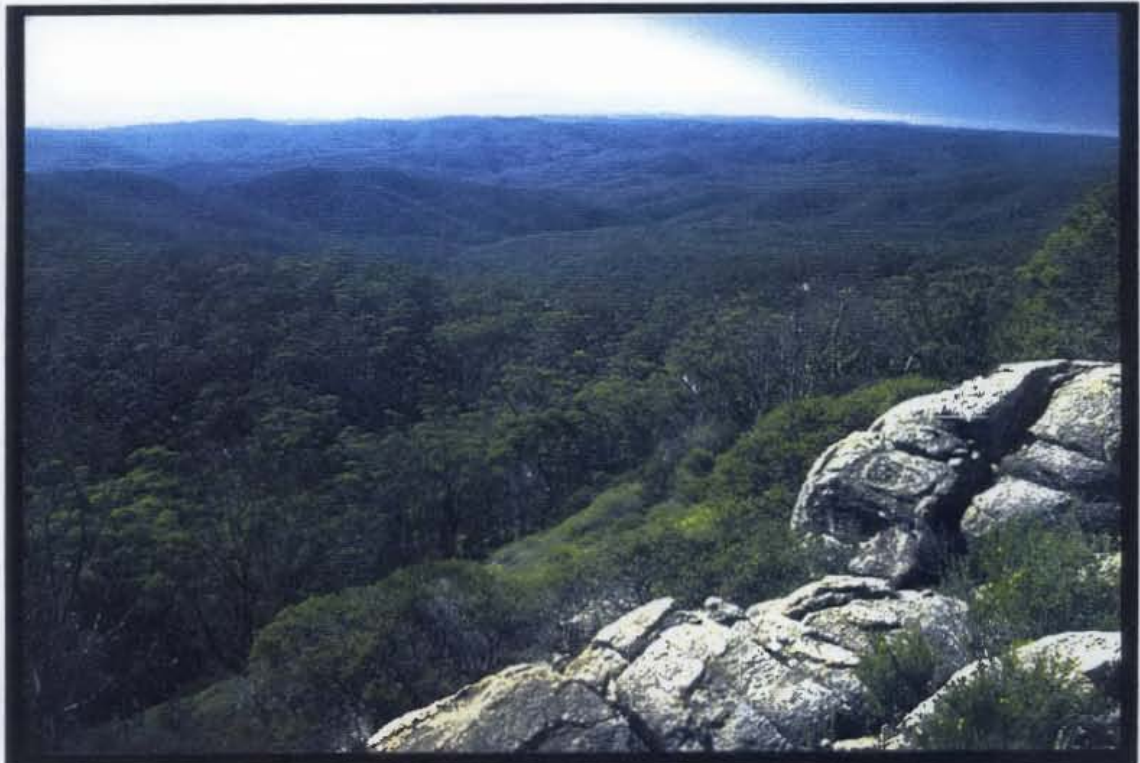


## Chapter 8: Areography



*The Devil's Forehead, Mount Chaelundi on the edge of the Guy Fawkes  
escarpment*

## Chapter 8

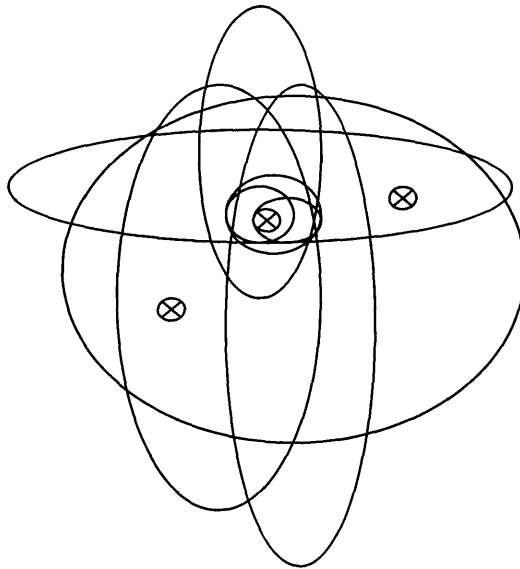
### Areography

#### 8.1 Introduction

Patterns in the sizes and distributions of species' ranges have been studied by biogeographers for over a century (Hughes *et al.* 1996). The term, 'areography' was first introduced and defined by Rapoport (1982). Areography is essentially the interspecific geographical variation in the structure and dynamics of species' ranges (Hengeveld 1990). The distribution of the frequency of species' range sizes is highly skewed with most species having relatively small ranges and few having large ones (Gaston 1990).

Investigations into the geographic ranges of species may provide insights about how species diversity and richness may be maintained. For instance, it has been shown that there is a correlation between species' range and local abundance (Hanski 1982; Lacy & Bock 1986; Gaston 1990; Gaston & Lawton 1990; Hengeveld 1990; Gaston 1994). Species with large range sizes more commonly exhibit, high local frequency, however, species with small ranges are only ever rare. Hence species with larger geographic ranges are less likely to go extinct for both reasons of range *per se*, and local abundance within that range. In conjunction with the previous phenomena it is theorised that in highly diverse communities there is a disproportionate number of species with small geographic ranges (Rapoport 1982; Gaston 1990). In other words species-poor sites should have species with large geographic ranges and species-rich sites are richer by the addition of species with small geographic ranges (endemics) (Figure 8.1). Despite many supportive findings, Holt *et al.* (1997) show that theoretically there is a number of instances where these correlations may not be found. Schoener (1987) coined the terms 'suffusive' rarity for rare species that are rare across their whole range and 'diffusive' rarity for those that are common in substantial portions of their ranges but rare in other parts of them.

In contrast to these predictions it has been shown in Chapter 3 that highly insular (outcrop endemic) species were more frequent and abundant on islands (outcrops) in the New England Batholith than comparatively widespread ubiquitous taxa with larger geographic ranges. Similarly, landscape ecologists have found that species that have evolved in highly fragmented systems usually evolve small range sizes and high local abundance due to a reduced ability to disperse and a strategy of local persistence (Green 1994; Dieckman *et al.* 1999). In addition, results from Chapter 5 indicate that where endemism and insularity is at its highest in the north east of the batholith (e.g. BR), species richness is comparatively low, and in contrast in areas to the west of the batholith where insularity and endemism are low, species richness is often comparatively high.



**Figure 8.1:** A collection of species with different range sizes, with X marking sites with different richness. It is postulated that species-poor sites have only species with large species' ranges and rich sites are richer due to the inclusion of endemic species (those with small range sizes).

Areography as a science attempts to understand the multifarious aspects of species' ranges, including their internal, external and temporal processes. Within this chapter analyses and interpretations will be confined to the size of species' ranges. It is the aim of this chapter to investigate the patterns of species' range sizes across the batholith at different scales and extent, in order to evaluate how differences in ranges may influence or maintain species richness and diversity. Furthermore, how such patterns may

correlate with or affect the results presented in previous chapters is also explored.

Specific questions include:

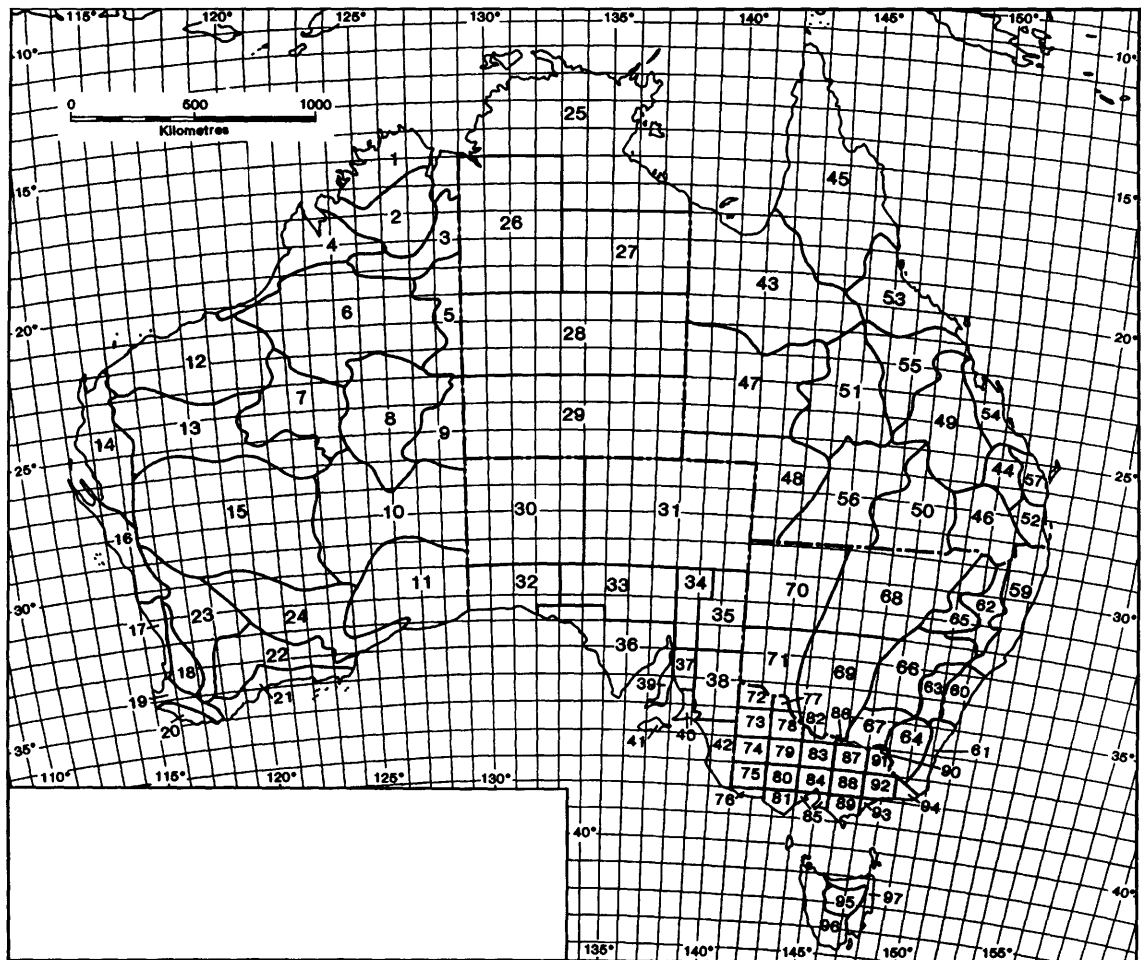
- Are there discernible patterns in species' range size across the batholith?
- Are there significant differences between species' range patterns on outcrops as compared to the surrounding vegetation ('sea')?
- Are differences in species' ranges significantly correlated with environmental variables?
- Is there a link between species' range size and local abundance?
- Is there a link between species' range sizes and local species richness?
- Do different life forms have differences in species' range size?

## 8.2 Methods

### 8.2.1 Measurement of species' ranges

Information on the geographic range of Australian vascular plant species is summarised by Hnatiuk (1990). This information has been updated by a number of State and regional censuses and floras (Chapter 2). The regions adopted are those recognized by the herbaria of each State and Territory within Australia, and are generally defined as capturing important ecological differences between regions (Oakwood *et al.* 1993; Figure 8.2). The availability of this information enables investigations into the relationships of geographic range (occupancy). Most analyses of geographic range do not differentiate between the limits of geographic range and the areas used within the range. Gaston (1991) referred to the former as the extent of occurrence and the latter as the area of occupancy. Occupancy within each of the 97 'ecological regions' has been chosen as the measure of geographic range size in this investigation. Occupancy is used as the questions asked are framed in terms of species ecology (Gaston 1991; Maurer 1994), and the environmental gradients across Australia are largely discordant. Quinn *et al.* (1996) investigated various means of measuring geographic range size and concluded that in most instances the methods were largely interchangeable.

Two measures are chosen here to describe and summarise aspects of species' range. The two measures summarise information contained in a matrix of species occurrences within the 97 defined 'ecological regions' of Australia. Evenness has been chosen to describe differences shown in between-row comparisons and Range Saturation (RS) is used to measure differences in information contained in, between-column comparisons.



**Figure 8.2:** Map of the 97 botanical regions within Australia. Figure taken from Hnatiuk (1990).

### 8.2.2 Distribution of species' ranges

The evenness index 'C' of Camargo (1993) has been discussed and used in Chapter 5. This same index is used here to describe the variance in occupancy of species within the 97 regions. Thus, this index will be a relative measure of the distribution of range sizes amongst species. The formula for 'C' and its derivation is given in Section 5.2.2.

### 8.2.3 Species' range saturation

Species' range saturation is a new concept developed by the author and is used here for the first time. Range saturation 'RS' is a quantitative measure of the distribution of range sizes within a sample of species. The measure is derived by ordering a presence-absence matrix of species incidences within each of the 97 Australian botanical regions. The following formula can be used to derive 'RS':

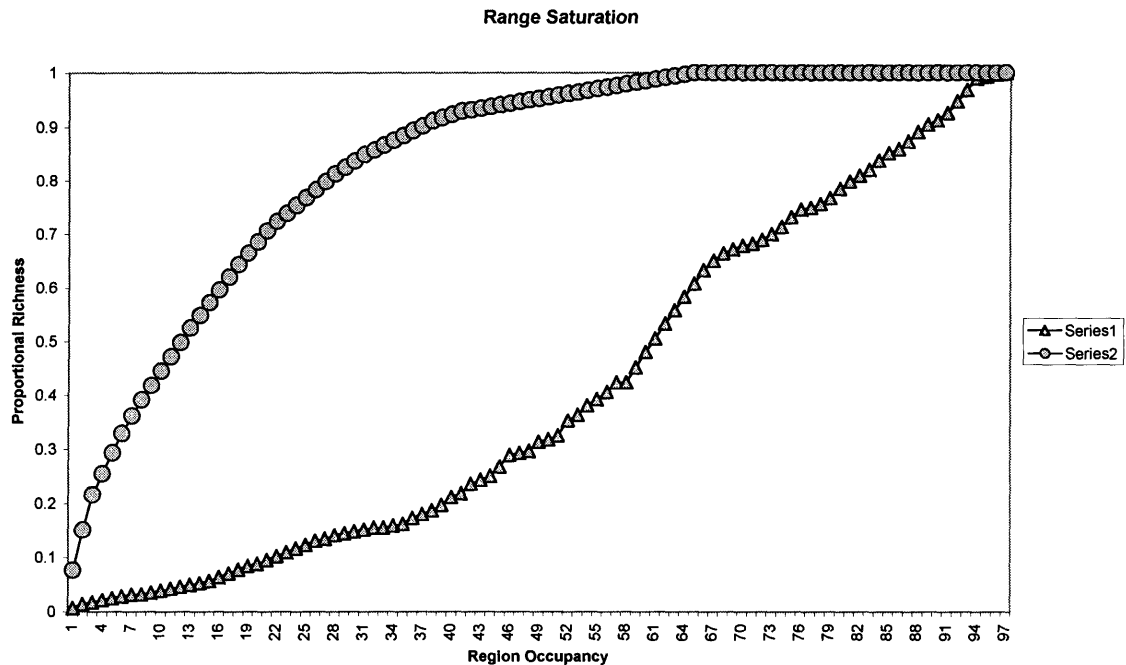
$$RS = 100 - \frac{1}{\sum_{i=1}^{97} r_i} (97r_1 + 96r_2 + \dots + r_{97}) / 0.97$$

$$RS = 100 - \frac{1}{\sum_{i=1}^{97} r_i} \left( \sum_{i=1}^{97} (97 - (i-1)) r_i \right) / 0.97$$

Where  $r_i = i$ th species.

The methodology is similar to the purely graphical cumulative range size frequency distribution curves used by Anderson and Marcus (1992). A presence-absence matrix is created with species in S rows and regions in K columns, with regions arranged in order of decreasing species richness. The sum of the richness of all regions is performed. The richness at any region is divided by the sum total of all richness scores for each botanical region in order to remove the affect of matrix fill. The resulting scores are cumulatively added to each following score, and the resulting figures summed and then divided by 0.97 (% of regions). The less widely dispersed a flora, the quicker it will reach saturation (saturation = 1; Figure 8.3). This final score is subtracted from 100.

The range saturation index (RS) is 0 when no species occur in any region and it is 100 when all species occur in all regions. Thus the greater the proportion of small range sizes the lower the range saturation score, and the larger the proportion of large range sizes the higher the score. 'RS' is not affected by matrix size (Figure 8.3).



**Figure 8.3:** An example of differences in range saturation derived from data presented in Table 8.3. Series 1 achieves an 'RS' score of 18.5 and Series 2 a score of 60.6. Thus series 2 has a greater proportion of widespread species and series 1 has a greater proportion of smaller range sizes (endemics).

#### 8.2.4 Species' range and local abundance

The mean species relative abundance (out of 10; Chapter 2), the sum of all relative abundance scores obtained and frequency (number of times a species occurred across quadrats) were used in conjunction with a score out of 97 (indicating occupancy in 'ecological regions') for each species in Forward Stepwise Multiple Linear Regressions. Regressions are made over a number of grain and extent sizes and included the entire flora of the outcrops ('islands') of the batholith, the 24 'archipelagos' as units, the nine Elements (Chapter 4), and individual quadrats of each of the 24 'archipelagos' and the major lifeform guilds separately. If species local abundance is related to species' range

then there should be a positive correlation between individual species' range size and measures of local abundance.

### **8.2.5 Species' range and local richness**

The 'RS' score was linearly regressed with richness. A negative correlation should be found if an increase in endemics (species with small range sizes) is associated with an increase in species richness as postulated in the introduction. Regressions were investigated in terms of the richness and 'RS' scores for the 24 'archipelagos', the nine Elements, the ten outcrops ('islands') with six quadrats placed, and the one quadrat sized outcrops ('islands') from Torrington (TT) (26), Flaggy Range (FR) (16) and Gibraltar Range (GR) (10) (see Chapter 2).

## **8.3 Results**

### **8.3.1 Range evenness and saturation**

The evenness of species' range distributions and range saturation of the outcrop and surrounding floras were calculated for each of the 24 'archipelagos' (Table 8.1). Analysis of the evenness ( $C$ ) of species' ranges shows that the floras of outcrops ('islands') and those of the surrounding vegetation ('sea') are significantly different ( $P < 0.004674$ ), with outcrops being more even in their range size distributions (average 0.682 and 0.670 respectively) (Table 8.1). Similarly, range saturation is significantly ( $P < 0.047807$ ) higher for the 'archipelago' outcrop flora as opposed to the surrounding flora ('sea') (average 27.91 and 26.99 respectively).

Between 'archipelago' comparisons, in terms of range saturation, highlight major changes across the batholith (Table 8.2). Five 'RS' scores (Moonbi (MB), Attunga (AT), Yarrowyck (YH), Kwiambal (KL) & Flaggy Range (FR)) were found to exceed 30, with Moonbi (MB) having the highest score (Figure 8.1). All of these high-scoring 'archipelagos' were found along the western side of the batholith. Five archipelagos



were found with lowest 'RS' scores (Cathedral Rock (CR), Butterleaf (BL), Gibraltar Range (GR), Mount Jondol (JB), Butterleaf (BL)) with Cathedral Rock (CR) having the lowest score. In contrast, all of lowest scores were from 'archipelagos' that occurred along the eastern margin of the batholith on the escarpment. Differences in range saturation are less extreme in comparisons of Element scores (Table 8.2). However, the general trend of lower 'RS' scores for Elements on the eastern escarpment and higher for those on the western margin of the batholith is maintained. Large differences were found in 'RS' scores between different life forms.

A comparison of the evenness and saturation of species' ranges across the nine floristic Elements described for granitic outcrops (Chapter 4) is presented in Table 8.2. Both the results within Tables 8.1 to 8.3 show a strong relationship between species' range evenness and saturation. This correlation is graphed for the data contained in Tables 8.1 and 8.2 in Figures 8.4 and 8.5 respectively. There is strong negative and highly significant correlation, between the measures *C* and *RS*. This indicates that the more widespread the flora becomes the less even is the distribution of range sizes. This correlation is improved when floristic groups (Elements) are plotted (Figure 8.5) as opposed to 'archipelagos' (Figure 8.4)

Comparisons between lifeforms in terms of species' range saturation and evenness are presented in Table 8.3. The data contained in this table indicates there is a great difference between the overall species' range sizes in different lifeform categories. In particular, trees and to a lesser extent shrubs were found to have very restricted distributions in general and Hemi-parasites to have comparatively very large range sizes, followed by herbs.

**Table 8.1:** Comparison of the evenness of species' ranges and range saturation of the flora of outcrops ('islands') and the surrounding vegetation ('sea') at each of the 24 'archipelagos' examined (Chapter 2).

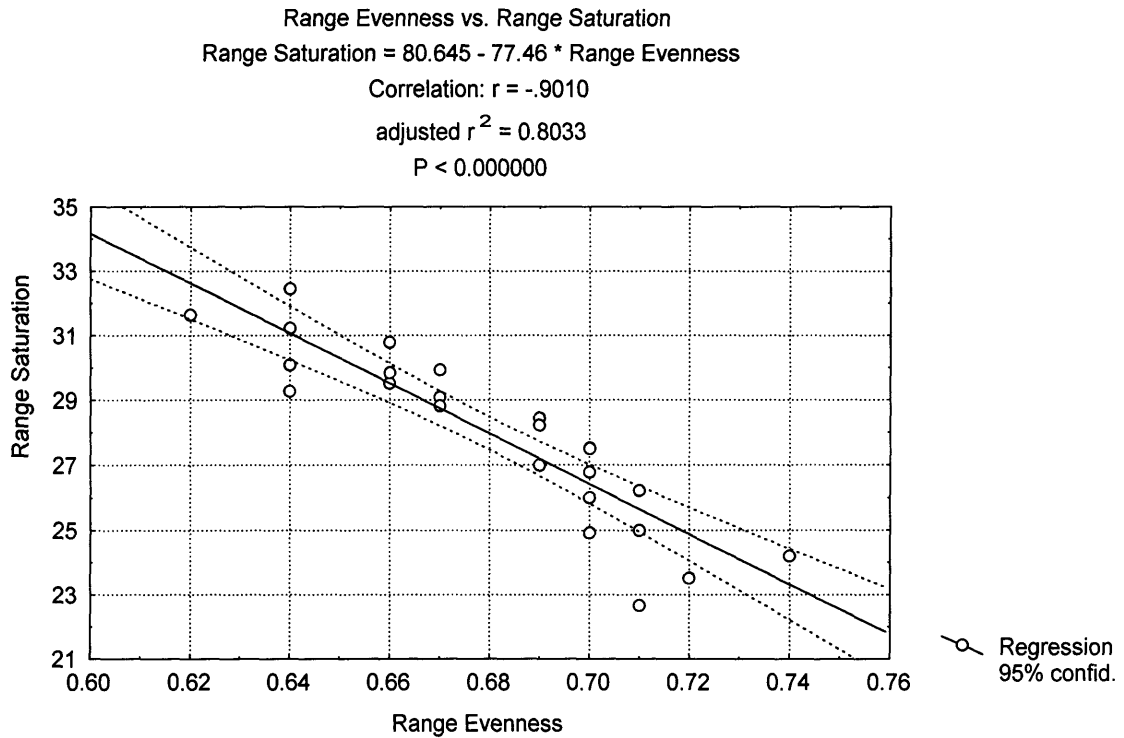
<b>Archipelago</b>	<b>Outcrop Range Evenness</b>	<b>'Sea' Range Evenness</b>	<b>Outcrop Range Saturation</b>	<b>'Sea' Range Saturation</b>
<b>Attunga (AT)</b>	0.618	NA	31.64	NA
<b>Backwater (BC)</b>	0.692	0.676	26.99	26.47
<b>Bolivia Hill (BH)</b>	0.701	0.664	26.78	27.82
<b>Butterleaf (BL)</b>	0.715	NA	23.51	NA
<b>Bald Rock/Girraween (BR)</b>	0.690	0.682	27.52	27.39
<b>Chaelundi (CH)</b>	0.712	0.692	24.99	25.32
<b>Cathedral Rock (CR)</b>	0.710	0.672	22.66	26.08
<b>Demon (DM)</b>	0.701	0.686	26.00	25.86
<b>Eagle Creek (EC)</b>	0.668	0.659	29.08	26.38
<b>Flaggy Range (FR)</b>	0.640	0.632	30.09	29.10
<b>Gibraltar Range (GR)</b>	0.737	0.751	24.20	20.87
<b>Howell (HC)</b>	0.669	0.670	29.93	24.41
<b>Ironbark (IB)</b>	0.656	0.657	29.52	28.18
<b>Mount Jondol (JB)</b>	0.695	0.672	24.92	25.92
<b>Kwiambal (KL)</b>	0.656	0.651	30.79	29.86
<b>Kings Plains (KP)</b>	0.711	0.665	26.22	28.83
<b>Moonbi (MB)</b>	0.637	0.631	32.44	29.93
<b>Mount Lookout (ML)</b>	0.641	NA	29.27	NA
<b>Parlour Mountains (PM)</b>	0.672	0.685	28.82	25.92
<b>Severn River (SR)</b>	0.688	0.692	28.44	27.41
<b>Torrington (TT)</b>	0.698	0.692	27.50	26.33
<b>Warrabah (WB)</b>	0.658	0.658	29.84	27.77
<b>Willows (WW)</b>	0.686	0.683	28.22	27.18
<b>Yarrowyck (YH)</b>	0.635	0.607	31.22	29.79
<b>NE Batholith</b>	0.706	0.705	29.23	27.85

**Table 8.2:** Comparison of the evenness of species' ranges and range saturation within each floristic Element (Chapter 4).

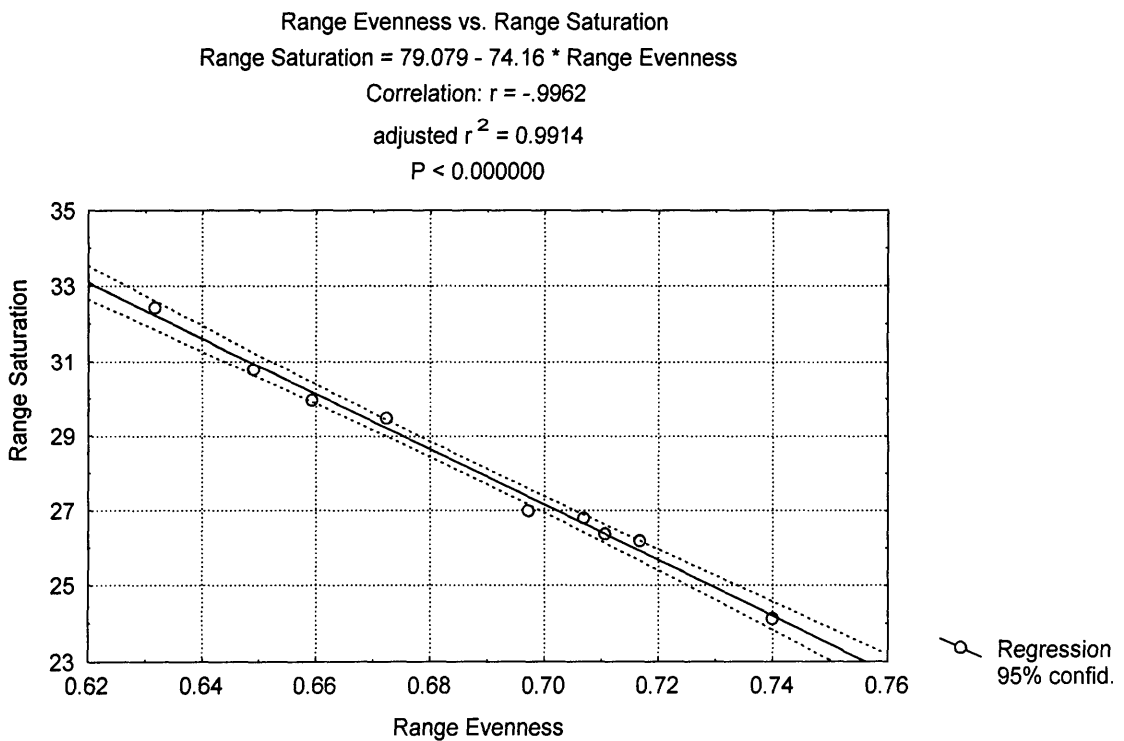
<b>Floristic Element</b>	<b>Range Evenness</b>	<b>Range Saturation</b>
<b>Element 1</b>	0.697	26.99
<b>Element 2</b>	0.717	26.18
<b>Element 3</b>	0.740	24.12
<b>Element 4</b>	0.711	26.37
<b>Element 5</b>	0.707	26.80
<b>Element 6</b>	0.632	32.43
<b>Element 7</b>	0.672	29.48
<b>Element 8</b>	0.649	30.78
<b>Element 9</b>	0.659	29.96

**Table 8.3:** Comparison of the evenness of outcrop ('island') species' ranges and range saturation within each major lifeform guild. A graphical representation of the saturation curves of 'Trees' and 'Epiphytes & Hemi-parasites' is given in Figure 8.2.

<b>Lifeform</b>	<b>Range Evenness</b>	<b>Range Saturation</b>
<b>Trees</b>	0.807	18.50
<b>Shrubs</b>	0.777	21.83
<b>Herbs</b>	0.658	30.63
<b>Lianas &amp; Vines</b>	0.604	25.06
<b>Epiphytes &amp; Hemi-parasites</b>	0.546	60.62



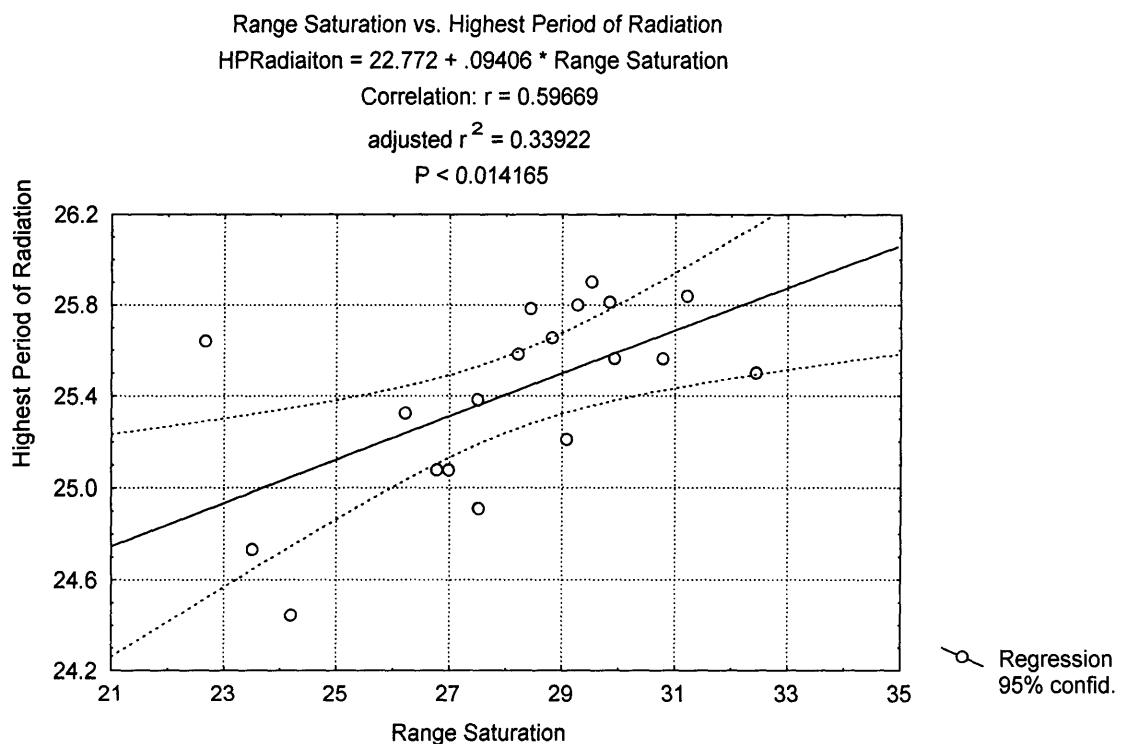
**Figure 8.4:** Comparison of the range saturation and evenness scores based on the results of Table 8.1.



**Figure 8.5:** Comparison of range saturation and evenness using scores obtained from the nine Elements (Table 8.2).

### 8.3.2 Range saturation and environmental variables

Forward Stepwise Multiple Linear Regression analyses were performed on 'RS' values derived from the 24 'archipelagos' and the environmental variables used in Chapter 3. Only one significant correlation was found. There was a significant positive correlation between 'RS' scores and the Highest Period of Radiation (Figure 8.6). This indicates that the component flora is more widespread in areas where there is higher incident radiation.



**Figure 8.6:** Comparison of range saturation scores and the Highest Period of Radiation for the 24 'archipelagos'. As the highest period of radiation increases the more widespread the component flora becomes.

### 8.3.3 Range saturation and species local abundance

Local abundance scores as measured by frequency of occurrence, relative abundance scores and the sum of all abundances (frequency times relative abundance) were

regressed against the range saturation scores obtained from the same sample.

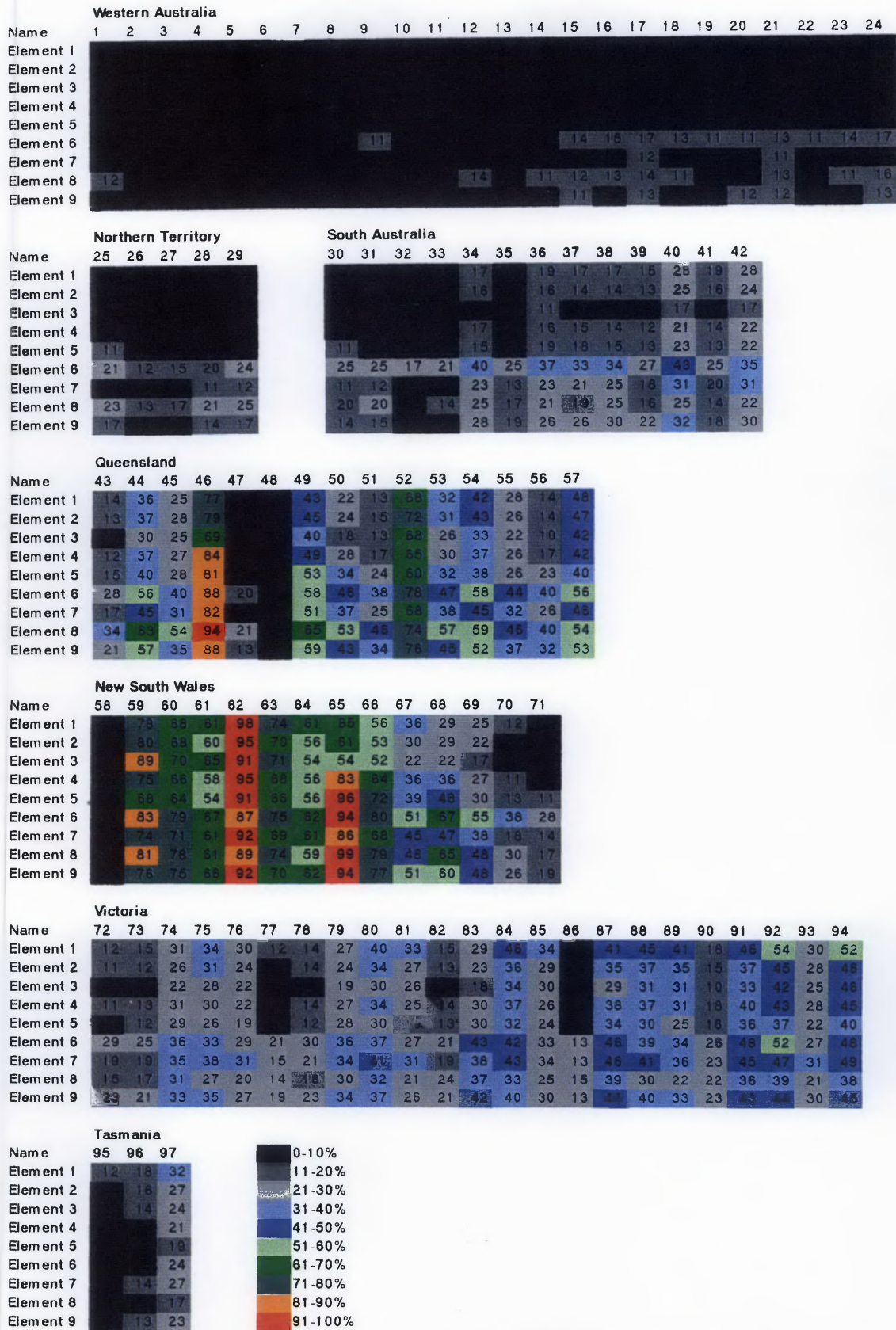
Regressions were performed from data obtained from a number of grain and extent sizes including the batholith as a whole, cross-‘archipelago’ comparisons and between different lifeforms. No statistically significant correlations were found between range saturation or any of the three measures of species abundance at any scale or extent.

#### **8.3.4 Range saturation and species richness**

Regressions between range saturation scores and species richness was performed. Richness data obtained from a number of grain and extent sizes including the batholith as a whole, cross-‘archipelago’ comparisons, within single outcrop size comparisons, or between different lifeform guilds were regressed against range saturation. Range saturation was not significantly correlated to species richness at any grain or extent size.

#### **8.3.5 Floristic elements and occupancy of regions**

Most species from all Elements are restricted to north eastern New South Wales and south eastern Queensland, as this is where the batholith is situated on the continent (Figure 8.2 & 8.7). The flora of the four Elements confined to the west of the batholith (6, 7, 8, & 9) show a wider geographic distribution, with more than 10% of the component flora also having distributions within a number of Western Australian regions on the other side of the continent. The first five Elements (1, 2, 3, 4 & 5) have component floras in which less than 10% of species occur in any of the Western Australian or Northern Territory regions. Comparatively more species from these first Elements are distributed down the east coast of Australia than the latter four. Overall, the results show that the Elements 6 to 9, to the west of the batholith are more widespread and occur in more arid regions (Figure 8.7). Conversely, the floras of Elements occurring at higher altitudes and to the east along the escarpment are less widespread (smaller ranges on average) and have trajectories along the east coast, particularly to the south (Figure 8.7).



**Figure 8.7:** Species' ranges within each of the nine Elements. The numbers in each of the 97 botanical divisions area percentage of the total flora of each element (i.e. 32% of the flora of Element 1 occurs in region 97). See Figure 8.1 for map of botanical districts.

## 8.4 Discussion

Both evenness of species' range size distribution and range saturation were lower for the surrounding ('sea') floras as opposed to the outcrop ('island') floras. This highlights the fact that species' ranges are in general smaller on outcrops ('islands') than in the surrounding flora ('sea'). Although statistically significant, these differences are only minor and certainly not as great as the differences between 'archipelagos'. This indicates that changes in species' ranges across the batholith are reflected in both the outcrop ('island') and the surrounding ('sea') floras in each 'archipelago' almost identically. The concordance of lower evenness and range saturation scores in surrounding ('sea') floras is difficult to explain in the light of the strong negative and highly significant correlation between range saturation (RS) and evenness. For such a high correlation to occur these two measures must be mathematically linked. Therefore, the difference between outcrop ('island') and surrounding ('sea') floras in respect to these two measures is contradictory.

The high correlation between the evenness of species' range sizes and range saturation is because they both measure different, but correlated aspects of matrix fill. The reasons for the correlation are graphically presented in Figure 8.8. Essentially as species become more widespread, the spread of differences between ranges sizes increases, thus increasing unevenness. It appears that either score could be used to describe the differences in species' range sizes across floras.

Differences between species' range sizes were found across the batholith.

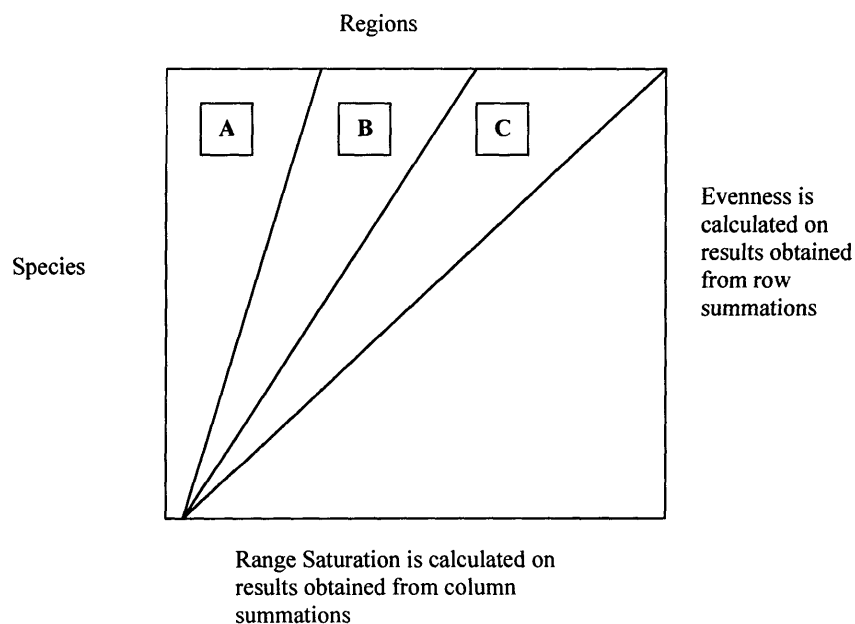
'Archipelagos' along the western margin of the batholith had larger range saturation scores. In concordance those 'archipelagos' along the eastern escarpment of the batholith had lower range saturation scores. Despite linear regression on a number of environmental descriptors only Highest Period of Radiation was significantly correlated to range saturation scores. This does explain the differences noted between the eastern and western 'archipelagos'. The distribution in range sizes across the batholith is therefore influenced, at least in part, by available energy. Hughes *et al.* (1996) found the range sizes of eucalypts expanded with increasing temperature (an energy descriptor).



There are large differences between species' range sizes across different life form groups. Differences in range sizes across lifeforms have been noted in other studies (Anderson & Marcus 1992; Oakwood *et al.* 1993; Kelly 1996). Trees in this investigation were found to have very small geographic ranges ('RS' = 18.50) with shrubs having slightly larger but also comparatively small geographic ranges. Epiphytes and hemi-parasites on the other hand had very large geographic ranges ('RS' = 60.62) with herbs to a lesser extent also having overall larger range sizes. The trees within this investigation are largely species of *Eucalyptus*. Hughes *et al.* (1996) found that 68% of eucalypts had range sizes of less than 1% of the Australian continent. Similarly, Oakwood *et al.* (1993) found that there was a tendency for taller growth forms of plants to occupy fewer regions. These findings are in contrast to those obtained by Kelly (1996) who found trees had larger ranges than shrubs. If larger growth forms in plants are analogous to larger body sizes in animals then the present results are also in contrast to Rapoport's rule that larger organisms have larger geographic ranges (Rapoport 1982). In general, herbaceous species have small diaspores and are often wind dispersed and most of the epiphyte and hemi-parasite species in this investigation were (bird-dispersed) mistletoes. Oakwood *et al.* (1993) found that vertebrate-dispersed plants had larger geographic ranges, as did species with smaller diaspores. This in part also helps to explain the higher range saturation scores obtained from Elements and 'archipelagos' restricted to the western side of the batholith as these had a higher percentage and greater dominance of herbs, while the eastern escarpment had a higher prominence of shrubs (Chapter 4).

Despite numerous regressions at a number of grain and extent sizes, range saturation scores could not be correlated with the Quotient of Insularity (Chapter 3) or measures of abundance and frequency, thus indicating that on granitic outcrops ('islands') of the New England Batholith local species frequency or abundance could not be related to species' geographic range size. This is in contrast to the results of a number of other investigations (Hanski 1982; Lacy & Bock 1986; Gaston 1990; Gaston & Lawton 1990; Hengeveld 1990; Gaston 1994). Most rare species on the batholith may be described as diffusely rare in the terms of Schoener (1987). Holt *et al.* (1997) theoretically described instances where correlations may not be found between abundance and range size. Many of these instances are defined as individualistic species responses to density dependent and independent extinction processes and should not be pronounced over

entire floras. They do however indicate that a correlation between local abundance and range size will be weaker over larger geographic range sizes due to a greater discordance in species responses. Research into naturally occurring fragmented systems have often found that species that are restricted to fragmented areas possess strategies that enable species to persist but at the expense of dispersal (Green 1994; Dieckmann *et al.* 1999). This certainly appears to be the case on the outcrops ('islands') of the batholith (Chapter 3) and thus explains the high local frequency and abundance of species with small geographic ranges. Ubiquitous species on the batholith are in low abundance on outcrops (Chapter 3). These species are less competitive on outcrops and less adapted to the extreme environmental conditions (Chapter 1) and are thus in low numbers. Gaston and Lawton (1990) found that negative relationships could result when the habitat in which species abundances are measured differs markedly from the spectrum of habitats in the region. They also found that no correlation, as is seen here, occurs when the reference habitat is neither sufficiently different from other habitats in the region nor sufficiently representative.



**Figure 8.8:** A rank ordered species matrix with three different levels of matrix fill (A, B, C). When a matrix has a low Range Saturation score (A) there is less difference between species' range sizes and hence the distribution of species occupancy scores is low and is therefore more even. As the Range Saturation score increases so too does the unevenness of the matrix (A to B to C).

Again in contrast to general areographical theory, no relationship was found between site richness and species' range sizes. Despite regressions performed at different grain and extent sizes no correlations either negative or positive could be found. Species richness at a local level on the batholith is entirely unrelated to the component species' range sizes.

The range size of species differs proportionately across the granitic outcrops ('islands') of the New England Batholith. In general range sizes increase in areas with higher incident radiation (higher available energy) and concordantly in areas with a greater proportion of hemi-parasites, epiphytes and herbs. Conversely, range sizes decrease in areas to the east of the batholith where incident radiation is lower and shrubs predominate. Although species' range size has been linked in a number of systems with increased species richness and local species abundance, such correlations were unobtainable in this investigation. However, investigations into other fragmented systems would suggest that this is likely to be the case. Therefore, the responses of species occurring in naturally fragmented systems may be different from those in less fragmented systems. Species on outcrops of the New England Batholith have evolved over millennia to persist in fragmented ecosystems and thus correlations in the dynamics of species' ranges may be different from the general patterns described elsewhere. Analyses of species' range sizes cannot be used in this system to infer directly on processes that maintain species richness or diversity locally.