

**Chapter 1: General Introduction and Aims**



# Chapter 1

## General Introduction and Aims

### 1.1 General Aims of Biogeography

Biogeography, in the simplest terms, is the investigation of the distribution of organisms. More precisely, biogeography attempts to determine how speciation, adaptation, extinction and ecological processes interact with the physical and climatic world to produce current distributional patterns (Dansereau 1957; Tivy 1971; Myers & Giller 1988; Hengeveld 1990). Any investigation into biogeography must begin with acquiring data on the distribution of the biota under research and the determination of these patterns (Seddon 1971; Myers & Giller 1988). Such patterns are amenable to analysis without any assumptions of underlying process, or they can be used to test hypotheses (Myers & Giller 1988).

One of the most commonly posed questions in biogeography is ‘what are the patterns of biodiversity and what maintains these?’ (Cox & Moore 1993). Biodiversity is of importance to humanity, and its geographic distribution is fundamental to its conservation. Biodiversity is related to environmental heterogeneity including aspects of habitat heterogeneity. Due to the complexity of scale, both spatial and temporal, there is little hope of understanding patterns of biodiversity and the underlying processes that form them, unless division into components is undertaken, within which repeatable and consistent patterns occur (Huston 1994). A natural form of compartmentalisation occurs within insular systems. Such ‘island-like’ systems provide a workable framework within which investigations into richness and diversity can be achieved. In many situations, islands and ‘island-like’ systems are ‘hotspots’ for biodiversity, or are places where a major disjunction in biotas occurs.

An understanding of the processes leading to the development and maintenance of biodiversity on such ‘islands’ will assist their conservation, and also be of relevance to conservation of other biotas. Fragmentation of ecosystems and the subsequent extinction of species resulting from human activities are occurring at an unprecedented

rate throughout the world (Huston 1994). Clearing within Australia is at an annual rate approaching that seen in Sudan, Thailand, Venezuela, Bolivia, Mexico and Zaire, being only overshadowed by Indonesia and the Brazilian Amazon (Hopper 1997b). As the fate of more species are tied to an 'island-like' reserve network, the study of natural insular systems is becoming more important. Such studies may aid in conservation and management decisions and theories on minimal viable population sizes (Sampson *et al.* 1988; Main 1997a). Within Australia, unlike other parts of the world, it is not tropical rainforests or temperate forests that are under greatest threat of loss of plant diversity. The greatest loss of biodiversity is in temperate lowland woodlands, grasslands, mallee and heaths (Hopper 1997b) of which the floras on granitic outcrops within eastern Australia are a part.

Granitic outcrops have long been considered to constitute 'habitat-islands' within a forested matrix (Smith 1962; Burbank & Platt 1964; Axelrod 1972; Erickson *et al.* 1973; Wyatt & Fowler 1977; Burbank & Phillips 1983; Ornduff 1987; Uno & Collins 1987; Baskin & Baskin 1988; Houle & Phillips 1989a; Houle 1990; Houle & Delwaide 1991; Pignatti & Pignatti 1994; Porembski *et al.* 1994; Ibisch *et al.* 1995; March & Bass 1995; Fleischmann *et al.* 1996; Gröger & Barthlott 1996; Bayly 1997; Main 1997a; Wyatt 1997). The constituent outcrop floras are thought to be insular, and thus the vegetation is strongly discordant with the adjacent vegetation. Granitic outcrops are particularly appropriate for studies of island biogeography as they have a worldwide occurrence with replicate geomorphological structure and equivalent environmental conditions (Burbank & Platt 1964; Walters & Wyatt 1982; Gröger & Barthlott 1996). Outcrops represent vegetated areas with comparatively low human impact, therefore offering possibilities for continuing long term studies of biodiversity (Gröger & Barthlott 1996). They provide natural instances of isolation of populations and gene flow (James 1982). Consequently, granitic outcrops provide excellent opportunities for comparative investigations of patterns, and the underlying factors that shape richness and diversity in insular systems (Porembski *et al.* 1994; Ibisch *et al.* 1995; Gröger & Barthlott 1996; Porembski *et al.* 1997).

This thesis aims to investigate and reveal the nature of vascular plant biodiversity on the ‘archipelagos’ of granitic ‘islands’ (outcrops), and the factors associated with its development and maintenance, and will explore the implications and ramifications of these findings for conservation of plant biodiversity generally. The granitic outcrops and the floras they support on the New England Batholith of eastern Australia are chosen as an insular system worthy of investigation in these terms.

The following sections of this introductory chapter first provide a discussion of boundary delineation and thus a working definition of a granitic outcrop. A discussion of the granitic outcrop environment then ensues that provides a framework in which patterns and processes of biodiversity are placed. A precis is then provided for the following chapters contained within this thesis. Each chapter provides its own specific literature review on the topics considered within them. A brief glossary of the land form terminology used in the following sections is provided in Chapter 2.

## **1.2 Island Systems**

Any system thought to be somewhat discordant from its surroundings may be considered insular, and thus an ‘island’ (Myers & Giller 1988). A vast range of systems other than true islands have been considered as islands and research has been undertaken on these based on their supposed insular qualities (for example Culver 1970; Brown 1971; Opler 1974; Abele & Patton 1976; Schoener & Schoener 1983; Elmberg *et al.* 1994; see Chapter 4 for a more thorough review). The proper definition and delineation of the boundary of a system is of importance, as it is at this point that species will be included or excluded from the system. The following sections provide information on how boundaries have been delineated both in other systems and for granitic outcrops. This information is used to present a clear definition of what an ‘outcrop’ is in terms of this investigation.

### **1.2.1 Boundaries and defining systems**

The determination of a boundary depends on its definition (identifying conceptual boundaries) and its delineation (identifying physical boundaries) (Winning 1991). All boundaries are arbitrary, and even when precisely defined criteria are used, some subjectivity is unavoidable (Canny 1981; Winning 1991). It is obvious that the delineation of boundaries (natural or artificial) is a major concern for most ecological investigations. The definition of boundaries between ecological systems and the delineation of the systems under investigation by ecologists are rarely, if ever, satisfactorily tackled. Most commonly, ecologically investigated systems are defined simply by name, such as rainforest or wetland, but their limits are not conceptualised. Canny (1981) states that boundaries drawn by ecologists may not be important to the organisms investigated, and that distinctions that are important to organisms are likely to go unnoticed by ecologists. Nevertheless, clear and distinct discontinuities do seem to occur and vegetation types dominated by different life forms usually coincide with steep gradients, or are a reflection of some ecological disequilibrium (Wardle 1981).

Boundaries consist of a series of barriers that are of differing effectiveness to each individual organism under investigation. A barrier may be simply defined as any environmental condition (discontinuity) which limits the dispersal or establishment of a taxon (Brandt & Wadley 1981). Where a number of barriers exist one would expect sharp discontinuities to be apparent (Brandt & Wadley 1981). Whether taxa have shared or disjunct responses to such barriers has important consequences for understanding the mechanisms that produce patterns (Keddy & Ellis 1984). Broadly, two types of barriers exist: ecological and physical (Brandt & Wadley 1981). Ecological barriers include competition, predators or limiting resources such as food. Physical barriers include factors such as degree of rockiness and frequency of storms. Physical barriers may coincide with ecological barriers and they often provide a template for ecological habitat partitioning, making it difficult to isolate the effects of each (Brandt & Wadley 1981).

Wetlands and rainforests are examples of frequently investigated systems that are not always clearly defined. Wetland boundaries are often defined as a line of best fit,

particularly in areas where gentle slopes are involved that cause gradual changes (Winning 1991). Researchers who attempt to classify and define wetlands are faced with the dynamic nature of these systems (Brock 1996). Changes in rainfall and climate, both seasonally and over longer periods, cause changes in floristics and boundaries. Similarly, although researchers often stress the sharp distinction, both structural and floristic, between rainforest and non-rainforest, many areas considered to be rainforest in Australia would not seem so to a visitor from overseas (Adam 1994). Rainforest boundaries are not stable either, but expand and contract over small periods. Ashton (1981) showed that the boundary between forests could be sharp, between 2-3 crown diameters, or extend over more than 500 m. Other supposedly clearly distinct systems have diffuse boundaries, for example riparian systems may extend their influence past where a river leaves its headwaters (Brown *et al.* 1997).

### **1.2.2 Boundaries and insular systems**

Many boundaries that have been defined are based on criteria that are likely to be of little importance to the biota investigated. For example many mountaintops have been considered insular, yet their boundaries are often defined purely by altitude (Vuilleumier 1970; Brown 1971). Other mountain areas have been defined simply by vegetation structure, such as the tree line (Johnson 1975; Lomolino *et al.* 1989). Although park or woodlot boundaries are clearly defined (Diamond *et al.* 1976; Gottfried 1977; Faeth & Kane 1978; Janzen 1983; Blake & Karr 1984), the boundary is likely to be of little consequence to a large part of the biota. Even in investigations of true islands it is often unclear whether strand areas or intertidal zones have been included. Lakes, similarly, are defined as the 'lake'. The effects of feeding tributaries or whether they should be included is rarely discussed. Many other insular systems are unlikely to sustain a constant or discernable boundary, for example marshes (Rey & Strong 1983; March & Bass 1995).

### 1.2.3 Definition of a granitic outcrop

In most instances granitic outcrops are defined simply by name or described as a domed shaped hill or bare rock face. Stricter geomorphologic terms have recently been applied (e.g. Hopper 1981) and names such as *inselberg* or *bornhardt* are now used. None of these terms can be used as an exact definition as the boundaries are not delimited in any strict sense.

Attempts have been made to create a definition of a rock outcrop or define the boundaries of outcrop communities. Burbank and Platt (1964) defined outcrop communities as those confined to soil depressions entirely surrounded by exposed rock. This neglects the many habitats on outcrops that are not soil depressions such as crevices, boulders or the bare rock surface itself. Murdy (1966) considered any exposure of rock above the surface of the soil as an outcrop, and the margin was defined by the edge of the exposed surface. Hambler (1964) and Axelrod (1972) used the terms *bornhardt* and *inselberg* in reference to granite outcrops. Such terms omit many smaller landforms that most would consider outcrops such as 'flatrocks'. Hopper (1981) more recently used the term *inselberg* as defining granite outcrops and stated that the rocks he surveyed were predominantly of this kind, presumably indicating that other undefined types were also studied. Burgman (1987) believed that there is a sharp boundary between the granite outcrops he investigated and the surrounding landscape. He defined granite outcrops as areas of 'dissected sheet granite supporting pockets of skeletal soil' whose margin was defined by a lack of exposed rock and a 'scree slope of shallow sand, gravel and boulders'. Ornduff (1987) stated that outcrops were any sizeable, isolated intrusion into the landscape. This definition does not aid in boundary delineation. Fuls *et al.* (1992) simply stated that outcrops were areas with a high percentage of surface rock. *Inselbergs* primarily of *bornhardts* and *whalebacks* along with flat-topped mountains and *ferricretes* or *iron pans* were defined as outcrops by Porembski *et al.* (1994), while Ibisch *et al.* (1995), Porembski (1995) and Wyatt (1997) also included *kopjes*. There is obvious difficulty in attempting to create a precise definition of an outcrop (Hopper *et al.* 1997; Main 1997a) particularly where the delineation of boundaries is concerned.

Gröger and Barthlott (1996) broadened the definition of the term inselberg to incorporate a greater diversity of rock outcrops. They believed that an inselberg in an ecological sense should include ‘...sites of more or less compact, crystalline rock surfaces scattered like islands in contrasting surroundings and covered by only a shallow soil layer or none at all...’ which excluded ‘...inselbergs in a progressed stage of disintegration (kopjes)...’ or ‘...table mountains’. Other researchers have attempted to define outcrops in a biological sense. Benwell (1995) defined the boundary of an outcrop (and hence an outcrop) as ‘the point where the upper stratum crown cover of eucalypt trees exceeded 20%’. The periodic death of individual trees or their establishment, could greatly affect which sites are included or not. Such a definition is also not transferable to other regions where trees may be less common. Hopper *et al.* (1997) used the distribution of plants that are locally endemic to outcrops to define the extent of outcrop communities. This neglects the possibility that endemic species may shift their niche breadth when growing with differing combinations of taxa or in areas at the species’ climatic limits thereby making their definition elastic under different climates or competitive regimes. Furthermore, outcrop endemics may not occur on all rocks. Wisser *et al.* (1996) attempted to combine both physical and ecological components in their definition of an outcrop. They considered that outcrops were to have ‘herbaceous plant species as a prominent component of the vegetation, > 5% of the area as exposed bedrock and > 75% of the area with bedrock within 20 cm of the surface’. Such an approach relies on the component flora of outcrops being primarily herbaceous, an assumption that is not always met (e.g. Ashton & Webb 1977; Beadle 1981; Binns 1995a).

A combination of biological and geomorphological terms in the definition of an outcrop will be more precise and easier to interpret in the field. However, inclusion of biological criteria in the definition of an outcrop may become circular in reasoning, if certain analyses or conclusions are made (for example, if species are used to define the boundaries of outcrops and then restriction to the outcrop is used to define endemism to the outcrop habitat). Therefore, a primarily geomorphic definition of an outcrop is used here. Granitic outcrops are defined here as: isolated and sizable positive relief intrusions into the landscape that are composed of dissected sheet granite supporting pockets of skeletal soil. This mainly includes inselbergs such as bornhardts, pediments, rock



platforms and tumuli if grounded on an exposed pavement, but does not include kopjes, nubbins, fugitive outcrops or tumuli on fugitive outcrops. The margins of these systems are defined by a clear break in the exposed granite sheet that is consistent, extended and with soil development greater than half a metre in depth. Such a definition of a granite outcrop and its boundaries will normally coincide with a number of biological gradients (see below). Hence the boundary will be delimited by marked changes in vegetation structure and composition but it is not defined by them.

### **1.3 The granitic outcrop environment**

Spatially, granitic outcrops frequently occur as clusters with exposures separated by a few kilometres or less, and much greater distances separating the clusters in turn from one another (Murdy 1968). This 'island-like' environment has ramifications for the distribution of plants and, potentially, the genetic divergence of their component populations. In addition outcrops, along with many other specialised systems (e.g. cliffs), are harsh and stochastic environments compared to others with the same macroclimate (Phillips 1981; Phillips 1982; Houle & Phillips 1989b; Dörrstock *et al.* 1996). In general it is not the average climate, as expressed in its many variables (e.g. mean daily temperature or yearly average rainfall), but the rarer extremes that limit plant survival. Granitic outcrops are systems in which the extremes of climate are encountered more frequently, and often with greater intensity (Dörrstock *et al.* 1996).

The microclimate of granitic outcrop systems is diverse over very small distances (Hamblen 1964; Uno & Collins 1987). Many extreme variations in microclimate may be persistent for extended periods (Hamblen 1964; Porembski *et al.* 1996), however most occur only temporarily (Hamblen 1964; Burbank & Phillips 1983). Thus there are 'stresses' that impede the establishment and persistence of plants on granite outcrops (Uno & Collins 1987). In turn, these same 'stresses' may also aid the rapid evolution of the component flora, both in terms of co-evolution of adaptive life history traits and in the divergence of individual populations. It is important therefore that a discussion of the current knowledge of the physical, climatic and temporal environments of granitic outcrops precedes the research chapters outlined in this thesis, as these variables provide a template on which richness and diversity are maintained. The following provides a

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brief outline of some of the known parameters circumscribed by the granitic outcrop environment.

The most noticeable feature of granitic outcrop environments is the lack of true soil development (Platt 1951). Plants often persist in a thin layer of organic dust overlain by coarse granite shingle (Gillham 1961). The skeletal soil, composed primarily of organic matter, is very acidic, commonly between pH 4 and 5 (Hamblen 1964; Jones 1964; Rundel 1975; Phillips 1981; Dörrstock *et al.* 1996). Such a low pH significantly affects the availability and/or toxicity of many nutrients (Meyer *et al.* 1960). An increase in soil depth has also been correlated with a higher average pH and a greater cation exchange capacity (Shure & Ragsdale 1977). One of the most pertinent effects of poor soil development for plants, is the lack of water retention. A relatively minor increase in soil depth can dramatically prolong water retention capabilities (Burbank & Platt 1964; Houle & Phillips 1989a). These thin soils rapidly dry out after rain and have little or no moisture available for extended periods (Murphy *et al.* 1970; Chapman & Jones 1975; Uno & Collins 1987; Baskin & Baskin 1988). The low water retention of soils is accentuated by heat absorption of granite, high incident radiation and winds, little cooling from evapotranspiration and high runoff (Phillips 1981; Phillips 1982; Walters 1982; Baskin & Baskin 1988; Houle & Phillips 1989a; Ware 1990; Dörrstock *et al.* 1996). It is estimated that 45 to 47% of rainfall is shed from outcrops after individual storms and that depending on the granitic outcrop characteristics, up to 95% runoff can be expected (Walters 1982; Moran & Hopper 1983; Lawler *et al.* 1997; Wyatt 1997). Such a high incidence of runoff means that at the least, the available moisture afforded to the vegetation on outcrops is almost half that of the surrounding vegetation matrix, if not a great deal less. Conversely, extended waterlogged conditions often occur depending on the topography of the available soil pans. Plants often have to contend with waterlogged situations followed by times of intense drought, within a matter of days. Few species are able to cope with such alternating submergence and desiccation (McVaugh 1943).

The overall macroclimate of a region is further modified on exposed granitic surfaces in terms of temperature. Temperatures are often 8—18°C higher than that of the ambient air (Winterringer & Vestal 1956; Shure & Ragsdale 1977). Platt (1951) recorded surface

temperatures of 63°C in summer with temperatures of 55—60°C being very common for 4—5 hrs of the day (Erickson *et al.* 1973; Phillips 1982; Walters 1982; Uno & Collins 1987; Reinhard & Ware 1989; Porembski *et al.* 1995; Dörrstock *et al.* 1996; Porembski *et al.* 1996). The low temperatures are also extreme, and the diurnal variations that are met by plants on outcrops are high (Jones 1964). Mares (1997) reported air temperature changes of up to 38°C over a 24-hour period on a granitic outcrop.

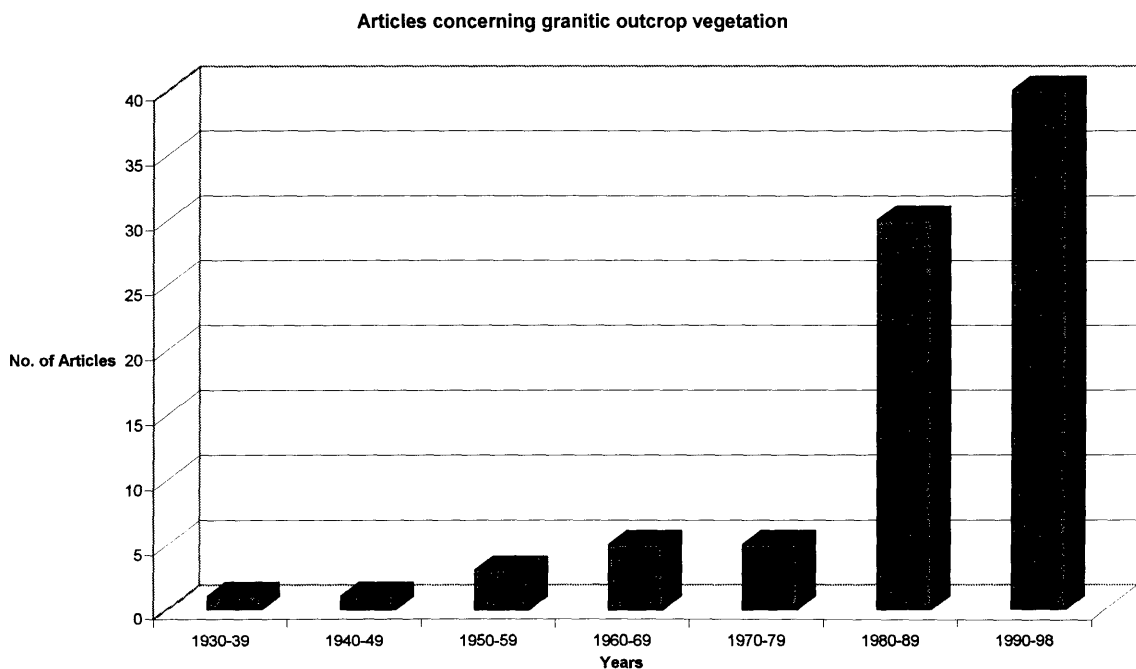
Variation in microclimate can be dramatic within a single granitic outcrop, due to aspect, slope, structural vegetation type and cover and topographic and micro-topographic variation (Ashton & Webb 1977). Hambler (1964) showed that the soil temperatures on a single vegetated patch on a granitic outcrop varied from 50°C in ephemeral flush vegetation to 35°C within the adjacent *Andropogonetum* patch. Uno and Collins (1987) showed that in an open herbfield the soil temperatures could be up to 6°C cooler under herbs than on unvegetated adjacent soil. Saplings and trees tend to stabilize the microclimate and contribute to the establishment of more mesic conditions (Phillips 1982; Burbank & Phillips 1983). Compared with large outcrops, small sized rock outcrops have less pronounced variation in microclimate (Porembski *et al.* 1996). The density of vegetation and the amount of exposed granite that surrounds a vegetation patch can dramatically ameliorate, or accentuate the extremes of environmental conditions (Houle & Delwaide 1991).

The wet and, more commonly, the dry extremes accentuate the severity of living conditions for outcrop taxa (Winterringer & Vestal 1956). Evaporation is rapid and drought is common. High temperatures, winds and incident radiation accentuate this. The majority of the rainfall that does occur is lost as surface runoff. In winter, cold temperatures and winds are just as detrimental to the survival of species (Hopper 1981; Phillips 1981). Such harsh conditions are met frequently and fluctuate greatly both seasonally and diurnally. Such abrupt changes are a strain physiologically on taxa (Oosting & Anderson 1937) and constitute extremely limiting environments (Maycock & Fahselt 1992). Granitic outcrops are environments that are commonly inhospitable to mesic invaders (Fleischmann *et al.* 1996) and constitute edaphic and micro-climatic deserts (Houle & Delwaide 1991; Porembski *et al.* 1994; Gröger & Barthlott 1996;

Porembski *et al.* 1996), even within macro-climates of high rainfall (Dörrstock *et al.* 1996). It is believed that coping with seasonal or unpredictable drought is the most significant survival strategy faced by the granitic outcrop flora (Kirkpatrick *et al.* 1988; Houle & Phillips 1989b; Gröger & Barthlott 1996; Hopper 1999).

#### 1.4 Research on the vegetation of granitic outcrops

The following provides an outline of the current published knowledge of the dynamics of the vegetation and vascular plant taxa found on granitic outcrops. Such investigations concentrating solely on the dynamics of granitic outcrop vegetation are becoming increasingly more popular in the English literature as Figure 1.1 illustrates.



**Figure 1.1:** The number of articles focused on the dynamics of the vegetation on granitic outcrops has increased dramatically over time. Based on current contents searches in the English literature and the subsequent incorporated references.

##### 1.4.1 Succession as documented on granitic outcrops

The documentation of supposed succession on bare granitic rocks has occupied much of the literature. Due to the large amount of research on this topic, and the possibility that

seral change may be a process by which richness and diversity are maintained on outcrops, this topic is reviewed here. Even in the earliest investigations on primary succession on granitic outcrops much contradictory evidence was found regarding seral changes. This had led some researchers to modify the concept of a linear progression of seral stages, or to completely abandon the belief that primary or other succession occurs at all.

Whitehouse (1933) was not able to accurately document replacement stages of succession, but still believed that succession followed a sequence from crustose lichens to mosses and finally to a grassland climax on granitic outcrops in Texas. Succession on granite outcrops according to Whitehouse (1933) was related to soil depth, and to accommodate what was found, four types of succession were described: rock surface; crevice; gravel; and rock pool. Without crevices, Bharucha and Ansari (1962) believed that only lithophytes could develop. Burbank and Platt (1964) showed that species richness increased with increasing soil depth and believed that this was evidence of a seral process. They attributed the increase in soil depth to purely physical agencies and stated that the conventional seral sequence was not important, but that progress was inevitable. Some hard soil lenses washed away during this investigation without ever having had a cover of vegetation (Burbank & Platt 1964). This evidence only applied to rock basins (gnammas) i.e. Whitehouse's (1933) rock pool or gravel succession. Changes in crevice vegetation, where soil depth is difficult to measure or of less consequence, was not mentioned. Winterringer and Vestal (1956) and Shure and Ragsdale (1977) also believed that soil depth was the most important feature in seral progression and that this was primarily achieved by physical means. Although vegetation patches were observed for five and a half years and no changes found, Hambler (1964) believed that the structural differences in the vegetation must have been seral. Ibisch *et al.* (1995), who studied outcrops in Africa over several years came to the conclusion that there was no evidence to suggest successional processes were occurring. Houle (1990) also did not observe succession, but was of the opinion that it did occur in soil islands although the development from a herb to a shrub and tree stage may take over 700 years. Lack of evidence was thought to be due to the small temporal scale of observations.

Keever (1957) provided evidence that mosses could establish on bare granite without the aid of lichens. A modified successional sequence was proposed by Rundel (1975) based functionally on physiographic weathering leading to the formation of fracture lines suitable for colonization, but not requiring initial colonization by lower forms, similar to that of Whitehouse (1933). Rundel showed that shrub seedlings could establish within crevices, and rarely did vascular plants colonize outcrops before physiographic weathering had occurred. Winterringer and Vestal (1956) stated that the role of lichens as rock destroyers and formers of soil had been considerably exaggerated. Although Rundel (1975) believed that bryophytes contributed little toward the development of advanced plant communities, succession was believed to proceed in a sequence once more advanced forms were established. Burgman (1987), however, collected 18 soil samples from unvegetated soil islands and showed that the only plants to develop were dicotyledons.

Some anecdotal evidence is provided which suggests that structurally less complex vegetation aids in the germination and establishment of 'higher' lifeforms. Seeds are thought to be trapped in moss and lichen mats, which provide a sponge of moisture and insulation that allow germination to occur (Oosting & Anderson 1937; McVaugh 1943; Winterringer & Vestal 1956; Richards 1957; Smith 1962; Burbank & Platt 1964; Ashton & Webb 1977; Sampson *et al.* 1988). A few published accounts have provided potential quantitative evidence of succession occurring on granitic outcrops (Ashton & Webb 1977; Burbank & Phillips 1983; Houle & Phillips 1989). Ashton and Webb (1977), while primarily presenting a critique of previous work on succession on outcrops, showed evidence that moss and lichen mats aided the germination and survival of vascular plant species, and thereby promoted changes in species composition and structural development. Burbank and Phillips (1983) quantified changes in vegetation patches on granitic outcrops over a 22-year period. Although photographs of communities showed no major increases or decreases in extent or shape, on average soil depth increased over time. With increasing soil depth, changes occurred in 16 out of 34 vegetation patches (47%) that enabled them to be reclassified into a different community. However, Burbank and Phillips (1983) had *a priori* and qualitatively circumscribed the seral communities and were not clear on how this occurred or where the boundaries of one community and another could be drawn. It appears that although changes were noted, whether these quantitatively constituted true, seral development or

were purely subjective, is unclear. Houle and Phillips (1989b) provided evidence similar to that of Ashton and Webb (1977) which showed that once the problem of seed availability was overcome, the presence of species able to grow in shallower soil often facilitated the establishment in shallow soil islands of species characteristic of deeper soil.

It appears that supposed successional stages are set back by purely climatic physical changes, thereby making successional development highly improbable. The large volume of runoff on granite outcrops (Section 1.4.) is considered to be a destabilising event, by washing away vegetation and soil (McVaugh 1943; Keever *et al.* 1951; Winterringer & Vestal 1956; Gillham 1961; Jones 1964; Wyatt & Fowler 1977). Conversely, rainless periods may kill all plants and increase the erosive action of runoff in subsequent rain periods (McVaugh 1943). Other destabilising events thought frequent enough to disrupt succession include strong winds, fire, disease and drought (Oosting & Anderson 1937; McVaugh 1943; Keever *et al.* 1951; Winterringer & Vestal 1956; Ashton & Webb 1977; Shure & Ragsdale 1977; Phillips 1981; Burbank & Phillips 1983; Houle & Phillips 1989b; Houle & Delwaide 1991; Dörrstock *et al.* 1996). Winterringer and Vestal (1956) concluded that there were no regular describable sequences, and that destructive events were so frequent that there was no tendency for a regular convergence to any sort of climax. Similarly, Shure and Ragsdale (1977) found the frequency and severity of destabilising events could affect the degree of community modification to such a degree that any successional stage should be viewed as potentially terminal, a theme reiterated by others (Ashton & Webb 1977; Dörrstock *et al.* 1996).

Oosting & Anderson (1937) believed that outcrops were a pioneer habitat of permanent duration and that composition of vegetation patches were based on what suitable species were immediately available. Once a taxon becomes established it is unlikely to have its place usurped. Ibsch *et al.* (1995) speculated that the harsh environmental conditions on outcrops required specialised lifestyles, that the very small lifeform pool was the most important factor determining composition rather than succession.

It is obvious from the published literature that what constitutes the change from one seral stage to another, particularly when 'higher' life forms are associated, is never clearly defined. Certainly a change in structural complexity is the most commonly used criterion for recognising seral changes. However, the presence or absence of a single individual of a tree or shrub will often place one vegetation patch within an earlier or a later seral stage. These criteria do not take into account overall floristic composition and relatedness, and it is possible that much of the supposed documented seral changes are purely subjective and may not constitute actual changes if quantitatively analysed. Furthermore, what constitutes the potential or ultimate climax is often not defined. It is obvious that some researchers believe the ultimate climax constitutes a vegetation matrix similar to that of the surrounding vegetation. Others seem to separate outcrops from the surrounding vegetation and believe that the vegetated patches have a climax of their own.

It appears that the different spatial and temporal scales used by various researchers have influenced the conclusions made. The temporal scale of observations may be too short to enable accurate conclusions. However, some research has shown that some outcrops have been exposed for at least 200 000 years and some may have been exposed for millions of years (Matthes 1930 quoted in McVaugh 1943) showing little evidence of modification.

There is a complex and stochastic process involved that, in part, allows seral changes to occur in some situations (soil depressions that increase in depth) but not in others (crevices). Only a limited species pool of colonisers is available that can establish and populate this 'arid' environment. Other species will germinate and grow for some seasons but will more regularly be killed by adverse conditions. Although the stage may be set for seral development, species may not be available before a disturbance event occurs (Houle & Phillips 1989b). Whether individuals of a species can establish and how long they persist depends primarily on the niche supplied by the physiological weathering. Ultimately, persistence is based on the physical attributes of the site (slope, crevice depth, soil accumulation etc.) and protection from stochastic destabilising events (fire, drought, winds, runoff).



It is apparent from this review that succession itself is unlikely to have a significant role to play in the development and maintenance of richness and diversity on granite outcrops, at least over short or medium time periods. However, the issues and processes that limit seral development such as destabilising events, chance colonisation and extinction and the various physiognomic habitats available by purely physiological weathering may be of utmost importance in maintaining richness and diversity across the landscape.

#### **1.4.2 Unique vegetation and flora on granitic outcrops**

Ornduff (1987) stated that granite outcrops supported an unusual array of vascular plant species and represent a distinctive edaphic and floristic intrusion in the woodland or forest communities in which they occurred. The 'arid' nature of the granite outcrop environment often sharply contrasts with the more mesic surroundings (Richards 1957; Murdy 1966; Axelrod 1972; Walters & Wyatt 1982; Ornduff 1987; Burgman 1987; Fanning & Mills 1991; Binns 1992; Porembski *et al.* 1994; Ibisch *et al.* 1995; Fleischmann *et al.* 1996; Main 1997a). It is evident that earlier publications have often confused this sharp discontinuity of the vegetation structure and the different assemblage of species as an indication of an almost entirely endemic flora. McVaugh (1943) thought that granite outcrops supported a more or less endemic flora of highly specialised species. At least one third of the species were considered to be restricted to the outcrops alone according to Hambler (1964). Murdy (1966; 1968) also stated that the flora of outcrops was unique and rich with a large assemblage of endemic species. Other authors (George *et al.* 1979; Walters & Wyatt 1982; Baskin & Baskin 1988; Ware 1990) have expressed such comments.

Despite many claims to the contrary, the actual number of true endemics is often low or non-existent in outcrop systems. McVaugh (1943) stated that at least 44 of the 200 species on granite outcrops in the southeastern United States were endemic to these systems. However, Murdy (1968) studying the same system found that only ten species were actually restricted to the granite outcrop environment. Platt (1951) found 8.5% of the outcrop flora to be endemic in the mid-Appalachians. Only three species were considered endemic in the Burbank and Platt (1964) study of granite outcrops in

Georgia. Similar low degrees of endemism were found in Texas (Walters & Wyatt 1982). Although Hambler (1964) had stated that one third of the flora of the African outcrops studied were endemic, other researchers have found that other African outcrop systems completely or almost entirely lack endemic species (Porembski *et al.* 1994; Porembski 1995; Fleischmann *et al.* 1996; Burke *et al.* 1998). A small number of species were found to be endemic on Venezuelan granite outcrops (Gröger & Barthlott 1996) but similar outcrop systems in Bolivia were noticeably lacking in endemic species (Ibisch *et al.* 1995).

Murdy (1968) showed that there was a centre of endemism in the southeastern United States and that the number of endemics decreased concentrically from this point. Where granite outcrops occur in more or less arid environments, such as in many of the African studies, the number of endemics is low or non-existent. Similarly, more endemics were found in the wetter Venezuelan than in the more arid Bolivian outcrop systems.

Hopper *et al.* (1997), comparing many of the investigations conducted on Western Australian outcrops, concluded that ‘...local endemism declines with increasing aridity, to the point where Kimberley and Pilbara outcrops show little discontinuity in species from the surrounding matrix’. Hopper (1999) has come to the conclusion that endemics, when they exist, originated via three different means, namely; 1) relictual with no obvious close relatives, 2) derived by speciation from allopatric congeners, and 3) derived by speciation from allopatric congeners of other granite outcrops.

It appears from these accounts that there are contrasting opinions as to the number, origin and importance of endemic species within the vegetation on granite outcrops. Endemic species may be found but their numbers are often low. The differences gleaned from the literature are only broadly comparative. The number of endemics varies across the landscape, particularly decreasing with increasing aridity. In at least some instances, the evolution of endemic species may have a role to play in the development of local richness and diversity on granitic outcrops. The differences between areas containing local endemics and those that do not, and the reasons for these observed patterns, may play a role in maintaining differences in diversity and richness across a landscape

containing granitic outcrop systems. Insights into these reasons will be valuable in conservation management planning for these and comparable environments.

### **1.4.3 Composition and definition of granitic outcrop vegetation communities**

The component outcrop flora has a sporadic and seemingly stochastic distribution (Platt 1951; Murdy 1966; Murdy 1968), which confounds the delineation of seral changes (Section 1.5.1). Similarly, it appears that traditional phytosociological techniques are difficult to apply to these systems. The origins of the constituent flora, and the persistence and prominence of individual populations, may play a significant role in the maintenance of richness and diversity, and the differences noted between contrasting outcrop systems. It is therefore important to discuss briefly some of these matters.

Earlier researchers believed that the flora of any given rock outcrop is recruited from the taxa of the surrounding district, supplemented by a minority of species distinctive to rock outcrops (Winterringer & Vestal 1956; Burbank & Platt 1964; Ornduff 1987). Species not restricted to rock outcrops can be further divided into those that are from the surrounding vegetated matrix and disjuncts from the flora of areas further afield some of which are introduced exotics.

Although the distribution of taxa across outcrops appeared to be random, Burbank and Platt (1964) realised there was a characteristic regional flora for outcrops. Axelrod (1972) further noted that the component regional outcrop floras had general affinities to taxa of arid environments. McVaugh (1943) divided the taxa from granite outcrops into two broad categories; 1) entirely restricted to outcrops and 2) not wholly restricted but largest populations occur on outcrops. Bharucha and Ansari (1962) divided outcrop flora species into seven phytosociological categories: 1) accidentals or escapes; 2) companion species; 3) species of alliance; 4) species of order; 5) differential species; 6) characteristic preferential; and 7) characteristic exclusive. Using preferential endemism and broader affinities Wyatt and Fowler (1977) used six divisions: 1) granite outcrop endemic; 2) restricted endemic; 3) near endemic; 4) coastal plains species; 5) mountain species; and 6) weedy species. Wyatt and Fowler (1977), and Fleischmann *et al.* (1996)

used similar categories: 1) outcrop endemic species; 2) indigenous species with restricted distribution; 3) indigenous species with widespread distribution; 4) naturalized species; and 5) status uncertain. Finally, within the Australian context Pignatti and Pignatti (1994) divided outcrop floras into four broad phytosociological groups: 1) endemics to the southwest province; 2) West and South Australian species; 3) southern Australian species; and 4) pan Australian species. There appears to be some utility in this divisive approach of compartmentalising the flora in order to understand the processes that act, potentially differently, on such subjective groupings.

The patterns shown by disjunct, relict and introduced species are likely to be different to those of endemics. Burgman (1987) showed that granite outcrops in Western Australia were important sites for relictual and recently evolved taxa. Some notable records are of disjunctions over 1500 km (Porembski *et al.* 1994). Within perhumid areas, outcrops provide opportunities for disjunct occurrences of arid adapted species (Erickson *et al.* 1973; Porembski *et al.* 1994; Ibisch *et al.* 1995; Porembski *et al.* 1996). Outcrops also provide, through their diverse range of microhabitats and low competition niches, for other relictual species to persist in fluctuating environments beyond their main range (Erickson *et al.* 1973; Abbot 1984; Hopper *et al.* 1997; Main 1997a; Burke *et al.* 1998; Hopper 1999). Main (1997a) believed that outcrops provided opportunities for the maintenance of a co-operative of refugees. It has been hypothesised that within fire prone environments, such as those in many areas of Australia, granite outcrops also provide places for relictual taxa that have not evolved to cope with this factor (Moran & Hopper 1983; Craven & Jones 1991; Binns 1992; Fuls *et al.* 1992; Gröger & Barthlott 1996; Beard 1997; Hopper *et al.* 1997; Lawler *et al.* 1998). However, this may not be a universal feature (Ibisch *et al.* 1995).

Exotic species need to be acknowledged as a significant component that augment, or disrupt, the natural patterns of richness and diversity. Contradictory details have arisen from various studies as to the nature and importance of exotic taxa and some hypotheses have been proposed. During an investigation into the vegetation on granitic outcrops in Western Australia Ornduff (1987) found that 37% of all taxa were exotic in origin. This percentage of exotic taxa is far above that of other relatively unmodified communities within Western Australia (Hopper 1999). Wyatt and Fowler (1977) also found that

'weeds' were a common component of North Carolina outcrop communities. The competitive ability of these 'weeds' was thought to be much reduced on outcrops due to the harsh environmental conditions and it was considered that outcrop endemics did not suffer from their competition (Baskin & Baskin 1988; Binns 1995a; Fleischmann *et al.* 1996). To accommodate the differences found in exotic species numbers, Hopper (1999) proposed that high invasibility could be attributed to an absence of major glacial soil stripping as an evolutionary force acting on the outcrop flora. Uno and Collins (1987) showed that many outcrop species could be found off outcrops in disturbed habitats. Hopper (*pers. comm.* 1998) has also found that some granitic outcrop endemics may become weeds in other areas when transplanted from granitic outcrops in Western Australia. Such observations led Wyatt (1997) to postulate that some 'weedy' taxa may have originally been restricted to granitic outcrops and have since spread more recently to sites disturbed by human activities.

Winterringer and Vestal (1956) stated that the vegetation on outcrops was an incomplete mosaic of highly dissimilar elements. Hambler (1964) believed that, the mechanisms driving species occurrences on outcrops were so stochastic, that observed communities could not be fitted into traditional phytosociological classifications. He further stated that the systems were far too complex for casual elucidation. Tracy (1982) found that any one of the main floristic components could be extensive in any place but lacking nearby. Ornduff (1987) found it anomalous that '...habitats occupied by non-shared taxa seemingly occur at both sites, these distributional patterns are not easily explained, particularly when some of these taxa were very abundant where they occurred'.

Hopper *et al.* (1997) presented results of multivariate analyses on the distribution of orchid taxa on granitic outcrops. They remarked on the fact that closely adjacent rocks were widely separated in the classification yet some geographically separated rocks had similar orchid floras. It is evident that even the most prominent taxa exist in small isolated populations in which there is little migration (Wyatt 1984). Larger populations on outcrops are often found to be, on closer inspection, subdivided into a number of smaller stands isolated from each other by areas of sheet granite (Moran & Hopper 1983). In addition to the lack of some of the more prominent taxa, there is also the inclusion of a number of taxa with very low constance (Porembski 1995; Dörrstock *et*

*al.* 1996). However, investigations indicate the stochasticity of species occurrences is low in some outcrop systems. West African outcrops have low beta diversity, indicating high floristic uniformity (Porembski *et al.* 1994; Porembski 1995; Porembski *et al.* 1996).

Binns (1995a; 1995b) and Chapman and Binns (1995) believed that the floristic composition of outcrops was very variable and even after multivariate analyses no obvious patterns could be elucidated. Such reservations are mirrored in a number of publications (Ashton & Webb 1977; Tracy 1982; Maycock & Fahselt 1992; Ibisch *et al.* 1995; Porembski 1995; Hopper *et al.* 1997). Jarvis (1974) on the other hand, while studying similar habitats, thought that although the systems were complex, at least crude divisions within the vegetation complex were possible.

It appears that due to such difficulties, a number of researchers have subjectively, and *a priori*, defined a number of habitat delimited phytosociological units in order to simplify comparisons between different outcrop systems and enable subsequent analyses. Porembski *et al.* (1994) defined seven communities that they thought were somewhat unique to outcrops and that were common to all. It was believed that the subjective delineation of these seven habitat communities would aid cross comparison of floras from many areas of the world. Within these habitat types, communities could then be defined based on the dominants. The seven habitat communities are: 1) cryptogamic crusts; 2) drainage channels; 3) crevices; 4) rock pools; 5) shallow depressions; 6) ephemeral; and 7) wet flush vegetation. This approach negates the need for floristic multivariate analyses and avoids the problems associated with the common stochastic distribution of the component floras. Such an approach may be of value in preliminary investigations into the processes that maintain floristic diversity and richness on granitic outcrops. Using subjectively defined community types limits the type and intensity of the cross comparisons that can be made. Whether such habitat communities are universal is yet to be shown. Since no previous publications are based on extensive and intensive investigations, it may be too early to negate the use of multivariate analyses and the resolving power of comparative research undertaken using quantitatively defined floristic units.

Periodic disturbance and extinction of populations is a common feature of outcrops. This is expressed in the inexplicable lack of occurrence of some of the most prominent species (frequent and abundant) both in adjacent patches on individual outcrops or on nearby outcrops. The reasons for the variation in distributional stochasticity are worthy of resolution.

#### **1.4.4 Adaptations and lifeform traits of granitic outcrop vegetation**

Species have adapted to tolerate the harsh physiological conditions on granitic outcrops in a multitude of ways. The means by which species are able to endure this environment, the success of such adaptations or whether there has been time to evolve such adaptations has implications for the potential richness and diversity of these habitats. Certainly basic requirements of outcrop species are tolerances of high temperatures, desiccation and high light (Section 1.4). In addition to physiological adaptations, species that are more or less restricted to outcrops exist in a mosaic of small isolated populations that may be separated by great distances, and therefore the effectiveness of cross-pollination and dispersal may be limited. Some results from research into this area are discussed here.

Outcrop plants often show gross morphological characters that aid drought tolerance, such as root systems that can penetrate small fissures and hoary and narrow leaves (Erickson *et al.* 1973; Uno & Collins 1987). Other common morphological characteristics include succulence (Fleischmann *et al.* 1996) and storage organs. Survival via underground storage organs is a method of drought avoidance commonly noted (Pate & Dixon 1982; Houle & Phillips 1989b; Hopper *et al.* 1997; Hopper 1999). Pate and Dixon (1982) discovered that species from granitic outcrops in Western Australia commonly had storage organs with a high nitrogen content allowing almost total desiccation during aestivation. These adaptations were thought to be unique response to this type of habitat.

Chapman and Jones (1975) found that even ubiquitous taxa shared by outcrops and the surrounding vegetation could be physiologically and chemically differentiated, with outcrop forms being more drought tolerant. These differences persisted in

transplantation experiments. The growth and photosynthetic rates of outcrop endemics have been shown to be maximal in high light environments (Baskin & Baskin 1988; Houle & Delwaide 1991). Research has proven implicitly that outcrop taxa have a much higher drought tolerance than species from the surrounding communities (Ashton & Webb 1977; Ware 1991).

Other plants on outcrops have evolved dormancy and germination cues that enable them to avoid drought periods rather than persist through them. Baskin and Baskin (1982) discovered that 85—90% of freshly matured *Arenaria* seeds from outcrops were innately dormant and that the 10—15% that germinated only did so at temperatures lower than those that occur in the habitat at the time of seed dispersal in summer. Similarly, Wyatt (1983) found that seeds of *Sedum* required a period of physiological after-ripening and were therefore restricted to autumn germination. Dörrstock *et al.* (1996) also found that dormancy prevented germination of many species within the last weeks of the rainy season on outcrops of the Ivory Coast. Dormancy was only broken in this system by a period of high temperatures followed by rain thereby preventing germination after sporadic rains in the wrong season. Such dormancy and germination characteristics are usually coincident with an annual life history which is the most common lifeform on outcrops (Erickson *et al.* 1973; Ornduff 1987; Uno & Collins 1987; Baskin & Baskin 1988; Porembski *et al.* 1994; Ibisch *et al.* 1995; Dörrstock *et al.* 1996; Hopper *et al.* 1997; Wyatt 1997). Long-term dormancy of up to 100 years has been found in some outcrop species (Keever 1957). Avoidance of drought can also be achieved by survival during periodic drying out. Many species on rock outcrops have been termed 'resurrection' plants such as species of *Borya*, *Cheilanthes* and *Pleurosorus* on Western Australian outcrops (Pate & Dixon 1982; Hopper 1999).

Wyatt (1981; 1983) has shown some plant species on granitic outcrops demonstrate a syndrome of ant pollination. It has also been noted that a number of primarily outcrop-restricted species self-pollinate (Wyatt 1984; Ornduff 1987; Dörrstock *et al.* 1996; Hopper *et al.* 1997; Wyatt 1997; Hopper 1999). Dörrstock *et al.* (1996) found that 57% of plant species were entomophilous in the outcrop system they investigated. Hopper



(1981; 1999) found that a number of granite outcrop woody perennials in Western Australian are potentially bird pollinated.

Anemochory appears to be a common diaspore dispersal method (Porembski *et al.* 1994; Porembski *et al.* 1996). Dörrstock *et al.* (1996) found that up to 75% of species on the Ivory Coast granitic outcrops were anemochorous, although 77% were polychorous. Wyatt (1997) believed that in general diaspore dispersal was highly localized and was affected primarily by wind and water. Hunter *et al.* (1998) postulated that reptiles could effect dispersal of some outcrop taxa but that this was likely to be very localized. Conversely, Burke *et al.* (1998) believed that the long distance dispersal of outcrop taxa in the Hauchab might explain the lack of local endemics.

Species on granitic outcrops also contend with low nutrient soils of high acidity. This has led to the occurrence of a high number of carnivorous species (Dörrstock *et al.* 1996; Hopper 1999). Dörrstock *et al.* (1996) believed that the nutrient deficiencies of the soil also favoured the production of very small diaspores produced in large numbers. The fire refugial aspects of outcrops (Section 1.5.3) have also permitted the persistence or evolution of obligate seeder life history traits that often are contrast with features of the surrounding flora (Gillham 1961; Erickson *et al.* 1973; Ashton & Webb 1977; Fuls *et al.* 1992; Binns 1995a; Gröger & Barthlott 1996; Beard 1997; Hopper *et al.* 1997; Heinze *et al.* 1998; Hunter 1998a; Lawler *et al.* 1998; Hopper 1999).

It is clear that the lifeforms characteristic of floras of granitic outcrops are those most commonly associated with arid environments, and that many physiological and gross morphological features of these taxa are adaptations to drought. Some adaptations also pertain to the 'island-like' nature of the granitic outcrop systems, particularly in terms of pollination and dispersal.

#### **1.4.5 Evolutionary dynamics on granitic outcrops**

Granitic outcrops are ancient landscapes. They are arid environments, often in contrast to more mesic surroundings (Section 1.5.2). Many of the taxa on outcrops are relicts or

at their distributional limit (Section 1.5.3). In addition, populations are often small, inbreeding (Section 1.5.4) and prone to extinction (Section 1.5.1). Such conditions provide opportunities for the investigation of living collections of discrete, yet integrated, natural evolutionary experiments (Bussell & James 1997).

Earlier investigators believed that granite outcrops must be ancient landscape features due to the number of endemics found on them (McVaugh 1943; Burbank & Platt 1964; Murdy 1966; Murdy 1968). However, as has been previously discussed the number of endemic taxa was commonly overrated (Section 1.5.2). Despite this, many narrow endemics have evolved and species characteristic of this habitat share many common adaptations. Wyatt and Fowler (1977) proposed an island-hopping model to account for the discrepancy between the apparent antiquity of the flora and the relatively recent origin of specific outcrops. The habitat and flora are much older than the age of any one exposure. While individual outcrops have not persisted indefinitely, collectively outcrops of hard crystalline rocks have been available for occupation throughout angiosperm history (Burbank & Platt 1964; Murdy 1968; Axelrod 1972). Outcrops are exposed gradually in a patch like manner resulting in a series of discontinuous basement sites (Axelrod 1972). Main (1997a) believed that the evolution of many characteristic outcrop groups probably began in the Tertiary along with the development of sclerophylly. Outcrops have thus facilitated genetic divergence and speciation (Hopper *et al.* 1997).

Outcrops are believed to be sites with low levels of competition due to the harsh environment (McVaugh 1943; Baskin & Baskin 1988; Ware 1990; Ware & Pinion 1990; Porembski *et al.* 1994). Where species are at the edge of their range they may become saxicolous as the outcrop habitat may afford protection under unfavourable regional conditions and can offer a refuge from competition (Davis 1951; Murdy 1968; Baskin & Baskin 1988; Burke *et al.* 1998). Catastrophic selection on the marginal population could result in narrow edaphic endemics (Davis 1951; Baskin & Baskin 1988). Davis (1951), however, believed that evolution of this kind even at the species level was not progressive and that such species could do little but maintain themselves and that extinction would be inevitable.

Species that are largely or entirely restricted to granitic outcrops are prone to further selection due to having small populations existing in isolation (Murdy 1968; Chapman & Jones 1971; Axelrod 1972; Sampson *et al.* 1988; Bussell & James 1997). A few intensive genetic investigations have occurred regarding rock outcrop restricted species within Australia. Moran and Hopper (1983) showed that the genetic diversity within populations of *Eucalyptus caesia* was remarkably low. However the level of population differentiation was the highest reported for a tree species. The diversity estimates were more typical of an inbreeding annual rather than a tree species. In a study of the genetic variation within *Eucalyptus crucis*, Sampson *et al.* (1988) found that the heterozygosity of populations was low compared with other tree species. The level of population differentiation was as expected for small isolated populations undergoing genetic fixation from genetic drift. Bussell and James (1997) in summarising much of their work on *Isotoma petraea*, concluded that outcrops preserve a record of change both within single populations and across population systems. They are windows on evolutionary processes.

In contrast to the edaphic narrow endemism that has occurred on a number of granitic outcrops, research indicates that some widespread ruderals may have had their origin on granitic outcrops. These xeric sites can be regarded as perpetual pioneer areas somewhat similar to disturbed localities (Axelrod 1972; Wyatt & Fowler 1977). Outcrop endemics have occasionally been found off outcrops in disturbed habitats where there is high light and low competition. Some 'weedy' species of early successional sites may have originated on outcrops and spread more recently to sites disturbed by human activities (Porembski 1995; Porembski *et al.* 1996; Hopper 1999).

### **1.5 Aims of the thesis**

This thesis aims to investigate and reveal the nature of vascular plant biodiversity on the 'archipelagos' of granitic 'islands', and the factors associated with its development and maintenance, and will explore the implications and ramifications of these findings for conservation of plant biodiversity generally. Specific questions include:

- Is the vegetation on granitic outcrops insular, what is the nature of insularity and does insularity vary spatially and/or temporally?

- Are there discernible patterns in diversity and evenness across the batholith?
- Does equilibrium theory or structure as measured by Nested Species Subsets, Species Saturation and species range sizes (Areography) provide insights?
- Are climatic and habitat factors correlated with plant richness and diversity?
- Do temporal factors such as fire play a role in the maintenance of plant richness and diversity?
- Does scale play a role in the significance of correlations found?
- Do correlated factors differ on outcrops compared with the surrounding vegetation and thus are human induced and naturally fragmented systems the same?

## 1.6 Structure of the Thesis

Chapter 2 includes the circumscription of the study area, the development of floristic survey methodologies (including stratification), environmental data acquisition, data management and subsequent modifications of initial survey design. The stratification and data storage methodologies provide the framework in which the subsequent investigations are made. Each research chapter has its own methodology section that is applicable to that chapter only. Chapters 3 and 4 provide additional structure on which subsequent investigations of processes and patterns are framed. In Chapter 3 the nature of insularity and whether granitic outcrops provide a true 'island-like' scenario is investigated. Phytosociological units and their distribution are defined in Chapter 4. These units are used in the investigations of biodiversity that follow. Richness, evenness (rank order distribution of species abundances) and beta diversity patterns are presented and analysed in Chapter 5. Chapter 6 deals with aspects of island biogeography, including changes in the representation and strength of correlations in regression models at different scales. The structural arrangement of species richness as described by nested subset patterns and species saturation curves are circumscribed in Chapter 7. Patterns in the sizes and distributions of species ranges and their potential effects on species richness are analysed in Chapter 8. The compositional, diversity and richness changes caused by fire are examined in Chapter 9. A synthesis of the research is presented in Chapter 10, which also includes the conclusion. Appendices and publications arising from this thesis are provided at the back of the thesis.