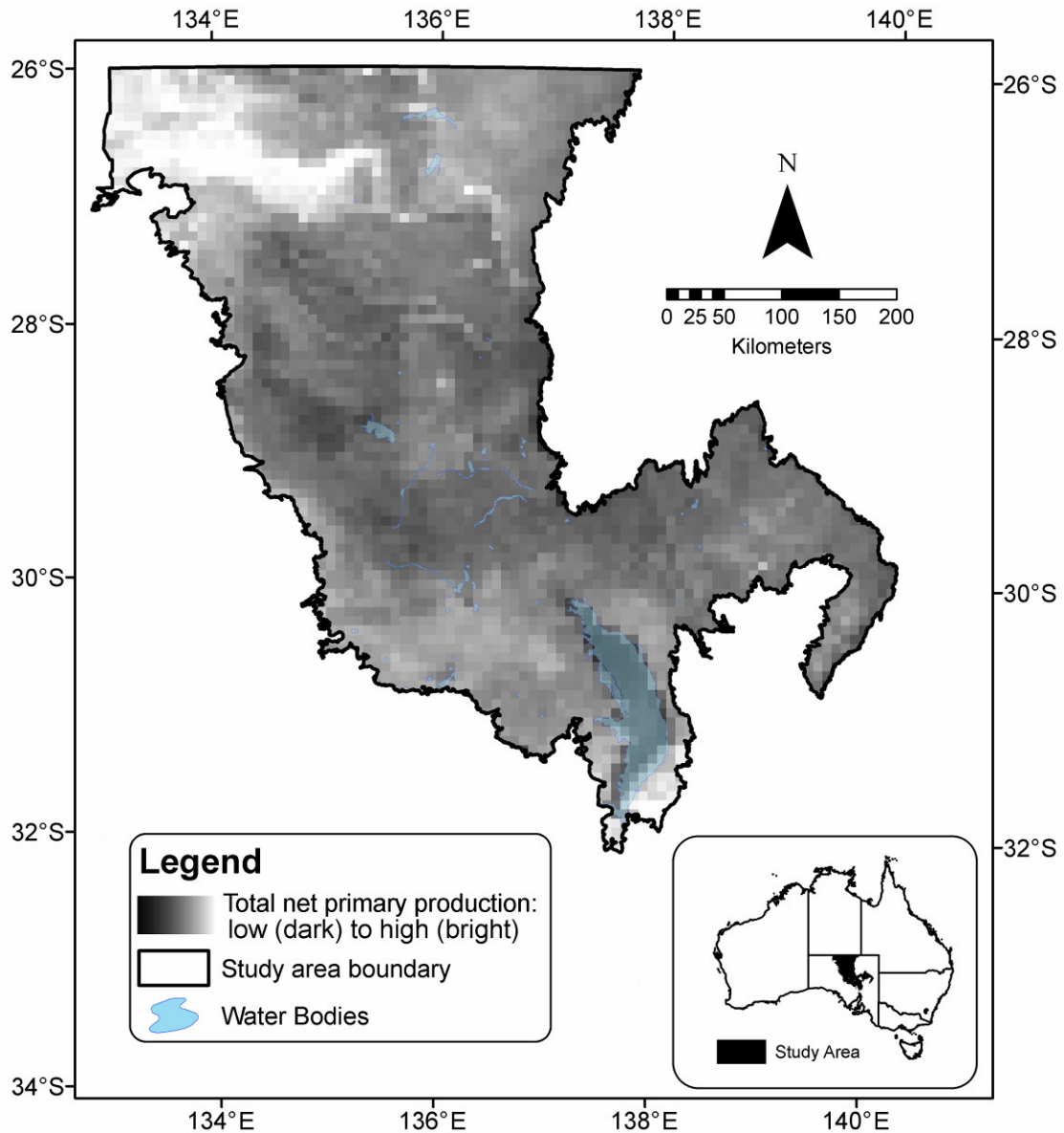


Figure 27. Index of total net primary production (TNPP) for the period 1990 – 2003, derived from accumulated NDVI (Σ NDVI). Resolution is 8 km.

The gradient displayed in the map is smooth, displaying no local or regional deviation. Due to the low density of climate stations in and around the study area, the AET at any given point is interpolated from data collected at climate stations ranging from a few kilometres to several hundred kilometres away. Thus, this measure of EPP makes no allowance for orographic influences on rainfall (uplift or rain-shadowing), or for the

topographic redistribution of rain by slopes (run-off areas) and valley flats and rivers (run-on areas).

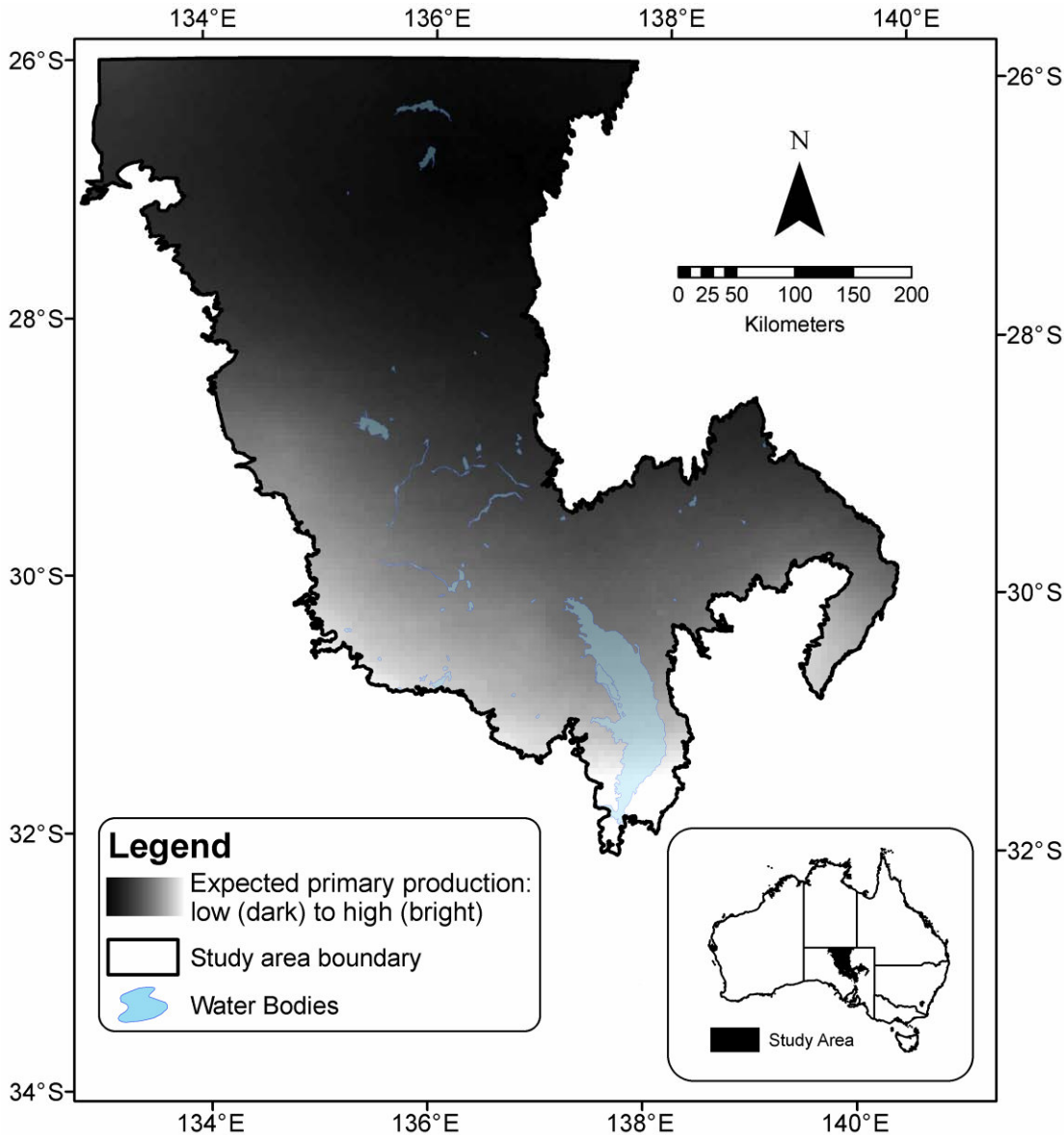


Figure 28. Accumulated Morton's actual evapotranspiration (AAET), interpolated from 18 climate stations surrounding the study area. Resolution is approximately 5 km. AAET is a theoretically sound surrogate for expected primary production (EPP).

Topographically scaled EPP (TEPP)

The topographically scaled index of expected primary production produced from the combination of EPP and VBF is presented in Figure 29. The TEPP is substantially different from the original EPP index, and show significant topographic influence. The sandy Simpson Desert in the north east (refer to Figure 25), Pedirka and Tiewon, Finke

sub-regions have higher TEPP than EPP. Additionally, local low points in the Kingoonya (approximately 135.5° E, 29.5° S) and Oodnadatta (approximately 136.5° E, 30.5° S) sub-regions have higher TEPP than EPP.

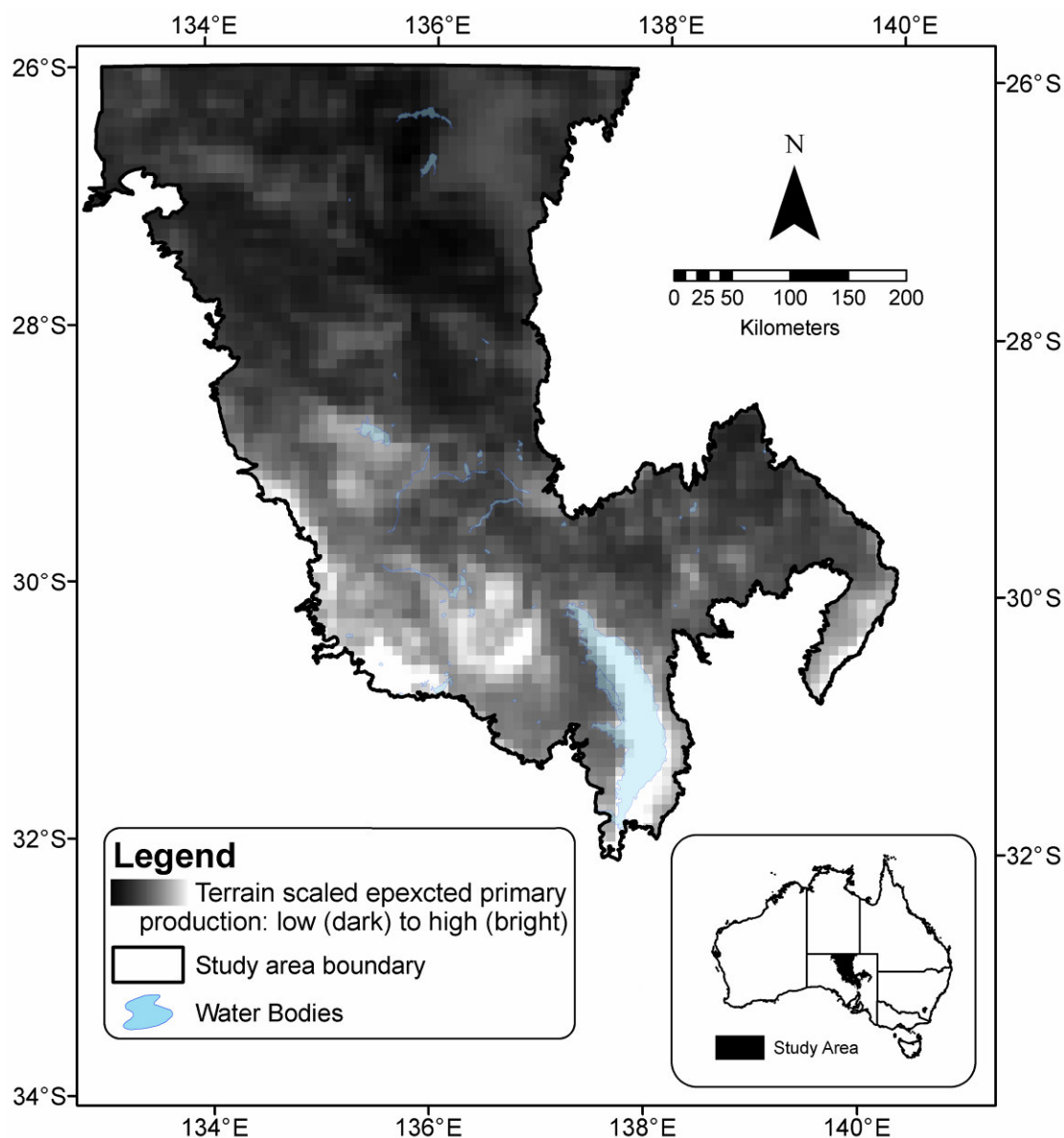


Figure 29. Morton's AAET scaled with VBF to account of topographic redistribution of rainfall and create a topographically scaled index of expected primary production (TEPP). Resolution is 8 km.

Surrogate 1: final index

The index of biodiversity-stress, Surrogate 1, based on the difference between net and expected primary production, is presented in Figure 30. The index is calculated using Equation 1, which produces an intuitively sensible index: low values of biodiversity-stress index indicate that actual primary production is close to climatic potential; while high

values of biodiversity-stress index indicate that actual primary production is falling short of climatic potential.

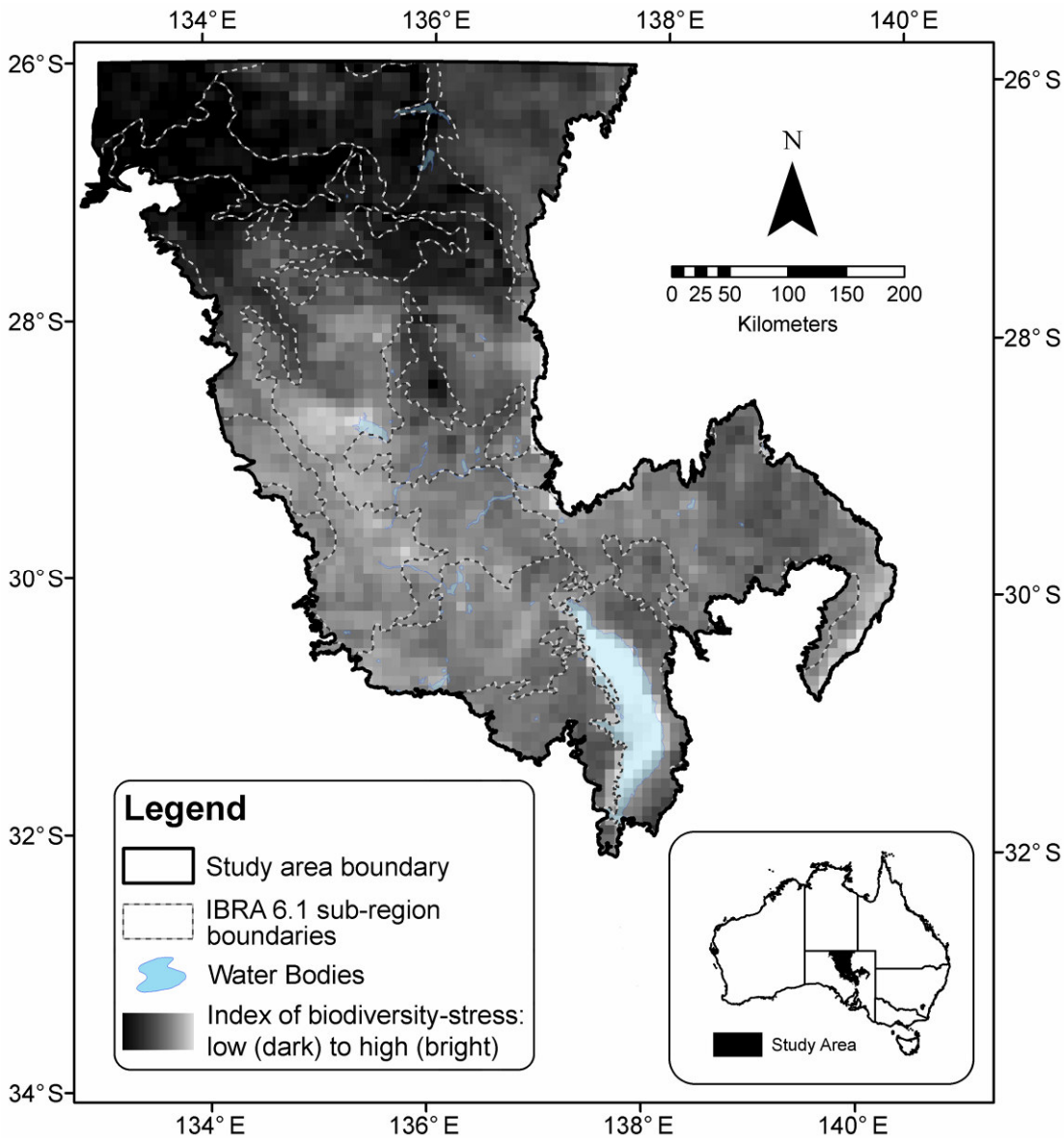


Figure 30. Surrogate 1: Index of biodiversity-stress, based on the difference between net and expected primary production.

The index of biodiversity-stress is dominated by low stress in the north, throughout the Teyon, Finke, Pedirka, Macumba and to a lesser extent the northern Breakaways, Stony Plains IBRA sub-regions. Another region of very low stress is located in the centre of the Peake-Dennison Inlier, near the centre of the study region. A few regions of elevated stress occur in the Breakaways, Stony Plains and Oodnadatta, between 135° E and 136° E,

and between 29° S and 30° S. Throughout the rest of the study area biodiversity-stress values are relatively uniform.

Evaluation of Surrogate 1

The sampling effort, woody perennial vegetation α -, β - and γ -diversity and average biodiversity-stress index values for both conventional vegetation surveys and all IBRA sub-regions is presented in Table 11. The presented α -diversity values are independent of sampling effort, while the β - and γ -diversity values are corrected for sampling effort using the method described in Clarke *et al.* (submitted). Sampling effort, in number of quadrats surveyed, is presented for reference only. The biodiversity-stress index has units of K/mm where K is an unknown constant relating NDVI to actual primary productivity.

For Biological Survey of South Australia the regression indicated a negligible relationship between biodiversity-stress index and α -, β - and γ -diversity when analysed by IBRA sub-region ($R^2 = 0.09$ (p 0.5), 0.04 and 0.05 respectively). There were similarly poor regression relationships between the biodiversity-stress index and South Australian Pastoral Lease Assessment α -, β - and γ -diversity when analysed by IBRA sub-region ($R^2 = 0.08$ (p 0.5), 0.01 and 0.00 respectively). Thus, there appears to be no relationship between elevated levels of our biodiversity-stress index and low values of α -, β - or γ -diversity.

Table 11. Sampling effort, woody perennial α -, β - and γ -diversity and average biodiversity-stress index values in each IBRA 6.1 sub-region

IBRA 6.1 Sub-region	Biological Survey of SA [§]					SA [§] Pastoral Lease Assessment				
	sampling effort*	α^\dagger	β^\dagger	γ^\dagger	BD-stress [‡]	sampling effort*	α^\dagger	β^\dagger	γ^\dagger	BD-stress [‡]
Arcoona Plateau	43	13.34	101.68	115.02	0.9909	113	9.35	59.17	68.51	0.9903
Breakaway, Stony Plains	216	12.12	118.96	131.08	0.9867	226	9.42	85.55	94.97	0.9898
Dieri	7	12.23	104.20	116.43	0.9888					
Gawler Lakes						59	11.48	85.64	97.12	0.9899
Kingoonya						243	8.93	67.03	75.96	0.9919
Macumba	46	9.23	103.87	113.10	0.9862	28	8.85	89.60	98.46	0.9850
Murnpeowie	192	10.98	104.02	114.99	0.9914	239	9.59	81.20	90.80	0.9911
Northern Flinders	51	12.32	92.63	104.94	0.9912	57	9.39	70.05	79.44	0.9906
Oodnadatta	230	10.65	92.32	102.97	0.9899	151	8.25	72.47	80.72	0.9909
Peake-Dennison Inlier	20	13.82	107.87	121.69	0.9865					
Pedirka	26	14.18	102.69	116.86	0.9817	19	8.35	69.87	78.21	0.9819
Simpson Desert	48	12.91	67.61	80.52	0.9878					
Tieyon, Finke						36	8.28	72.82	81.11	0.9822
Warriner	11	11.93	98.51	110.44	0.9926	17	7.50	73.77	81.27	0.9908

[§]South Australia

*Sampling effort in number of quadrats surveyed

[†] α -, β - and γ -diversity values corrected for sampling-effort differences, in units of species-richness.

[‡]Biodiversity-stress index, unitless.

5.3.3 Surrogate 2

Average annual NPP (mean-NPP)

The index of average annual net primary production (mean-NPP), derived from 14 annual Σ NDVI, is presented in Figure 31. Several interesting features become apparent by comparing NPP to IBRA sub-region boundaries (Figure 25). Firstly, the higher Σ NDVI values in the north-west of the study area correspond very closely to the Pedirka and Teyon, Finke sub-regions. Secondly, a region of high Σ NDVI around 136° E - 137° E, 26° S - 27° S corresponds to the eastern Macumba IBRA sub-region. Next, a line of high Σ NDVI pixels is visible around about 28° S, stretching east from the north-west of the Oodnadatta sub-region, and crossing the northern tip of the Peake-Dennison Inlier. Finally, a small area of high Σ NDVI appears in the far south of the study area. These areas of high Σ NDVI could be either the result of true variation in the spatial distribution of primary production as a result of soil type, rainfall and topography, or an error caused by the known influence of soil colour on NDVI.

Inspection of high-resolution QuickBird imagery (not shown) shows substantially greater vegetation cover in the Pedirka and Teyon, Finke sub-regions than in surrounding areas. The eastern Macumba IBRA sub-region is dominated by the ephemeral Oogawa and Ambullinna Waterholes, and Alkaowra Flood Flats. Additionally, two large tree-lined ephemeral rivers flow through the Oodnadatta and Peake-Dennison Inlier sub-region along 28° S, the Arckaringa Creek and the Neales (Nappamurra) River. Finally, the south of the study area is closer to Spencer Gulf and receives more rainfall, accounting for the mapped increase in mean-NPP in the southern tip of the study area. Thus, much of the spatial variation in mean-NPP corresponds to real terrain or climatic features which would be expected to increase mean-NPP.

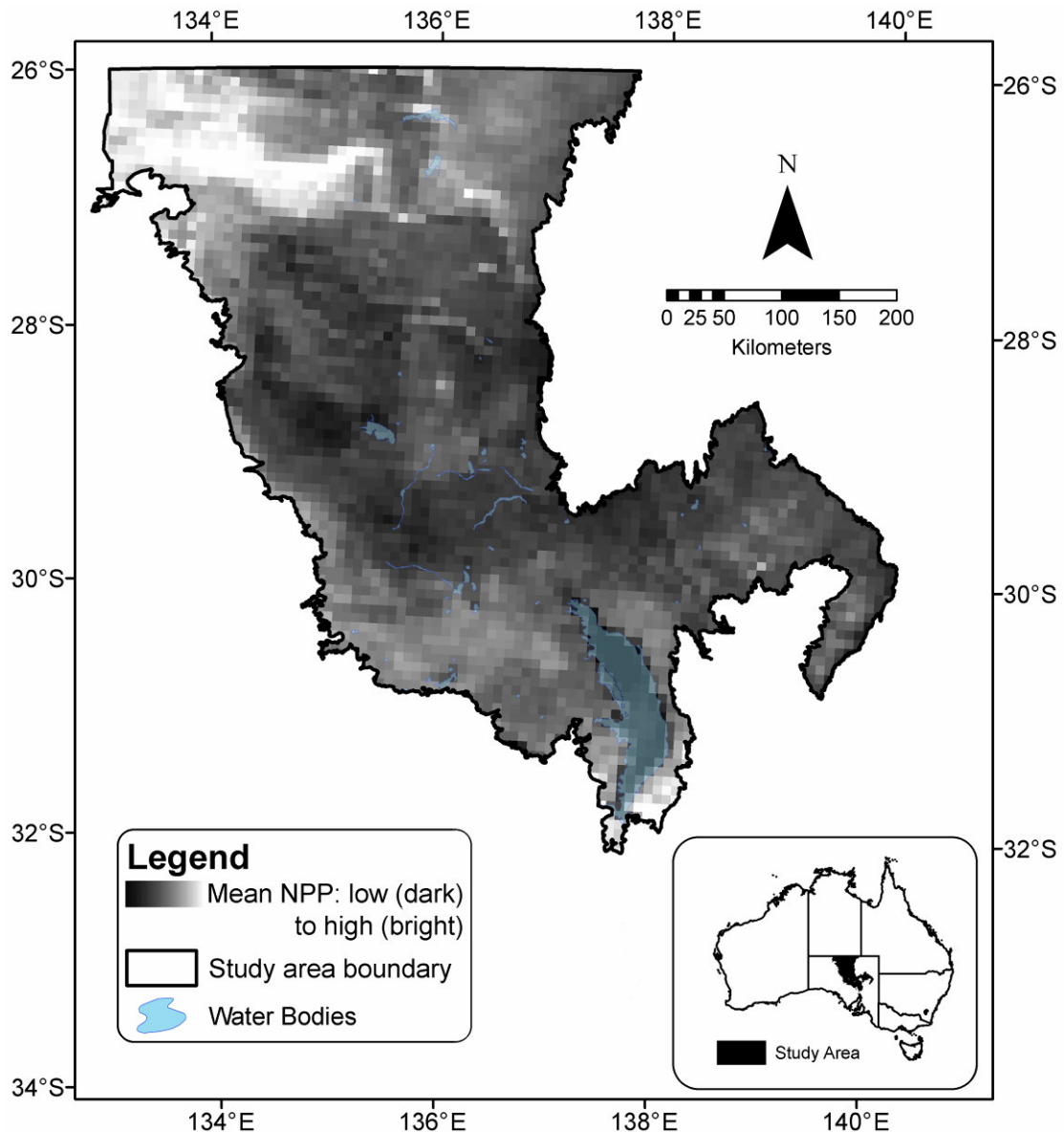


Figure 31. Index of average annual net primary production (mean-NPP), 1990 – 2003, derived from 14 annual Σ NDVI images. Resolution is 8 km.

Variation in annual NPP (std-NPP)

The index of variation in annual net primary production (std-NPP) is presented in Figure 32. The ephemeral wetlands in the eastern Macumba IBRA sub-region, and the ephemeral rivers along 28° S are visible once again. Thus, two of the major sources of spatial variation in std-NPP correspond to ephemeral wetlands, topographic features which would be expected to cause large variation in NPP from year to year.

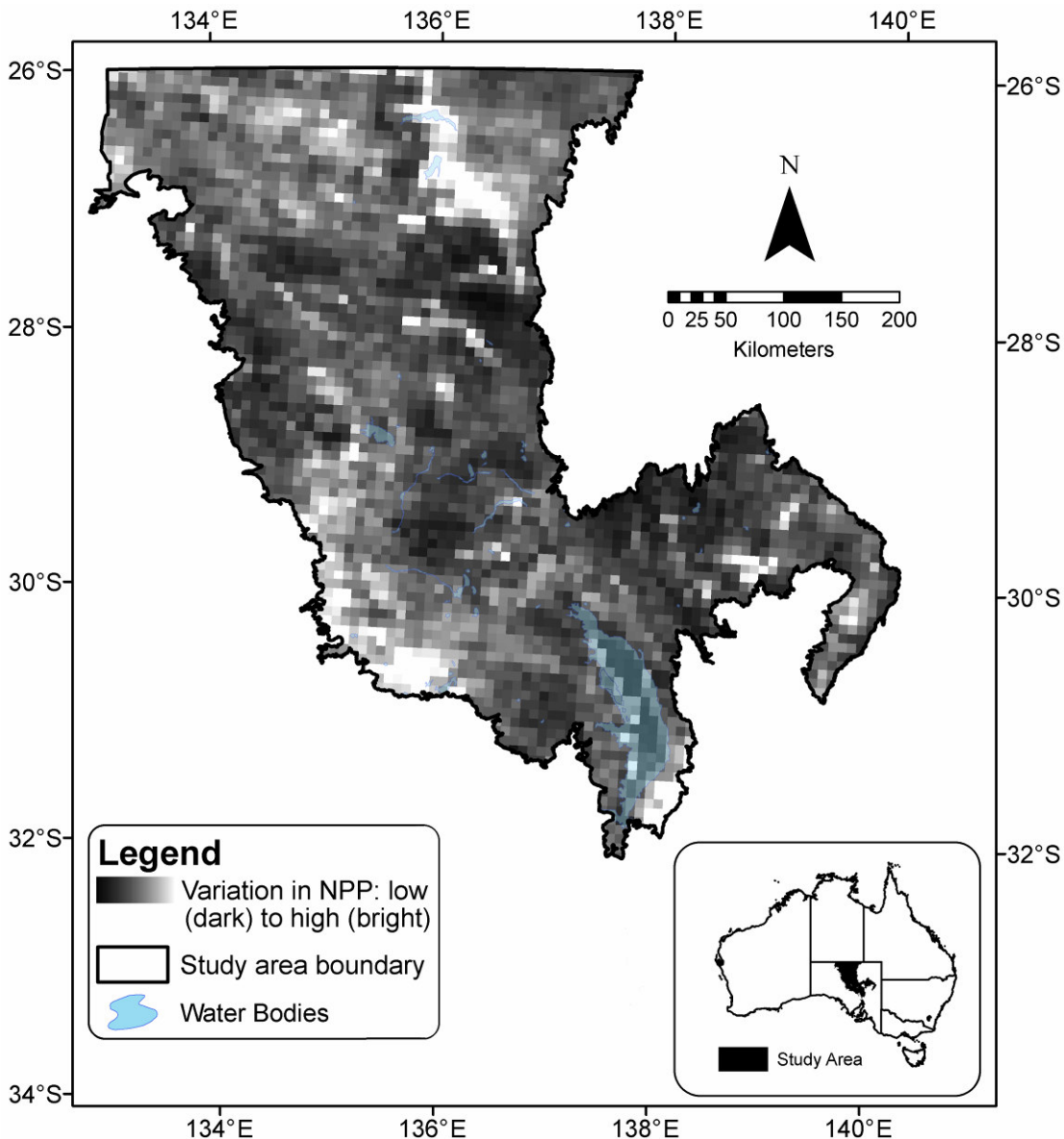


Figure 32. Index of variation in annual net primary production (std-NPP), 1990 – 2003, derived from 14 annual Σ NDVI images. Resolution is 8 km.

Average annual climatically distributed RUE (mean-CRUE)

The index mean-CRUE, produced from the combination of annual NPP and annual rainfall, is presented in Figure 33. The area of high mean-CRUE in the north-west corresponds closely to the eastern end of the Pedirka IBRA sub-region, and the ephemeral Hamilton Creek; the area in the north-east of the study area, in the eastern Macumba IBRA sub-region corresponds to the ephemeral Oogawa and Ambullinna Waterholes, and Alkaowra Flood Flats; and the area in the middle of the study area (135.5° E, 29° S) corresponds closely to the Warriner IBRA sub-region, a region of vegetated dunes.

The area of high mean-CRUE in the far east of the study area (138.5° E, 29° S) is the result of an apparent anomaly in the rainfall data in 1994 and 1995. The SILO rainfall data for these two years records almost no rainfall in a circular zone just north and east of the study area, centred around 139° E, 27° S, and just entering the study area. However, during these two years NPP in this region was not reduced from its low but consistent level. Therefore, it seems that the region of low rainfall is an artefact of the data generation method rather than a real climatic event.

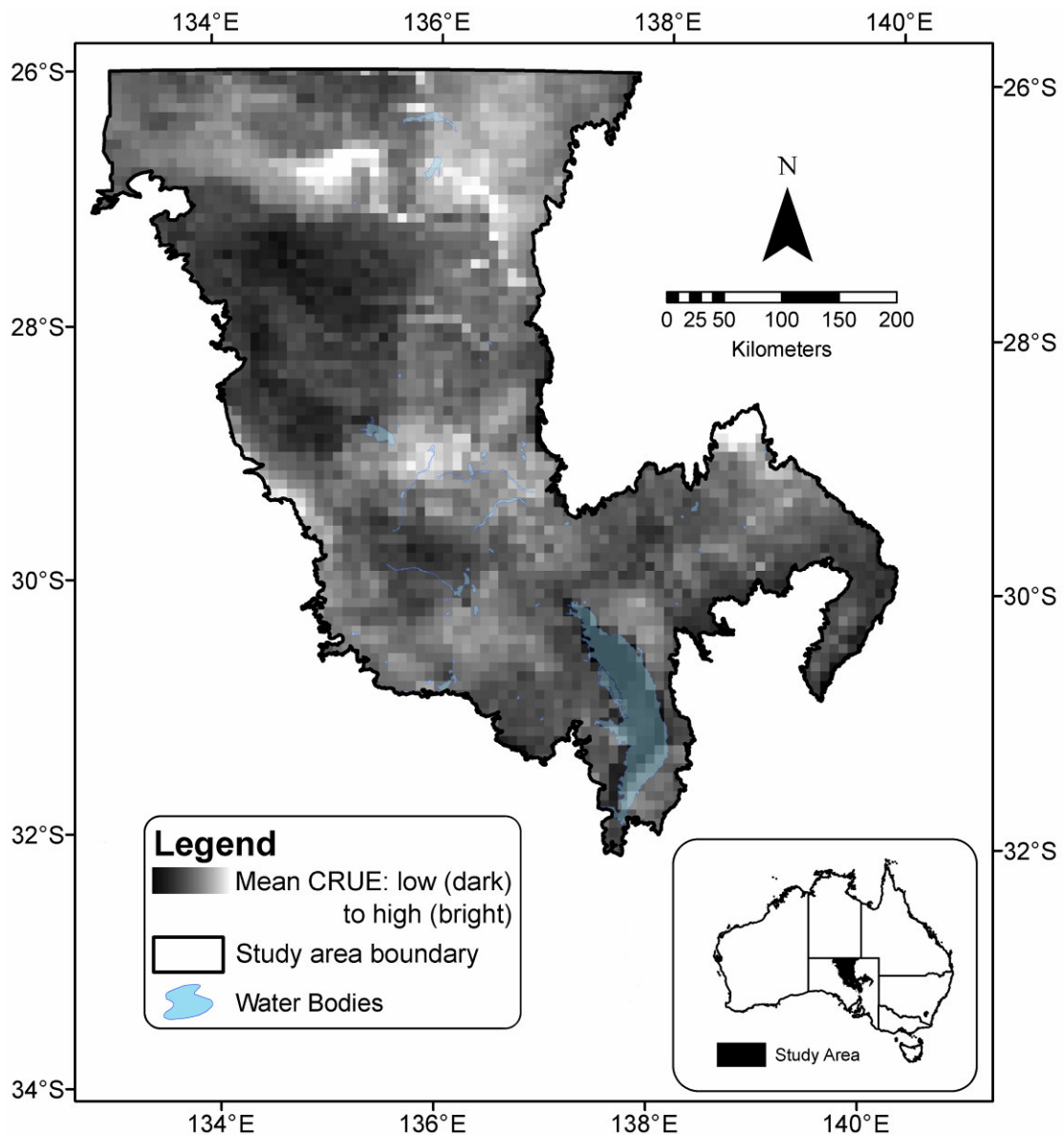


Figure 33. Index of average annual climatically distributed rainfall use efficiency (mean-CRUE), 1990 – 2003, derived from 14 annual CRUE images. Resolution is 8 km.

The rainfall data are interpolated from point climate stations ranging from a few to several hundred kilometres away: because of the circular shape of the rainfall anomaly, and the lack of any corresponding decrease in NPP, we assume the anomaly is a result of locally unusually low rainfall or error at one climate station, and of the interpolation process.

Variation in annual climatically distributed RUE (std-CRUE)

The index of variation in CRUE, or std-CRUE is presented in Figure 34. The area of high std-CRUE in the middle-north of the study area (135° E, 27° S) corresponds with the eastern end of the Pedirka IBRA sub-region, specifically the ephemeral Hamilton Creek.

The area of high std-CRUE in the far east of the study area (138.5° E, 29° S) is a result of the previously mentioned anomaly in the rainfall data.

Average annual topographically scaled RUE (mean-TRUE)

The index of mean-TRUE, produced from the combination of annual NPP and topographically re-distributed rainfall is presented in Figure 35. There is an area of high mean-TRUE in the north-west of the study area, corresponding to the eastern end of the Pedirka IBRA sub-region, and the ephemeral Hamilton Creek. The band of generally high mean-TRUE in the middle of the study area (136° E - 137° E, 27° S – 29.5° S) does not seem to relate to any specific topographic features, except for the Neales (Nappamurra) River (136° E, 28° S). The area contains both hills and valley bottoms, and spans IBRA sub-regions. The one common feature of this bright central region is that it is toward the lower end of the catchment. However, the area around Lake Torrens in the south of the study area is also low in the catchment and does not have a similarly high mean-TRUE.

The area of high mean-TRUE in the far east of the study area (138.5° E, 29° S) is a result of the previously mentioned anomaly in the rainfall data.

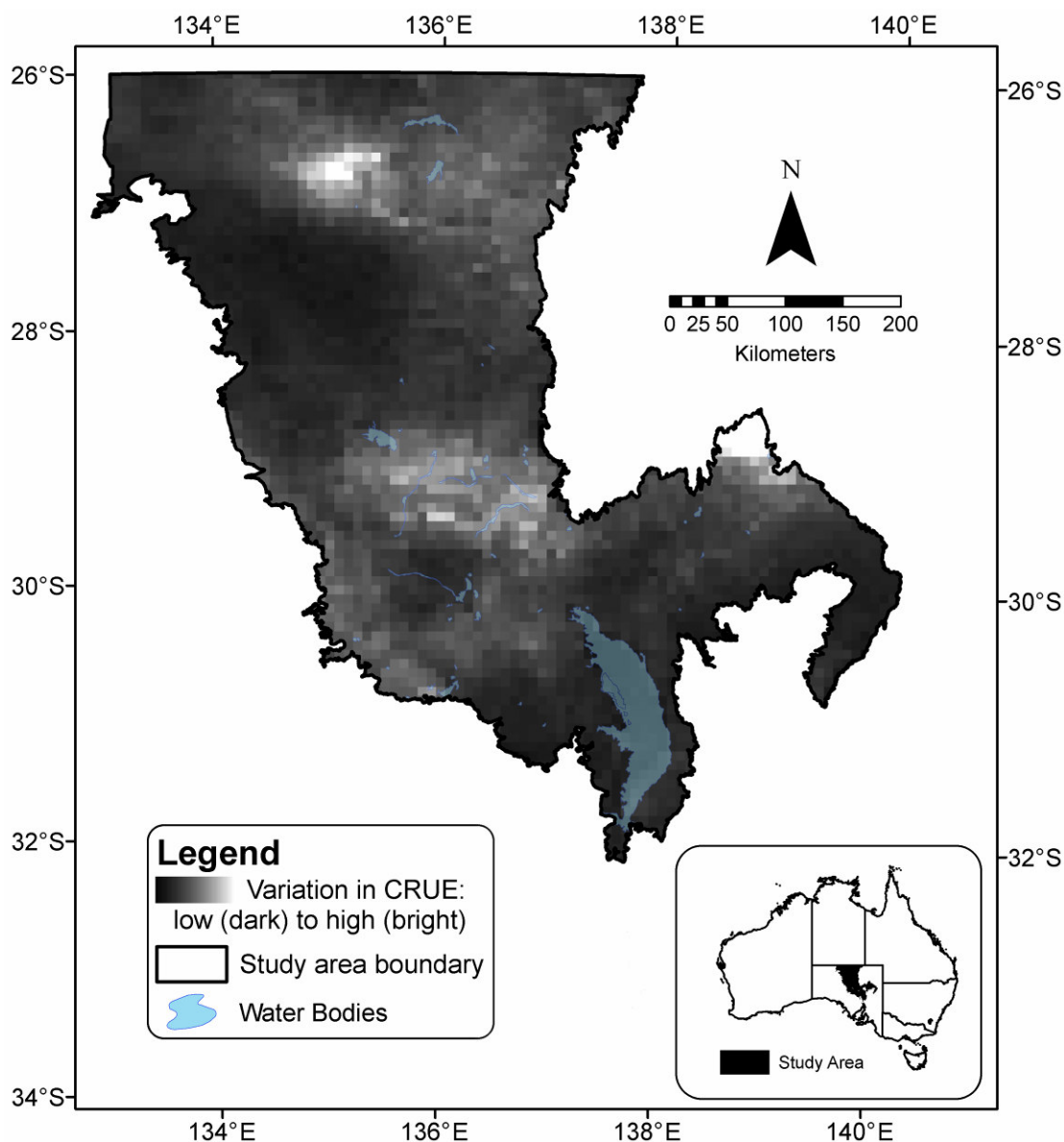


Figure 34. Index of variation in annual climatically distributed rainfall use efficiency (std-CRUE), 1990 – 2003, derived from 14 annual CRUE images. Resolution is 8 km.

Variation in annual topographically scaled RUE (std-TRUE)

The index of variation in annual TRUE, or std-TRUE, is presented in Figure 36. The area of high std-TRUE in the north of the study area corresponds to the eastern end of the Pedirka IBRA sub-region, and the ephemeral Hamilton Creek. The area of variably high std-TRUE in the lower middle of the study area covers parts of the Oodnadatta and Warriner IBRA sub-regions, and does not appear strongly related to topographic features.

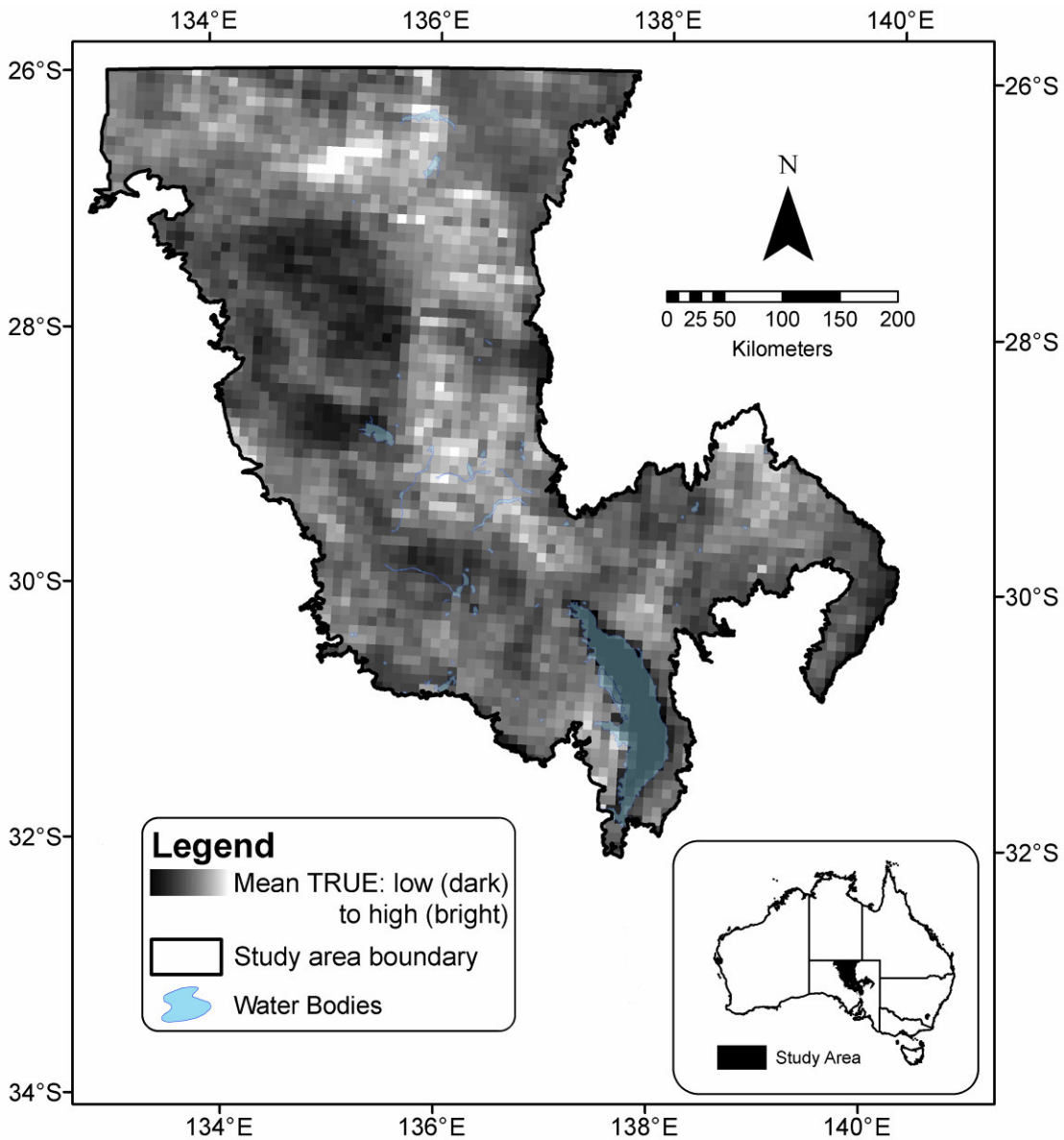


Figure 35. Index of average annual topographically scaled rainfall use efficiency (mean-TRUE), 1990 – 2003, derived from 14 annual TRUE images. Resolution is 8 km.

The area of high std-TRUE in the far east of the study area (138.5° E, 29° S) is a result of the previously mentioned anomaly in the rainfall data.

Evaluation of Surrogate 2

The correlation between each potential biodiversity stress index and all diversity types for both conventional vegetation surveys is presented in Table 12.

Table 12. Coefficient of determination (R^2): woody perennial α -, β - and γ -diversity and potential biodiversity stress indices

Biodiversity Stress index	Biological Survey of South Australia			South Australian Pastoral Lease Assessment		
	α	β	γ	α	β	γ
mean-NPP	0.24 (p 0.5)	0.00	0.01	0.01	0.00	0.00
mean-CRUE	0.23 (p 0.5)	-0.07 [‡] (p 0.5)	-0.05 [‡]	-0.24 [‡] (p 0.5)	0.00	0.00
mean-TRUE	0.35 (p 0.1)	0.05	0.08 (p 0.5)	-0.30 [‡] (p 0.1)	-0.03 [‡]	-0.05 [‡]
std-NPP	<i>0.19 (p 0.5)</i>	<i>0.18 (p 0.5)</i>	<i>0.21 (p 0.5)</i>	0.00	0.00	0.00
std-CRUE	0.08 (p 0.5)	-0.01 [‡]	-0.01 [‡]	-0.33[‡] (p 0.1)	0.03	0.06 (p 0.5)
std-TRUE	0.07 (p 0.5)	0.01	0.01 [‡]	-0.40[‡] (p 0.05)	0.06 (p 0.5)	0.03

[‡]Although coefficient of determination is always positive, we use sign to denote the direction of the relationship: minus sign indicates a negative slope.

***Bold** indicates the direction of the relationship is expected from the literature; *italics* indicates the direction of the relationship is the opposite to that expected from the literature; plain text indicates the relationship is too weak for interpretation.

There is no clear relationship between β - or γ -diversity and the indices of biodiversity stress. The correlation between β - and γ -diversity and the biodiversity stress indices is negligible ($R^2 \leq 0.07$) in all but two instances in which it is very-poor; std-NPP and BSSA β -diversity ($R^2 = 0.18$) and γ -diversity ($R^2 = 0.21$).

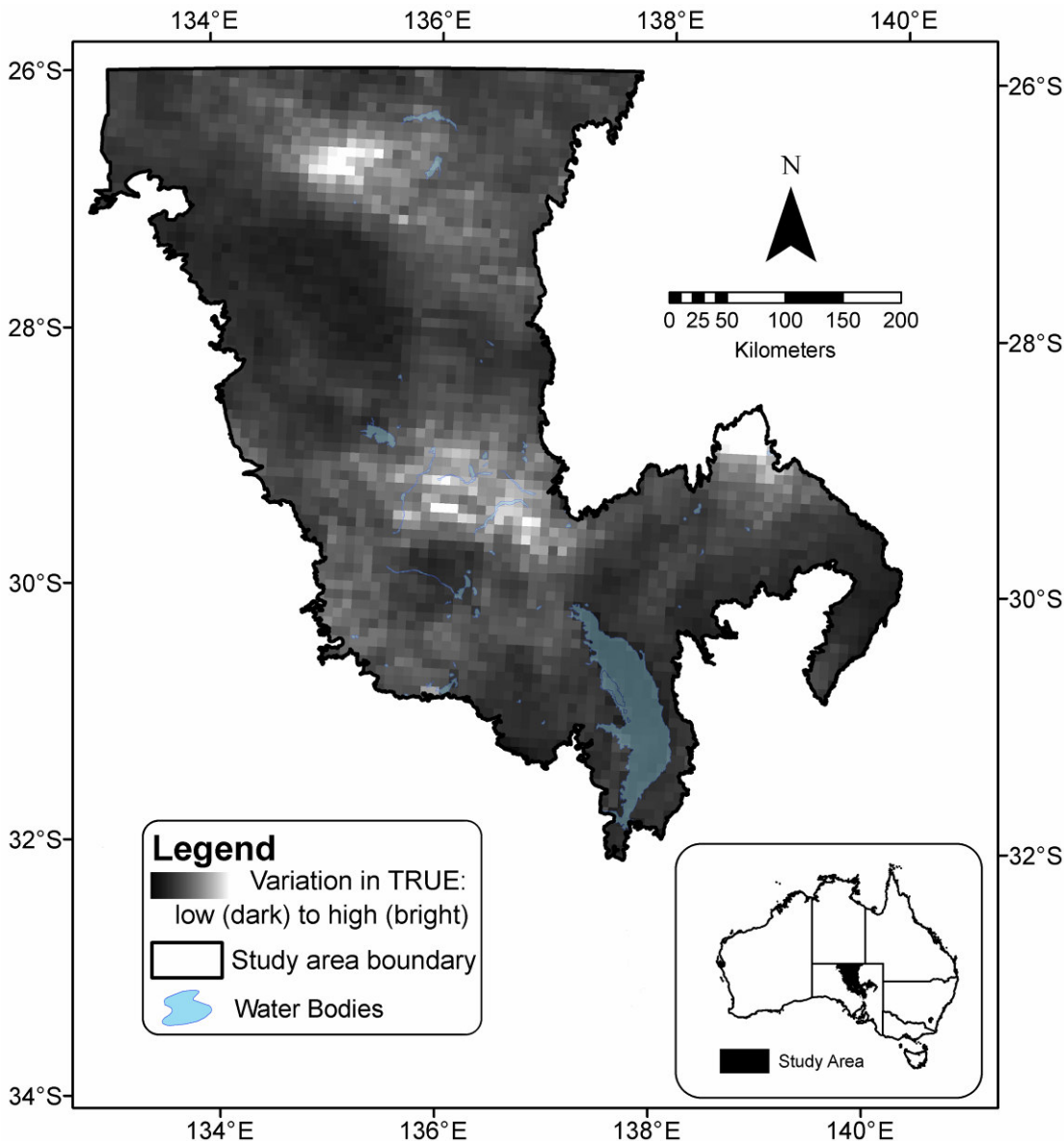


Figure 36. Index of variation in annual topographically scaled rainfall use efficiency (std-TRUE), 1990 – 2003, derived from 14 annual TRUE images. Resolution is 8 km.

While the relationships between α -diversity and biodiversity stress indices are slightly stronger, interpretation is not simple. There is a weak correlation between mean-NPP and BSSA α -diversity ($R^2 = 0.24$), but not with SAPLA α -diversity ($R^2 = 0.01$). Likewise, there is a weak correlation between std-NPP and BSSA α -diversity ($R^2 = 0.19$), but not with SAPLA α -diversity ($R^2 = 0.00$). There are weak ($R^2 = 0.0.23$) to moderate ($R^2 = 0.35$) correlations between mean-CRUE or mean-TRUE and BSSA α -diversity respectively, and correlations of a similar magnitude, but with a negative correlation, between mean-CRUE or mean-TRUE and SAPLA α -diversity ($R^2 = 0.24$ and $R^2 = 0.30$ respectively). Conversely, while there is a negligible correlation ($R^2 \leq 0.08$) between std-

CRUE or std-TRUE and BSSA α -diversity, there is a moderate correlation with a negative correlation between std-CRUE or std-TRUE and SAPLA α -diversity ($R^2 = -0.33$ and $R^2 = -0.40$ respectively).

In most cases the index of topographically scaled rainfall use efficiency correlated more strongly with α -diversity than the index of climatically distributed rainfall use efficiency.

5.4 Discussion

We proposed two surrogates of biodiversity stress based on the causes of and pressures on biodiversity and validated these using an index of perennial vegetation species diversity. Surrogate 1 was based on the hypothesis that the difference between net primary production (NPP) and expected primary productivity (EPP) was an index of biodiversity stress. Surrogate 2 was based on the hypothesis that overgrazing decreases average NPP and rainfall use efficiency (RUE), and increases variation in NPP and RUE. Our validation is based on an index of α -, β - or γ -diversity and review of the literature which suggested that α - and γ -diversity decrease with increasing severity of grazing induced degradation.

Evaluation of the performance of Surrogate 1 is simple: our analysis found no relationship between Surrogate 1 and woody perennial vegetation α -, β - or γ -diversity extracted from either of the conventional vegetation surveys. Evaluation of Surrogate 2 is more difficult: We found no consistent relationship between any form of species-diversity derived from either conventional vegetation survey and any of the potential image indices of biodiversity pressure. Some of our results supported the hypothesis that overgrazing decreases average NPP and RUE: BSSA α -diversity decreased with decreasing average NPP, CRUE and TRUE. However, some of our other results contradicted this hypothesis: SAPLA α -diversity declined with increasing average CRUE and TRUE. Likewise, the hypothesis that overgrazing increases variation in NPP and RUE is supported by some of our results and contradicted by others: SAPLA α -diversity decreased with increasing temporal variation in CRUE and TRUE, as expected; while contrary to expectations BSSA α -, β - and γ -diversity all increased with increasing temporal variation in NPP. Finally, none of our results supported the most important part of our hypothesis; that the proposed indices of biodiversity pressure would co-vary with woody perennial γ -diversity.

The lack of detected relationship between Surrogate 1 and vegetation species diversity may be due to either of, or a combination of two factors; data limitations obfuscating the relationship, or an un-accounted for source of variation preventing the water-energy hypothesis from being the primary determinant of diversity in the study area. Likewise, the complex relationship of Surrogate 2 to vegetation species diversity may be due to one of two factors; the same data limitations suffered by Surrogate 1, or the difference in site placement of the two vegetation surveys from which the species diversity index was extracted. We will deal with the factors unique to Surrogates 1 and 2 first, and then discuss the common data limitations.

Considering Surrogate 1 first; if another factor is similarly or more limiting to primary production than the balance between water and energy availability, then we would expect the relationship between Surrogate 1 and vegetation species diversity to be weak or non-existent. We suggest that the variation in soils in the study area is such a factor.

The extreme age of soils and the internal drainage of the study area combine to provide serious impediments to plant growth. The combination of these two factors means that soils in the upper parts of catchments are heavily leached and contain only very small amounts of soluble salts, while the lower parts of catchments are heavily salinised to the point of forming salt-encrusted pans (Hubble *et al.* 1983). In addition to these general problems, the specific soils covering the study area present their own unique obstacles to plant growth: the deep sands suffer gross deficiencies of both major and minor elements; the calcareous soils are strongly alkaline, with typical pH > 9 and sometimes suffering zinc, iron or copper deficiencies; and most of the texture-contrast soils are low in phosphorus and many are both saline and sodic (Northcote and Skene 1972; Hubble *et al.* 1983). Hence, the soils of the study area present many challenges to plant growth. However, the study area is relatively vegetated, considering its aridity, and each soil type is characterised by a specialised vegetation community adapted to dealing with the specific challenges presented by that soil (Specht and Specht 1999).

Secondly, the complex relationship of Surrogate 2 to vegetation species diversity may result from the differences in survey design, and hence site placement. To clarify the following discussion we will briefly reiterate the differences in the two vegetation survey

methodologies. Firstly, the surveys differ in intent and hence site placement: the BSSA is an inventory survey, and where possible sites are placed in locations remote from water, to avoid regions more heavily grazed by domestic stock; the SAPLA is a pastoral range condition monitoring survey, all sites are placed within the piosphere to measure the magnitude of grazing pressure. Secondly, surveyor expertise differs: the BSSA employs botanical experts, while the SAPLA employs range monitoring professionals with some botanical training.

All SAPLA sites are within the piosphere, and therefore grazed to some extent. Thus, the intermediate disturbance hypothesis (Connell 1978; Menge and Sutherland 1987) may explain the relationship between SAPLA α -diversity and average rainfall use efficiency. Under this hypothesis, moderate degradation would reduce average rainfall use efficiency and increase α -diversity, as compared to low degradation. Additionally, according to our hypothesis, moderate degradation would increase variation in rainfall use efficiency and decrease α -diversity, as compared to low degradation.

Alternatively, the BSSA is an inventory survey; sites are placed with the intent of recording as many present species as possible. Hence, sites are generally placed in areas of good condition remote from stock watering points. However, some sites must necessarily be placed close to water, when the landscape type is by its very nature associated with close proximity to water, or when the only accessible examples of a landscape type are close to water. Thus we expect that BSSA sites might cover a wider range of grazing conditions than SAPLA sites, from no grazing to heavily grazed. If this is the case, and we do not invoke the intermediate disturbance hypothesis, then our original arguments would explain the relationship between BSSA α -diversity, average net primary production and average rainfall use efficiency.

However, we find these explanations unsatisfying. We can find no difference in vegetation survey methodologies which would allow the invocation of the intermediate disturbance hypothesis for one survey and not the other. Neither can we find an adequate explanation for the increase in variation in net primary production with increasing BSSA α -, β - and γ -diversity, which is contrary to our predictions. Ultimately all of the Surrogate 2

correlations are weak, and the differential response of the BSSA and SAPLA α -diversity casts doubt on the significance of any of our relationships.

We feel that the confusing and weak relationships derived in the validation of Surrogates 1 and 2 are the result of two factors. The first and more serious is the interpolation of the rainfall and evapotranspiration surfaces used in the analyses. The second is that the NOAA NDVI data, from which net primary production is calculated, is of a relatively coarse spatial resolution in relation to the scale of variation in species diversity and grazing management.

The rainfall surface is, as previously mentioned, interpolated from a minimum of 30 climate stations, only 22 of which are located inside the study area. Thus, the rainfall, and hence evapotranspiration, at any given point is interpolated from data collected at stations ranging from a few kilometres to several hundred kilometres away. As a result of this interpolation from an originally low data density, the rainfall surfaces do not truly represent any of the localised variation in rainfall. The study area does not experience reliable seasonal rainfall, and localised thunderstorm activity can provide a significant boost to annual rainfall in a small area. Likewise, orographic precipitation and rain-shadowing are not represented in the interpolated rainfall, and could both influence rainfall in the study area. Additionally, interpolation of rainfall from few climate stations will mean that a localised extreme weather event over one of the climate stations can significantly affect a large area of the rainfall surface. We believe such a localised event caused a large circular area of extremely low rainfall, centred at 138.5° E, 29° S, in two years rainfall surfaces. Such a severe absence of rainfall should have caused a visible reduction of net primary production over a similar area, however none was visible. Thus, while the SILO rainfall and evapotranspiration data (Jeffrey *et al.* 2001) is the best available for the study area, it does not accurately reflect rainfall throughout our study area.

The NOAA NDVI data are likewise the best existing data of its type for the study area and period. However, the smallest element of the NOAA NDVI data, the pixel, is 8 x 8 km (64 km²). This contrasts strongly with the scale of our species diversity measurements: BSSA sites are 100 x 100 m (0.01 km²); SAPLA sites range from 100 to 200 m radius (0.03 – 0.13 km²). Thus the vegetation survey sites cover a very small proportion of a single

NDVI pixel, and therefore the condition of either BSSA or SAPLA sites may not be representative of the majority of the pixel area.

The NDVI pixel area is a good match to the area typically utilised by cattle, but not to the area utilised by sheep. Cattle grazing is predominant in the north of the study area, and cattle are expected to move as little as 4 km from water when forage is plentiful, and as much as 20 km from water when forage is very scarce or in winter (Hodder and Low 1978; Low *et al.* 1978). Given that the study area is amongst the most arid of Australia's rangelands, we therefore expect that forage will rarely be plentiful and that cattle will usually utilise an area as large, or larger than, one NDVI pixel around a watering point. Sheep, the grazing of which predominates in the south of the study area, utilise a smaller portion of the landscape. In hot, dry conditions, and especially in chenopod shrublands sheep must remain close to water, and forage range is reduced to 3 km (Lange 1969; Lynch 1974; Squires 1976; Squires 1978; Wilson and Graetz 1980). However, in cooler or wetter weather sheep may graze further from watering points (Osborn *et al.* 1932; Wilson 1978). We expect that the majority of grazing induced degradation will occur in hotter, dryer parts of the year when the sheep grazing is focused in a smaller area. Therefore, the area degraded by sheep grazing will be less than half of the area of one NDVI pixel, while the rest of the pixel may cover non-grazed landscape. We would expect this mixture of grazed and non-grazed landscape to reduce the impact of grazing induced degradation on NDVI in the southern portion of the study area dominated by sheep grazing.

5.4.1 Summary

To summarise, we proposed two surrogates of biodiversity stress: Surrogate 1, based on the well supported Productivity Theory (O'Brien 1993; Whittaker *et al.* 2003; Cardinale *et al.* 2006) and the difference between indices of net and expected primary production; and Surrogate 2, based on average and variation in net primary production and rainfall use efficiency. We validated Surrogates 1 and 2 against an index of woody perennial vegetation α -, β - and γ -diversity, assuming that prolonged biodiversity stress would cause low vegetation species diversity.

We have thoroughly tested Surrogates 1 and 2 in the South Australian rangelands with the best available remotely sensed data and climate data for the study area and period. Our

analysis did not reveal a convincing link between either Surrogate 1 or 2 and vegetation species diversity. However, we feel that the analysis was hampered to a large degree by the rainfall data, which is interpolated from climate stations up to several hundred kilometres away. Additionally, the relatively coarse scale of the NOAA NDVI data, and the fine scale over which sheep graze may have hampered detection of the impact of sheep grazing. Finally, analysis by IBRA sub-regions accounted for some, but not all, of the influence of soil type on vegetation community. Differing amounts of soil variation in IBRA sub-regions may have confounded evaluation of Surrogate 1 by providing a source of variation in species diversity as or greater than that caused by primary productivity.

It is difficult to draw any conclusions regarding rainfall use efficiency, due to the limitations of the rainfall data. However, the NOAA NDVI data does not impose similar limitations in drawing conclusions about net primary productivity. The area utilised around water points by cattle grazing is a good match with the scale of the NDVI imagery, and sheep grazing affects a smaller but still substantial portion of an NDVI pixel. Therefore, it is interesting that we did not find the expected link between grazing induced degradation, decreased average net primary production and increased temporal variation in net primary production. It appears that this link, found elsewhere in Australia and other parts of the world, is substantially weaker or does not exist in the study area.

This analysis has highlighted the lack of high resolution climate data in the Australian rangelands. This gross deficiency must be addressed before many forms of environmental modelling can assist in range management at any but the broadest of scales; including understanding and mitigating the effects of climate change. We recommend that the resolution of climate data in the rangelands should be improved, to better reflect meso-scale variation.

5.5 References

Andres, L., W. A. Salas and D. Skole (1994) Fourier analysis of multi-temporal AVHRR data applied to a land cover classification. *International Journal of Remote Sensing* **15**(5): 1115 - 1121.

Asrar, G., E. Kanemasu, R. Jackson and P. Printer (1985) Estimation of total above-ground phytomass production using remotely sensed data. *Remote Sensing of Environment* **17**: 211-220.

Badgley, C. and D. L. Fox (2000) Ecological biogeography of North America mammals: species density and ecological structure in relation to environmental gradients. *Journal of Biogeography* **27**: 1437-1467.

- Box, E., B. Holben and V. Kalb (1989) Accuracy of the AVHRR Vegetation Index as a predictor of biomass, primary productivity and net CO₂ flux. *Vegetatio* **80**: 71-89.
- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran and C. Jouseau (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**: 989-992.
- Clarke, K. D., M. M. Lewis and B. Ostendorf (submitted) Additive partitioning of rarefaction curves: removing the influence of sampling on species-diversity in vegetation surveys. *Ecological Indicators*?(?): ?
- Connell, J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science* **199**(4335): 1302-1310.
- Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. O'Neill, J. Paruelo, R. Raskin, P. C. Sutton and M. van den Belt (1997) The value of the world's ecosystem services and natural capital. *Nature* **387**: 253-260.
- Currie, D. J. (1991) Energy and large-scale patterns of animal-species and plant-species richness. *American Naturalist* **137**(1): 27-49.
- Currie, D. J. and V. Paquin (1987) Large-scale biogeographical patterns of species richness of trees. *Nature* **329**: 326-331.
- Gallant, J. C. and T. I. Dowling (2003) A multiresolution index of valley bottom flatness for mapping depositional areas. *Water Resources Research* **39**(12).
- Hawkins, B. A. and E. E. Porter (2003) Does herbivore diversity depend on plant diversity? The case of California butterflies. *American Naturalist* **161**(1): 40-49.
- Hawkins, B. A. and E. E. Porter (2003) Water-energy balance and the geographic pattern of species richness of western Palearctic butterflies. *Ecological Entomology* **28**: 678-686.
- Hawkins, B. A., E. E. Porter and J. A. F. Diniz-Filho (2003) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology* **84**(6): 1608-1623.
- Hobbins, M. T., J. A. Ramirez, T. C. Brown and L. H. J. M. Claessens (2001) The complementary relationship in estimation of regional evapotranspiration: The Complementary Relationship Areal Evapotranspiration and Advection-Aridity models. *Water Resources Research* **37**(5): 1367-1387.
- Hodder, R. M. and W. A. Low (1978) Grazing distribution of free-ranging cattle at three sites in the Alice Springs district, central Australia. *The Australian Rangeland Journal* **1**: 95-105.
- Holben, B. N. (1986) Characteristics of maximum-value composite images from temporal AVHRR data. *International Journal of Remote Sensing* **7**(11): 1417-1434.
- Holm, A. M., I. W. Watson, W. A. Loneragan and M. A. Adams (2003) Loss of patch-scale heterogeneity on primary productivity and rainfall-use efficiency in Western Australia. *Basic and Applied Ecology* **4**: 569-578.
- Hubble, G. D., R. F. Isbell and K. H. Northcote (1983) Features of Australian soils. *Soils: an Australian viewpoint*, CSIRO: Melbourne / Academic Press: London.
- Huete, A. R. and R. Jackson (1987) Suitability of spectral indices for evaluating vegetation characteristics on arid rangelands. *Remote Sensing of Environment* **23**: 213-232.
- Jeffrey, S. J., J. O. Carter, K. M. Moodie and A. R. Beswick (2001) Using spatial interpolation to construct a comprehensive archive of Australian climate data. *Environmental Modelling and Software* **16**(4): 309-330.
- Lambin, E. F. and A. H. Strahler (1994) Change-vector analysis in multitemporal space: a tool to detect and categorize land-cover change processes using high temporal-resolution satellite data. *Remote Sensing of Environment* **48**(2): 231-244.
- Lange, R. T. (1969) The piosphere: sheep track and dung patterns. *Journal of Range Management* **22**: 396-400.
- Low, W. A., R. M. Hodder and D. E. Abel (1978) Watering behaviour of British breed cattle in central Australia. *Studies of the Australian Arid Zone III. Water in rangelands*. K. M. W. Howes. Perth, Australia, CSIRO.

- Lynch, J. J. (1974) Merino sheep: some factors affecting their distribution in very large paddocks. The behaviour of Ungulates and its relation to management. V. Geist and F. Walther. Morges, Switzerland, International union for the conservation of nature new series.
- Menge, B. A. and J. P. Sutherland (1987) Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment doi:10.1086/284741. *The American Naturalist* **130**(5): 730.
- Morton, F. I. (1983) Operational estimates of areal evapotranspiration and their significance to the science and practice of hydrology. *Journal of Hydrology* **66**: 1-76.
- Northcote, K. H. and J. K. M. Skene (1972) Australian soils with saline and sodic properties. CSIRO Soil Publications.
- O'Brien, E. (2006) Biological relativity to water-energy dynamics. *Journal of Biogeography* **33**: 1868-1888.
- O'Brien, E. M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of Southern Africa's woody flora. *Journal of Biogeography* **20**: 181-198.
- O'Brien, E. M. (1998) Water-energy dynamics, climate, and prediction of woody plants species richness: an interim general model. *Journal of Biogeography* **25**: 379-398.
- Osborn, T. G., J. G. Wood and T. B. Paltridge (1932) On the growth and reaction to grazing of the perennial saltbush *Atriplex vesicarium*: an ecological study of the biotic factor. *Proceedings of the Linnean Society of New South Wales* **57**: 377-402.
- Rasmussen, M. S. (1998) Developing simple, operational, consistent NDVI-vegetation models by applying environmental and climatic information: Part I. Assessment of net primary production. *International Journal of Remote Sensing* **19**(1): 97-117.
- Reed, B. C., T. R. Loveland and L. L. Tieszen (1996) An approach for using AVHRR data to monitor U.S. Great Plains grasslands. *Geocarto International* **11**(3): 13-22.
- Ricotta, C., G. Avena and A. De Palma (1999) Mapping and monitoring net primary productivity with AVHRR NDVI time-series: statistical equivalence of cumulative vegetation indices. *Isprs Journal of Photogrammetry and Remote Sensing* **54**(5-6): 325-331.
- Sarkar, S. (2002) Defining "Biodiversity"; Assessing Biodiversity. *The Monist* **85**(1): 131-155.
- Smyth, A. K., V. H. Chewings, G. N. Bastin, S. Ferrier, G. Manion and B. Clifford (2004) Integrating historical datasets to prioritise areas for biodiversity monitoring? Australian Rangelands Society 13th Biennial Conference: "Living in the outback", Alice Springs, Northern Territory.
- Specht, R. L. and A. Specht (1999) Australian plant communities: dynamics of structure, growth and biodiversity, Kyodo, Singapore.
- Squires, V. R. (1976) Walking, watering and grazing behaviours of Merino Sheep on two semi-arid rangelands in south-west New South Wales. *The Australian Rangeland Journal* **1**: 13-23.
- Squires, V. R. (1978) Distance trailed to water and livestock response. *Proceedings of the First International Rangelands Congress, Denver, USA, Society for Range Management*.
- Tucker, C., B. Holben, J. Elgin and J. McMurtrey (1981) Remote Sensing of Total Dry-Matter Accumulation in Winter Wheat. *Remote Sensing of Environment* **11**: 171-189.
- Tucker, C. and P. J. Sellers (1986) Satellite remote sensing of primary production. *Int. J. Remote Sensing* **7**(11): 1395-1416.
- Whittaker, R. J., K. J. Willis and R. Field (2003) Climatic-energetic explanations of diversity: a macroscopic perspective. *Macroecology: concepts and consequences*. T. M. Blackburn and K. J. Gaston. Oxford, Blackwell Science: 107-129.
- Wilson, A. D. (1978) Water requirements of sheep. *Studies of the Australian Arid Zone: Water in Rangelands*. K. M. W. Howes. Perth, Australia, CSIRO. **3**: 178-189.

Wilson, A. D. and R. D. Graetz (1980) Cattle and sheep production on *Atriplex vesicaria* (saltbush) community. *Australian Journal of Agricultural Research* **31**: 369-378.

Chapter 6: Discussion and conclusions

6.1 Introduction

The overarching goal of this thesis was to contribute to the development of better tools for the monitoring of biodiversity in the Australian rangelands. Specifically, this work aimed to extract indices capable of measuring and/or monitoring biodiversity from vegetation quadrat survey data and remotely sensed data over the Australian rangelands.

This thesis has contributed significantly to this goal by providing new tools for biodiversity measurement, including a method for extracting α -, β - and γ -diversity from vegetation quadrat survey data and removing the influence of sampling effort, and two remote sensing based indices of pressure on biodiversity. Additionally, this work has contributed to the research goal by raising awareness of the limitations of vegetation quadrat surveys and hence accelerating the development of more robust and meaningful analyses of vegetation, and by identifying limitations in climate monitoring data, which if addressed may allow for better modelling of biodiversity in the arid rangelands.

Our analysis of false-negative errors in conventional vegetation survey data provided an important cautionary lesson on the limitations of such data in the study area (Chapter 3). Significant rates of false-negative errors remained, even after limiting analysis to the most persistent, most detectable species. Therefore, any biodiversity metric derived from such survey data collected in the study area must account for the expected false-negative errors or be seriously flawed.

In Chapter 4, a regional index of vegetation α -, β - and γ -species diversity was derived from extensive vegetation quadrat survey data, as a surrogate for biodiversity. This index accounted for regional differences in sampling effort, and the γ -diversity index is theoretically insensitive to false-negative errors.

Finally, two spatially distributed surrogates of biodiversity stress, based on the causes of and pressures on biodiversity, were derived from the best available remotely sensed and climate data (Chapter 5). These surrogates were thoroughly tested against the index of α -, β - and γ -diversity, and no convincing link was found between either surrogate and

vegetation species diversity. However, this analysis was probably limited by the available climate data.

Thus, this thesis has addressed the original goal identified in Chapter 1. The specific contributions to knowledge made by each of the research chapters is discussed in Section 2; the broader implications of the research findings, and the factors which limit the extent to which the findings may be generalised are discussed in Section 3.

6.2 Summary of specific contributions to knowledge

6.2.1 False-negative errors in a survey of vegetation species

The Biological Survey of South Australia (BSSA) was identified as the best available biodiversity survey in the study region. This prompted an evaluation of the BSSA data to determine their quality and potential to supply a ground based biodiversity indicator for comparison with remotely sensed surrogates of biodiversity. This led to the analysis in Chapter 3, the major aim of which was to conservatively estimate false-negative error rates of the perennial vegetation species data collected by the BSSA. It was hoped that quantification of false-negative error rates would facilitate the development of corrective measures, and therefore the derivation of more meaningful information from the BSSA data.

The analysis was performed on data collected from four BSSA sites visited twice yearly for eight years. Even after limiting the study to the most easily-detected perennial vegetation species, and controlling for observer skill, we revealed frequent false-negative errors by all surveyors, at all sites, for all species examined. Thus, we demonstrated in the study area that even highly detectable vegetation species often have detection probabilities significantly less than one.

In addition to the BSSA, there are other broad scale vegetation surveys in the region, such as the South Australian Pastoral Lease Assessment (SAPLA), that generate vegetation data which may be used for similar purposes, and which may also suffer from false-negative errors. An evaluation of the differences between the BSSA and the SAPLA led us to expect higher rates of false-negative errors in the SAPLA.

The problem of false negative errors in vegetation surveys has not featured prominently in the literature, unlike false negative errors in fauna surveys, which has received significant attention (see MacKenzie *et al.* 2002; Tyre *et al.* 2003; Gu and Swihart 2004; MacKenzie 2005; MacKenzie 2005). It appears that vegetation species are assumed to be highly or perfectly detected by conventional vegetation surveys. We have demonstrated that this assumption is not necessarily warranted, and would recommend that vegetation surveys adopt measures to gauge the detectability of species, and to correct for false-negative errors, as is already done in some fauna surveys.

Finally, for more mundane reasons we would also caution against the use of raw vegetation quadrat survey data to assess regional variation in biodiversity. The data collected by these surveys may not be representative without additional analysis, due to the small size of the quadrats in relation to the extensive scale of landscapes. Additionally, differences in sampling effort may confound regional measures which fail to account for the influences of sampling effort.

6.2.2 Additive partitioning of rarefaction curves species diversity surrogate

The aim of Chapter 4 was to develop a biodiversity metric free from the influence of sampling effort. The γ -diversity of woody-perennial vegetation was identified as an estimator-surrogate for biodiversity, and we hypothesised that rarefaction to a common sampling effort and extraction of α -, β - and γ -diversity through additive partitioning of species diversity would remove the influence of sampling effort.

The analysis demonstrated that rarefaction to a common sampling effort did not completely remove the influence of sampling effort. However, the influence of sampling effort on γ -diversity was predictable, and therefore it was possible to correct for the influence. Additionally, this index of woody perennial vegetation γ -diversity theoretically minimises the influence of false negative errors, especially for well-sampled regions.

While the index developed in Chapter 4 is specific to the study area, the method for creating the index is not. This method is transferable and can conceivably be employed to extract a sampling effort corrected measure of γ -diversity from any vegetation data obtained from site-based surveys following prescribed methodologies.

Furthermore, our work answers the call by Fleishman *et al.* (2006) to standardize measures of species richness for differences in survey effort. However we have demonstrated a significant point not previously reported in the literature, that rarefaction alone does not adequately control for the influence of sampling effort. If this relationship exists in other areas, then interpolation or extrapolation of rarefaction relationships, a common use of rarefaction, will produce erroneous results.

However, this woody perennial vegetation γ -diversity does not address the need for a spatially extensive, fine scale measure of biodiversity at the scale of the Australian rangelands. The aggregation of point data to large regions, a necessary part of this index, produces spatially coarse results.

6.2.3 Remotely sensed biodiversity stress surrogates

The major aim of Chapter 5 was to develop an index of pressure on biodiversity capable of covering the extensive Australian rangelands at a fine scale. We developed two indices of biodiversity stress based on the causes of and pressures on biodiversity, and produced from the best available remotely sensed and climatic data. Surrogate 1 was based on the supported Productivity Theory (O'Brien 1993; Whittaker *et al.* 2003; Cardinale *et al.* 2006) and the difference between indices of net and expected primary production; and Surrogate 2, based on average and variation in net primary production and rainfall use efficiency. We validated Surrogates 1 and 2 against the index of woody perennial vegetation α -, β - and γ -diversity developed in Chapter 4. The rationale of the validation was based on the literature which suggests that that α - and γ -diversity decrease with increasing severity of grazing induced degradation, the most prevalent source of biodiversity stress in the study area.

Surrogates 1 and 2 were thoroughly tested with the best available remotely sensed and climate data for the study area and period. There was no relationship between the first surrogate and woody perennial α -, β - or γ -diversity extracted from either the BSSA or the SAPLA data. The relationship of the second surrogate to the validation data was more complex. While some of the results supported the hypothesis that overgrazing decreases α -diversity and average NPP and RUE, other results did not. Importantly, none of our results supported the most important part of our hypothesis; that the proposed indices of

biodiversity pressure would co-vary with woody perennial γ -diversity. Thus, the analysis did not reveal a convincing link between either Surrogate 1 or 2 and vegetation species diversity. However, the analysis was hampered to a large degree by the rainfall data, which is interpolated from climate stations up to several hundred kilometres away.

Additionally, while soil heterogeneity probably influences vegetation γ -diversity in the study area (Chapter 2, Section 2.1.4), we were not able to account for this effect. While the extent of the study area and the coarse scale of available soil maps precluded meaningful analysis, stratification of analysis by IBRA sub-region has accounted for the influence of soil heterogeneity on vegetation diversity as best as possible.

While the rainfall data limited the conclusions which could be drawn from these analyses, the satellite data was of sufficient quality to allow a robust examination of net primary production. Therefore, it is interesting that the analysis found no link between grazing induced degradation (measured by reduced α - or γ -diversity), decreased average net primary production and increased temporal variation in net primary production, contrary to expectations from the literature (see Le Houerou 1984; Snyman and Fouché 1993; Snyman 1997; Snyman 1998; Holm *et al.* 2002; Holm *et al.* 2003).

It is important to note that this climate data has been identified as a limiting factor by other research into biodiversity surrogates in the study area. Smyth *et al.* (2007) attributed the inability of their study to detect the expected relationship between vegetation species diversity (as a surrogate for biodiversity) and any of several potential biodiversity surrogates to the low resolution of the climate information in the study area.

6.3 Limitations to generalisation

While the work presented in this thesis made some important contributions to knowledge, the extent to which the conclusions of this work can be generalised are limited in scope. This section covers the specific limitations to generalisation of each of the research chapters.

6.3.1 False-negative errors in a survey of vegetation species

While the analysis of false-negative errors presented in Chapter 3 was performed on data collected by a specific vegetation quadrat survey, the Biological Survey of South Australia (BSSA), the methods used by this survey are typical of vegetation quadrat surveys. Therefore, the results of this analysis should be considered quite general: any vegetation survey may contain significant false-negative errors.

By critically evaluating the differences between the BSSA and another vegetation survey in the study area, the South Australian Pastoral Lease Assessment (SAPLA), it was possible to estimate the relative level of false-negative errors in the SAPLA. All differences between the BSSA and SAPLA lead to an expectation of higher rates of false-negative errors in the SAPLA.

Similar comparisons of the methodology of BSSA and other vegetation surveys of interest may help gauge the probable magnitude of false-negative errors in these other surveys. However, such comparisons should only be used as a guide, and should not replace a proper analysis of false-negative error rates.

6.3.2 Diversity indices

The diversity indices derived in Chapter 4 are specific to the study area, the taxa studied, and the vegetation survey method, and should not be applied outside of these bounds. However, the methods used to derive the diversity indices are wholly transferable, and provides a theoretically sound framework for deriving an indicator of α -, β - and γ -diversity which is comparable between regions of different sampling effort. This index can conceivably be generated from any vegetation quadrat survey data obtained within a prescribed methodology.

Through the use of additive partitioning, α -, β - and γ -diversity are expressed in the same units of species richness, and are therefore directly comparable. While the indices do not directly model and account for false-negative errors in the vegetation survey data, the methods used theoretically reduce these errors to varying degrees depending on the type of diversity. The γ -diversity index is theoretically insensitive to false-negative errors, and becomes even less sensitive at higher sampling efforts: a species must be recorded at only

one site in a region to contribute to γ -diversity. The index of α -diversity is theoretically vulnerable to the effect of false-negative errors. Although steps have been taken to minimise the number of false-negative errors contained in the vegetation survey data by limiting it to persistent perennial species, the analysis in Chapter 3 demonstrated that the data were still likely to contain significant rates of false-negative errors. Finally, β -diversity is generated from α -, and γ -diversity, through additive partitioning. Therefore, the sensitivity of β -diversity to false-negative errors will be an average of the sensitivity of α -, and γ -diversity: β -diversity is less sensitive than α -, and more sensitive than γ -diversity. As with γ -diversity, β -diversity will become less sensitive to false-negative errors at higher sampling efforts.

While the diversity indices derived in Chapter 4 are in the strictest sense specific to the taxon studied, this ignores the issue of surrogacy. This thesis has made the argument that one taxon may act as a surrogate for one or several other taxa (see Chapter 1, section 1 Motivation for the research; Chapter 3, section 1 Introduction; Chapter 4, section 1 Introduction), and the literature supports the use of the use of cross-taxon biodiversity surrogates (Rodrigues and Brooks 2007). In this sense, the diversity indices are not specific to the taxa studied, but may be considered indicative of overall taxon diversity.

6.3.3 Remotely sensed surrogates of biodiversity stress

The two surrogates derived in Chapter 5 are theoretically sound measures of grazing pressure on biodiversity, and are calculated from reliable, calibrated data. Therefore, it would be reasonable to compare surrogate values derived in the study area to values derived elsewhere with the same surrogate, from similar quality data; at the same scale; and if grazing pressure is a major source of biodiversity pressure. However, the limitations of the climate data used in the generation of the surrogates should be considered before such comparisons are made: the climate data are interpolated from climate stations up to several hundred kilometres away.

6.4 Broader implications

6.4.1 False-negative errors in a survey of vegetation species

The analysis presented in Chapter 3 has implications for vegetation surveying in general. The results suggest that a single site-survey may miss some of the most detectable vegetation species, and will probably miss an even greater proportion of the less detectable vegetation species. This finding has serious ramifications for the interpretation of vegetation survey data as well as those managing the surveys.

The data collected by quadrat vegetation surveys are often analysed on the assumption that they are presence-absence data (e.g. Brandle 1998; Robinson and Armstrong 1999; Brandle 2001; Smyth *et al.* 2007). However the work presented herein suggests that this assumption should be checked: these data may only be reasonably considered presence-only data. The use of an inappropriate analysis, the assumptions of which are not met, will produce erroneous results. Hence, this finding will guide the use of more appropriate analyses of vegetation survey data in the future, and a concurrent increase in the quality of knowledge extracted from vegetation surveys.

For managers of vegetation surveys the ramifications are methodological, as many vegetation surveys aim to collect presence-absence data. The high frequency of false-negative errors revealed by Chapter 3 demonstrates that data collected by the vegetation survey examined, and by extension the data collected by similar vegetation surveys, may only reasonably be considered presence-only data. If it is essential that the data collected by a survey can be considered presence-absence data, then simple alterations to that surveys methodology should allow for the measurement and correction of false-negative errors. In particular, we would recommend the same measures that are taken to counteract false-negative errors in fauna surveying: multiple sampling occasions at each site within a short time (MacKenzie *et al.* 2002; Gu and Swihart 2004), specifically three repeat visits (Tyre *et al.* 2003).

6.4.2 Diversity indices

Rarefaction is commonly used to standardise sampling effort for comparison between populations. The analysis in Chapter 4 revealed that, at least in the study area, rarefaction

did not wholly remove the influence of sampling effort on γ -diversity. While determining the cause of this relationship was beyond the scope of the work in Chapter 4, it was hypothesised that the non-detection errors identified in Chapter 3 may be the source of the relationship between rarefied γ -diversity and sampling effort. As a result of this work, rarefaction should not be used to control for differences in sampling effort without additional testing to determine whether there is any residual influence from sampling effort.

6.4.3 Remotely sensed surrogates of biodiversity stress

While there was no convincing link between the surrogates of biodiversity stress derived in Chapter 5 and woody perennial vegetation α -, β - or γ -diversity, the analysis was hampered by the low resolution of the available climate data. The surrogates are theoretically sound, and could be applied in any region in which the assumptions of their theoretical framework holds: arid to semi-arid rangelands.

While these surrogates need to be evaluated with adequate climate data, they offer great potential for biodiversity management in arid and semi-arid rangelands. The surrogates are derived from low-cost, extensive data, and are relatively easily produced. An adequate, extensive measure of biodiversity would provide important information, and assist in the management of rangelands for biodiversity conservation.

6.5 Recommendations and future research

The following areas of necessary research were identified through the work presented in this thesis.

- Assessment of the extent of false-negative errors in vegetation quadrat surveys is necessary to identify which surveys are more or less likely to contain significant false-negative errors, and therefore when to include false-negative error mitigation in survey methodology design.
- To minimise the impact of false-negative errors on vegetation quadrat surveys, error mitigation strategies need to be evaluated so that appropriate recommendations can be made.

- To allow the re-interpretation and valuation of past analyses, work should be undertaken to quantify the impact on analyses of treating presence-only data as presence-absence data.
- The extent to which rarefaction to a common sampling effort still suffers residual influence from sampling effort needs to be evaluated in different taxa and in data collected by different survey methodologies.
- The source of the residual influence of sampling effort after rarefaction to a common sampling effort should be identified.
- To evaluate the extent to which they may be generalised, the measures developed in this thesis to extract sampling effort corrected measures of α -, β - and γ -diversity should be employed in other regions.
- The generation of α -, β - and γ -diversity surfaces in sample rich regions through the use of a moving window and custom additive-partitioning-rarefaction software would produce more easily used, contiguous data, and should be investigated.
- The efficacy of the surrogates of biodiversity stress should be evaluated in regions where adequate climate data are available.
- The resolution of climate data in general and specifically in the Australian rangelands should be increased to facilitate better environmental modelling and management.
- The development of other remotely sensed surrogates of biodiversity should be investigated, to address the need for spatially comprehensive tools for monitoring biodiversity across the globe.
- Examine the relationship between total net primary production (TNPP) and total expected primary production (TEPP) with quantile regression to determine whether there is a strong positive relationship between TEPP and the upper quantiles of TNPP, and a weaker relationship at lower quantiles, as predicted by the hypothesis on which Surrogate 1 was based.

6.6 Conclusions

This thesis has contributed to the measurement and monitoring of biodiversity. The identification of false-negative errors as a cause for concern will allow future analyses of the vegetation survey data to adopt methods to counteract these errors, and hence extract more robust information. The method for extracting sampling effort corrected indices of α -, β - and γ -diversity allow for the examination and comparison of species diversity across regions, regardless of differences in sampling effort. These indices are not limited to rangelands, and can be extracted from any vegetation quadrat survey data obtained within a prescribed methodology. Therefore, these tools contribute to global biodiversity measurement and monitoring. Finally, the remotely sensed surrogates of biodiversity are theoretically sound and applicable in any rangeland where over-grazing is a significant source of degradation. However, because the evaluation of these surrogates in this thesis was hampered by available data, further testing is necessary.

6.7 References

- Brandle, R., Ed. (1998) A biological survey of the north west Flinders Ranges, South Australia, Dec-1997, Biological Survey and Research, Department for Environment, Heritage and Aboriginal Affairs, South Australia.
- Brandle, R., Ed. (2001) A biological survey of the Flinders Ranges, South Australia 1997-1999, Biodiversity Survey and Monitoring, National Parks and Wildlife, South Australia, Department for Environment and Heritage.
- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran and C. Jouseau (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**: 989-992.
- Fleishman, E., R. F. Noss and B. R. Noon (2006) Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators* **6**(3): 543-553.
- Gu, W. and R. K. Swihart (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation* **116**(2): 195-203.
- Holm, A. M., W. A. Loneragan and M. A. Adams (2002) Do variations on a model of landscape function assist in interpreting the growth response of vegetation to rainfall in arid environments? *Journal of Arid Environments* **50**: 23-52.
- Holm, A. M., I. W. Watson, W. A. Loneragan and M. A. Adams (2003) Loss of patch-scale heterogeneity on primary productivity and rainfall-use efficiency in Western Australia. *Basic and Applied Ecology* **4**: 569-578.
- Le Houerou, H. N. (1984) Rain use efficiency: a unifying concept in arid-land ecology. *Journal of Arid Environments* **7**: 213-247.
- MacKenzie, D. I. (2005) Improving inferences in population studies of rare species that are detected imperfectly. *Ecology* **86**(5): 1101-1113.
- MacKenzie, D. I. (2005) What are the issues with presence-absence data for wildlife managers? *Journal of Wildlife Management* **69**(3): 849-860.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle and C. A. Langtimm (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**(8): 2248-2255.

- O'Brien, E. M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of Southern Africa's woody flora. *Journal of Biogeography* **20**: 181-198.
- Robinson, A. C. and D. M. Armstrong, Eds. (1999) A biological survey of Kangaroo Island, South Australia, 1989 & 1990, Heritage and Biodiversity Section, Department for Environment, Heritage and Aboriginal Affairs, South Australia.
- Rodrigues, A. S. L. and T. M. Brooks (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics* **38**(1): 713-737.
- Smyth, A. K., R. Brandle, A. Brook, V. H. Chewings, M. Fleming and J. L. Read (2007) Methods for identifying, selecting and interpreting indicators for assessing biodiversity condition in desert Australia, using the Stony Plains bioregion as a case study, Desert Knowledge Cooperative Research Centre.
- Snyman, H. A. (1997) The influence of range condition on the hydrological characteristics in semi-arid rangeland. The XVIII International Grassland Congress.
- Snyman, H. A. (1998) Dynamics and sustainable utilization of rangeland ecosystems in arid and semi-arid climates of southern Africa. *Journal of Arid Environments* **39**(4): 645-666.
- Snyman, H. A. and H. J. Fouché (1993) Estimating seasonal herbage production of a semi-arid grassland based on veld condition, rainfall, and evapotranspiration. *African Journal of Range and Forage Science* **10**(1): 21-24.
- Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris and H. P. Possingham (2003) Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications* **13**(6): 1790-1801.
- Whittaker, R. J., K. J. Willis and R. Field (2003) Climatic-energetic explanations of diversity: a macroscopic perspective. *Macroecology: concepts and consequences*. T. M. Blackburn and K. J. Gaston. Oxford, Blackwell Science: 107-129.