



Habitat islands in fire-prone vegetation: do landscape features influence community composition?

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Abstract

Aim, Location Landscape features, such as rock outcrops and ravines, can act as habitat islands in fire-prone vegetation by influencing the fire regime. In coastal and sub-coastal areas of Australia, rock outcrops and pavements form potential habitat islands in a matrix of fire-prone eucalypt forests. The aim of this study was to compare floristic composition and fire response traits of plants occurring on rocky areas and contrast them with the surrounding matrix.

Methods Patterns of plant community composition and fire response were compared between rocky areas and surrounding sclerophyll forests in a range of climate types to test for differences. Classification and ordination were used to compare floristic composition and univariate analyses were used to compare fire response traits.

Results The rock outcrops and pavements were dissimilar in species composition from the forest matrix but shared genera and families with the matrix. Outcrops and pavements were dominated by scleromorphic shrubs that were mainly killed by fire and had post-fire seedling recruitment (obligate seeders). In contrast, the most abundant species in the adjacent forest matrix were species that sprout after fire (sprouters).

Main conclusions Fire frequency and intensity are likely to be less on outcrops than in the forest matrix because the physical barrier of rock edges disrupts fires. Under the regime of more frequent fires, obligate seeders have been removed or reduced in abundance from the forest matrix. This process may have also operated over evolutionary time-scales and resulted in convergence towards obligate seeding traits on outcrop fire shadows. In contrast, there may have been convergence towards sprouting in the forest matrix as a result of selection for persistence under a regime of frequent fire.

Keywords

Habitat islands, fire regime, fire response traits, obligate seeding, persistence, sprouting.

INTRODUCTION

In fire-prone landscapes, fire regime can have a major influence on the composition of present-day vegetation by regulating demographic processes such as mortality, reproduction, germination and survival of plant populations (Whelan, 1995; Bond & van Wilgen, 1996). Spatial variation in physical landscapes, as well as human impacts, influences fire regime (intensity, frequency and season) and therefore has the potential to influence plant population and

community patterns in vegetation (e.g. Bowman, 2000). In turn, over time, the fire regime can act as a selective force in the evolution of plant traits and result in convergent characteristics of species in fire-prone habitats (Bond & van Wilgen, 1996). In Australia, much of the landscape is fire-prone because of the climate, to the flammability of the vegetation and frequent sources of ignition (human and lightning) (Bradstock *et al.*, 2002). Nevertheless, the composition, structure and functional traits of species are not uniform within the open forest (dry sclerophyll) formations of Australia (Beadle, 1981; Williams & Woinarski, 1997).

One aspect of the spatial heterogeneity in vegetation that has received little attention is the relationship between

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landscape features and fire regime. Distinctive plant communities have been reported in parts of the landscape that act as 'fire shadows' such as riparian forests, topographic barriers and rocky refugia (Clayden & Bouchard, 1983; Bond *et al.*, 1988; Geldenhuys, 1994; Bond & van Wilgen, 1996). True islands within lakes in boreal forests have, in contrast, a history of more frequent but less intense fires than do surrounding lakeshores and this results in the decreased abundance of serotinous conifers (Bergeron, 1991). In the Australian landscape, there are potential fire 'shadows' and 'refugia' around topographic discontinuities (Gill & Bradstock, 1995). In many parts of Australia, such habitat 'islands' exist on scree slopes and canyons as patches of rain forest in a matrix of sclerophyllous fire-prone vegetation (Ash, 1988; Adam, 1994; Bowman, 2000). However, the physiognomic differences between many communities recorded on the rocky outcrops and the adjacent matrix are generally much smaller than the differences between rain forest and the sclerophyll forest matrix. Similarly, the growth form contrast between xerophytes on large rock outcrops (inselbergs) and mesophytes in surrounding vegetation elsewhere in the world (Porembski *et al.*, 1997; Porembski & Barthlott, 2000a,b) is not apparent in Australia (Clarke, in press). Instead, the rock outcrop and the surrounding matrix vegetation of Australia are both sclerophyllous (Hunter & Clarke, 1998; Clarke & Knox, 2002; Clarke, in press).

Links between plant fire response and fire regime have often focused on large spatial scales by examining biogeographical patterns (e.g. Pate *et al.*, 1990; Lamont & Markey, 1995; Ojeda, 1998; Bowman, 2000; Clarke & Knox, 2002). However, at local scales, fire regimes may influence community composition through different demographic processes associated with fire response (Bond & van Wilgen, 1996). In Mediterranean-type ecosystems and in other sclerophyllous vegetation, frequent high-intensity fires are thought to promote sprouters, whilst intermediate fire intervals favour obligate seeders (Keeley & Zedler, 1978; Morrison *et al.*, 1995a; Keith, 1996). Thus, in 'insular' habitats, where fire is less frequent but not excluded, obligate seeders should be more common than sprouters (Bond *et al.*, 1988; Gill & Bradstock, 1995; Hopper *et al.*, 1997; Clarke & Knox, 2002). Some insular habitats (rock

outcrops and pavements) may also be more open and promote seeders although the availability of open spaces where competition from sprouters is reduced (Keeley, 1977; Keeley & Zedler, 1978; Clarke & Knox, 2002).

The aim of this study was to compare floristic composition and fire response traits of plants occurring on potential habitat islands and contrast them with the surrounding open forest matrix. Examining different types of rock outcrops (sandstone pavements and granite outcrops) tested the generality of this pattern across contrasting climate types within Australia. The specific questions asked were whether: (1) physical features (rock outcrops and pavements) provide habitat islands and result in different community composition from the surrounding vegetation, and (2) fire responses of species differ between 'island' and matrix habitats across a wide range of climate types.

METHODS

Study areas and design

Four study areas were selected for each of the habitat contrasts (rock outcrop vs. matrix) so that regional climate variation was included (Table 1). In each study area, the potential habitat islands were in a matrix of eucalypt open-forest (Fig. 1). Quadrat-based data were collected from two areas (Sydney Basin and New England Tablelands), whilst vascular plant floristic lists were used from existing sources (southern Western Australia and Kakadu) so that sampling was contrasted between habitats (Table 1). Where existing species lists were used (Western Australia and Kakadu) locations were visited to ensure that the data was applicable to the region. Sources and type of the floristic data are shown in Table 1.

Quadrat-based sampling for sandstone pavement Sydney Basin (Dharug and Brisbane Waters National Parks) and granite outcrop New England Tableland Torrington State Recreation Area were stratified across rainfall gradients [low: < 800 mm, high: > 1200 mm mean annual rainfall (MAR)], but in each case the underlying lithology was the same for 'island' vs. 'matrix' sampling. Thus, there were four strata; 'island' vs. 'matrix' and 'low' vs. 'high' mean annual rainfall (MAR). In each stratum, 10–16 sites (0.1 ha) were

Table 1 Locations used to contrast floristic composition and functional traits of species between potential habitat islands and adjacent habitats in sclerophyllous, nutrient-poor landscapes in coastal and sub-coastal areas of Australia. Quantitative quadrat data were collected for New England Tablelands and for the Sydney Basin. Other sources of fire response data and observations on floristic differences are listed

Lithology	Climate type			
	Warm temperate	Cool temperate	Mediterranean	Monsoon
Sandstone pavements and matrix	Sydney Basin*			Kakadu escarpment [†]
Granite outcrops and matrix		New England Tablelands [‡]	South Western Australia [§]	

*Benson & Fallding, 1981; Clarke & Benson, 1986; Benson & McDougall, 1993; Clarke & Fulloon, 1997.

[†]Brock, 1993; Bowman, 2000; Russell-Smith *et al.*, n.d.

[‡]Hunter & Clarke, 1998; Clarke & Knox, 2002.

[§]Hopper *et al.*, 1997.

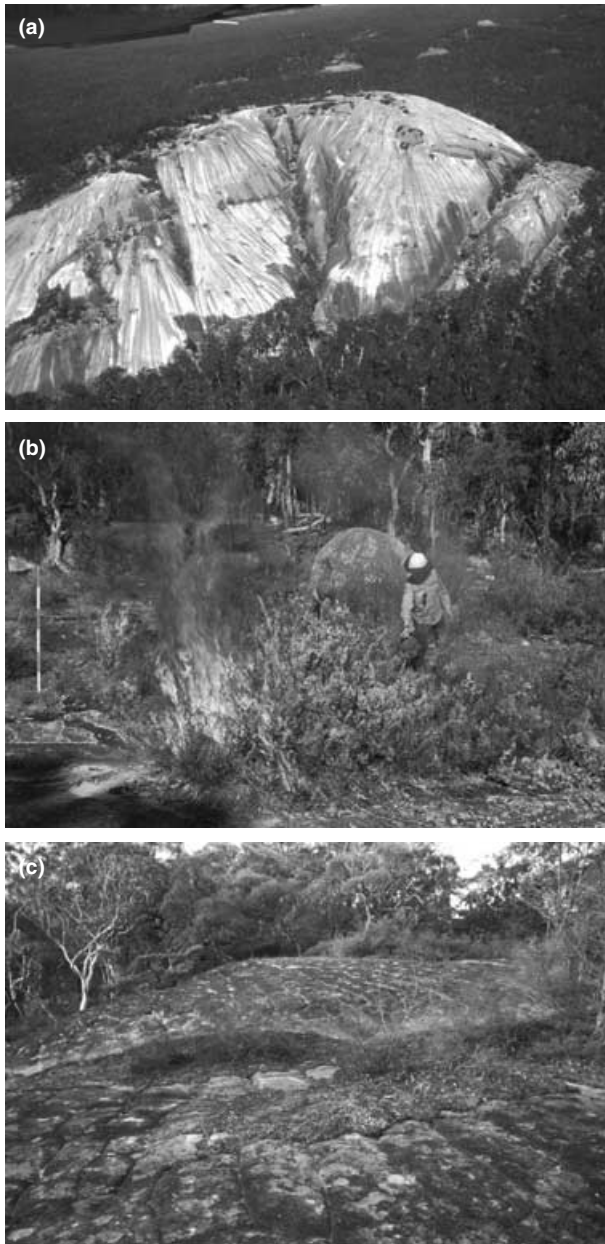


Figure 1 (a) Aerial view of a large granite outcrop on the New England Tablelands (Bald Rock) with smaller 'islands' in the background. The matrix consists of open eucalypt forests and the outcrop vegetation consists of sclerophyllous heath and woodland. (b) Ignition of a granite outcrop endemic shrub (*Prostanthera staurophylla* F. Muell.) on the New England Tablelands to test for fire response (fire-killed). The small eucalypt (*Eucalyptus prava* L. Johnson), top left, associated with the edges of the outcrops is a sprouter. (c) Sandstone pavement in the Sydney Basin with prostrate shrubs and small eucalypts. The shrubs (*Allocasuarina distyla* L. Johnson, *Woollisia pungens* F. Muell. and *Darwinia fascicularis* Rudge) are all killed by fire (obligate seeders). The small eucalypt (*E. sclerophylla* L. Johnson & Blaxell), top left, is associated with the edges of outcrops and is a sprouter.

sampled using semiquantitative abundance scores that reflect the density of species rather than their cover (Morrison *et al.*, 1995b). Sites were chosen from aerial photography and on ease of access and outcrop size (>0.1 ha). At each site, all vascular plants were recorded from 0.1 ha paired samples from rock pavement and outcrops (islands) and the adjacent open forest matrix. Paired samples were arranged so that they were 100–500 m apart. Nomenclature for species used in data matrices follows Harden (1990–93). Details of the community descriptions, species composition and fire related traits have been published elsewhere (Clarke & Benson, 1986, 1987; Hunter & Clarke, 1998; Clarke & Knox, 2002).

Data analyses

Quadrat data collected in the New England Tablelands and in the Sydney Basin (see Table 1), were used to examine patterns of floristic similarity (Bray-Curtis) among habitats within regional climates. An agglomerative classification (UPGMA) (Belbin, 1993) was used for clustering whilst non-metric ordinations of floristic distance among samples were calculated using hybrid multidimensional scaling (HMDS default) (Belbin, 1993). Where only species lists were available (Western Australia and Kakadu), the floristic similarity (Bray-Curtis) of the matrix and outcrop were compared within climate regions.

The growth form composition and fire response of species in two major groups from the agglomerative classification was compared for data collected in the New England Tablelands and in the Sydney Basin. Plant species were initially classified into one of the seven classes of fire-response syndromes, as defined by Gill & Bradstock (1992), based on observations after wildfires and research burns (Fig. 1b). The seven fire response syndromes were then aggregated into two groups (obligate seeders and sprouters) and compared. The relative frequency of fire response was compared among the habitat groups using a G-test for association (Sokal & Rohlf, 1981).

RESULTS

Multivariate patterns and floristics

Classification of quadrat data at the species level clearly reflected the floristic difference between habitat islands and the adjacent vegetation matrix for granite outcrops and for sandstone pavements (Fig. 2a, b). This pattern was generally maintained across 'high' and 'low' rainfall strata, which formed a secondary dichotomy in the New England data (Fig. 2a) and in the Sydney Basin data (Fig. 2b). In contrast, no dichotomy of outcrops and matrix or rainfall was detected in classifications at the rank of genus or family. This reflects the large number of genera and families that share distributions among both habitats. Between habitat floristic similarity at the species level was generally low (0.30–0.66), but at the genus and family rank it was higher (0.70–0.90).

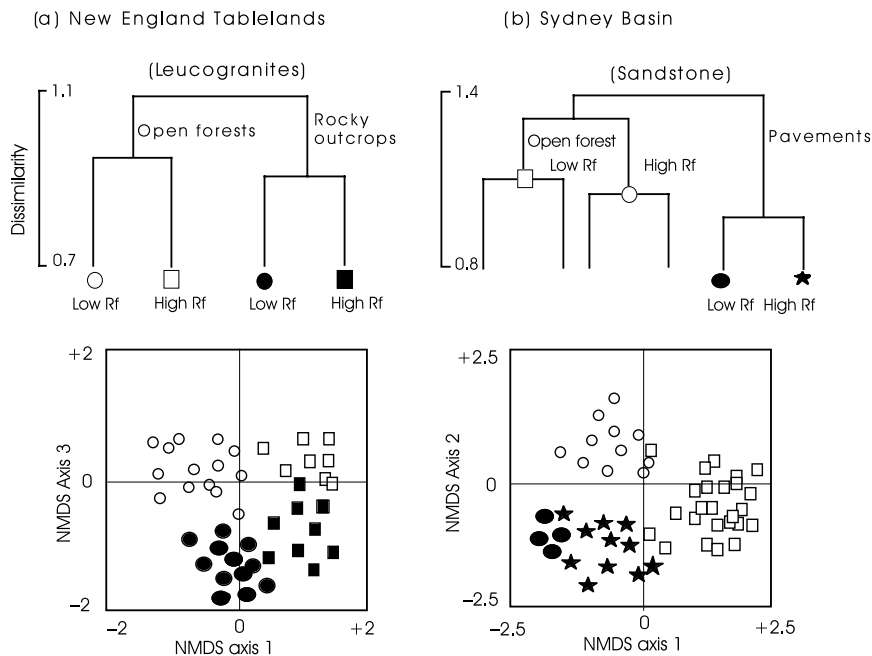


Figure 2 Classification (top) and ordination (bottom) of sample sites (0.1 ha) from the vascular plant flora of outcrops and matrix vegetation. (a) granitic outcrops in the New England Tablelands in an open forest (dry sclerophyll forest) matrix, and (b) sandstone pavements in the Sydney Basin in low open forest/woodland and shrubland matrix ('dry sclerophyll forest' and 'wet heath'). Secondary division in the classification followed a rainfall gradient. The tertiary division in the Sydney Basin open forests relates to fire frequency within the forests. Classification at the rank of genera or families did not produce such clear dichotomies between the outcrops and matrix. Abbreviations: NMDS, non-metric multidimensional scaling; Rf, rainfall. Low and high mean annual rainfall are defined in the text.

Growth forms

The most frequent and most species-rich growth forms on the New England Tablelands in the quadrat-based data were scleromorphic shrubs (160 spp.), followed by forbs (113 spp.), tussock grasses (forty-three spp.), trees (twenty-two spp.) and graminoids (mostly sedges) (eighteen spp.) (Fig. 1b, c). There was, however, no significant difference in the frequency of species in the various growth forms between outcrops and the matrix ($G = 39.9$, $P > 0.05$), i.e. the spectrum of growth forms was similar among habitats despite the marked structural differences between open forest in the matrix and heath or scrub on outcrops (Fig. 1b, c). This pattern appears to also hold for sites where quantitative data were not available. Growth forms of both the Western Australian outcrops and the Kakadu escarpment species were not markedly different from those in the adjacent 'matrix' vegetation, other than in the scarcity of trees on pavements and on rock outcrop fissures. At Kakadu, however, monsoon rain forest is found in ravines that form fire refugia (Bowman, 2000). Similarly, in deep valleys on the New England and in the Sydney Basin, open forests (dry sclerophyll) can grade into tall open (wet sclerophyll) forests and can even develop into rain forest in fire refugia (Benson & Fallding, 1981; Clarke & Benson, 1987).

Whilst the cover of individual species was not measured, the overall cover of trees (eucalypts), shrubs and herbaceous species was measured at each quadrat-based sampling site. There were significant differences in canopy (trees), mid-stratum (low trees and shrubs) and ground cover (herbaceous and subshrubs) between habitats. All strata had significantly higher cover in the matrix than in the outcrops ($F_{1,68} = 139.1$, $P < 0.001$). This pattern confirmed the

initial designation of outcrop fissures being more in open habitats (Fig. 1b, c).

Species fire response

The ratio of fire responses among species between the New England granite outcrops and shrubby open forest was significantly different ($G = 23.5$, $P < 0.05$), with the ratio of all obligate seeder species to sprouters being higher on outcrops (66 : 84) than in the forest matrix (70 : 190). This pattern was stronger for shrub species where the ratio on outcrops was 52 : 6, but in the forests it was 30 : 81 ($G = 29.8$, $P < 0.001$). The Sydney Basin showed similar patterns, with higher proportions of obligate seeding shrub species on sandstone pavements than in adjacent shrubby open forests and woodlands (Table 2). Whilst there are no comparative data between outcrop and matrix vegetation for Western Australia and Kakadu, the ratio of obligate seeders to sprouters is high in both cases. Field observations suggest that, if measured, the number and density of woody sprouters in the matrix in both these locations would likely exceed obligate seeder shrubs.

The number of species in quadrats with different fire responses also diverged between granite outcrops and the shrubby forest matrix on the New England ands (Fig. 3). There were significantly more obligate seeder species on outcrops (mean 19.2/0.1 ha high and 16.5/0.1 ha low rainfall) than in the forest matrix (mean 10.9 high and 12.9/0.1 ha and low rainfall) ($F_{3,68} = 10.3$, $P < 0.001$). Conversely, there were significantly more species of sprouters in the matrix (mean 42.9/0.1 ha high and 44.2/0.1 ha low rainfall) than on the granite outcrop (mean 22.8/0.1 ha high and 17.7/0.1 ha low rainfall) ($F_{3,68} = 37.2$, $P < 0.001$) (Fig. 3).

Table 2 Ratios of shrub species killed by fire (obligate seeders) vs. species that resprout after fire (sprouters). Note that species with a highly variable response to crown fires in the Sydney Basin have been excluded from the data set as these taxa may have different ecotypes associated with different fire regimes

Habitats	Fire response ratio (obligate seeder : sprouter)
Granite outcrops*	91 : 9 ($n = 58$)
Granite matrix*	28 : 72 ($n = 111$)
Granite outcrops [†]	77 : 23 ($n = 50$)
Sandstone pavements [‡]	65 : 35 ($n = 34$)
Sandstone matrix [‡]	46 : 54 ($n = 122$)
Sandstone pavements [§]	62 : 38 ($n = 28$)

n = number of taxa observed.

*New England Tablelands (Clarke & Fulloon, 1997; Hunter & Clarke, 1998; Clarke & Knox, 2002).

[†]Southern Western Australia (Hopper *et al.*, 1997; P.J. Clarke, pers. obs.).

[‡]Sydney Basin shrubs (Benson & Fallding, 1981; Benson & McDougall, 1993; P.J. Clarke, pers. obs.).

[§]Kakadu escarpment shrubs (Brock, 1993; Russell-Smith *et al.*, n.d.; P.J. Clarke, pers. obs.).

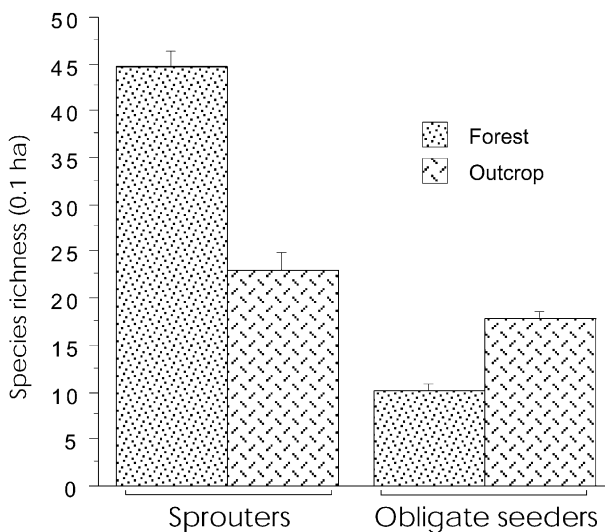


Figure 3 Mean (+SD) species richness of vascular plant species killed by fire (obligate seeders) and those that resprout after fire (sprouters) on rocky outcrops (open shading) and in the adjacent forest matrix (dark shading) on the New England Tablelands of New South Wales, Australia.

DISCUSSION

Do landscape features influence community composition?

I found distinct floristic differences at the species and infraspecific rank between rock outcrops and adjacent matrix open forests in two bioregions (New England Tablelands and

Sydney Basin) that have a similar rainfall pattern (aseasonal), but different lithologies (leucogranite vs. sandstone) and temperature regimes (warm vs. cool temperate). These patterns were consistent across high (>1200 mm) and low (<800 mm) MAR strata within each of the two bioregions, although the lower rainfall sites had a smaller proportion of obligate seeders. Floristic differences at the species level have also been distinguished between granite outcrops and adjacent vegetation in the Mediterranean-type climate of Western Australia (Hopper *et al.*, 1997) and sandstone pavements and adjacent matrix in the monsoon climate of Kakadu (Brock, 1993; Bowman, 2000). Differences in the community composition between outcrops and the open forest matrix appear to be consistent across a range of spatial scales from small-scale climate gradients to regional differences in geology through to continental-scale differences in climate. This pattern shows that rock outcrops in the higher rainfall regions of Australia are floristically distinct from the forest matrices at the species and infraspecific rank.

Whilst community composition has been acknowledged as being 'distinct' on rocky outcrops in Australia, the similarities of the flora with the matrix have not been emphasized. These phylogenetic similarities result from common sclerophyllous families (Epacridaceae, Fabaceae, Myrtaceae, Proteaceae, Rutaceae) being shared between habitats and a pattern of congeners being found on granite outcrops and in the matrix (Clarke, in press). This landscape pattern within the 'sclerophyll' forest differs from the marked dichotomy of families and genera between rain forests in fire refugia and the adjacent sclerophyll matrix in Australia (Bowman, 2000) and elsewhere (e.g. Bond *et al.*, 1988). It also differs from the marked higher-level taxonomic differences between the 'inselberg' floras and matrix found elsewhere in the world (Porembski & Barthlott, 2000b).

Do rocky habitat 'islands' show different fire responses?

In all locations where data have been collected, the most abundant species on rocky outcrops were shrubs killed by fire (obligate seeders) whereas the most abundant species in the forest matrix were shrub species that sprout after fire (sprouters). Similarly, the total number of species killed by fire was higher on rocky outcrops and pavements than in the surrounding forests across a wide range of climate types (see also; Hopper *et al.*, 1997; Clarke & Knox, 2002). Unlike the 'inselberg' floras of many parts of the world, the vascular rock outcrop flora of Australia is not dominated by annual, succulent or resurrection plant species characteristic of xeric landscapes (cf. Porembski *et al.*, 1997; Porembski & Barthlott, 2000a, b). Instead, they are dominated by a diverse array of flammable sclerophyllous shrubs in the cracks between the cryptogam-covered rock surfaces. The 'island' flora also shows no pattern of asexual reproduction, dioecy or gigantism associated with true island floras (Clarke, in review). This suggests that the low nutrient status of the soils is the main factor in determining the growth form composition of outcrops and the matrix rather than drought

tolerance. This model is supported by the presence of congeneric pairs of species on outcrops and in the adjacent matrix. These congeners have different fire responses, but no apparent morphological differences associated with water stress (Clarke, in press).

The contrasting adult fire response between outcrops and matrix is also mirrored in the post-fire seedling recruitment for two study areas (Sydney Basin sandstone pavement, and New England leucogranite outcrops). Those habitats dominated by obligate seeders (pavement and outcrops) have been observed to have large numbers of seedlings whereas the resprouting shrubs in the matrix rarely have abundant seedlings present in the post-fire environment (Clarke & Knox, 2002). This is consistent with studies of resource allocation in congener sprouter and seeders, where sprouters typically produce fewer seedlings after fire (Enright & Lamont, 1989; Enright & Goldblum, 1999).

Why is the fire response different on outcrops?

Throughout the coastal and subcoastal areas of Australia, shrub species on rock outcrops appear to have converged on a similar fire response trait, obligate seeding. This can be explained in terms of differences in the fire regimes between the matrix and the rock outcrops. On rocky outcrops, fire frequency and intensity are likely to be less than in the matrix because fires are disrupted by the physical barrier of bare rock, especially when outcrops are domed or have cliff edges. Hence, with more frequent fires, obligate seeders in the forest matrix have been removed or reduced in abundance because seedlings have not reached the primary juvenile period and seed banks have been exhausted. This disturbance frequency model is supported by studies that show the reduction of obligate seeding species after frequent fires in the forest matrix (Morrison *et al.*, 1995b; Keith, 1996). Differences in the regeneration niche of seeders and sprouters may also explain the low abundance of sprouters on outcrops because of differences in seedling growth patterns (Clarke & Knox, 2002). Preliminary transplant experiments of obligate seeding species into the forest matrix suggest, however, that there is no physiological barrier for growth of obligate seeding outcrop species in the forest matrix (P.J. Clarke, unpublished data).

Outcrop habitats should not be regarded as fire 'refugia' in the sense that their vegetation is not flammable or is rarely burnt (> 100 years intervals). They are rarely free from fires as there is evidence of burning in the form of fire scars on trees and charcoal in the soil. Thus, the obligate seeding species on the rock outcrops are not fire 'intolerant' *per se* but are 'sensitive' to the frequency of fires. Hence, too many or too few fires may eliminate obligate seeders because most species have a fire-related germination cue and are fire-event dependent (Clarke & Fulloon, 1997). Whatever the proximal cause of the differences in fire responses between outcrops and the matrix, it is likely that these landscape features have acted as fire 'shadows', resulting in different community composition.

The distribution of congeners in the New England Tablelands granite outcrops showed a pattern of species

segregation among outcrops and the forest matrix that also has evolutionary implications (Clarke, in press). In this more detailed study, Clarke (in press) found twenty-three genera in sixteen families had habitat differences, with those species on outcrops being killed by fire whilst their sister taxa in the forest matrix were sprouters. Such a pattern of convergence among so many unrelated groups suggests that the interaction of fire frequency and landscape features has influenced speciation. Conceivably, there has been functional divergence across the landscape over a range of time scales from relatively recent, e.g. subspecies differentiation, to older divergence of distantly related species as a result of the Miocene/Pliocene drying of the Australian climate (Hill, 1994). Implicit in this model is that sprouting is a derived state, resulting from selection for persistence in more dry and stochastic fire-prone environments. This is consistent with the model of how persistence traits (resprouting) maintain populations under adversity (Bond & Midgley, 2001). Increased aridity during the late Tertiary and through the Quaternary may have increased fire frequencies and selected for a sprouting response in the scleromorphic matrix taxa. Subsequent isolation of ancestral obligate seeding species in poorly dispersed genera (*Acacia*, *Darwinia* and *Homorathus* in eastern Australia and *Acacia*, *Grevillea* and *Verticordia* in southern Western Australia) on outcrops may then have resulted in radiation of these genera. This may have been influenced by isolation, genetic drift and through enhanced local adaptation resulting from the shorter generation times of obligate seeders.

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BIOSKETCH

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