Chapter 3: Outcrop Insularity

Angoparran Hill near Bolivia Hill – A small patch may contain many plants entirely restricted to granitic outcrops. This patch contains the granitic outcrop endemics: Acacia pycnostachya, Boronia boliviensis, Brachyscome stuartii, Brachyloma saxicola, Cryptandra lanosiflora, Homoranthus croftianus, Isotoma anethifolia, Kunzea bracteolata, Leptospermum novae-angliae, Leucopogon neo-anglicus and Philotheca myoporoides subsp. epilosum

Chapter 3

Outcrop Insularity

3.1 Introduction

A diverse range of systems has been investigated based on their insular qualities. The first insular systems that often to come to mind are oceanic islands. Much work within the biogeographic literature has concentrated on investigating the controlling factors affecting biodiversity on islands, particularly since the seminal work of Macarthur and Wilson (1967) (Chapter 6). Such work has often been transferred to insular 'island' like systems such as 'ecological' or 'habitat islands' within a continental landscape. Investigations include those on mountain 'islands' (Vuilleumier 1970; Brown 1971; Johnson 1975; Lomolino 1984; Wilcox *et al.* 1986; Davis & Dunford 1987; Lomolino *et al.* 1989; Nores 1995), but a number of other insular systems have also been investigated: caves (Culver 1970; Culver *et al.* 1973; Christiansen & Culver 1987); trees and shrubs (Opler 1974; Southwood & Kennedy 1983; Brown *et al.* 1995; Little & Hebert 1996); coral heads (Abele & Patton 1976); wooded lots (Helliwell 1976; Gottfried 1977; Shreeve & Mason 1980; Janzen 1983; Schoener & Schoener 1983a, b); city parks (Faeth & Kane 1978); rivers and streams (Ward 1995); rodents (Gilbert 1980); limestone pavements (Margules *et al.* 1982); shelter belts (Martin 1981); bracken fronds (Higgs 1981); inter-tidal boulders (McGuinness 1984); bodies of rainwater (Kholin & Nilsson 1998); canyons (Kenneally *et al.* 1991); lakes (Elmberg *et al.* 1994); and soil patches (Collins *et al.* 1989), to name a few.

One issue that is little discussed in reference to 'ecological islands', is whether these systems are indeed insular. Insularity is usually taken for granted. Such affirmations often require a 'leap of faith' from the reader that may not be justified in all situations (Janzen 1983). Another variable that is rarely quantified in this type of investigation is; does the degree of insularity vary spatially and/or temporally? Lomolino (1986) and

Whittaker (1995) demonstrated that even over small periods isolating mechanisms may change in effectiveness, such as seasonally, when lakes freeze over or after periodic storms. Variation over longer time periods also affects the degree of isolation. For example, differences have been shown between continental and oceanic islands, with many continental islands still showing ‘relaxation’ (Heaney 1984; Lawlor 1986). Spatial scale is also important in determining the degree of isolation in island systems (Schoener & Schoener 1983b; Doak *et al.* 1992). Examples are distance from the mainland or direction of water currents (Lomolino 1984; Boomsma *et al.* 1987; Lomolino 1994). Disturbance has also been shown as an important factor that affects the degree of insularity (Humphreys & Kitchener 1982; Janzen 1983).

The effectiveness of barriers, even when constant, is taxon specific (Abbott 1977; Buckley 1985; Chaloupka & Domm 1986; Wilcox *et al.* 1986; Quinn *et al.* 1987; Glenn & Nudds 1989; Haila 1990; Heatwole 1991) and barriers should be thought of as filters of varying quality (Lomolino *et al.* 1989; Lomolino 1994). Whittaker (1992) saw great utility in the sorting of taxa into different groups for understanding insular systems and he believed that there should be a shift in emphasis from number, to composition, and to the forces that shape it. Diamond and Gilpin (1982) and Blake and Karr (1984) believed that analyzing the whole species pool, rather than ecologically defined guilds, buried distributions in a mass of irrelevant data. Those researchers who have understood the usefulness of partitioning taxa into different response groups have used one of two pathways when investigating insular systems: to investigate those taxa thought to be the most ‘insular’; or to divide all taxa into differing guilds and analyze the guilds separately.

McCoy (1982) who used the first option believed taxa that were adept at crossing barriers should be eliminated from insular analyses. Johnson (1975) similarly only included taxa thought to be sedentary. Vuilleumier (1970) and Lomolino *et al.* (1989) who studied ‘insular’ mountain tops only included taxa that were restricted to areas above specified altitudes. Opler (1974) divided taxa into feeding guilds and only included the most-endemic guild. Heaney (1984) chose the most common ‘insular’ mammals. Simberloff (1976) only included species capable of reproduction on mangrove islands in his analysis. Culver *et al.* (1973) while investigating cave fauna only included those taxa thought to be cave limited.

Other research has concentrated on the need to assess the contributions each guild may make to insular communities or to assess the differential effects each insular barrier has on separate guilds. In insular vegetation studies, plants are often divided into lifeform categories for separate analysis (Linhart 1980; Humphreys & Kitchener 1982; Woodroffe 1986). In other investigations plants and animals have been subdivided in groups based on their habitat preference within insular systems (Buckley 1981; Butcher *et al.* 1981; Buckley 1982; Schoener & Schoener 1983b; Buckley 1985; Quinn *et al.* 1987; Quinn & Harrison 1988; Kohn & Walsh 1994). Vagility categories have also been used to subdivide the resident taxa (Diamond 1974; Diamond *et al.* 1976; Nilsson & Nilsson 1978; Schoener & Schoener 1983b; Chaloupka & Domm 1986; Wilcox *et al.* 1986).

Martin (1981), who investigated the distribution of birds in remnant patches, believed that an ideal index would allow subtraction of a certain fraction of each species' abundance due to the time spent outside the remnants. This approach would lead to taxa being segregated based on their restriction to the insular habitat in question. Blake and Karr (1984) analyzed taxa based on their presumed restriction to the habitats under investigation using period of residency and habitat preference; some guild designations were modified based on personal observations. Adler and Wilson (1985) also subdivided taxa into distributional guilds based on their restriction to the region under investigation.

The flora on outcrops is considered insular (Burgman 1987; Ibisch *et al.* 1995; Hopper *et al.* 1997; Porembski *et al.* 1997). It is the aim of this chapter to assess by explicit analysis whether granitic outcrops of the New England Batholith constitute a true insular system and are subsequently 'archipelagos' of 'ecological islands'. Other questions include:

- Can the vascular flora of outcrops be segregated into guilds based on their edaphic endemism to granitic outcrops similar to the categories of Gröger and Barthlott (1996)?
- Are there differences spatially and temporally in the degree to which granitic outcrops are insular?
- If differences are found, can they be predicted by selected environmental variables?
- Can the contribution of each guild to the insularity of outcrop floristic communities be assessed?

3.2 Methods

3.2.1 Insularity guilds

Taxa found during this survey were divided *a priori* into seven distributional guilds to enable analyses of the contribution that the various guilds give to insularisation of outcrops. Similar categories of edaphic endemism for granite outcrop plant species were established by Gröger and Barthlott (1996). The ranked distributional guilds are as follows:

0. Never found on outcrops, taxa restricted to the surrounding vegetation;
1. Taxa predominately found in surrounding vegetation rarely on outcrops;
2. Ubiquitous taxa found equally on outcrops or in the surrounding vegetation;
3. Taxa common on outcrops but occasionally found in the surrounding vegetation;
4. Taxa restricted to outcrops on the New England Batholith but not elsewhere in their distribution;
5. Taxa restricted to outcrops throughout their distribution but not necessarily granitic outcrops;
6. Taxa apparently restricted to granitic outcrops throughout their distribution.

Several sources were used to help decide which guild each taxon belonged. Initial comparisons were made on the distribution and frequency of each taxon from surrounding vegetation and outcrop sites. Reference was made to relevant floras, published articles, herbarium records (NE and NSW), and personal experience of the author and other workers. While the choice of taxa scored is biased by those found in the present survey no placement of taxa was made solely on information found in the surveyed distributions. Naturally, some taxa did not fit easily into only one guild, and in such situations a value judgment was made as to which was the most appropriate. The taxa and their subsequent guild classification are given in Appendix D.

A Quotient of Insularity (QI) was calculated for each quadrat based on the guild score given to each taxon. The QI number is an average of all taxon guild scores given as a percentage to allow comparison between quadrats. Effectively the higher the score given by QI the comparatively more 'insular' a quadrat is. This same process was repeated for outcrops and each of the 24 areas under investigation.

3.2.2 Numerical analysis

The PATN Analysis Package (Belbin 1995a, b) was used for initial classification and ordination. All species and their relative abundance scores were used in the classification analysis. PATN was developed for manipulation, analysis and display of patterns in multivariate biological data (Belbin 1995a). Both classification and ordination were performed on data as each technique is complementary and the use of both highlights anomalies produced by the other (Gauch 1982). Ordination will detect natural clusters if they are present and highlight overall trends clarifying relationships alluded to with classification (Belbin 1991; Belbin 1995a). Classification techniques will impose groups on continuous data even if they are not present (Belbin 1991; Faith 1991; Belbin 1995a). Even in such situations utility can be found in imposed divisions (Gauch 1982). Classification is useful in detecting outliers that may affect ordination procedures (strong discontinuity). This technique also aids in the detection of smaller groupings or trends within the data that may be difficult to see from an ordination where groupings may be less obvious (Faith 1991).

Site classification was achieved using the Kulczynski association measure that has proven to be a superior measure of association with ecological data (Faith *et al.* 1987;

Belbin 1995b). Agglomerative hierarchical clustering using flexible UPGMA (Unweighted Pair Group arithMetic Averaging) was used for group joining, this optimises the hierarchy and not the groups. UPGMA gives equal weight to objects not groups in the fusion process thereby groups are weighted proportionally to the number of objects contained (Belbin 1995b). This method has been widely tested and is the most frequently used classification technique (Gauch 1982; Belbin 1995b) and it provides the best fit between the association measure and the distances implied from the dendrogram (Belbin 1991). Flexible UPGMA enables the value of β, which ranges from –0.1 to 1.0 to be changed, this controls the amount of space dilation during the fusion process (Belbin 1991; Belbin 1995b). A β value of –0.1 was used to enable slight dilation to occur; this has been shown to better recover known partitions (Belbin 1995b).

Semi- Strong- Hybrid Multidimensional Scaling (SSH) was used as the ordination technique. Multidimensional scaling (MDS) moves objects around in a space defined by the number of dimensions chosen and the dissimilarities among sites in terms of their composition (Faith 1991; Belbin 1991). SSH calculates the level of stress, which is the miss-match between distances between points and the best estimate of the same values (Belbin 1995b). Subsequently all points in the initial ordination are moved slightly to reduce stress, this process is iterated a specified number of times or until a minimum stress is achieved (Orlóci 1978; Belbin 1995b). MDS has been shown to be a robust method (Minchin 1987; Faith 1991). SSH has the advantage of being designed to cope with unimodal responses of taxa replacing the assumption of linearity used by many other ordination procedures (see e.g. Noy-Meir & Whittaker 1978; Orlóci 1978; ter Braak & Prentice 1988; Faith 1991; Belbin 1995a).

In total 51 variables were measured or modeled for each quadrat (Chapter 2). This large number of variables included many that were significantly auto-correlated. For this reason the most strongly auto-correlated variables (multi-colinear) were removed and replaced with one variable that could be used to explain most of the variance of the others. This was achieved via examination of correlation matrices (any variables over 95% correlated) and subsequent 'Principle Components Analysis' using STATISTICA (StatSoft 1994—1995). This enabled a quantitative choice of the most appropriate replacement variable when more than two variables were highly auto-correlated (those with the highest factor loading and partial correlations).

'Canonical Correspondence Analysis' (CCA) via CANOCO (ter Braak 1987-1998), a direct gradient analysis technique was used for exploration of factors affecting the insular nature of quadrats, outcrops and regions. The input to this analysis included the 51 environmental variables and all 399 survey plots. The data attached to each survey plot included only sex pseudo-species (the six insular guilds). The values assigned to each insular guild was the percentage of representation of each within the flora of each site. Forward selection of variables was used for data reduction, ranking of variable importance and significance testing (ter Braak & Verdonschot 1995). This was achieved by using the forward selection module in CANOCO. Here the variation explained by each variable is partitioned and a model of significant variables is constructed (i.e. all environmental variables are ranked based on the fit of each variable separately). The significance of the effect of each variable is tested by a Monte Carlo permutation test (in this case 999 iterations). A variable was added if its significance was at the 5% level or less. As each variable is selected, the remaining variables are reassessed based on the fit that each variable gave in conjunction with the variables already selected (ter Braak & Verdonschot 1995). Forward selection ceased when the significance based on the Monte Carlo tests was greater than 5%. The overall significance of the CCA ordinations was tested by Monte Carlo permutation (999 iterations) of residuals of the taxa after fitting environmental variables (ter Braak 1992).

Simple rules are associated with the interpretation of CCA biplots. These include: sites with similar distributions will be close and those with divergent distributions will be distant; arrows point in the direction of maximal change in that variable; the longer the arrow the more important the variable; the order of perpendicular projected points on the variable arrows gives an inferred ranking; points on the same side are positively correlated; those on the opposite side are negatively correlated; those that are perpendicular are not correlated at all.

The indirect gradient analysis technique of Forward Stepwise Multiple Linear Regression via the program STATISTICA (StatSoft 1994—1995) was used on the insular guild scores. Linearity of response is assumed in these analyses, however, multiple regression procedures are not greatly affected by minor deviations from this assumption. For each independent variable, partial and semi-partial correlations were viewed to identify variables that were redundant with other variables. Analysis of residuals was conducted in order to identify outliers. Once significant variables were selected, probability plots of the raw data and residuals were inspected to test the normality of distributions.

3.2.3 Geostatistical analysis

In this study, geostatistical methods are used to analyze the changes in the comparative insular nature of the granite outcrops. Cesaroni *et al.* (1997) discusses the relative merits of using geostatistical methods in ecology and biogeography. Kringing analysis is performed on *x, y* geographic coordinates and a *z* coordinate. In this case the *z* coordinate is the insular score (QI) derived for each of the 399 outcrop sites. Intervening geographic *z* values are interpolated from the raw data set provided. The program SURFER for Windows (Ver. 6.0; Golden Software 1997) was used to perform the analysis.

3.3 Results

3.3.1 Classification and ordination of sites

The 21 areas ('archipelagos') which had their adjacent forests and woodlands ('sea') sampled were initially analyzed separately. In every instance, all outcrop sites and forest and woodlands sites were separated on the dendrograms and ordinations. No instances of mixed outcrop and forest sites were found confirming that granite outcrops are insular systems. The magnitude at which the outcrop ('island') and forest ('sea') sites were separated from each other varied considerably indicating that some 'archipelagos' were comparatively more insular than others. A summary of the dissimilarity figures associated with the first split on each of the dendrograms is given in Table 3.1.

Analyses performed on the complete data set of all 522 quadrats (803 taxa) showed almost complete separation of outcrop ('island') sites from forest and woodland sites ('sea'). It appears that the western outcrop and surrounding flora sites are different from the eastern outcrop and surrounding floras. This east west difference has an overriding influence on the partitioning of the dendrogram (Figure 2.2). Within these two 'sub-regions' the outcrop floras are indeed 'insular' in comparison to the surrounding floras ('sea'). The initial division between east and west and the second division between outcrop and surrounding flora sites is very close. Ordinations generally distinguish natural clusters more clearly than dendrograms. The ordination scattergram clearly shows a separation between outcrop and surrounding flora sites (Figure 3.3). The differences between the western and the eastern sites on the dendrogram are not clear in the ordination. This is likely to be an instance where the overriding difference between the outcrop and the surrounding vegetation sites obscures the differences between east and west on the ordination. The ordination result confirms that the outcrop sites are insular to those of the surrounding floras.

A few sites were anomalous in their positions either on the dendrogram or on the ordination. The sites that were outliers or anomalous in the dendrogram were not the same as those that were anomalous on the ordination. In total only 13 sites (2.5% of the total sites) where unusual in their placement on either the dendrogram or ordination. All of the outcrop sites anomalously placed with forest sites are outcrops of only 1 ha in size.

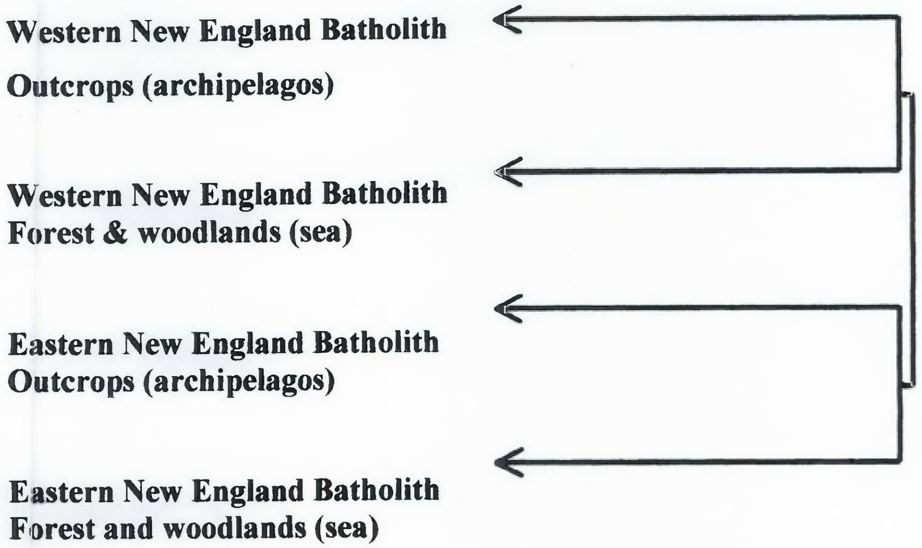

Figure 3.1: Summary dendrogram of the full floristic dataset of sites using the Kulczynski association and flexible UPGMA fusion strategy and a β value of –0.1. The full dendrogram is given in Appendix C.

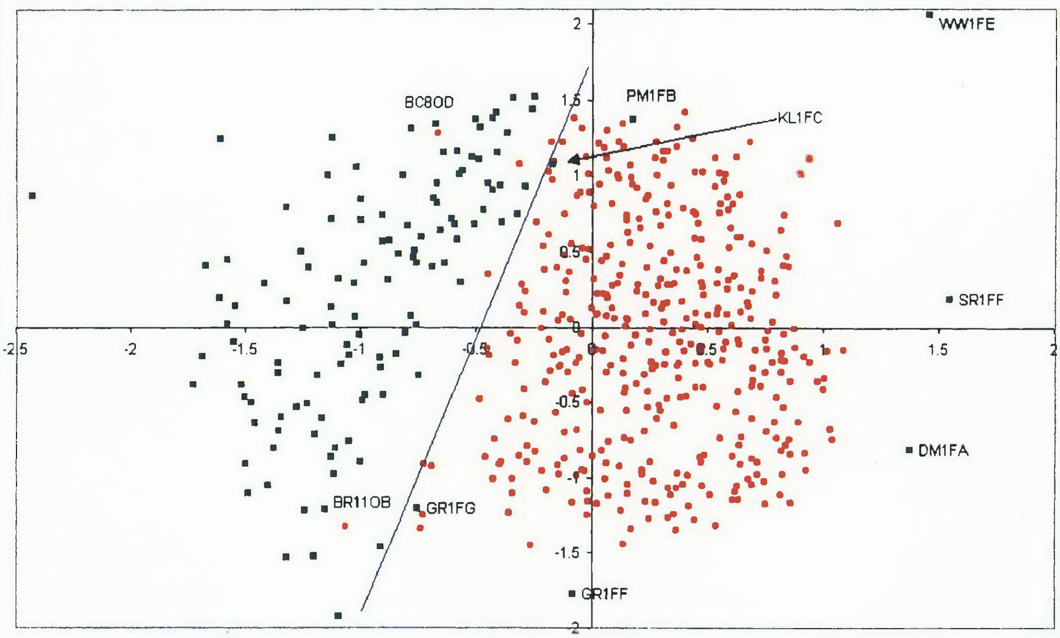

Figure 3.2: Ordination scattergram of all sites sampled based on full floristics and analysis by Flexible UPGMA association measure and Semi-Strong-Hybrid Multi-Dimensional Scaling. Green squares represent quadrats placed within the surrounding vegetation. Red circles represent quadrats placed on outcrops. The blue line is arbitrary and represents the demarcation between outcrop ('island') and surrounding flora ('sea') sites. Site codes are shown for sites deemed to be anomalous in their association (outliers) on the ordination.

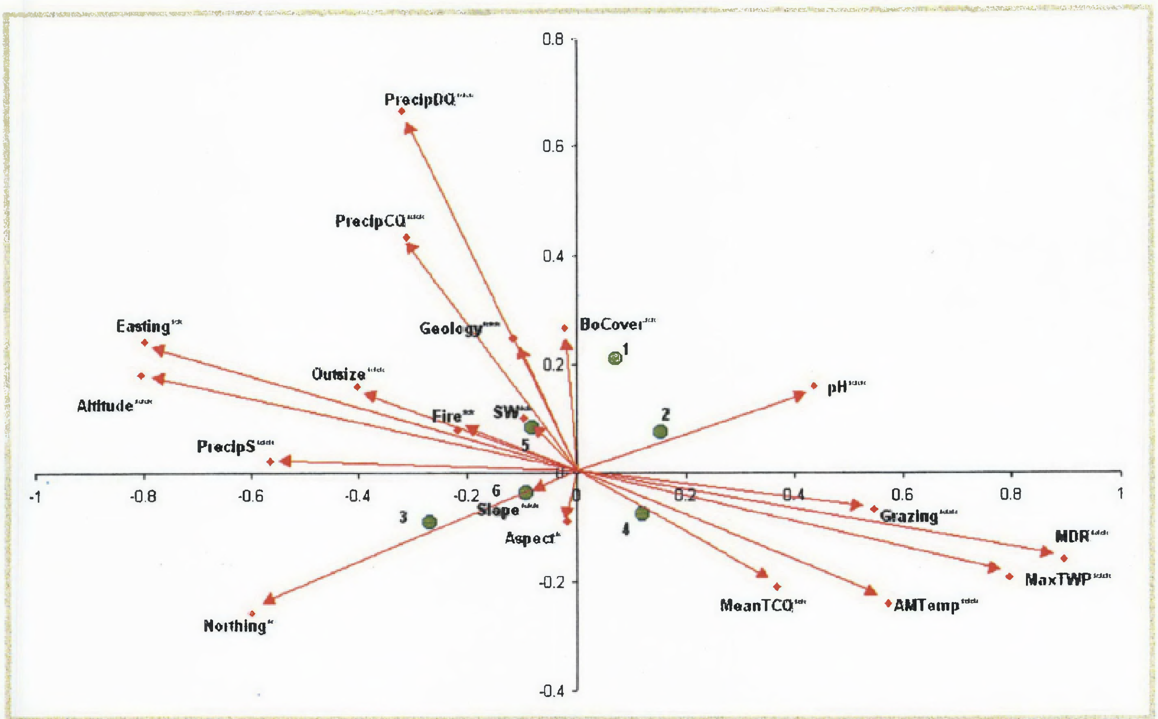

Figure 3.3: CCA biplot of the 19 significant environmental variables (of 39) as chosen by forward selection and Monte Carlo significance testing (Section 3.2.4) and the six insular guild classes (Section 3.2.2). Significance of the variables based on Monte Carlo simulations are; *P < 0.05, **P < 0.01, and ***P < 0.001. PrecipDQ = Precipitation of the Driest Quarter; PrecipCQ = Precipitation of the Coldest Quarter; Outsize = Outcrop Size; Easting = AMG east coordinate; PrecipS = Precipitation Seasonality; SW = horizontal protection from the south west; Northing = AMG north coordinate; Aspect = increasing southward site projection; BoCover = Boulder Cover; MDR = Temperature Mean Diurnal Range; MaxTWP = Maximum Temperatuer of the Wettest Period; AMTemp = Annual Mean Temperature; MeanTCQ = Mean Temperature of the Coldest Quarter.

3.3.2 Outcrop insular differences and geostatistical plotting

The Quotient of Insularity (QI) effectively represents the difference between forest ('sea') and outcrop ('island') sites in a single number. Surrounding forest and woodland sites ('sea') are distinctly separated from outcrop sites ('island') in terms of the QI number. The QI number varied from 37% to 95% for outcrops with a median of 50%

('islands') and from 27% to 40% with a median of 32% for forest and woodland sites ('sea'). Only 23 sites (4.4% of all sites), seven from the surrounding forest and woodlands ('sea') (5.7%) and sixteen from the outcrop sites ('islands') (4%) overlap in their QI scores. These did not occur in the same region.

The very few sites of mixed distribution in the full site classification and ordination were also anomalous in their Quotient of Insularity (QI). Four of the five forest and woodland sites ('sea') from Kwiambal (KL), are amongst the seven forest and woodland sites with the highest QI numbers. Hence, overall the Kwiambal (KL) forest and woodland sites have a high proportion of taxa that are shared with outcrops on the batholith. Furthermore, one of the Kwiambal (KL) outcrop sites had a very low QI score (42%) and in the full site dendrogram, this site was placed with the forest and woodland sites from Kwiambal (KL). Similarly, a forest site ('sea') from Gibraltar Range (GR), which was anomalous in the ordination, has the highest QI score (40%) of any forest or woodland site.

The difference between the overall outcrop Quotient of Insularity (QI) and the forest and woodland Quotient of Insularity (QI) can be used as an indication of overall dissimilarity or overall insular nature of an 'archipelago' (Table 3.2). Bolivia Hill (BH) was the most insular 'archipelago' (26%) with the highest overall Quotient of Insularity for its outcrops (58%) and an overall average Quotient of Insularity (32%) for its forests and woodlands (Table 3.3). Other 'archipelagos' that are more comparatively insular from their respective forests and woodlands were Bald Rock (23%), Backwater (22%), Mt Chaelundi (21%) and Torrington (20%) (Table 3.3). In general, this degree of difference is mostly accounted for by the high Quotient of Insularity (QI) for the outcrop vegetation; i.e. a high number of taxa restricted to outcrops compared to other more generalist species. All of these 'archipelagos' occur at high altitudes in the north east of the region.

Two 'archipelagos', Kwiambal (7%) and Demon (8%) had extremely low differences between their outcrop vegetation Quotient of Insularity and their forest and woodland Quotient of Insularity. These 'archipelagos' had the lowest Quotient of Insularity for their outcrop flora ('island') with Kwiambal (KL) also having the highest Quotient of Insularity for its forests and woodlands ('sea').

The overall discernable pattern is that outcrops are comparatively more 'insular' in the north east of the batholith and that outcrops become less 'insular' particularly along the west (Figure 3.4). This is also true of the 24 'archipelagos' investigated, with those groups of outcrops in the north east being more divergent from their surrounding forests and woodlands ('sea').

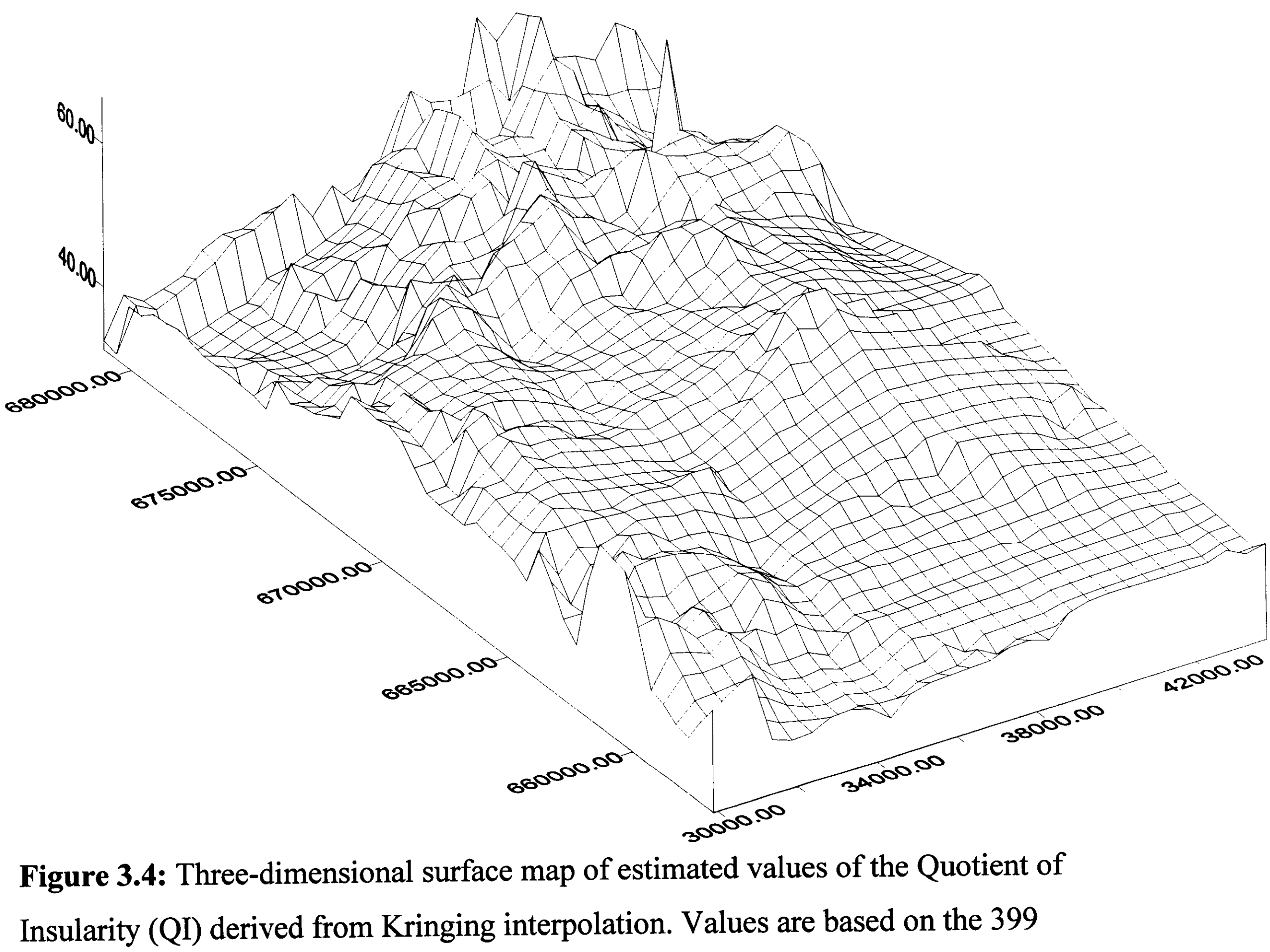

Figure 3.4: Three-dimensional surface map of estimated values of the Quotient of Insularity (QI) derived from Kringing interpolation. Values are based on the 399 outcrop sites and their subsequent Quotient of insularity. Note that outcrops are comparatively more 'insular' in nature in the north east of the region. X axis = easting, Y axis = northing and Z axis = Quotient of Insularity score.

3.3.3 Distribution of insular guilds on outcrops

Only a small percentage of taxa are apparently entirely restricted to granite outcrops (insular guild 6: 4.6%) (Table 3.3). About 20% of all taxa surveyed and about 24% of all taxa found on outcrops are primarily restricted to granitic outcrops (insular guild 3—6) within the New England Batholith. This 24% accounted for *c.* 45% of all species incidences on outcrops. Forty-five taxa were restricted to granite outcrops on the New England Batholith, yet in most other areas of their distribution are rarely found on outcrops of any sort (insular guild 3). These taxa were often at their geographic limits. Half of all taxa surveyed and *c.* 60% of all taxa on outcrops were generalists (insular guild 2) and occurred equally within the surrounding flora or on outcrops.

Ubiquitous taxa accounted for about half of all records on outcrops. The more restricted a taxon was to outcrops, the more abundant it was on the outcrops. The granitic outcrop specialists (insular guild 6) had the highest average relative abundance scores (Chapter 2) on outcrops and although only accounting for *c.* 6% of taxa on outcrops they accounted for *c.* 12% of all records. Conversely, taxa rarely found on outcrops accounted for *c.* 17% of all taxa found on outcrops but only for *c.* 2% of all records.

Table 3.1: The Kulczynski dissimilarity level at which the vegetation of each of the 21 outcrop areas ('archipelagos') were different from the surrounding forests and woodlands ('sea').

Outcrop area ('archipelago')	Kulczynski dissimilarity
Backwater (BC)	1.4700
Bald Rock (BR)	1.4800
Bolivia Hill (BH)	1.2000
Cathedral Rock (CR)	1.0600
Demon (DM)	0.8050
Mt Chaelundi (CH)	1.0100
Eagle Creek (EC)	1.2300
Flaggy Range (FR)	0.9050
Gibraltar Range (GR)	1.3200
Howell (HC)	1.3100
Ironbark (IB)	1.1000
Mt Jondol (JB)	1.0600
Kwiambal (KL)	0.8080
Kings Plains (KP)	1.1800
Moonbi (MB)	1.2000
Parlour Mt (PM)	1.2100
Severn River (SR)	1.1200
Torrington (TT)	1.3000
Warrabah (WB)	1.0800
Willows (WW)	1.1500
Mt Yarrowyck (YH)	0.9110

Table 3.2: Quotient of Insularity (QI) for total outcrop vegetation ('islands') and forest and woodlands ('sea') floras from the 24 areas investigated ('archipelagos'). The Quotient of Insularity is a reflection of how much of the flora is outcrop restricted. The differences between the forest and woodland and outcrop scores is an indication of how 'insular' the area investigated was.

Name of area ('archipelago')	QI score for all outcrops ('islands')	QI score for all forest and woodlands ('sea')	Difference: outcrop – forest and woodlands
Attunga (AT)	40%	NA	NA
Backwater (BC)	52%	30%	22%
Bolivia Hill (BH)	58%	32%	26%
Butterleaf (BL)	52%	NA	NA
Bald Rock (BR)	54%	31%	23%
Mt Chaelundi (CH)	51%	30%	21%
Cathedral Rock (CR)	46%	30%	16%
Demon (DM)	39%	31%	8%
Eagle Creek (EC)	47%	31%	16%
Flaggy Range (FR)	44%	31%	13%
Gibraltar Range (GR)	51%	33%	18%
Howell (HC)	51%	33%	18%
Ironbark (IB)	48%	32%	16%
Mt Jondol (JB)	50%	33%	17%
Kwiambal (KL)	42%	35%	7%
Kings Plains (KP)	48%	33%	15%
Moonbi (MB)	44%	31%	13%
Mt Balala (ML)	47%	NA	NA
Parlour Mt (PM)	48%	30%	18%
Severn River (SR)	46%	33%	13%
Torrington (TT)	53%	33%	20%
Warrabah (WB)	44%	33%	11%
Willows (WW)	47%	32%	15%
Yarrowyck (YH)	45%	33%	12%

Table 3.3: Summary of the importance of the insularity guilds. An increase of guild ranking is effectively an increase in how restricted or 'insular' species are to outcrops of the New England Batholith.

Insular guild score	Richness	Percent of all taxa found (% of all outcrop taxa)	Average relative abundance on outcrops (/10)	Percent of all records on outcrops
0	146	18.2% (NA)	NA	NA
1	111	13.8% (16.9%)	2.0	1.8%
2	391	48.7% (59.5%)	3.0	53.1%
3	45	5.6% (6.9%)	3.5	15.2%
4	56	7.0% (8.5%)	3.9	15.7%
5	17	2.1% (2.6%)	3.5	2.1%
6	37	4.6% (5.6%)	4.9	11.5%

3.3.4 Direct gradient analysis

Nineteen environmental variables were significant at the 5% level based on forward selection and Monte Carlo significance testing. Figure 3.5 gives the subsequent biplot from the CCA analysis of environmental variables and the distribution of insularity guilds. The axes shown account for 32.8% of the variance (axis one = 22.2%) of the constrained ordination. The species environmental relations shown account for 85.9% (58.1% on the first axis) of the total sum of squares of the first two axes of the equivalent unconstrained ordination. Monte Carlo permutations on the first constrained axis and the overall model are significant at the 1% level.

The climatic variables: rainfall; Precipitation Driest Quarter (PrecipDQ), Precipitation Coldest Quarter (PrecipCQ), Precipitation Seasonality (PrecipS); Temperature Mean Diurnal Range (MDR), Maximum Temperature of the Wettest Period (MaxTWP), Mean Temperature of the Coldest Period (MeanTCP), Annual Mean Temperature (AMTemp); and other variables somewhat correlated with these such as altitude (Altitude); and geographic position (Easting, Northing) are of greatest explanatory power. Proximal site characteristics are of secondary importance. The most explanatory site characteristics are pH, grazing, outcrop size (Outsize) and geology. Of least effect are some proximal site characteristics that influence microclimate such as the presence of boulders (BoCover), slope, aspect, fire and protection from the south west (SW).

Taxa that are most common in the surrounding vegetation but rarely occur on outcrops are represented by guild one. This guild increases in importance with an increase in winter rainfall (PrecipDQ & PrecipCQ), protection with boulders (BoCover), a less acidic soil (pH), the granodiorite end of the geology spectrum (Geology), and a southerly distribution (-ve Northing). Of minor influence is a level slope (-ve to slope), a northerly aspect (-ve Aspect), protection from the south west (SW) and an increase in grazing pressure (Grazing). Most other variables are not correlated or are only very weakly correlated with insular guild one.

Guild two represents ubiquitous and widespread taxa. These taxa appear to be positively correlated with a less acidic soil (pH), grazing and an overall increase in temperature (MDR, MaxTWP, AMTemp, MeanTCQ). They are more common in the south of the batholith (-ve Northing). Minor negative correlations also occur with slope, outcrop size (Outsize), easting, aspect and fire.

Guild three and six respond in a similar way to the significant environmental variables displayed. Taxa from these categories are more common in the north east of the batholith at higher altitudes (+ve Northing, Easting, Altitude). Guilds three, and six are correlated with increasing precipitation seasonality (PrecipS), slightly to increasing precipitation (PrecipDQ, PrecipCQ) and decreasing overall temperatures (-ve MDR, MaxTWP, AMTemp, MeanTCQ). Strongly acid soils are favoured (-ve pH) along with more exposed positions (Outsize, Slope; -ve BoCover), but southerly aspects (+ve Aspect) and protection from the south-west (SW) are partially correlated with guild three occurrence. Disturbance from grazing is negatively correlated but fire is positively correlated with guild three occurrence.

Taxa that are not found on outcrops outside of the batholith are classed as insular guild four. These taxa are correlated with a lower rainfall (-ve PrecipDQ, PrecipCQ), higher temperatures (MDR, MaxTWP, AMTemp, MeanTCQ) and an associated westerly distribution (-ve Easting) and decreasing altitude. Minor correlation also occurs with a greater exposure to the south west and a decrease in boulders (-ve BoCover). Soils with a higher pH, grazing and smaller outcrops are also favoured while fire is not. Overall, taxa in this category are in general associated with warm, dry and exposed situations.

Insular guild class five includes species that are restricted to outcrops but not always granitic ones. Positive correlations occur with increasing precipitation (PrecipDQ, PrecipCQ) and an easterly distribution (Easting) with its associated decrease in temperatures (-ve MDR, MaxTWP, AMTemp, MeanTCQ) and increase in altitude. Other correlations occur with protection from the south west (SW), grazing (-ve Grazing), and boulders (BoCover), an increase in outcrop size (Outsize), fire, slope and the granite *sens. strict.* end of the geological spectrum.

In summary, taxa restricted to outcrops (guilds 3—6) are positively correlated with a north eastern distribution within the batholith and the associated increase in altitude, precipitation and a decrease in temperatures. Disturbances have a mixed effect with a positive correlation to fire and a negative correlation to increased grazing pressure. These taxa are also correlated with an increase in outcrop size and slope, acidity and protection from the south west. Insular guild four is slightly different from the other categories in that it is correlated with a south-west distribution and its reduced rainfall and increased temperature. The taxa primarily from the surrounding forests and woodlands ('sea') and those common to both areas (guilds 1—2) are correlated with a less acidic soil, protection from boulders, a decrease in slope and geology on the granodiorite side of the spectrum.

3.3.5 Indirect gradient analysis

Overall, climatic variables such as precipitation, temperature and radiation had the highest significant correlations with insular guild scores. More minor correlations occurred with other climatic variables and proximal quadrat variables such as geology, outcrop size, pH and with microclimate variables for example boulders, slope, protection from various directions etc. The significant correlations are very similar to those found significant in the CCA analysis. All but three variables (PrecipS, Aspect and MeanTCQ) of the 19 found significant in the CCA analysis are significant in the forward stepwise linear regression. Although mean temperature of the coldest quarter (MeanTCQ) was not found in the stepwise regression, its counterpart (highly intercorrelated) variable mean temperature of the driest quarter (MeanTDQ) was. In most instances the additional variables found significant in stepwise regression not significant in the CCA analysis are climatic variables associated with radiation.

Five significant correlated variables were found associated with insular guild one and these explained 13% of the variation (Table 3.4). Insular importance of insular guild one is positively correlated with rainfall in winter (PrecipDQ), protection from the south west (SW) and from an increase in anthropogenic disturbance (Pollut). Guild one was slightly negatively correlated with an increase in slope and in outcrop size (Outsize).

Seven significant variables explain 25% of the variance in insular guild two (Table 3.5). Guild two is positively correlated with an increase in overall radiation (Rads), a more neutral soil (pH), an increase in temperature of in winter (MeanTDQ) and slightly to the granodiorite end of the geology spectrum. Minor negative correlations also occur with precipitation in summer (PrecipWQ), fire and to slope.

Guild class three is significantly correlated with nine variables that account for 18% of the variation (Table 3.6). Negative correlations occur with increasing temperature (MaxTWP, AMTemp, MDR) and disturbance by grazing (Grazing). Positive correlations occur with an increase in precipitation (PrecipWQ, PrecipDQ), northing and slope.

Thirty-four percent of the variation in insular guild four is correlated with six variables (Table 3.7). Positive correlations occur with an increase in radiation (Highest Period of Radiation (HPRad); –ve to Lowest Period of Radiation (LPRad)) and +ve to grazing. A decrease in precipitation (-ve PrecipDQ), increase in exposure (-ve BoCover), and geology on the granodiorite side of the spectrum (-ve Geology) are associated with insular guild four.

Forty-five percent of the variation in insular guild five is explained by 11 significant variables (Table 3.8). An increase in precipitation (PrecipWQ, PrecipDQ) accounts for a significant portion of the variation accounted for. An increase in outcrop size (Outsize), Altitude, easting and protection from the east is also positively correlated to insular guild five. Minor negative correlations also occur with protection from the north (N) and north east (NE) and the lowest period of radiation (LPRad).

Table 3.4: Results of forward stepwise linear regression of environmental variables on insular guild one ('sea' taxa). R – squared values are semi-partial correlations.

Variable	R – squared	R	Beta	P value
Precipitation Driest Quarter (PrecipDQ)	0.054842	+ 0.23418	+ 0.256	0.000000
Slope	0.021419	- 0.0925	+ 0.135	0.004705
Protection from the South West (SW)	0.020250	+ 0.15986	+ 0.165	0.007200
Outcrop Size (Outsize)	0.016045	- 0.0687	- 0.15	0.002055
Anthropogenic Disturbance (Pollut)	0.017607	+ 0.15311	-0.14	0.005038
Total	0.130164		F = 11.76184	0.000000

Table 3.5: Results of forward stepwise linear regression of environmental variables on insular guild two (ubiquitous taxa). R – squared values are semi-partial correlations.

Variable	R – squared	R	Beta	P value
Radiation load (Rads)	0.089385	+ 0.2989	+ 0.601	0.000000
pH	0.037094	+ 0.26128	+ 0.153	0.001211
Mean Temperature of the Driest Quarter (MeanTDQ)	0.015649	+ 0.17584	+ 0.652	0.000000
Precipitation of the Wettest Quarter (PrecipWQ)	0.053798	- 0.1473	+ 0.647	0.000000
Geology	0.034432	+ 0.03788	+ 0.255	0.000002
Slope	0.014700	- 0.0781	- 0.11	0.021455
Fire	0.007723	- 0.0454	+ 0.095	0.045094
Total	0.252781		F = 18.89627	0.000000

Table 3.6: Results of forward stepwise linear regression of environmental variables on insular guild three (most common on outcrops but also in the 'sea'). R – squared values are semi-partial correlations

Variable	R – squared	R	Beta	P value
Maximum Temperature of the Wettest Period (MaxTWP)	0.065890	- 0.2567	- 1.8	0.000075
Precipitation of the Wettest Quarter (PrecipWQ)	0.032426	+ 0.03470	- 0.53	0.000000
Grazing	0.025532	- 0.2253	- 0.22	0.000061
Slope	0.020400	+ 0.12024	+ 0.147	0.002032
Northing	0.003963	+ 0.11838	+ 0.117	0.020401
Precipitation of the Driest Quarter (PrecipDQ)	0.003963	+ 0.09200	+ 0.333	0.001574
Annual Mean Temperature (AMTemp)	0.006984	- 0.2285	+ 0.991	0.000745
Mean Diurnal Range (MDR)	0.017418	- 0.2260	+ 0.647	0.004298
Total	0.176593		F = 10.45524	0.000000

Table 3.7: Results of forward stepwise linear regression of environmental variables on insular guild four (outcrop restricted on the batholith but not elsewhere). R- squared values are semi-partial correlations.

Variable	R – squared	R	Beta	P value
Highest Period of Radiation (HPRad)	0.141908	+ 0.45452	+ 0.176	0.000000
Grazing	0.070214	+ 0.35410	+ 0.324	0.000000
Precipitation of the Driest Quarter (PrecipDQ)	0.049945	- 0.3176	- 0.40	0.000000
Geology	0.029020	- 0.1971	- 0.24	0.000001
Boulder cover (BouldCov)	0.024730	- 0.1559	- 0.17	0.000093
Lowest Period of Radiation (LPRad)	0.021151	- 0.1109	- 0.16	0.002885
Total	0.336968		F = 29.57793	0.000000

Table 3.8: Results of forward stepwise linear regression of environmental variables on insular guild five (outcrop restricted by not always granite outcrops). R – squared values are semi-partial correlations.

Variable	R - squared	R	Beta	P value
Precipitation of the Wettest Quarter (PrecipWQ)	0.222887	+ 0.47211	- 0.29	0.006207
Outcrop size (Outsize)	0.070577	+ 0.32731	+ 0.197	0.000002
Precipitation of the Driest Quarter (PrecipDQ)	0.030929	+ 0.46783	+ 0.387	0.000007
Radiation load (Rads)	0.033280	+ 0.3107	- 0.43	0.000065
Lowest Period of Radiation (LPRad)	0.007902	- 0.0179	- 0.43	0.000014
Easting	0.008058	+ 0.43533	+ 0.739	0.000000
Maximum Temperature of the Wettest Period (MaxTWP)	0.006498	- 0.4301	+ 2.53	0.000000
Altitude	0.001952	+ 0.44956	+ 2.14	0.000000
Protection from the North (N)	0.002464	- 0.0577	+ 0.14	0.006812
Protection from the North East (NE)	0.001854	- 0.0850	- 0.19	0.006594
Protection from the East (E)	0.009714	+ 0.00172	+ 0.152	0.008904
Total	0.4561368		F = 29.50416	0.000000

Table 3.9: Results of forward stepwise linear regression of environmental variables on insular guild six (restricted to granite outcrops). R – squared values are semi-partial correlations.

Variable	R – squared	R	Beta	P value
Mean Diurnal Range (MDR)	0.332463	- 0.5766	- 0.29	0.015134
Precipitation of the Driest Quarter (PrecipDQ)	0.070746	+ 0.03102	- 0.35	0.000000
pH	0.022470	- 0.3192	- 0.17	0.000018
Outcrop Size (Outsize)	0.016699	+ 0.2373	+ 0.112	0.003591
Fire	0.012754	+ 0.13628	- 0.14	0.000700
Maximum Temperature of the Wettest Period (MaxTWP)	0.011132	- 0.4808	- 0.38	0.000322
Radiation of the Coldest Quarter (RadCQ)	0.006923	+ 0.49382	+ 0.086	0.022896
Protection from the South-west (SW)	0.006928	+ 0.08662	+ 0.082	0.023167
Total	0.480114		F = 45.02061	0.000000

Eight significant variables help to explain 48% of the variation in insular guild six (Table 3.9). Most of the variation is explained by a decrease in temperature (-ve MDR, MaxTWP) and an increase in precipitation in the driest months (PrecipDQ). Minor partial correlations also occur with more acidic soils (-ve pH), outcrop size (Outsize), fire, protection from the south west (SW) and radiation during the coldest quarter (RadCQ).

3.4 Discussion

The flora on granite outcrops within the New England Batholith is insular, and there is evidence to prove that outcrops are 'ecological islands'. The distinctiveness of these communities has often been taken for granted. This assumption has also been made for a number of other supposedly insular systems. Such systems may not all prove to be insular if tested statistically. Margules *et al.* (1982) showed that of 311 species found on limestone pavements in England, only one was largely restricted to this system. The same could also be true for many remnant patches or nature reserves. Proving a system is insular should be the first step in all studies of 'habitat islands'.

The insular nature of the granite outcrops of the batholith was by no means uniform. There is significant variation shown in the distinctiveness of the flora of individual outcrops. The Quotient of Insularity (QI) for individual sites ranged from 37% to 95%, indicating that there was nearly a three-fold difference between the insular nature of some outcrops. This in itself has significant implications for the maintenance of biodiversity on outcrops along with other biogeographic investigations such as island biogeography. Geostatistic plotting and interpolation show (Figure 3.4) that there is a distinctive increase in the comparative insular nature (as indicated by the Quotient of Insularity) of sites and therefore outcrops ('islands') in the north east of the region. Sites and subsequently outcrops were comparatively less insular all along the western side of the batholith. Kwiambal (KL) showed only a 6% difference between the average Quotient of Insularity for outcrops ('island') and forests and woodlands ('sea') indicating that floristically this area is barely insular. The average Quotient of Insularity of outcrops ('island') also decreased in the most eastern part of the batholith. In particular the most eastern area sampled, Demon (DM), only had a 7% difference between its outcrop and forest Quotient of Insularity. Kwiambal (KL) and Demon (DM) are at the western and eastern extremes of the batholith and at both only very small outcrops were found. Although, Kwiambal (KL) and Demon (DM) also had the smallest differences between their outcrop ('island') and forest and woodland ('sea') vegetation (in terms of Quotient of Insularity) this was achieved via different means. Kwiambal (KL), while having a relatively low Quotient of Insularity for its outcrops had the highest insular score for its forests and woodlands. At Demon (DM), the low difference between outcrop and forest insular scores is attributable to the very low outcrop Quotient of Insularity, which is the lowest average recorded for any of the areas investigated.

The separation of species into guilds, defined by degree of restriction to granite outcrops of the batholith, has highlighted some significant patterns. Only 24% of species are primarily outcrop occurring within the batholith. Similar results were obtained by Benwell (1995) who considered that at least one third of the species found on rhyolite and trachyte outcrops of the Mt Warning Shield of eastern Australia were restricted to such habitats. In general, the more restricted to outcrops a species was the more abundant it was. The 24% of species primarily restricted to outcrops accounted for 45% of all relative abundance records. The more restricted a taxon was to outcrops the more 'island' like the outcrops were and hence the less connected was the landscape (the more insular). This pattern of increased abundance with increasing restriction is typical of species from poorly connected systems, where species often show poor dispersal and subsequently clumped distributions (Green 1994; Dieckmann *et al.* 1999). Such clumped distributions may aid the persistence of small populations even in the face of superior competitors (Green 1994).

The results of direct and indirect gradient analysis of guild scores are similar, indicating that the results obtained are robust. The strong east west environmental gradient is an obvious feature affecting the abundance of the guild classes. The large increase in altitude from west to east and its associated changes in rainfall and temperature are some of the main correlative factors identified in both direct and indirect gradient analyses. Guilds one and two, which represent those that are less restricted to outcrops, increase in importance with an increase in temperature. Some more proximal correlations are also discernable. These species increase in importance on smaller outcrops with a flatter topography and northern exposure. A decrease in the acidity of soils, along with a more weathered geology (granodiorite side of the geology spectrum) and an increase in disturbance from grazing and anthropogenic sources is also correlated with guilds one and two.

For species more or less restricted to outcrops of the batholith the opposite ends of the environmental gradients are important. These species increase with a decrease in temperatures, an increase in solar radiation and an overall increase in rainfall associated with an easterly distribution. Proximal effects such as; an increase in acidity, a more granite *sens. strict.* geology, an increase in slope and outcrop size and a decrease in grazing and anthropogenic disturbances are correlated with species of this guild. Baskin and Baskin (1988) have shown that endemic rock outcrop species are shade intolerant and require high levels of light. Porembski *et al.* (1996) also found that an increase in outcrop size increased the number of typical inselberg species.

Some more subtle correlations exist. Insular guild five, which are those species not normally restricted to outcrops outside of the batholith, did not respond to the environmental gradients as other more outcrop restricted species. These species were more prominent further west where precipitation was lower and temperatures were higher. They were also correlated with an increase in radiation loads (Chapter 8) and to exposure (-ve BoCover). Kirkpatrick *et al.* (1988) found that rockiness was a significant factor in their analyses of vegetation on granite outcrops through its influence on increasing local soil moisture. Perusal of the species within this category explains these correlations. Many of these species restricted to the western portion of the study area are at their distributional and climatic limits within the batholith. These species are often tropical species found usually in parts of the northern Australia (Chapter 8).

The occurrence of fire was significantly correlated, in both direct and indirect analyses, with increased abundance of some of the outcrop-restricted species. This factor, which changes with time appears to be a feature unique to some areas (Chapter 9). The relationship with fire and outcrop restricted species is more complex than it initially seems. Fire did not increase the numbers of what were the common outcrop restricted species, in fact many of these are killed outright by fire (Gröger & Barthlott 1996; Hopper *et al.* 1997; Hunter 1998c). Other research and observations carried out on the batholith (Hunter 1995; Richards & Hunter 1997; Hunter 1998b; Hunter 1998c; Hunter *et al.* 1998), show that there is a short-lived, primarily outcrop restricted, fire-ephemeral flora (Chapter 9). This flora only appears on outcrops after large fires in only some areas of the batholith (e.g. Bald Rock, Backwater). Essentially there is a replacement fire-ephemeral flora that is short lived and largely restricted to outcrops and which is eventually replaced by the original pre-fire flora (Chapter 9). The above discussion illustrates the essential need to integrate ecology and life history of species in order to understand complex distributions and correlations (Brown 1986).

This research has shown that the insular nature of ecological islands can be quite complex. There are some distinct gradients in variation in the nature of outcrop insularity. There is an increase in the relative insular nature of outcrops in the east of the batholith, and in particular to the north east of the region. This is associated with an increase in altitude and subsequent decrease in temperatures and increase in rainfall. Previous investigations suggest that granite outcrops behave as 'xeric islands' within a mesic forest matrix (Hopper 1981; Phillips 1981; Phillips 1982; Baskin & Baskin 1988; Houle & Phillips 1989a, b; Houle & Delwaide 1991; Ware 1991; Porembski *et al.* 1994; Gröger & Barthlott 1996; Porembski *et al.* 1996; Wyatt 1997; Burke *et al.* 1998). The changes in insularity seen here support this hypothesis. Outcrops become more insular as they occur in increasingly less xeric surroundings. This also explains the decreasing insular nature of outcrops further west in the region and in particular at Kwiambal (KL), which is in the driest and warmest part of the batholith. At Kwiambal (KL), low differences between outcrops and woodland sites were attributed to an increase in the number of shared species (high Quotient of Insularity for woodland sites). There is a lack of distinction between outcrops and the surrounding flora in areas where climatic differences between 'island' and 'sea' are less marked. On a larger geographic scale, this would also explain the occurrences on outcrops of species that are at their climatic limits (Chapter 8). Similar results were obtained by Porembski *et al.* (1996) when investigating outcrops within West African rainforest. These species, normally from warmer and drier climates can only survive on the warmer and drier outcrops in the region. Burke *et al.* (1998) found lack of endemic species on granite outcrops in the Namib Desert and a high number of species at there distributional limits. They attributed this pattern to the outcrops being insufficiently isolated and to the long-range dispersal of the many of the species found. Hopper (1999) also found that areas of high rainfall in the south west of Western Australia had outcrop floras that were more insular, with the drier climate outcrop floras being virtually identical with the surrounding terrain. This change was attributed by Hopper (1999) to a mirroring of the dynamics of other Western Australian communities whereby, the higher rainfall areas have had a more variable climate in the past enabling greater opportunities for speciation. The evidence here suggests the arid nature of the surrounding communities alone could explain these differences.

Insularity shows a unimodel response. Demon (DM), an extreme eastern site, has a low Quotient of Insularity. The lack of difference between outcrops and forests at Demon (DM) is due to a lack of outcrop restricted species. This lack is partly explained by the fact that only small outcrops were found at Demon (DM) but it may also be explained by the high rainfall and warmer temperatures associated with the edge of the eastern escarpment. Here and in other localities in the extreme east some closed forest species began to appear on outcrops. There are two possible explanations for this phenomenon. At a certain threshold on the moisture gradient, some of the xeric features of outcrops are ameliorated. Small outcrops are also prone to an increase in fire frequency. The Demon (DM) and other sites at the extreme east of the batholith were exposed to a comparatively higher fire frequency. Many of the common outcrop restricted species were wiped out by the frequent fires (Binns 1992) (Chapter 9). Both of these phenomena can account for the low insular scores at the extreme east of the batholith.

The results presented here are primarily a static picture of events and this is typical of many insular biogeographic studies (Levin & Heatwole 1973). Some historical factors have been assessed in the analysis, which has shown a temporal aspect to the insular nature of outcrops on the batholith. Disturbance has been found to affect the insular nature of other systems (Butcher *et al.* 1981; Janzen 1983) and is indicated as having significant affects in these analyses. Grazing pressure was significant, in both direct and indirect gradient analyses by reducing the number of outcrop restricted species and increasing the number of ubiquitous or forest species. Although of minor influence in direct gradient analysis, fire was significantly correlated with an increase in outcrop restricted species (Chapter 9). These changes by their nature are more proximal and will usually only affect individual outcrops or a small group of outcrops. An important extension of this research would be to follow individual outcrops and monitor the changes in their insular nature.

Each insular system is unique and needs to be assessed on its own merits (Heatwole 1991). The research presented here shows the value of addressing whether insular systems are indeed insular. It is also important to describe both spatial and temporal changes in the insular nature of systems. It is only after this variation has been explained that useful analyses of the factors affecting the biodiversity and dynamics of species occurring on ecological or real islands can be assessed.