Chapter 6: Island Biogeography and Granitic Outcrops

Moonbi: Granitic Outcrops are like islands in a sea of forest

Chapter 6

Island Biogeography and Granitic Outcrops

6.1 Introduction

MacArthur and Wilson (1963; 1967) initially proposed the Equilibrium Theory of Island Biogeography. As with many major theoretical issues in biology, there are precursors who highlighted many of the aspects covered by the theory (Thornton 1992; Wilkinson 1993). The Equilibrium Theory is important as it shifted the emphasis of biogeographic investigations from reconstructing the life histories of individual taxa to a concerted effort to understand the general processes that determine the richness, diversity and composition of biotas (Brown 1986). It is difficult to ignore this theory in any investigation of insular systems, as islands (including 'habitat islands') exist in biogeographical science largely in the light of interpretations of the MacArthur and Wilson theory (Haila 1990). Williamson (1989) states that the emphasis and impetus that the theory has given to the study of the species area relationship is its most important legacy. This introduction provides an outline of some of the major variations of, and aspects pertaining to, the Equilibrium Theory of Island Biogeography.

The Equilibrium Theory was developed in an attempt to describe observations summarised by Preston (1962) and Williams (1964) (Gilbert 1980). The basis of the Equilibrium Theory is that there is an equilibrium number of species, which is controlled by a balance between immigration and extinction rates. The slope of the immigration curve is distance dependent and the extinction curve is area dependent (and to a lesser extent the immigration curve). As a species poor island approaches the equilibrium number of species, the immigration rate drops and the extinction rate increases towards equality (MacArthur & Wilson 1967). In addition, it is suggested that larger islands will intercept a larger number of disseminules per unit time because small islands represent smaller targets. An increase in distance lowers the immigration curve while an increase in area lowers the extinction curve and the species number increases with area more rapidly on distant islands than on proximate ones (MacArthur & Wilson

1967; Whitehead & Jones 1969). Wilson (1969) subsequently recognised four types of semi-equilibria that could exist successively in long-lived communities to account for observations that certain favourable species combinations are more likely, and that greater species richness may develop over time by speciation (evolutionary equilibrium) (Smith 1979).

Observations contrary to the theory have led to refinements to it. Vuilleumier (1970) and Abbott (1977) point out that several sources may contribute to species richness on an island and therefore distance (isolation) should not be taken solely from the mainland. Brown and Kudrick-Brown (1977) and Wright (1985) provide evidence that extinction rates are directly related to isolation in contrast to the MacArthur and Wilson (1967) hypothesis. As such, the process of island hopping (stepping stones) and its effects on isolation and population persistence may be an important process and adjunct to the equilibrium theory (Gilpin 1980; Kareiva 1990). Guilds of species can respond individualistically, some seemingly corroborating the theory and others not. Abbott (1977) found that annual plant species had higher extinction and immigration rates than other plant taxa. The vagility of species or groups of taxa significantly affects immigration and extinction rates and consequently the effectiveness of isolation (Johnson 1975; Nilsson & Nilsson 1978; Buckley 1981; Bengston & Bloch 1983; Schoener & Schoener 1983b; Buckley 1985; Lomolino 1986; Wilcox *et al* 1986; Blake & Karr 1987; Quinn & Harrison 1988; Thornton 1992). Buckley (1981; 1985) formulated the terrain floristic element model in which he suggested different floristic assemblages on islands respond to aspects of the equilibrium theory differentially, and therefore they should be tested separately. Investigations have shown that in continental 'islands' a stronger species-area relationship is obtained if vagrants (those not restricted to the system) are removed (Johnson 1975; Quinn *et al.* 1987; Haila 1990). Other factors that have been shown to influence the outcomes of analyses pertaining to the Equilibrium Theory include: habitat disturbance (Abbott 1977; Whittaker 1995; Ward & Thornton 1998); island age or time since isolation (Wilcox 1978; Crowell 1986; Cutler 1991; Saunders *et al* 1991; Deacon & MacNally 1998); source pool richness and composition (Lawlor 1986; Lomolino 1986; Quinn *et al.* 1987; Deshaye & Morisset 1988; Kholin & Nilsson 1998; Roden 1998; Vilenkin & Chikatunov 1998); predation and release from competition (Wilson 1969; Smith 1979; Heaney 1984; Lawlor 1986; Paulay 1994).

The universality of the theory was thought by some to be confirmed by reports of positive correlation between island size and richness, and in some cases residual variance explained by distance (isolation) (Case 1975; Abele & Patton 1976; Gottfried 1977; Faeth & Kane 1978; Nilsson & Nilsson 1978; Lomolino 1982; Heaney 1984;). Lomolino (1984) pointed out that consistency did not constitute proof. Finding a close relationship between island size and species richness does not validate the theory (Gilbert 1980; Brown & Dinsmore 1988), only observations on turnover (extinction and immigration over time) could provide direct evidence. Nonetheless the reporting of close relationships between species number and area are still popularly discussed in terms of equilibrium theory (Lomolino 1984; Buckley 1985; Crowell 1986; Martin & Lepart 1989; Brown *et al.* 1995; Nores 1995; Burbidge *et al.* 1997; Davies & Smith 1998). Some studies of turnover have affirmed the predictions of the equilibrium hypothesis (Browne 1981; Nilsson & Nilsson 1982; Rey & Strong 1983; Lomolino 1990). However, a number of other studies were unable to show significant species area or turnover relationships as predicted by the model (Brown 1971; Helliwell 1976; Simberloff & Abele 1976; Abbott 1977; Smith 1979; Buckley 1981; Jones *et al* 1985; Dunn & Loehle 1988; MacNally & Watson 1997). As with positive reports of species area relationships, consistent negative reports do not constitute proof that the theory should be rejected.

An adjunct to the equilibrium theory is the habitat heterogeneity model. In this model it is proposed that increasing area increases the number of habitats, and that it is the latter that species are responding to and not area *per se*. Suggestions that habitat may play a more important role in species richness relations occurred soon after the introduction of equilibrium biogeography (Whitehead & Jones 1969). In comparisons between the explained variance due to habitat heterogeneity or island area a number of studies found the former of greater predictive power (Heatwole & Levins 1973; Johnson 1975; Bengston & Bloch 1983; Schoener & Schoener 1983b; Westman 1983; Buckley 1985; Boecklen 1986; Quinn *et al.* 1987; Williamson 1989; Perry *et al.* 1998). Conversely, other studies have shown habitat to be of little significance with area having greater explanatory value (Simberloff & Abele 1976; Dueser & Brown 1980; Shreeve & Mason 1980; Rey & Strong 1983; Elmberg *et al.* 1994). Kohn and Walsh (1994) proposed that an area habitat relation is an essential part of observed species area relationships and for this reason the effect of habitat on species number cannot be dissociated from the overall effect of area (Simberloff & Abele 1976; Benwell 1995).

Deshaye and Morisset (1988) found that within habitats there is a genuine influence of area on species richness, but the strength of this relation depends on the size of the habitat species pool. Therefore, at the level of whole islands, species richness is controlled by both area and habitat diversity. Schoener and Schoener (1983b) also noted area was a more important predictor of species number on geographically extensive archipelagos. Kholin and Nilsson (1998) found no correlation between habitat heterogeneity and species diversity at the regional scale, but a correlation at the local level. Böhning-Gaese (1997) showed that small spatial scales emphasize the importance of habitat diversity whereas, geographical studies at large spatial scales emphasize variables related to available energy such as temperature. Lomolino (1994) and MacNally and Watson (1997) believed that much of the controversy over area as opposed to habitat heterogeneity effects is related to scalar issues. In addition to the equilibrium and habitat heterogeneity theories, the random placement hypotheses has also been proposed to account for observed species area relationships on islands (Fisher *et al.* 1948). The random placement hypothesis points out that if individuals are distributed at random, larger samples will contain more species.

Species/genus ratios have also played a minor but significant role in a number of insular studies. It is predicted that the mean number of species per genus on an island will be lower than the ratio for a mainland source area (Simberloff 1970; Linhart 1980). Simberloff (1970) believed that congeners are more likely to occur together despite competition due to their ecological requirements and dispersal abilities. Grant (1966) argued the converse, i.e. congeners would exclude each other due to their common ecological requirements. Abele and Patton (1976) found that congeneric exclusion occurred on small coral head 'islands'.

Both Böhning-Gaese (1997) and MacNally and Watson (1997) proposed a 'zoom sampling' technique to determine which environmental factors are scale dependent and which are not. Kelly *et al.* (1989), Holt (1992) and Thiollay (1998) proposed that fixed area sampling should be used in investigations of the Equilibrium Theory as this gives a fairer comparison because it avoids bias caused by decreasing per species sampling effort as richness increases. Both of these methodological techniques are used in this investigation (Chapter 2).

The aim of this study is to examine how equilibrium theory, or its variants, might provide insights into how floristic richness and diversity is derived or maintained on the granitic outcrops ('islands') of the New England Batholith of eastern Australia. Specific questions include:

- Can the Equilibrium Theory of Island Biogeography and/or its variants provide insights into processes that maintain richness on granitic outcrops?
- Are patterns discernable in species/genus ratios?
- Are the results obtained based on the grain size of the sample?
- Are the results obtained based on extent of the area investigated?
- Does how insular (Quotient of Insularity; Chapter 3) an outcrop or 'archipelago' is affect the results obtained?
- Do different lifeform guilds respond differently to significant correlative variables?

6.2 Methods

The terminology relating to spatial scale is defined in Section 5.2.

6.2.1 Design of analysis

Considerable overlap occurs between some Elements and 'archipelagos' (Chapter 4), in particular Howell and Element 9 and Gibraltar Range and Element 3. Additionally, some 'archipelagos' and Elements are small being sampled by only a small number of quadrats and outcrops ('islands') or outcrop sizes. Within the following analyses only Elements 1, 2, 4, 5 and 7 were chosen for detailed investigations as these encompassed outcrops of a range of sizes. The same reasoning limited the number of 'archipelagos' chosen to only Backwater (BC), Bald Rock/Girraween (BR) and Howell (HC). Each of these archipelagos received a number of survey sites additional to that allocated (Chapter 2) to enable a broader range of replicate island sizes to be sampled. This research design allows for analyses at three sizes of grain and extent, however, statistical inference is limited because quadrats are not independent. This is essentially a nested design where one grain contributes to the data of the next highest grain (Palmer & White 1994). Therefore no formal attempt is made to test statistical hypotheses.

6.2.2 Forward stepwise multiple linear regression

The indirect gradient analysis technique of Forward Stepwise Multiple Regression via the program STATISTICA (StatSoft 1994—1995) was used against richness and species/genus ratios and the variables used in Chapter 3, the Quotient of Insularity (Chapter 3), evenness scores (Chapter 5), area and log of area, isolation distance, and habitat heterogeneity.

Isolation distance was derived by triangulation of the AMG co-ordinates of each quadrat enabling the distance between objects (i.e. quadrats, outcrops, 'archipelagos') to be derived. The smallest distance in metres was used as a measure of isolation. This measure of isolation was chosen as this is a continental insular system with no direct 'mainland'. The nearest (and not the nearest largest) object was chosen as studies have shown that 'stepping-stone' islands of any size may be important in aiding the distribution of taxa (Gilpin 1980). All habitat scores (i.e. Vegetation Cover, Boulder Cover, Faulting etc; Chapter 2) were summed and then divided by the number of included attributes into a single score of Habitat Heterogeneity and this is included as an additional variable. Scores for environmental variables for larger extents (outcrops, 'archipelagos', Elements) are based on the means derived from cumulative quadrat data (Chapter 2). 'Archipelago' area is derived from Table 2.1 (Chapter 2).

6.2.3 Multivariate analysis

Canonical Correspondence Analysis' (CCA) via CANOCO (ter Braak 1987—1998) was used for exploration of variation in the distribution of lifeforms across all islands. Values where assigned to each lifeform based on the percentage of representation of each within the flora. Forward selection of variables was used. For a further explanation of these techniques see Section 3.2.2.

The overall significance of the CCA ordinations was tested by Monte Carlo permutation (999 iterations) of residuals of the species after fitting co-variables and environmental variables (ter Braak 1992).

6.3 Results

6.3.1 Forward stepwise multiple linear regression on species richness

The predictive power of the models presented increases with increasing grain and extent size (Table 5.1). Vegetation cover and the Quotient of Insularity (Chapter 3) figure prominently in most of the quadrat grain models. At the outcrop (island) grain, area becomes the predominant predictive variable. The Quotient of Insularity (QI) along with habitat heterogeneity variables (e.g. Vegetation Cover) are also of strong predictive power at this size of grain. At the largest grain, area is of greatest importance and the Quotient of Insularity (QI) has no explanatory value. Climatic variables appear to be of primarily subordinate importance at all grain and extent sizes. The affects of fire appear to be of importance in a number of models, being positively correlated with richness.

Table 6.1: Comparison of significant correlations from forward stepwise multiple linear regression to species richness at three sizes of grain and extent for the outcrop flora of the New England Batholith. P – level significance * < 0.05, ** < 0.005, *** < 0.0005, **** < 0.00005, ***** < 0.000005, ****** < 0.0000005. Values in brackets are R^2 change.

Extent	Grain =	Object	Outcrop ('Island')	Quadrat
New England Batholith			Overall Significance ******* (0.63)	Overall Significance ***** (0.35)
			+Log Island Size ****** (0.44)	+Vegetation Cover****** (0.17)
			-Quotient of Insularity ****** (0.06)	-Quotient of Insularity***** (0.07)
			+Fire *** (0.05)	+Precipitation Driest Quarter***** (0.04)
			+Vegetation Cover ***** (0.04)	+Radiation Driest Quarter* (0.03)
			-Annual Mean Temperature *** (0.02)	+Fire***** (0.02)
			+Mean Temp. Cold Quarter **** (0.01)	+Annual Mean Temperature*** (0.01)
			+Acidity (pH) * (0.01)	-AMG Northing * (0.01)

Element	Overall Significance *** (1) +Log Element Area *** (0.62) -Distance *** (0.16) -Vegetation Cover *** (0.13) -Mean Temp. Coldest Quarter ** (0.07) -AMG Easting ** (0.02) -Radiation Seasonality ** (0.001) +Annual Mean Temperature ** (0.006)	**Element One**	Overall Significance ***** (0.88) +Log Island Size ****** (0.78) -Quotient of Insularity ** (0.11)	Overall Significance ***** (0.40) -Quotient of Insularity **** (0.32) -AMG Northing ** (0.10)
		Element Two	Overall Significance **** (0.57) +Acidity (pH) ***** (0.30) +Boulders (Number & Size) *** (0.27)	Overall Significance ***** (0.65) +Mean Diurnal Range ** (0.31) +Precipitation Driest Period ***** (0.18) +Vegetation Cover **** (0.09) -Temperature Annual Range ** (0.07) +Mean Temp. Driest Quarter * (0.02)
		Element Four	Overall Significance **** (0.40) +Log Island Size *** (0.29) -Quotient of Insularity * (0.10)	Overall Significance ***** (0.43) -Quotient of Insularity ****** (0.37) -Slope ** (0.08)
		Element Five	Overall Significance ***** (0.90) +Log Island Size ****** (0.75) +Fire ** (0.10) +Temperature Range * (0.05)	Overall Significance ***** (0.60) +Vegetation Cover ** (0.34) +Faulting * (0.14) -AMG Easting ** (0.09) +Fire * (0.08)

		Element Seven	Overall Significance ***** (0.59) +Log Island Size ****** (0.22) +Vegetation Cover ** (0.12) +Annual Mean Radiation * (0.08) +Acidity (pH) ** (0.06) -Geology **** (0.05) -Quotient of Insularity ** (0.05)	Overall Significance ***** (0.29) +Annual Mean Temperature *** (0.17) +Vegetation Cover *** (0.11) +Acidity (pH) * (0.04)
Archipelago	Overall Significance ***** (0.84) +Log Archipelago Area ****** (0.71) +Protection from North West *** (0.07) -Protection from the North * (0.06)	**Backwater (BC)**	Overall significance ***** (0.55) +AMG Easting** (0.37) -Quotient of Insularity ** (0.15) -Boulder Cover * (0.07)	Overall Significance ***** (0.55) +AMG Easting ** (0.37) -Quotient of Insularity ** (0.15) -Boulder Cover * (0.07)
		Bald Rock / Girraween (BR)	Overall Significance ***** (0.90) +Radiation Coldest Quarter**** (0.51) +Radiation Seasonality ****** (0.23) -Quotient of Insularity ** (0.09) +Log Island Size **** (0.08)	Overall Significance ***** (0.50) +Vegetation Cover ***** (0.33) -Quotient of Insularity *** (0.17)
		Howell (HC)	Overall Significance ***** (0.97) +Log of Island Size ****** (0.73) -Quotient of Insularity * (0.12) +Radiation Seasonality ** (0.04) -AMG Northing ** (0.04) +Lowest Period of Radiation ** (0.03)	Overall Significance **** (0.47) +Mean Temp. Wettest Quarter ** (0.29) -Quotient of Insularity ** (0.14) -AMG Northing ** (0.08)

6.3.2 Regression on species/genus relationships

The taxon ratios plotted against area for the surrounding flora ('sea') and outcrop flora ('island') within 'archipelagos' are similar (Figures 6.1 & 6.2). However the steepness of the slopes is greater in the surrounding flora ('sea'). A paired *t*-test on individual records shows that only the species/genus ratios are significantly different (S/G $P<0.04$; S/F $P<0.33$; G/F $P<0.77$). The species/genus ratios are lower on the 'archipelagos' compared to those of the surrounding flora ('sea').

Table 6.2 summarises the results of multiple linear regression conducted at three sizes of grain and extent. Overall, only small amounts of variation are explained by the analyses. The explanatory power of the models increases with increasing grain and extent size (0 to 0.95). Neither area nor habitat effects are of major importance at the smallest grain. However, area becomes an important correlative variable in a number of the outcrop ('island') grain analyses, and the most significant explanatory variable at the largest grain. In most analyses some form of energy relationships (climatic variables) are of secondary importance.

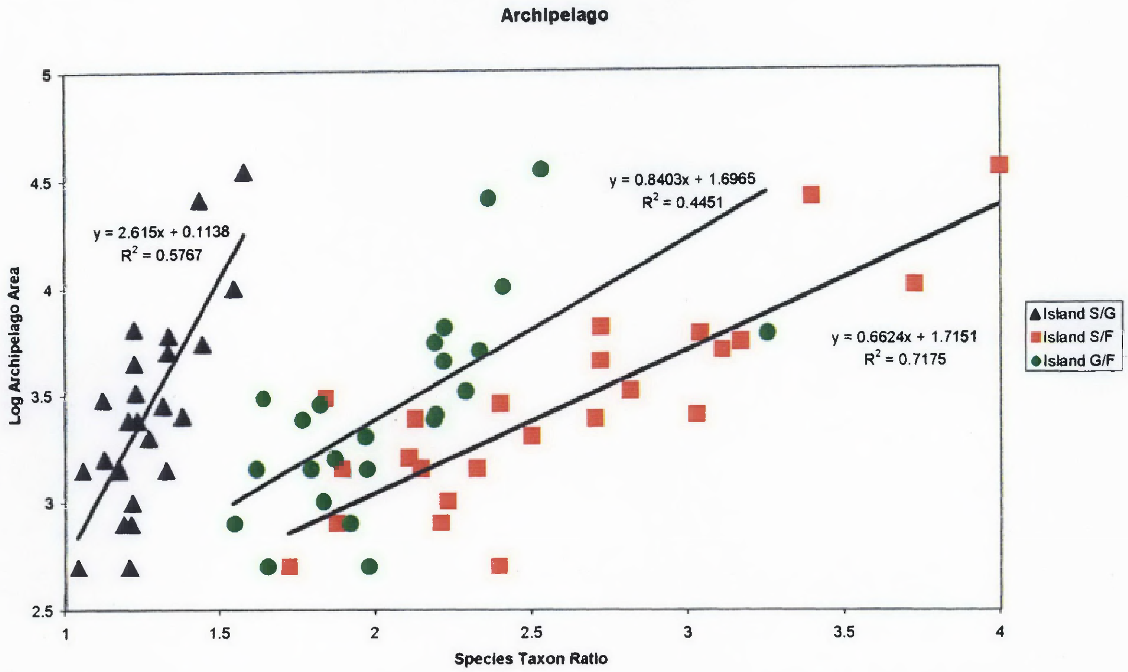

Figure 6.1: Species/Genus, Species/Family and Genera/Family ratios for virtual 'archipelagos' based on data from outcrops ('islands'). All are positively correlated with 'archipelago' area.

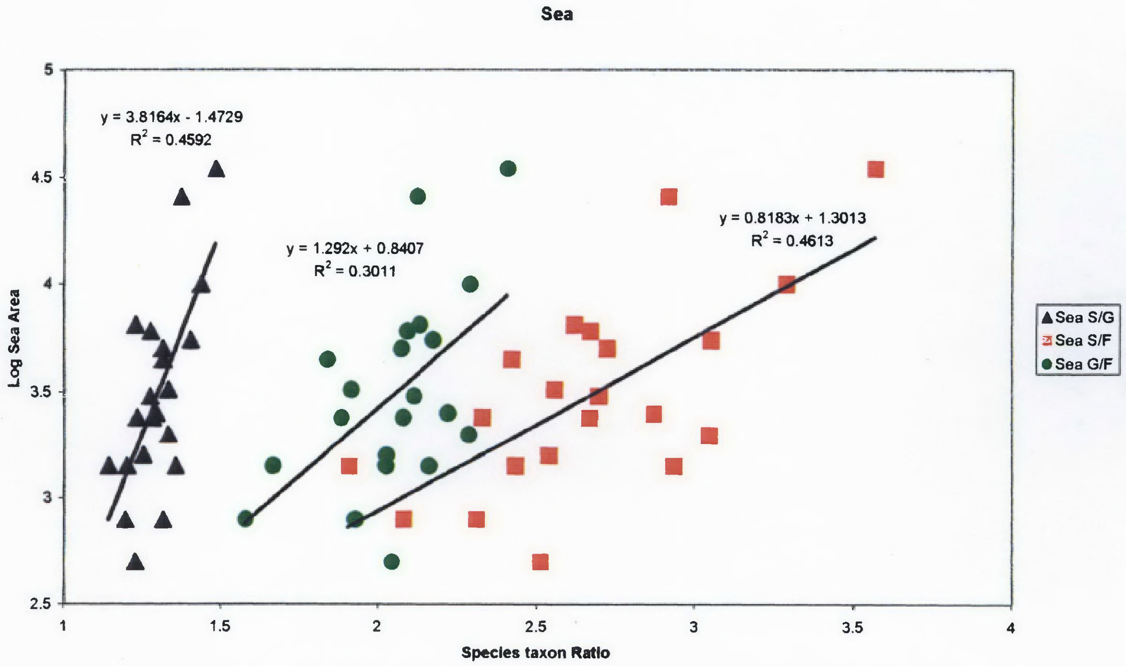

Figure 6.2: Species/Genus, Species/Family and Genera/Family ratios for the surrounding flora ('sea') of each 'archipelago'. All are positively correlated with 'sea' area.

Table 6.2: Comparison of significant correlations from forward stepwise multiple linear regression to species/genus ratio at three grain and extent sizes for the outcrop flora of the New England Batholith. P – level significance * < 0.05, ** < 0.005, *** < 0.0005, **** < 0.00005, ***** < 0.000005, ****** < 0.0000005. Values in brackets are R^2 change.

Extent	Grain =	Object	Outcrop ('Island')	Quadrat
New England Batholith			Overall Significance ***** (0.33) +Log Island Size ****** (0.18) -Average Temp. Range ****** (0.08) -Altitude *** (0.06) -Protection from South East ** (0.03)	Overall Significance ***** (0.12) +Quotient of Insularity ****** (0.09) +Boulder Cover *** (0.04)
Element	Overall Significance *** (0.95) +Log Element Area **** (0.89) +Boulder Cover * (0.06)	**Element One**	Overall Significance *** (0.55) +Log Island Size *** (0.55)	Overall Significance * (0.14) +Precipitation of the Wettest Quarter * (0.14)
		Element Two	Overall Significance *** (0.50) -Protection from South ** (0.23) +Protection from South West ** (0.14) +Clearing ** (0.11)	Overall Significance ***** (0.36) +Quotient of Insularity ***** (0.15) +AMG Easting ** (0.13) +Vegetation Cover * (0.07)
		Element Four	Overall Significance * (0.11) +Vegetation Cover * (0.11)	Overall Significance * (0.11) -Precipitation Seasonality * (0.11)
		Element Five	Overall Significance *** (0.61) +Log Island Size *** (0.61)	Overall Significance * (0.14) Radiation of the Driest Quarter * (0.14)

		Element Seven	Overall Significance *** (0.22) +Radiation Warmest Period *** (0.09) +Precipitation Wettest Quarter ** (0.07) +Habitat Heterogeneity * (0.06)	No significant variables
Archipelago	Overall Significance ***** (0.83) +Log of Archipelago Area *** (0.54) +Fire ** (0.10) +Boulder Cover * (0.07) -Precipitation Coldest Quarter ** (0.07) -Radiation of the Wettest Period * (0.05)	**Backwater (BC)**	Overall significance *** (0.72) +Log Island Size *** (0.72)	No significant variables
		Bald Rock / Girraween (BR)	Overall Significance *** (0.55) -Protection from the West *** (0.55)	No significant variables
		Howell (HC)	Overall Significance *** (0.8) Radiation of the Driest Quarter *** (0.61) Radiation of the Warmest Quarter * (0.19)	Overall Significance * (0.10) -AMG Northing * (0.10)

6.3.3 CCA of lifeform distributions

Overall, Monte Carlo significance testing (999 iterations) of the first canonical axis and the overall test on trace are highly significant ($P<0.001$) for the CCA. The first canonical axis accounts for 60.6% of the variation. Habitat Heterogeneity was the strongest explanatory variable followed by the correlated Vegetation Cover variable and finally Altitude and Outcrop Insularity (Figure 6.3). All variables are somewhat positively auto-correlated as they occur on the same side of the ordination space and are more or less projected in the same direction (Figure 6.3). Shrubs are most strongly positively associated with an increase in each of the significant variables. The occurrence of Hemi-parasites is weakly positively correlated but Herbs, Vines and Trees are all negatively correlated with an increase in each of the significant variables.

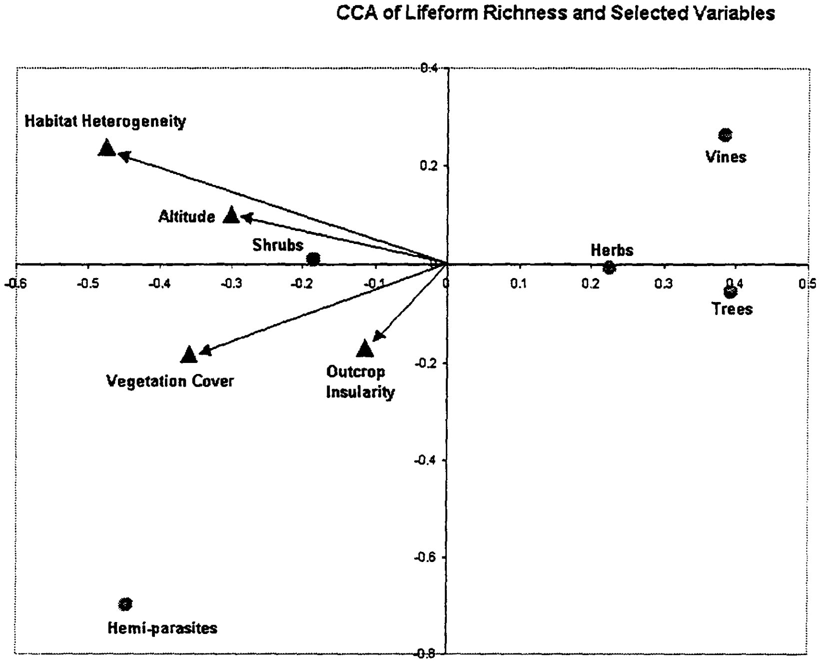

Figure 6.3: CCA ordination of selected variables on the distribution of life forms on the 217 outcrops ('islands'). Habitat Heterogeneity $P<0.001$; Altitude $P<0.001$; Vegetation Cover $P<0.001$; Quotient of Insularity $P<0.005$.

6.4 Discussion

6.4.1 Species richness

Overall, the predictability of models is increased with increasing grain size. This is probably due to the effects of local heterogeneity being averaged out at broader scales (Wiens 1989; Reed *et al.* 1993; Bellehumeur *et al.* 1997). Essentially, extreme values disappear and variation occurring at smaller spatial scales is filtered out (Bellehumeur *et al.* 1997). It is evident from the results (Table 5.1) that many of the significant variables that account for much of the variation in species richness are indeed scalar dependent both in terms of grain and extent size. At the quadrat grain size there is a mixed response in the most significant explanatory variables. There is a positive increase in species richness with Vegetation Cover, and in general, with an increase in temperature but a lowering of species richness as the degree of insularity increases. These three types of variables account for the majority of significant correlations at the quadrat grain size. The Quotient of Insularity is the most common significant variable occurring in six of the nine models. Outcrop ('island') area does not appear as a significant explanatory variable in any of the analyses performed at this size of grain.

Using the outcrop ('island') as the grain size, area becomes the most consistent explanatory variable. The log of outcrop area accounts for most of the explanatory variance in six of the nine models and occurs as a subordinate variable in a seventh model. Vegetation Cover only occurs as a subordinate variable in two models. Although the Quotient of Insularity is not of major explanatory value in any of the models, it does occur in seven out of the nine models as a subordinate variable. Although area is overall the most significant explanatory variable, there is evidence to suggest that its influence is dependent on extent size. Of the nine models area is unimportant in two and of minor significance in a third. These models constitute three of the four smallest cumulative areas and species pool sizes. Hence, at this level of grain size, some evidence is provided corroborating the findings of Deshaye and Morisset (1988), who found the strength of the relation of area depends on the size of the habitat species pool.

At the largest grain, area becomes the most significant correlative variable explaining a large amount of variation. The Quotient of Insularity is unimportant at this size of grain. Vegetation Cover is of subordinate importance in one of the two models and for the first time the relationship is negative. Also for the first time the degree of isolation (distance) becomes significant with greater isolation decreasing species richness.

Of note is the significant explanatory value of the Quotient of Insularity both at the quadrat and outcrop ('island') grain sizes and across the three extent sizes. As discussed in Chapter 3, the Quotient of Insularity varies greatly over the batholith. As insularity increases species richness decreases. This factor is shown to have a significant underlying correlative effect on richness that is independent of extent, and to a large degree, grain size. Thus reinforcing the need to quantify and understand the distribution of insularity across a landscape of continental insular systems, as this factor may play an important role in species richness (Chapter 3).

Böhning-Gaese (1997) believed that large spatial scales emphasize variables related to available energy such as temperature. Present analyses show that although energy variables were rarely of major explanatory value, they were significant at all sizes of grain and extent. At small spatial scales energy variables are rarely tested for their effects. These results show that even at a small grain and extent available energy may still play a significant, if only minor, role in explaining variance in richness studies.

Fire, although not of major importance has been found to be a significant variable in a number of models of species richness across various scales. This evidence corroborates results presented in Chapters 3 and 9 that show fire being an important issue affecting species richness across the New England Batholith.

6.4.2 Species/genus ratios

The species/genus ratios for all 'archipelagos' and the surrounding floras ('seas') (Figures 6.1 & 6.2) are very similar ('archipelago' average 1.27; sea average 1.30). This difference though small is consistent and the outcrop insular systems have a significant lowering of the species/genus ratio. The results confirm the results of other studies that show lower species/genus ratios in insular systems (Simberloff 1970; Linhart 1980).

Overall, much less variance was explained by regression on species/genus ratios than was obtained for richness. Again, with a fixed quadrat sampling method, area should still explain some variance in species/genus ratios at the level of individual quadrats if it is of overriding importance. Area was not a significant correlative value in any of the quadrat grain size models. The Quotient of Insularity (QI) was of major importance in explaining variance in two models at the quadrat grain size. In contrast to species richness, insularity had a positive effect, increasing the species/genus ratio. In other words, as insularity increases there is an increase in the number of species per genus possibly indicating speciation with increasing isolation from the surrounding floras ('seas'). Again, this evidence indicates that the level of insularity and its variance across the landscape needs to be quantified (Chapter 3). Insularity is scale dependent as it does not appear in any of the models presented based on larger grain sizes.

As with species richness, energy variables (radiation, temperature etc.) are significant in explaining variance at all sizes of grain and extent. Thus emphasising their importance in any analyses of pattern at whatever scale. Unlike the investigations of species richness, fire was found to be significant in only one model. The positive correlation of fire with increasing species/genus ratios indicates that at least at this grain size, fire may play a role in increasing the number of species per genus. This may be due to shared congeneric fire responses being reinforced (i.e. phylogenic predisposition).

6.4.3 Lifeform richness

The richness of lifeform groups across the New England Batholith is significantly affected by habitat heterogeneity, vegetation cover, altitude and outcrop ('island') insularity (QI). Although tested for, area was found to be of no statistical significance. The lifeforms reacted differently to each of the significant variables. Shrub richness was positively correlated with each of the significant variables. However, Herbs, Vines and Trees were all negatively correlated with all of the significant variables. These findings corroborate those highlighted in Chapter 3 and Chapter 4 which show herbs and trees being more prevalent at less insular sites and site insularity decreasing towards the west of the batholith where altitudes are lower. Significantly, this analysis highlights that individual groups of species will react differently to correlates of species richness in an insular system. Such results have been commonly found and many examples have been given in the introduction to this chapter. Although not elaborated on in this research, these results indicate that an important extension of this work would be to investigate the relationship of scale with correlates of individual guild richness.

6.4.4 Conclusion and further research

Variables relating to available energy or resources such as temperature, rainfall, radiation loads, and soil acidity etc. have all been shown to be significant correlations at all grain and extent sizes. Such variables are most often left out of this type of investigation, and in particular, are rarely thought of at smaller scales. Yet the results presented here indicate such variables are important at all scales of investigation. The Quotient of Insularity was important in a number of models. This emphasises the importance of allowing for the lack of insularity in continental insular systems, as this factor significantly affects richness levels across the batholith (Chapter 4).

The species/genus ratios of the floras on the outcrops ('islands') of the New England Batholith are lower than those of the surrounding floras ('seas'), yet not as low as would be predicted by random sampling of a large species pool. As with richness, area is ruled out as the most significant factor correlated to species/genus ratios, even though, at larger grain sizes it was the most significant variable. Scale was noted to affect the significance of a number of variables. Insularity was an important factor in species/genus ratio analyses.

It is clear that scale is of great importance when analysing and understanding the effectiveness of correlations (Addicott *et al.* 1987; Wiens 1989; Kotliar & Wiens 1990; Lord & Norton 1992; Reed *et al.* 1993). Without testing for scale one cannot be sure that the results obtained are correct and this can lead to incorrect hypotheses. The effects of scale need to be tested for in any biogeographic phenomenon. Correlated variables affect different species or guilds in different ways, as has been shown briefly in the lifeform richness analysis performed here. For a comprehensive understanding of the effects of scale, analyses need to be performed on groups of species, which may posses similar lifeform traits or dispersal mechanisms.

In a sense many aspects of biogeography have come full circle. Brown (1986) stated that the importance of the equilibrium theory is that it shifted the emphasis of biogeography from reconstructing life histories to understanding processes that determine richness. However, now that processes are beginning to be understood and many limitations are known, their affects on individuals and their life histories are now of importance.

Chapter 7: Nested Species Subsets and Species Saturation on Granitic Outcrops

Chapter 7

Nested Species Subsets and Species Saturation

7.1 Introduction

Nested species subsets describe the tendency for species to have non-random distribution patterns, whereby larger more species-rich islands contain all species present on the next less species-rich island (Paterson & Atmar 1986). Species saturation describes the degree to which spatial structure or the arrangement of islands effects species richness (Quinn & Harrison 1988). Both are methods in which the nature of species richness and species distribution patterns can be described. Wright and Reeves (1992) demonstrated a significant negative correlation between species saturation and nestedness indicating that the two measures may describe interrelated processes effecting patterns of species richness across the landscape. Both measures describe how richness may be derived and maintained by non-stochastic (orderly) processes.

The recognition of nested patterns in species richness was thought to have originated from the studies of Darlington (1957) (Heaney 1984; Yiming *et al.* 1998). Similar patterns were described in a number of research papers studying island biogeography from the mid-1970s to the early 1980s (Abele & Patton 1976; Helliwell 1976; Browne 1981; Diamond 1982; Diamond & Gilpin 1982; Simberloff & Abele 1982; Schoener & Schoener 1983b; Blake & Karr 1984; Heaney 1984; Lomolino 1984; Simberloff & Gotelli 1984; Jones *et al.* 1985). Diamond (1982) appears to be the first to have formally described the orderliness of species pool decline as a subset pattern and later Diamond and Gilpin (1982) used the term 'nestedness'.

Patterson and Atmar (1986) were the first to concentrate research solely on nestedness patterns and to try to describe and compare them statistically. The study of nested subsets arose from studies of the Equilibrium Theory and hence this topic naturally follows the work presented in the previous chapter (Chapter 6). Nested patterns represented orderliness in nature. Prior to the formal introduction of nestedness, much research after the rise of MacArthur and Wilson's (1967) theory of island biogeography

(Chapter 6), concentrated on the underlying stochasticism of patterns precluding or hindering the development of equilibrium (Cutler 1991; Whittaker 1992; Atmar & Patterson 1993). Much of the initial research concentrated on describing patterns of nestedness in terms of islands of decreasing area (Crowell 1986; Patterson & Atmar 1986). However, by evaluating nestedness strictly by richness, no *a priori* assessments of the underlying importance of particular environmental factors are made (Patterson 1990). Nestedness is thus an area independent concept (Whittaker 1992; Cook 1995). Even so, some researchers still equate ‘rich’ with ‘large’ in nestedness investigations, assuming that once a nested pattern is shown, proof that larger areas contain more species is the logical conclusion (Wright & Reeves 1992; Cantrell & Cosner 1994; Yiming *et al.* 1998).

Non-nested patterns of distribution were predicted by Diamond and Gilpin (1982), whose supertramp theory predicts that some species are confined to small, less rich islands and are absent from the most species rich islands. Wright and Reeves (1992) in producing their index of nestedness theorized that some patterns could be significantly less nested than random. Endemic species were shown to reduce nestedness (Cook & Quinn 1995). Introduced predators were thought to cause a non-nested pattern in Guam (Perry *et al.* 1998). Wright *et al.* (1998) found that experimental studies showed statistically significantly non-nested or anti-nested patterns but did not find any non-experimental examples. Some evidence suggests that different groups of taxa show greater or lesser nestedness in the same systems (Schoener & Schoener 1983b; Patterson 1990; Cook 1995; Kadmon 1995). However, Cutler (1991) and Wright *et al.* (1998) were unable to find significant differences in nestedness across taxa.

Overall, it appears that some degree of nestedness is the norm in nature and is widespread in natural and anthropogenically sub-divided habitats across a range of taxa, both plants and animals (Patterson & Atmar 1986; Paterson 1990; Bolger *et al.* 1991; Cutler 1991; Wright & Reeves 1992; Atmar & Patterson 1993; Cook 1995; Downs & Wirminghaus 1997; Cook & Quinn 1998; Ganzhorn 1998; Hoekstra & Fagan 1998; Patterson *et al* 1998; Perry *et al.* 1998; Wright *et al.* 1998). While nestedness may be common, the degree of nestedness varies greatly (Cook & Quinn 1998). Debate over the causes of nestedness still occurs. This debate is primarily over the effects of extinction and colonisation (Patterson & Atmar 1986; Patterson 1990; Bolger *et al.* 1991; Cutler

1991; Wright & Reeves 1992; Cook & Quinn 1995). Wright *et al.* (1998) found in their comprehensive investigation that nestedness was more prevalent in extinction prone systems. Cook and Quinn (1998) summarised the major factors that are thought to promote nested patterns in species distributions. In theory, nestedness may result from; selective extinction, deterministic patterns of colonisation in which the smallest or most remote sites are only inhabited by the best dispersers, nested habitats or niche space, or passive sampling. Ganzhorn (1998) theorized that nested patterns are produced in biotas that share a common biogeographic history, occupy a similar environment, and have a hierarchical organization of niche relationships.

The flora of granitic outcrops on the New England Batholith of eastern Australia represent a biogeographic system that incorporates all of Ganzhorn's (1998) criteria for nested patterns. Nested species subsets and species saturation are relatively new means by which patterns of biodiversity and richness across a landscape may be investigated. It is the aim of this chapter to investigate the patterns of species nestedness and saturation across the batholith at different grain and extent sizes, in order to evaluate how these may influence or maintain species richness and diversity. Specific questions include:

- Are statistically significant nested patterns in floristic species richness present on granitic outcrops of the New England Batholith?
- Does the spatial structure of outcrops affect species richness patterns as determined by species saturation?
- Are nested subset and species saturation patterns effected by the scale of the investigation?
- How do nested subset and species saturation patterns compare with those found elsewhere?
- Are differences in nested subset and species saturation patterns correlated with environmental variables?
- Is there a correlation between the measures of nestedness and species saturation?

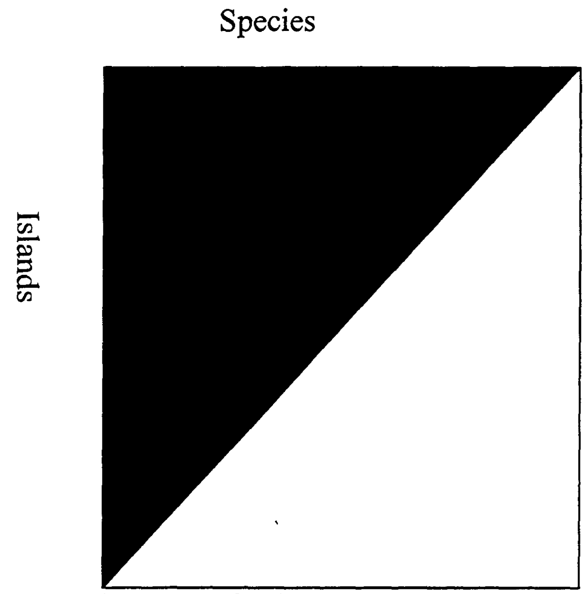

Figure 7.1: An example of a perfectly nested pattern of species occurrences. The black area denotes species presences. Note the richest site contains a full complement of all the species found in all less rich sites. Species abundances should be higher in the top left hand corner.

7.2 Methods

The terminology relating to spatial scale is defined in Section 5.2.

7.2.1 Analysis of nested subset patterns

The metric N_c and its standardization C (Wright & Reeves 1992) are the indices chosen here to describe nested subsets. The index C is a quantitative measure of nestedness whose statistical properties are well understood (Wright & Reeves 1992; Cook & Quinn 1995; Yiming *et al.* 1998). Unlike earlier measures of nestedness, including Atmar and Patersons' (1993) T, C is not affected by the size of the matrix (Wright & Reeves 1992; Wright *et al.* 1998; Yiming *et al.* 1998), nor is it based on any underlying assumptions of causality (Wright *et al.* 1998). N_c takes into account ties between sites in species richness in assessing nestedness (Wright *et al.* 1998). N_c is the total number of times a species presence is predicted by its presence at a richer site. It is directly related to the conditional probability of a species being present at a site given that it is present at a more depauperate site (Wright & Reeves 1992). As nestedness and matrix rank increase the value of N_c increases. In addition, Wright *et al.* (1998) have shown that, compared to other measures of nestedness, N_c is weakly related to matrix fill. N_c can be calculated using the equation below:

$$N_c = \frac{1}{2}\sum_{j=1}^{s} J_j\left(J_j - 1\right)$$

Where J_j is the total incidence of species 'j' (number of times it occurred).

N_c is standardized so that it is not affected by the size of the matrix using the following equation:

$$C = \frac{Nc - E\{Nc\}}{\max\{Nc\} - E\{Nc\}}$$

Where *E {N$_c$}* is the expected N_c and the *max {N$_c$}* is the maximum value for N_c.

C is '0' when nestedness does not differ from expectation and is '1' for perfect nestedness. Wright and Reeves (1992) have indicated that negative values are possible and these suggest that the matrices are less nested than random expectations, such as might be expected in the checkerboard patterns of Diamond (1975) and Diamond and Gilpin (1982).

If the presence-absence matrix is arranged as 'K' rows of sites and species in 'S' columns (Figure 7.1), then the expected value of N_c ($E\{N_c\}$) is calculated as the number of species shared by sites '*i*' and '*m*', is R_iR_m/S, and summing over all pairs of sites. R_i is the richness at site '*i*'. $E\{N_c\}$ is the value for N_c that would be expected by the null hypothesis of random distribution. This is calculated using the following equation:

$$E\{Nc\} = \frac{1}{S} \sum_{i+1}^{K-1} \sum_{M=i+1}^{K} R_i R_m$$

The maximum value for N_c is derived using:

$$\max\{Nc\} = \sum_{i=1}^{K} (i-1) R_i$$

Max $\{N_c\}$ is the maximum value for N_c possible with the given species richness totals for each site.

Wright and Reeves (1992) discuss the use of Cochran's Q statistic and state that N_c is completely determined by the observed incidence totals, and because the null hypothesis of equiprobable species implies that all species should have equal incidence totals, a test for equality of incidence totals constitutes a test of the significance of N_c or C. The Cochran Q test is an extension of McNemar's *Chi-squared* test for changes in frequencies or proportions to dependent samples (StatSoft 1984—1995). It tests whether several matched frequencies or proportions differ significantly among themselves. Cochran's Q is used here to evaluate the significance of C.

7.2.2 Cumulative-species-area relations and species saturation

The cumulative species-area relations for each inclusive dataset have been calculated in two ways. Within each data set the objects ('archipelagos', Elements, outcrops) were ranked in size. Cumulative curves were plotted by beginning with the largest object and adding successively smaller objects, and by starting with the smallest object and adding progressively larger objects. Both curves pass through the origin. The small-to-large curve represents a curve in which the greatest number of objects is initially added. This maximizes the degree of sub-division and minimizes the mean object size (Quinn & Harrison 1988). Conversely the large-to-small curve minimizes the degree of sub-division and initially maximizes the mean object size. This represents the minimum number of objects required to add up to a cumulative area (Quinn & Harrison 1988). If spatial structure does not affect diversity the two curves will be the same. Saturation indices are calculated as the ratio of the area under the small-islands-first cumulative species-area curve to the area under the large-islands-first cumulative species-area curve.

7.2.3 Forward stepwise multiple linear regression

Forward Stepwise Multiple Linear Regression of values of *C* and saturation scores against the variables used in Chapter 6 (Section 6.2.2) was performed. These analyses were conducted in order to assess any significant correlations with nestedness.

7.3 Results

7.3.1 Nested species subsets

Analysis of nestedness across the New England Batholith at different grain and extent sizes yielded a wide range of results (Tables 7.1—7.3). The lowest *C* scores were in fact weakly negative (-0.098), a feature that is theoretically possible in checkerboard communities but one that is rarely found (Cook & Quinn 1995; Hunter 1999c). However, only the Mount Lookout (ML) 'archipelago' was statistically significant in the negative (-0.014) (Table 7.1). The highest recorded value for *C* was the Torrington (TT) 'archipelago', which was as high as 0.489 (Table 7.1). Wright and Reeves (1992) considered those values above *c.* 0.6 to be high values of nestedness and those below 0.3 to be low and other values to be medial. Using such broad classifications it is noted that none of the values obtained could be considered of high nestedness. Around 62% (24) of *C* values recorded from outcrops of the New England Batholith show low nestedness with the remaining 38% (18) of medial value (Figure 7.14). The granitic outcrops show low relative nestedness even when comparisons are made between the same floristic groupings (communities and Elements) or even sites from the same outcrops ('islands') (Table 7.3).

Table 7.1: Relative nestedness index, *C*, and associated probability values (*Q*) for all 'archipelagos' with more than two sampled outcrops ('islands').

'Archipelago'	***C***	**No. of Islands**	**Cochran's *Q***	***P*<**
Backwater (BC)	0.340	12	99.26	0.000000
Bolivia Hill (BH)	0.344	10	34.18	0.000000
Butterleaf (BL)	0.208	7	35.78	0.000000
Bald Rock/Girraween (BR)	0.279	17	88.02	0.000000
Chaelundi (CH)	-0.098	3	4.61	0.099918
Demon (DM)	-0.090	3	3.40	0.180000
Eagle Creek (EC)	0.288	8	32.20	0.000037
Flaggy Range (FR)	0.349	20	133.72	0.000000
Gibraltar Range (GR)	0.366	15	138.30	0.000000
Howell (HC)	0.458	15	149.74	0.000000
Ironbark (IB)	0.247	8	41.05	0.000001
Mount Jondol (JB)	0.042	4	3.52	0.318759
Kwiambal (KL)	0.304	9	20.10	0.009985
Kings Plains (KP)	0.354	9	31.47	0.022496
Moonbi (MB)	0.427	3	29.40	0.000000
Mount Lookout (ML)	-0.014	3	48.32	0.022496
Parlour Mountains (PM)	0.352	6	7.60	0.000000
Severn River (SR)	0.285	11	141.01	0.000000
Torrington (TT)	0.489	31	124.27	0.000000
Warrabah (WB)	0.316	13	56.94	0.000000
Willows (WW)	0.217	4	15.16	0.001689
Yarrowyck (YH)	0.302	4	30.75	0.000001

Table 7.2: Relative nestedness index, *C*, and associated probability values (*Q*) for all higher level grain sizes. Elements 3 and 8 are represented by the 'archipelagos' Gibraltar Range (GR) and Howell (HC) (Table 7.1).

Grain	*C*	No. of Samples	Cochran's *Q*	*P* <
NE Batholith	0.228	216 outcrops	134.13	0.000000
Element	0.277	9 Elements	666.58	0.000000
Element 1	0.347	18 outcrops	153.12	0.000000
Element 2	0.205	25 outcrops	132.57	0.000000
Element 4	0.227	40 outcrops	158.05	0.000000
Element 5	0.272	18 outcrops	198.31	0.000000
Element 7	0.328	71 outcrops	193.87	0.000000
Community	0.281	27 communities	796.15	0.000000
'Archipelago'	0.212	24 'archipelagos'	480.11	0.000000

Table 7.3: Relative nestedness index, *C*, and associated probability values (*Q*) for all outcrops ('islands') with five or more plots.

Outcrop (Island)	*C*	No. of Quadrats	Cochran's *Q*	*P* <
BR5O	0.198	7	25.03	0.000339
BC12O	0.438	6	14.08	0.015200
BC8O	0.232	6	11.39	0.044562
BR11O	0.189	6	10.09	0.022536
BR17O	0.171	6	10.90	0.027716
BR18O	0.204	6	25.98	0.000090
GR10O	0.268	6	28.54	0.000090
HC14O	0.296	6	0.17	0.673557
HC5O	0.336	6	11.57	0.041134
MB2O	0.454	6	6.83	0.145074
SR5O	0.310	6	21.42	0.000676
BC4O	0.220	5	2.14	0.709769
BC7O	0.150	5	10.53	0.032419
BL7O	0.189	5	11.39	0.022536
BR15O	0.195	5	10.90	0.027716
IB1O	0.454	5	6.83	0.145074

7.3.2 Cumulative-species-area relations

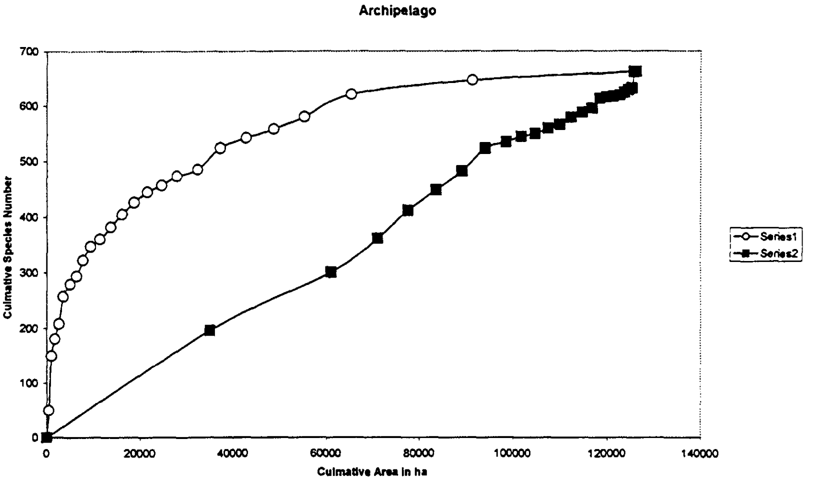

Figure 7.2: Cumulative species-area curves for the 24 'archipelagos'. Circles = 'archipelagos' ranked smallest-to-largest. Squares = ranked largest-to-smallest.

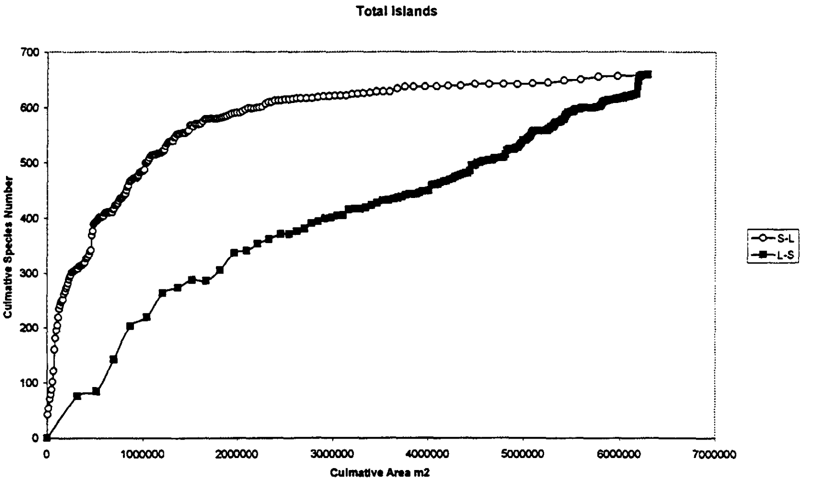

Figure 7.3: Cumulative species-area curves for all outcrops ('islands') (217). Circles = outcrops ranked smallest-to-largest. Squares = ranked largest-to-smallest.

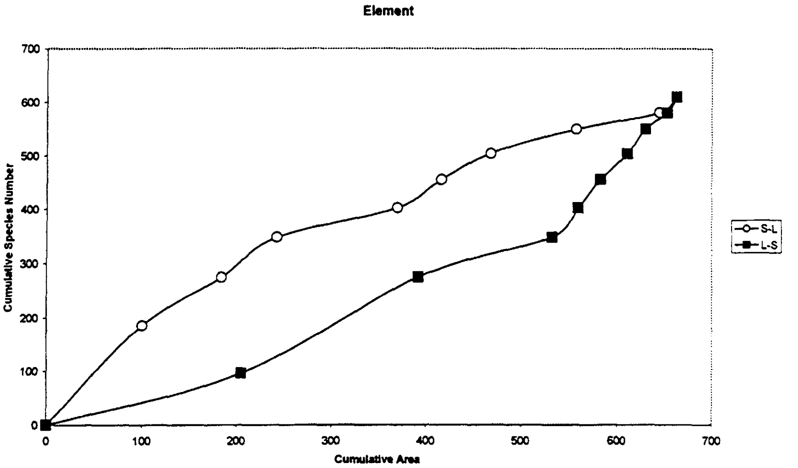

Figure 7.4: Cumulative species-area curves for the 9 Elements (Chapter 4). Circles = Elements ranked smallest-to-largest. Squares = ranked largest-to-smallest.

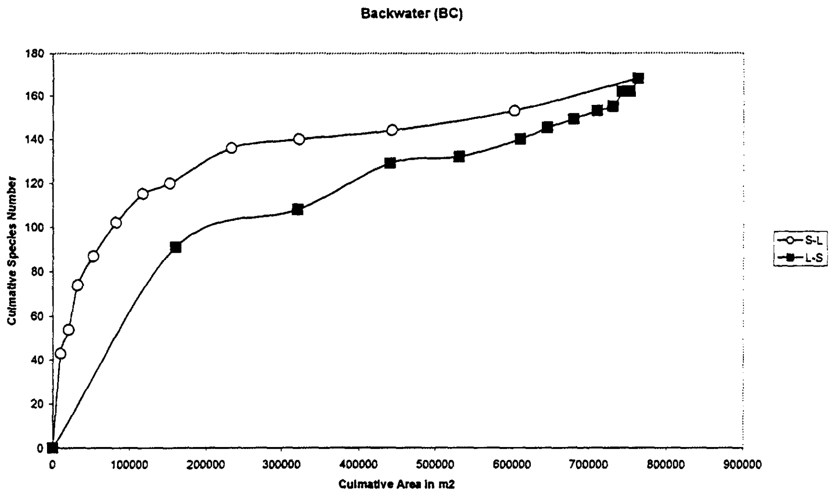

Figure 7.5: Cumulative species-area curves for the outcrops at Backwater (BC). Circles = outcrops ranked smallest-to-largest. Squares = ranked largest-to-smallest.

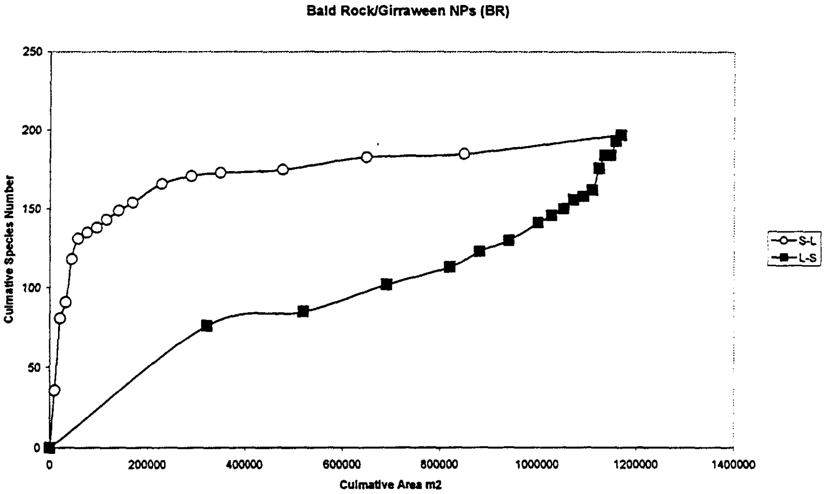

Figure 7.6: Cumulative species-area curves for the outcrops at Bald Rock (BR). Circles = outcrops ranked smallest-to-largest. Squares = ranked largest-to-smallest.

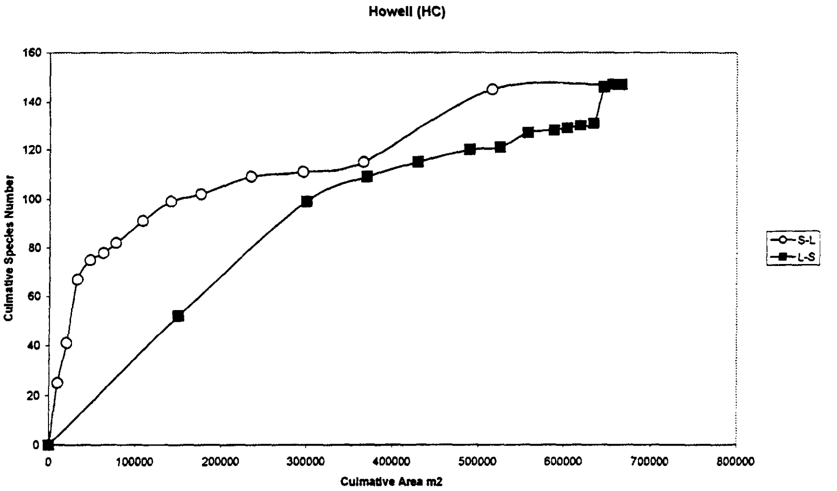

Figure 7.7: Cumulative species-area curves for the outcrops at Howell (HC). Circles = outcrops ranked smallest-to-largest. Squares = ranked largest-to-smallest.

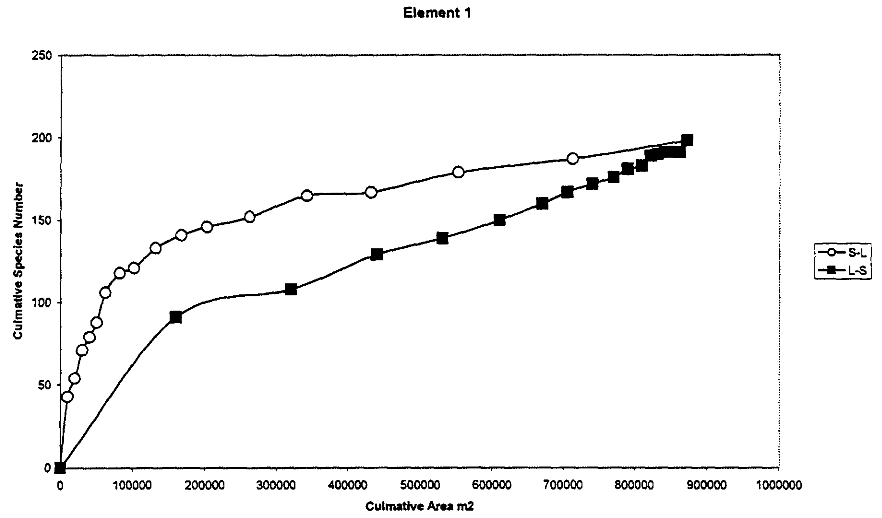

Figure 7.8: Cumulative species-area curves for the outcrops in Element 1. Circles = outcrops ranked smallest-to-largest. Squares = ranked largest-to-smallest.

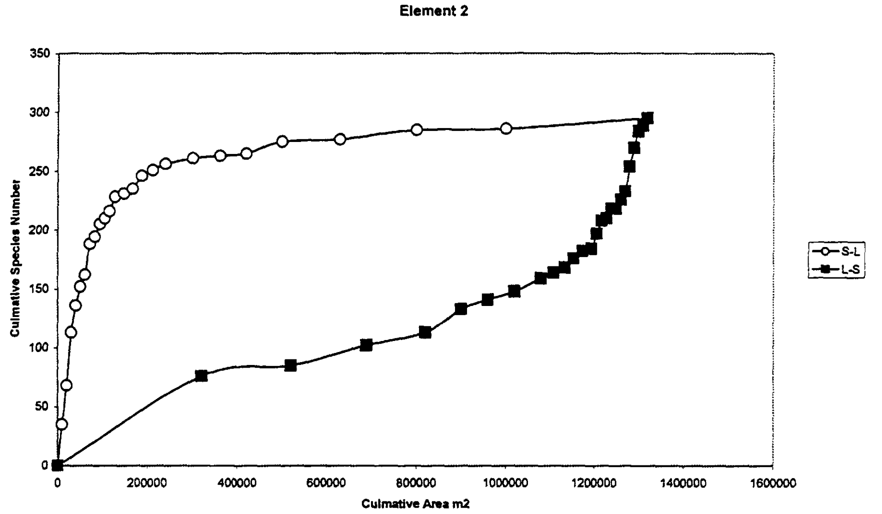

Figure 7.9: Cumulative species-area curves for the outcrops in Element 2. Circles = outcrops ranked smallest-to-largest. Squares = ranked largest-to-smallest.

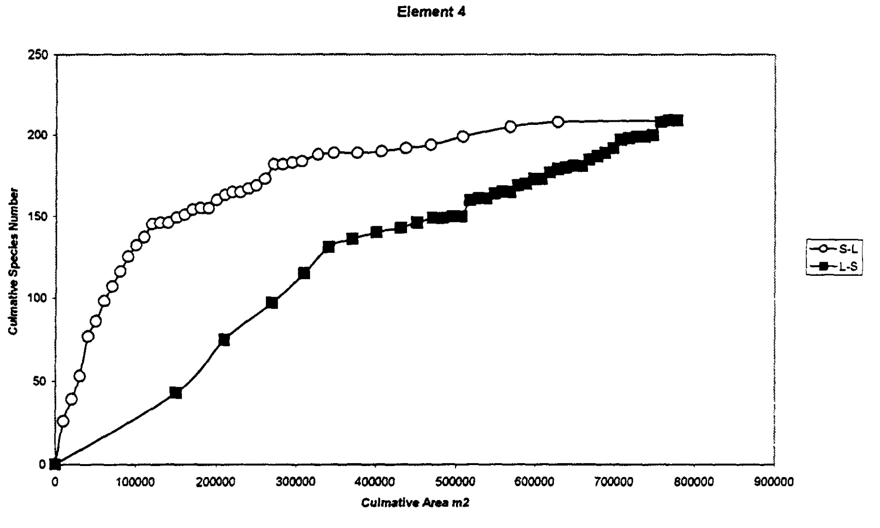

Figure 7.10: Cumulative species-area curves for the outcrops in Element 4. Circles = outcrops ranked smallest-to-largest. Squares = ranked largest-to-smallest.

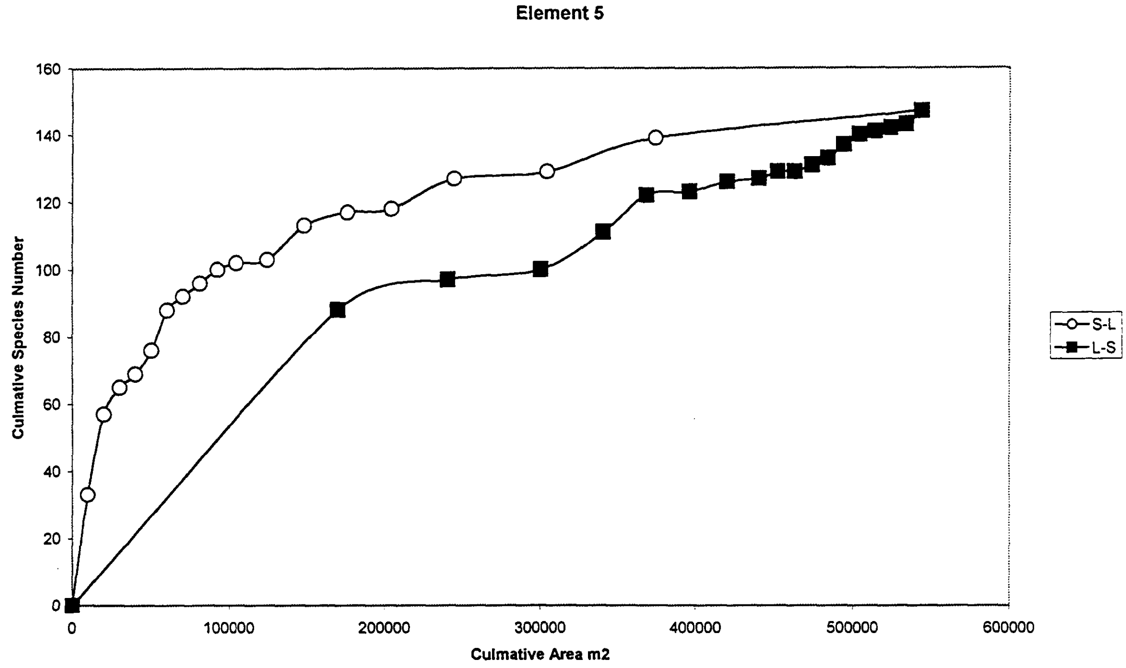

Figure 7.11: Cumulative species-area curves for the outcrops in Element 5. Circles = outcrops ranked smallest-to-largest. Squares = ranked largest-to-smallest.

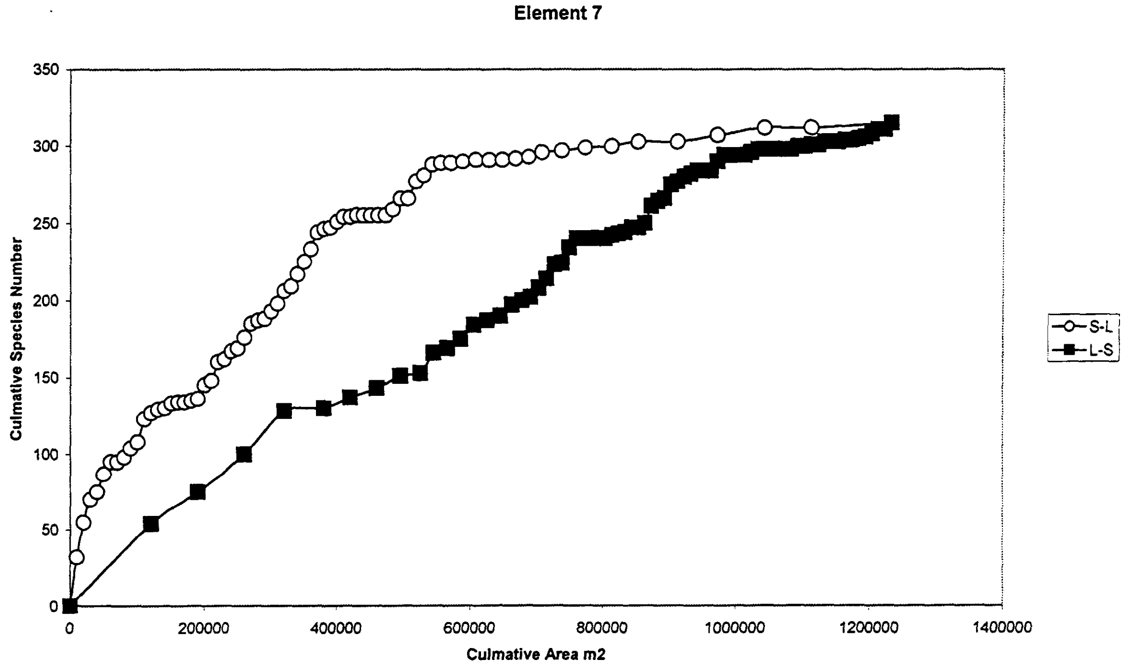

Figure 7.12: Cumulative species-area curves for the outcrops in Element 7. Circles = outcrops ranked smallest-to-largest. Squares = ranked largest-to-smallest.

Table 7.4: Saturation indices calculated as the ratio of the area under the small-islands-first cumulative species-area curve to the area under the large-islands-first cumulative species-area curve.

Extent	**Saturation Index**
All 'archipelagos'	0.896475
All Elements	0.755072
New England Batholith Outcrops ('Islands')	0.747947
Element 1 Outcrops ('Islands')	0.765502
Element 2 Outcrops ('Islands')	1.126769
Element 4 Outcrops ('Islands')	0.923417
Element 5 Outcrops ('Islands')	0.781553
Element 7 Outcrops ('Islands')	0.859015
Backwater (BC) Outcrops ('Islands')	0.788666
Bald Rock/Girraween NP (BR) Outcrops ('Islands')	0.979806
Howell (HC) Outcrops ('Islands')	0.756614

All the cumulative species-area relationships regardless of extent or grain sizes were consistent in the results presented (Figures 7.2—7.12; Table 7.4). The small-to-large cumulative species-area curves rise quickly with inclusion of the smallest islands and remain consistently above those of the large-to-small curves. The ratios of the integrals of the small-to-large over the large-to-small curves constitute a single figure index for the effect of subdivision on species richness (Quinn & Harrison 1988). The larger the number the stronger the effect of subdivision on species richness. The effect of subdivision on species richness is least pronounced in the analysis of all outcrops ('islands') surveyed within the New England Batholith with the Element level analysis (9 groups) and the Howell (HC) 'archipelago' (Table 7.4). Element 2 has by far the most significant effect of subdivision on richness with Bald Rock (BC) and the 'archipelago' (24 groups) wide analysis. The results are unrelated to scale.

7.3.3 Forward stepwise multiple linear regression

Forward Stepwise Multiple Linear Regression analyses were performed on values of *C* and saturation index scores. Despite using all criteria available no significant correlations with *C* or saturation could be found. A significant negative correlation occurs between the saturation index and *C* (Figure 7.13). This indicates that low nestedness favours the many small reserves of the Single-Large-Or-Several-Small reserves (SLOSS) debate.

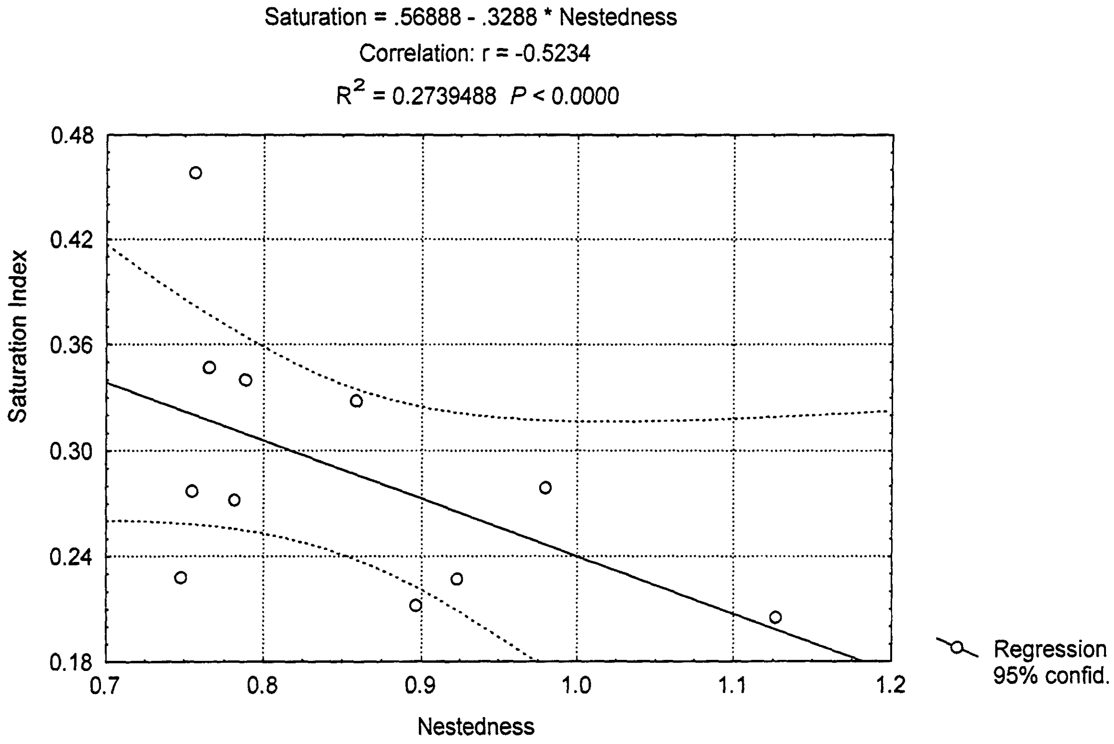

Figure 7.13: Nestedness (*C*) versus the saturation index. There is a significant negative relationship between the saturation index and nestedness. Comparisons are based on results from Tables 7.2 and 7.4.

7.4 Discussion

7.4.1 Nested species subsets

Compared to previously published *C* values, those obtained from the granitic outcrop flora of the New England Batholith are of low nestedness (Figure 7.14). The highest derived value was 0.489, which is considered to be medial by Wright and Reeves (1992). No matrix combinations were highly nested and most (60%) were of low nestedness. Values greater than 0.8 have been recorded in the literature (Wright & Reeves 1992; Cook 1995; Cook & Quinn 1995; Yiming *et al.* 1998). Although three of the *C* values (CH, DM & ML) were anti-nested, only one (ML) was significantly so (Table 7.1). Cook (1995), Cook and Quinn (1995) and Hunter (1999) both present some negative *C* values. However only Cook and Quinn (1995) and Hunter (1999c) give statistical significance for their results, all but one of those reported were non-significant (Hunter 1999c). Despite their negative values and relatively low nestedness, granitic outcrops are still generally nested and significantly so. In addition, it appears that the scale of observation both in terms of grain and extent did not overly effect the spread of *C* values. However it is noted that the anti-nested scores occurred on the three smallest datasets. Wright *et al.* (1998) found that reducing the size of samples made them more heterogeneous. This finding may explain the anti-nested scores that were non-significant for two of the datasets.

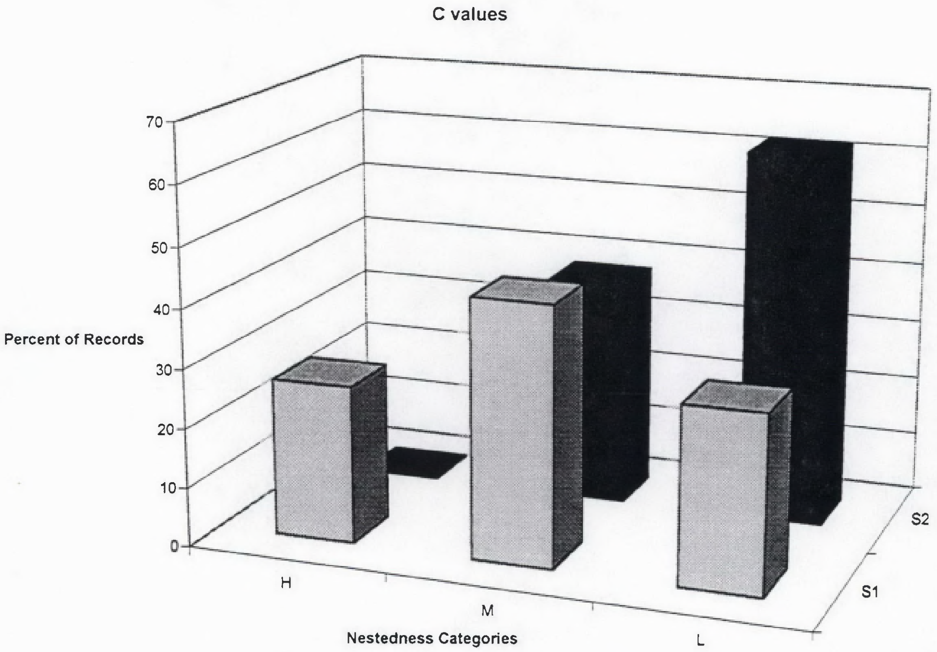

Figure 7.14: Comparison of published nestedness (*C*) values in the high (>0.6), medium (0.3-0.6) and low (>0.3) categories. S1 = *C* values obtained from Wright and Reeves (1992), Cook (1995), Cook and Quinn (1995), and Yiming *et al.* (1998). S2 = data presented here. Note granitic outcrops are of comparatively low nestedness.

Atmar and Patterson (1993) derived a number of reasons for relatively low nested scores and these included; post isolation immigration, presence of a fundamental disjunction in the historical evolution of community structure, competitive exclusion, or the presence of unique ecogeographical features. Perry *et al.* (1998) also found that introduced predators might disrupt nested patterns. Additionally, Cook and Quinn (1995) found that endemic species were more likely to be on species poor islands thereby reducing overall nestedness. This is in contrast to many Areographic analyses that show endemics are more likely to occur in species rich sites (e.g. Hengeveld 1990) (Chapter 8). Understanding the reasons for deviations from high nestedness are of importance in understanding the processes that effect diversity within the Batholith. The relatively low nestedness values for the New England Batholith are difficult to interpret in the light of previous investigations.

Disjunction in the historical evolution of community structure are unlikely, as the New England Batholith forms a single unit and this would not explain the low nested values across all grain and extent sizes. Similarly, it would be unreasonable to assume that there are unique ecogeographical features across all grains and extents. Goats and rabbits are introduced pests that are found across the batholith and grazing was found to be of significance in affecting insularity (Chapter 3). However, no factors recorded on a site basis including grazing, outcrop size or isolation were correlated with *C*. It is possible that competitive exclusion may account for lower nested scores in some situations as outcrop floras have low competitive abilities (Chapter 1). It is unlikely that competitive exclusion would affect nested scores across the board, particularly at larger grains and extents. There are a number of unique endemics within the batholith and these endemics are highly localised in many situations (Chapter 3). Endemics may play a small role in causing a lack of nested patterns as shown by Cook and Quinn (1995) as they were not restricted to the richer sites (Chapter 8). This cannot explain the low nested scores across the batholith, as endemics were not a major component of most outcrop floras, particularly in the west (Chapter 3). Low values of *C* were found at the sampling level of individual outcrops, where one would not expect the exclusion of endemics to play a role. Furthermore, low and medium *C* scores were found across the batholith both in Elements and 'archipelagos' that were rich in endemics and in those that had few to no endemics.

The degree of effective fragmentation and the likelihood of species colonising outcrops are linked to their degree of isolation that is reflected by insularity. In less insular systems one would expect that colonisation is more likely, both because species are more likely to disperse widely in less fragmented systems (Green 1994; Dieckmann *et al.* 1999) and because the filters between the outcrop and surrounding floras is less effective. The Elements and communities (Chapter 4) on the batholith include areas dominated by highly dispersed grasses and herbs from outcrops with a low Quotient of Insularity (Chapter 5). Conversely, shrubs that in many instances are poorly dispersed dominate other outcrops with a high Quotient of Insularity (Chapter 5). Yet, both medium and low *C* scores are found in both situations. Therefore, although lifeforms or taxa with different dispersal abilities have been found to be differentially nested in a few studies (Schoener & Schoener 1983b; Cook 1995; Kadmon 1995; Patterson *et al.* 1998), cross Element and community comparisons would suggest that this does not play a significant role on the batholith. Using the same reasoning it can be assumed that colonisation is not the sole or major cause of the nested scores found within the batholith.

High values of nestedness are more often found in extinction prone environments (Patterson 1990; Wright & Reeves 1992; Wright *et al.* 1998). The relatively low nestedness of communities within the batholith may in part be due to their stability and age. Granitic outcrops have been shown to be ancient and stable landscape features (Chapter 1). Therefore, these systems may no longer be controlled by deterministic patterns of colonisation or extinction. Determinism may be more prevalent at intermediate stages. Early stages are highly stochastic, as systems have not yet begun to relax. At later stages, after deterministic patterns of colonisation and extinction have occurred random patterns of extinction, colonisation and unlikely persistence patterns become highly likely with increasing time. The degree of nestedness may be a temporally dependent.

Nestedness is correlated to diversity. Systems with low nestedness have high beta diversity (Chapter 5). Wright and Reeves (1992) state that if differences in species richness among sites are not an issue, nestedness provides a more sensitive measure of beta diversity than similarity indices. As the granitic outcrop flora has a relatively low nestedness it also has a high degree of beta diversity across all levels of grain and extent (Chapter 5). Wright and Reeves (1992) also demonstrated a significant negative correlation between saturation index and nestedness. A similar significant negative correlation was also demonstrated by the data presented here (Figure 7.13). Therefore, beta diversity, nestedness and saturation indices are all correlated phenomena. The results presented here on nestedness, reinforce the message given by beta diversity results (Chapter 5), which all indicate that many small outcrops will preserve the greatest amount of species. As nestedness is relatively low and beta diversity high, then the richest sites will not include all species found in less rich sites.

7.4.2 Cumulative species-area curves

All of the cumulative species-area curves showed that the small-to-large curve was higher than the large-to-small curve (Figures 7.2—7.12). This is not always the case in such analyses and Quinn and Harrison (1988) present of examples where the converse may be true. Essentially this indicates that at all levels of grain and extent the spatial structure of islands significantly affects species richness. The degree of the spatial structure effect (Table 5.3), however, is very different across the landscape and at different sampling scales.

The most significant implication of these results is that small islands contain more species than a comparable area composed of a few very large islands. In all cases the small islands first curve saturates much faster and the two curves never intersect. It is clear therefore, that in all cases maximising the number of islands maximises species richness. This naturally has implications for conservation management. The Single-Large-Or-Several-Small reserves (SLOSS) debate has been of significance to biogeographic literature since the introduction of the equilibrium theory (Diamond 1975; Simberloff & Abele 1976; Usher 1979; Gilpin & Diamond 1980; Higgs & Usher 1980; Cole 1981; Humphreys & Kitchener 1982; Margules *et al.* 1982; Simberloff & Lawrence 1982; McCoy 1983; Boecklen & Gotelli 1984; Harris 1984; Simberloff & Gotelli 1984). However, this debate has largely been a matter of semantics as the equilibrium theory is neutral on the subject (Simberloff & Lawrence 1982). Furthermore, more than just species richness is important in reserve design, for example species may occur only on large islands and not at all in smaller ones. Using the cumulative species-area curves however, the plots are constrained by the total known species richness. Thus unlike predictive models the results shown are constrained by the system. In many of the small-to-large accumulation curves presented here almost the full compliment of species is reached with a distinct leveling of the curve at half the area needed for the large-to-small curve. Variation is noted though with some curves not leveling off as quickly. Even so, it appears that there is strong evidence to support the notion that if the number of outcrops is maximised, which may be achieved by many small reserves, then the maximal amount of species will be preserved on outcrops of the New England Batholith.

7.4.3 Conclusion

The granitic outcrop flora of the New England Batholith is in almost all situations significantly nested. However, the degree of nestedness varies considerably across the landscape with no apparent correlation with any measured environmental or landscape features. Nestedness is correlated to the degree to which fragmentation affects species richness and to beta diversity. Overall the degree of nestedness within the New England Batholith, at all grain and extent sizes, is relatively low compared to other published studies. The reasons for the low nestedness on outcrops are hard to determine, and may be due to the age and stability of the system. The relatively low nestedness also reinforces the notion that several small reserves with many small outcrops will preserve the greatest number of species.

The spatial structure of the granite outcrop islands has a significant affect on species richness. These analyses show graphically how area *per se* has little direct affect on richness as the same area of outcrop may contain many more or many less species depending solely on fragmentation. Such evidence supports the view that many small reserves with many small islands are more likely to preserve the greatest number of species.

The low nested values and their link with high beta diversity and saturation indicate that diversity and richness across the New England Batholith at all scales of sampling are maintained at the landscape (gamma diversity) level by highly idiosyncratic distributions. The idiosyncratic nature of species distributions is associated with difficulties in community definition (Chapter 4) and the insular nature of sites (Chapter 3). The methods used here and the results presented are at the resolution limit of correlative analyses and further insights may only be obtained through direct manipulative experimentation.