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Habitat insularity and fire response traits: evidence from a sclerophyll archipelago

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Abstract Rock outcrops are landscape features that may form habitat islands in a matrix of more widespread vegetation. The patterns of floristics, reproduction, gender, life span, growth forms, and fire response traits were compared between rock outcrops and matrix sclerophyll vegetation to test for insularity in taxon composition and functional traits. The outcrops and matrix had similar reproduction, gender, life span, and growth form traits, being dominated by co-sexual sclerophyll shrubs. The outcrops, however, were dissimilar in species composition and functional traits forming an archipelago of habitat islands in a forest matrix. Rank abundance curves were less even on rock outcrops than in adjacent forests, being dominated by shrubs that were killed by fire (obligate seeders). The ratio of shrubs killed by fire (obligate seeders) to resprouters was 70:30 on the outcrops compared with 38:62 in the matrix. Evidence for functional convergence in fire response traits comes from 27 genera, in 17 families, which have congeners in each habitat. Most shrub congeners on or near rocky outcrops were killed by fire whereas related taxa in the forests resprout after fire. Functional convergence can be related to disturbance frequency and/or differences in regeneration niche among habitats. A resprouting response appears to be related to more frequent fires in the matrix as outcrops experience fires less often. The dominance of obligate seeding shrubs on high rainfall outcrops may also be related to better resources in an environment where allocation to growth rather than storage could be advantageous. In drier and shadier habitats, however, resprouting may be promoted over seedling recruitment as the risks of recruitment failure are higher.

Keywords Convergence · Fire shadows · Resprouting · Rocky outcrops · Sclerophyll shrubs

Introduction

Fire is one of many factors that mould plant form and function. Until recently fire has received relatively little attention as a selective force despite the frequent reference to some characteristics as ‘adaptations’ to fire (Bond and van Wilgen 1996; Whelan 1996). Links between life-history traits and the selective regime of fire have focused on smaller scale spatial patterns (e.g. Keeley 1977; Bond et al. 1988), biogeographic patterns (e.g. Lamont and Markey 1995; Ojeda 1998) and landscape features (Bond et al. 1988; Clarke 2002). At local scales frequent fires are thought to promote selection for sprouting whilst intermediate fire intervals favour seeders in Mediterranean-type ecosystems. Thus in insular habitats, where fire is less frequent, seeders should be more common than resprouters (Bond et al. 1988; Hopper et al. 1997; Clarke and Knox 2002). Insular habitats may also be more open and promote seeders though the availability of open spaces where competition from sprouters is less (Keeley 1977; Keeley and Zedler 1978; Myerscough et al. 1995). However, the role of competition and fire-mediated open space in selection for sprouting remains contentious (Bond and van Wilgen 1996). In dry habitats post-fire gap sizes may be expected to be large and hence recruitment of seeders is enhanced (Keeley and Zedler 1978; Carrington and Keeley 1999; Enright and Goldblum 1999). Alternatively, in environments with low, or more variable, rainfall persistence (sprouting) may be favoured over seedling recruitment as the risks of failure are higher (Higgins et al. 2000; Clarke and Knox 2002).

Potential natural habitat islands occur as granitic boulder fields and rock outcrops on the New England Tablelands of Australia in a region where rainfall is summer dominated and rapidly declines east to west (Beadle 1981). These outcrops are in a matrix of species rich sclerophyll forests that are prone to wildfires (Bradstock et al. 2001), whilst the outcrops have longer fire-free intervals. As such they provide model systems for generating and testing hypotheses about the effects of fire inter-

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val, openness and isolation on the composition and functional traits of species. In this system, isolated outcrops are more open than the surrounding eucalypt forest. This can result in more adverse habitats on rocky outcrops in terms of moisture stress and select for species with xeromorphic traits (Porembski and Barthlott 2000a, b). Outcrop isolation may also give rise to species radiation (Givnish and Sytma 1997), 'disharmonic' or filtered floras (Carlquist 1974), and selection for traits such as dioecy and insular woodiness as found on true islands (Carlquist 1974).

The aim of this study was to compare taxon composition and functional traits of rocky outcrops with the surrounding forest matrix. It examined whether (1) rocky outcrops provide habitat islands and result in floristic insularity from the surrounding vegetation across a rainfall gradient, (2) there are functional differences between island and matrix species in response to isolation, adversity and fire response, and (3) trait differences of species on outcrops and in the matrix show convergence among unrelated genera and families.

Materials and methods

Study area

The study area is located in the New England Bioregion of eastern Australia on a granite pluton known as the Mole Pluton. This pluton is a part of the New England Batholith extending 400 km in length and 100 km in width (Barnes et al. 1988) that falls within the cool to mild temperate climate region. The Mole pluton covers an area ca. 80,000 ha and has extensive areas of exposed granite outcrops and granitic boulder fields. A detailed account of the plant composition and floristic variation across the New England Batholith is described in Hunter and Clarke (1998) and in Clarke and Knox (2002). Much of the vegetation on the Mole Batholith is within a conservation reserve known as Torrington State Recreation Area that has been intensively surveyed (Clarke et al. 1998). The 30,000 ha conservation reserve contains approximately 730 vascular plant species in seven sclerophyllous plant communities (Clarke et al. 1998).

Sampling design

Sampling of vegetation was stratified over two spatial scales to assess the composition and abundance of vascular plant species. The first stratification was between higher altitude and rainfall (1,200 mm mean annual rainfall) sites to the east of the study area and lower altitude and rainfall (750 mm mean annual rainfall) sites in the west of the study area (referred to as rainfall). The second stratification within each of the rainfall zones was between rocky outcrops and adjacent areas (within 1 km) without exposed rock surfaces (referred to as habitats). Within each of the four strata 18 replicate sites were randomly chosen from a large pool of sites (ca. 100 outcrops) and sampled. Thus, a total of 72 sites were sampled (18 replicates \times 2 habitats \times 2 rainfall levels). At each site a nested series of quadrats were placed to sample areas of 1, 2, 4, 8, 16, 32, 64, 128, 512, and 1,024 m². The presence/absence of plant species were recorded in each annulus such that a score out of 10 was recorded for each species (see Morrison et al. 1995a, b). This method allows for species area curves to be calculated and for the relative abundance of species to be compared. Nomenclature of species follows Harden (1990–3).

Multivariate patterns

Classification and ordination of data from each of the 72 sites (samples) were used to examine patterns of floristic similarity in sites. Species (attributes) with occurrences in less than 1% of sites were excluded from the analysis. The Bray-Curtis coefficient was used to calculate association matrices on species, genera and family data. The coefficient is non-linear and is robust to variations in models of species distributions (Faith et al. 1987). Two classifications were applied to the association matrix: a divisive classification (TWINSPAN) and an agglomerative classification (UPGMA) (Belbin 1993). Ordinations of floristic distance among samples were calculated using hybrid multidimensional scaling (HMDS default) (Belbin 1993). The Bray-Curtis association matrix for species in sites was compared to a Euclidean distance matrix of the geographic distance among all sites using the Mantel test (Burgman 1988; Belbin 1993). Separate matrices were also constructed for each of the two habitat types and the test computed for each.

Species richness, abundance and rank abundance

Numbers of species found among major habitat groups, defined by classifications, were compared among spatial factors (rainfall and habitats) using two-factor ANOVA at each of the 10 nested sampling scales. Species area curves were also constructed for each group. Summed abundance and frequency values for each species across each of the four classification groupings were tabulated. Species rank order of abundance was sorted and plotted for the two major groups in the classification. The abundance of species was also compared among four habitats defined by classification in a one-factor ANOVA after square-root transformation of data. Species that had a relative frequency of presence in all quadrats of less than 1% were excluded from the analysis because of heterogeneous variances. Data were also tested for homogeneity of variance using Cochran's test (Sokal and Rohlf 1981), and species that failed this test were also excluded from the analysis. Post hoc multiple comparisons were done using Scheffe's test (Sokal and Rohlf 1981).

Floristics and functional traits

The taxonomic composition of each of the four major groups was compared in terms of (1) species in genera and genera in families, (2) the ratio of exotic to native species, (3) the ratio of habitat restricted to non-restricted species and (4) the ratio of rare to widespread species. The 'functional' composition of each of the four major groups was compared in terms of growth forms, reproduction, gender, and life span. Species' growth forms were classified into eleven broad classes; tree, shrub, vine, rosette forb, clonal forb, herbaceous geophyte, clonal grass, tussock grass, clonal sedge, tussock sedge, and parasites. Plant species were also classified into one of the seven classes of fire-response syndromes as defined by Gill and Bradstock (1992) based on observations at Torrington after wildfires and research burns. The seven fire response syndromes were further aggregated into two groups (obligate seeders and resprouters) and compared. Additionally, the numbers of species per quadrat that were obligate seeding shrubs or resprouting shrubs were compared across habitats by single-factor ANOVA after assumptions were tested. The relative frequency of traits was compared among the habitat groups using a *G*-test for independence (Sokal and Rohlf 1981). No attempt was made to apply 'phylogenetic control' to the data as the taxa came from a wide variety of families and genera and no one lineage was numerically more species rich across contrasting habitats.

Results

Multivariate patterns

Classification of site data by both divisive and agglomerative methods revealed identical patterns at the two-group level, but less correspondence at smaller group sizes. The two-group level clearly reflects the floristic difference between large rocky outcrops and adjacent forest matrix, while the four-group level reflects more subtle difference within vegetation types that is related to rainfall (Fig. 1a). Seven small-sized rocky pavement sites classified with adjacent forests indicating that size of outcrop influences insularity. Two-dimensional ordination of samples showed that there was less floristic difference between outcrops and forest in the lower rainfall sites (west) than between outcrop and forest in higher rainfall sites (east) (Fig. 1b). Overall there was no corre-

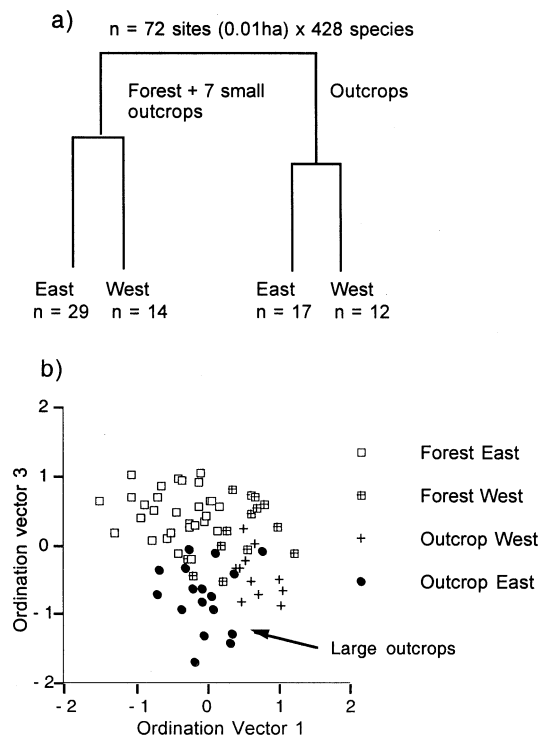


Fig. 1 Classification (a) and ordination (b) of site data collected from rocky outcrops and adjacent forests. Sites located on large outcrops are at the periphery of the ordination diagram. Smaller outcrops are floristically similar to adjacent forest sites

lation between geographic and floristic distance using matrix correlations (sensu Burgman 1988).

Floristic dissimilarity at the species level was about the same within outcrop and forest subgroups (Table 1). The most dissimilar groups were adjacent outcrops and forest sites in the higher rainfall area. This pattern was maintained at the genus and family level but the magnitude of the relative difference comparing within and between fell from 0.35 at the species level to 0.10 at the genus and family level. This suggests there is relatively little 'disharmony' or filtering of species between habitats.

Floristics, species richness and rank abundance

The total number of species, genera and families recorded in the 72 sites was 428, 233 and 77 respectively, most of which are native to the region (Table 2). The major plant families include Poaceae (27 taxa), Asteraceae (18 taxa), Myrtaceae (16 taxa), Fabaceae (16 taxa), Mimosaceae (13 taxa), Epacridaceae (12 taxa), Rutaceae (12 taxa), Orchidaceae (10 taxa), and Cyperaceae (10 taxa). This rank closely matches patterns found in a broader bioregional analysis (Hunter and Clarke 1998). No major differences in the presence of families or genera were detected among habitats. Similarly, the relative ratio of species in genera and genera in families was not significantly different among habitats ($G=5.0$, $P>0.5$) (Table 2) indicating similar patterns of speciation in each habitat. Exotic species, comprising mostly of annuals, showed no enhanced presence on the more open rocky habitats ($G=1.4$, $P>0.5$).

Overall, the number of species recorded differed significantly between outcrops and forest and between high and low altitude clusters within them (Table 2, Fig. 2). Species richness was consistently less on rocky outcrop (mean 46.4/0.1 ha) than in the forest (mean 65.9/0.1 ha) at all spatial scales ($F_{1, 52}=26.4$, $P<0.001$). Rank abundance curves were different between habitats (Fig. 3) but similar within them. Rocky outcrop vegetation had steeper rank abundance diagrams than adjacent forest vegetation being dominated by shrubs functionally different from the forest dominants (see below) (Fig. 3).

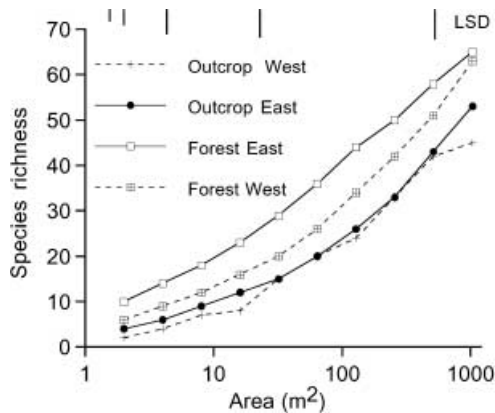
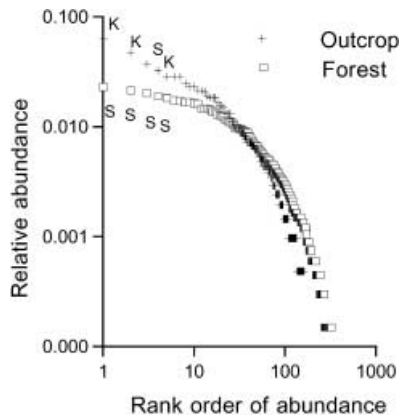
Of the 428 species recorded, 111 showed significant differences in abundance between habitat and these were across a range of genera and families. There were significant differences in the ratio of habitat restricted and rare

Table 1 Bray-Curtis dissimilarity (1= similar) measures among numerically defined habitats at the species, genus and family taxon level. Summed abundance scores across 16 replicates are used for calculation of dissimilarity among strata

Habitat	Outcrop east			Outcrop west			Forest east		
	Species	Genus	Family	Species	Genus	Family	Species	Genus	Family
Outcrop west	0.46	0.68	0.80	–	–	–	–	–	–
Forest east	0.21	0.59	0.65	0.22	0.55	0.65	–	–	–
Forest west	0.39	0.56	0.70	0.28	0.65	0.70	0.44	0.74	0.84

Table 2 Summary of floristics characteristics of rocky outcrop and adjacent forest communities

	Forest east (<i>n</i> =29)	Forest west (<i>n</i> =14)	Outcrop east (<i>n</i> =17)	Outcrop west (<i>n</i> =12)	Total (<i>n</i> = 72)	<i>G</i> test
Taxon						
Families	67	66	46	50	77	<i>G</i> =5.0
Genera	179	173	106	112	233	<i>P</i> >0.5
Species	321	267	160	165	428	
Origin						
Exotic	7	9	3	5	11	<i>G</i> =1.3
Native	314	258	157	160	417	<i>P</i> >0.5
Habitat affinity						
Forest restricted	78	55	0	0	81	<i>G</i> =18.3
Outcrop restricted	0	0	28	15	30	<i>P</i> <0.001
Non-restricted	243	212	122	150	317	
Endemism						
Regionally rare	6	3	13	3	16	<i>G</i> =20.4
Narrow endemic	2	2	3	4	6	<i>P</i> <0.001
Other	313	262	144	158	406	

**Fig. 2** Species accumulation curves for forest and outcrop classified sites. Species richness is not significantly different at the smallest spatial scales but diverges at larger scales. Western sites also tend to be less species rich than eastern sites. *LSD* Least significant difference by Scheffe's test**Fig. 3** Rank abundance curves for forest and outcrop sites for all species recorded in samples. Shrub species killed by fire dominate outcrop sites whereas shrub species sprouting after fire dominate the forests. *K* Killed by fire, *S* sprout after fire

species among outcrop and forest habitats (Table 2). Relatively more species in forests are restricted to that habitat than species found on outcrops. In other words, outcrops contain more shared taxa with the forests than vice versa. However, outcrops contain more regionally rare and endemic taxa than forests and this pattern decreases east to west (Table 2).

Growth forms

The most common growth forms were shrubs, followed by forbs, tussock grasses, trees, and graminoids (mostly sedges) in terms of abundance (Table 3). The *G*-test for association for frequency of growth form of species in forests and outcrops was not significant ($G=39.9$, $P>0.05$) i.e. the spectrum of growth forms was similar among habitats. Significant variation was, however, detected in the number of species with different growth forms within habitats rather than between them. Both forbs and grasses had more species in the lower altitude habitats than in the higher altitude ones. There were also significantly more species of vine in the forests (1.2/0.1 ha) than in the high altitude outcrops (0.2/25 m²) ($F_{3, 68}=3.8$, $P<0.05$). Trees, shrubs and geophytes did not differ significantly in the mean number of species per sample area between or within habitats.

Whilst the cover of individual species was not measured the overall cover of trees, shrubs and herbaceous species was measured at each site. Significant differences in canopy (trees), mid stratum (low trees and shrubs) and ground (herbaceous and sub-shrubs) were detected between habitats. All strata had significantly higher cover in the forests compared with the outcrop habitats and this decreased east to west ($F_{1, 68}=139.1$, 145.0, 10.5, $P<0.001$). This pattern confirmed the initial designation of outcrops being more open habitats.

Table 3 Summary of growth form, reproduction, gender and life span characteristics of rocky outcrop and adjacent forest communities

	Forest east (n=29)	Forest west (n=14)	Outcrop east (n=17)	Outcrop west (n=12)	Total (n=72)	G test
Growth form						
Tree	21	12	6	7	22	$G=39.9$ $P>0.1$
Shrub	121	85	74	63	160	
Vine	4	5	1	2	5	
Forbs	84	88	21	46	113	
Clonal herbs	11	13	8	9	13	
Tussock grass	35	31	21	16	43	
Clonal grass	3	4	2	1	5	
Tussock graminoid	14	9	7	7	14	
Clonal graminoid	7	11	7	5	18	
Geophytes	17	7	11	5	29	
Mistletoe	4	2	2	4	6	
Reproduction						
Clonal	21	28	17	15	36	$G=3.7$ $P>0.01$
Non-clonal	300	239	143	150	392	
Gender						
Co-sexual	314	261	157	160	420	$G=0.6$ $P>0.1$
Dioecy	7	6	3	5	8	
Life span						
Annual	16	18	7	10	23	$G=1.4$ $P>0.5$
Perennial	305	249	153	155	405	

Table 4 Summary of fire response syndromes of rocky outcrop and adjacent forest communities. Response syndromes are: I, killed by fire with canopy held seed bank; II, killed by fire with soil stored seed bank; III, killed by fire no seed bank; IV, basal stem resprouts; V, sub-surface resprouts; VI, stem shoots; VII, apical shoot resprouts

	Forest east (n=29)	Forest west (n=14)	Outcrop east (n=17)	Outcrop west (n=12)	Total (n=72)	G test
Fire response						
I Killed	1	1	5	1	5	$G=33.1$ $P<0.05$
II Killed	67	50	60	56	92	
III Killed	2	2	1	2	2	
IV Resprouts	40	35	24	20	67	
V Resprouts	132	110	56	56	154	
VI Resprouts	16	10	3	4	17	
VII Resprouts	2	1	1	1	2	
Unknown	61	58	10	25	89	
Fire response						
Killed	70	53	66	59	99	$G=23.5$ $P<0.001$
Resprout	190	156	84	81	240	
Fire response shrubs						
Shrubs killed	46	28	52	36	67	$G=29.8$ $P<0.001$
Shrubs resprout	75	57	22	27	70	

Species fire syndromes

The most common fire syndrome was resprouting from basal stem buds or lignotuber, followed by species regenerating only from seed, and then those resprouting from rhizomes (Table 4). The G -test for association for frequency of fire syndromes among species between outcrops and forest was significant ($G=33.5$, $P<0.05$), i.e. the spectrum of syndromes was different with the percentage of resprouters being higher in the forest. This pattern was stronger when only the shrub species were compared among habitats ($G=29.8$, $P<0.001$). In the forests 38 (east) and 33% (west) of shrub species were

killed by fire whereas the outcrops had 70 (east) and 57% (west) of shrub species killed by fire.

Significant differences were detected in the number of species in samples with different fire syndromes between habitats. There were significantly more species of obligate seeders in outcrops (mean 19.2 and 16.5/0.1 ha) than in the forest (mean 10.9 and 12.9/0.1 ha) ($F_{3, 68}=10.3$, $P<0.001$). Conversely, there were significantly more species of resprouters in the forest (mean 42.9 and 44.2/0.1 ha) than in the outcrop (mean 22.8 and 17.7/0.1 ha) ($F_{3, 68}=37.2$, $P<0.001$). Significant differences between habitats were also detected for species with type I, III response syndromes. More type I species,

those killed by fire and having a canopy held seed-bank, were found on the higher altitude outcrops (Table 4). Fire-ephemeral species (type III) were also more common on the lower altitude outcrops. Patterns of difference among resprouting syndromes (types IV, V, VI and VII) were similar in that the outcrops consistently had lower numbers of species with type IV, V, VI and VII responses (Table 4).

Congeneric comparisons

Genera that had species with contrasting or overlapping habitats were compared in terms of their fire response syndromes (Appendix). About half the genera in the samples (33 genera) showed some habitat differences in their species (Appendix). Twenty-four shrub genera had species with habitat differences whilst only seven herbaceous genera and one tree genus had species showing habitat differences. Congeners of the shrub species showed differences in fire response syndromes between habitats in 23 of the 24 genera (Appendix). Those species in the outcrop habitat or overlapping in habitat preference were obligate seeders whereas their sister taxa in the forest were mostly resprouters (Appendix). This pattern is also present in three of the seven herbaceous genera (*Gonocarpus*, *Isotoma*, and *Stylidium*). Species in the tree genus *Eucalyptus* did not show differences in fire response syndromes, but those in *Allocasuarina* did (Appendix).

Discussion

Floristic composition, species richness, rank abundance and numbers of species in categories of post-fire regeneration correlate with environmental differences between outcrops and the forest matrix, but growth form, asexual reproduction, gender and dispersal do not. In the floristic variation, species in the same genus tend to show clear environmental segregation among habitats and fire response traits. The functional significance of these patterns in relation to insularity, fire frequency, and environmental variability is discussed below.

Do rocky outcrops show floristic insularity?

Floristic insularity of outcrops, measured by comparisons of similarity with surrounding matrix, is rarely measured because habitat islands are often distinct at family or generic rank (e.g. Bond et al. 1988; Porembski et al. 1997). The flora recorded on the rocky outcrops in my study is less distinct at the genus and family rank than those described for granite inselbergs elsewhere (Porembski et al. 1997; Porembski and Barthlott 2000a, b). This results from genera being shared between habitats and the relative number of shared species increasing with decreasing size of outcrops. This is shown on the ordina-

tion diagram where outcrops adjacent to forest sites were characterized by their small size and flatness whilst those at the extremes were approaching the status of an inselberg (Porembski et al. 1997). Relative similarities in the flora also appear to be influenced by rainfall as the low elevation western sites show less dissimilarity in composition between outcrop and surrounding vegetation. Overall, however, the outcrops are distinct in species composition compared with the matrix as shown by a consistent dichotomy in the site classification.

Relatively more species in forests are restricted to that habitat than species on outcrops. What makes the outcrops stand out, floristically, is that they support fewer species than comparable areas of the surrounding matrix as sampling area increases. This is due to the lack of habitat, as richness at the scale of rock fissures (1 m²) was similar among habitats, rather than any difference in colonization and extinction rates. Outcrops also have steeper dominance curves where a few species are abundant but the tail species are less abundant and contain more endemic and regionally rare taxa. To begin to explain these patterns an understanding of the traits of component species is required.

Isolation, species radiation and divergence

Island traits such as asexual reproduction, dioecy, and gigantism were not prominent in the rocky outcrop species and these findings are consistent with habitat islands in the Fynbos (Bond et al. 1988). In the present study, most congeners were spatially separated or if they were in the same habitat they had different post-fire regenerative attributes (see Appendix). By detailed analysis of gradients in heaths Myerscough et al. (1995) showed that, in general, sclerophyllous congeners are not found in the same habitat. Whilst patterns of congeners across habitats show divergence within genera there was little evidence for radiation of species among habitat islands either at a local level (this study) or at a regional level (Hunter and Clarke 1998). This differs from other fire prone regions in southern Western Australia where orchids, sundews (*Drosera*), and trigger plants (*Stylidium*) have shown marked speciation on outcrops in comparison with adjacent matrix communities (Hopper et al. 1997). The reason for this difference may lie in the fact that there is no strong seasonality and less rainfall predictability in the study region.

Do rocky outcrops show functional insularity?

Unlike the rock outcrop floras of many parts of the world the New England rock outcrop flora has few annual, succulent, or resurrection plant species (cf. Porembski et al. 1997; Porembski and Barthlott 2000a, b), and shows little evidence for 'adversity' selection. Instead, both the outcrops and surrounding matrix are dominated by sclerophyllous shrubs suggesting that moisture stress may be

less important than fire in determining the functional composition of the flora.

The most abundant species on rocky outcrops are shrubs killed by fire (obligate seeders) whilst the most abundant species in the forests were shrub species that sprout after fire (resprouters). In addition, the ratio of shrubs killed by fire (obligate seeders) to resprouters was 38:62 in the forest matrix compared with 70:30 on the adjacent outcrops in the higher rainfall sites. These results are also consistent with a regional analysis of where 90% of shrubs on rocky outcrops were killed by fire (Clarke and Knox 2002). These patterns suggest that obligate seeders have been removed or reduced in abundance from the forest matrix by more frequent fires (Bond et al. 1988; Morrison et al. 1995a, b; Bond and van Wilgen 1996). Conversely, less frequent fires on outcrops may enhance the survival of obligate seeding species (Clarke and Knox 2002). Field observations after major wildfires and after controlled burns showed that either outcrops are patchily burnt within crevices or escape burning because of their rock surrounds. European fire regimes to reduce hazards may also have distorted seeder: resprouter ratios in the forest matrix but these effects are difficult to assess because pre-European fire regimes are not known. Increased hazard reduction burning will, however, reduce or eliminate obligate seeders from the matrix and may threaten outcrop obligate seeders.

Fire response differences among habitats can also be explained by differences in the regeneration niche and/or disturbance frequency (Clarke and Knox 2002). In more open habitats (outcrops) there are increased opportunities for faster growing seeders to complete their life cycles as long as fire intervals are less than the primary juvenile period (Keeley 1977; Myerscough et al. 1995). Water and nutrient utilization may also be different for obligate seeders (Davis and Mooney 1986; Pausas 1999; Wisheu et al 2000) with allocation to growth and reproduction rather than persistence (Higgins et al. 2000; Bond and Midgely 2001).

Evidence for functional convergence in fire response traits in the two habitats comes from 27 genera, in 17 families, that have congeners in each habitat. Almost invariably shrub congeners on or near rocky outcrops are killed by fire whereas their related taxon in the forests are resprouters. This suggests that landscape features have influenced fire frequencies over evolutionary time scales resulting in convergence toward obligate seeding in fire shadows.

How does climate influence functional insularity?

If the above models apply, why do the more open drier outcrops and forests have less fire-killed shrubs given that they have the similar fire regimes? At sites with less and more varied rainfall, the seeder ratio decreased both in the forest (33:67) and on outcrops (58:42). Similarly, the mean number of obligate seeding species per sample area was also significantly reduced from a mean of 19.2 in the east to 16.2 in the west. These patterns suggest that both insularity and climate interact with fire intervals influence present day patterns of fire response syndromes.

One model that explains this is the 'environmental variance' model where less predictable environments favour plant allocation to persistence (resprouting organs) because of greater risks involved in seedling germination and recruitment (Higgins et al. 2000; Bond and Midgely 2001). Such effects should be strongest in fire-killed species with short-lived seed banks that lack a 'storage effect'. This idea is supported by the lack of obligate seeding serotinous shrub species (*Hakea*, *Callistemon*, *Grevillea*) in low rainfall western sites. This is also consistent with biogeographic studies of *Erica* and *Banksia* that have shown obligate seeders to be more common in predictable environments and resprouters to be more widespread (Lamont and Markey 1995; Ojeda 1998; Bell and Ojeda 1999).

Clearly, the above models invoke processes in time that may underlie the patterns I have described in space. To test these ideas experiments are needed that couple demography and physiology by following plant recruitment, growth and resource allocation in contrasting environments (e.g. Pate et al 1990). Such experiments should consider not only the effects of insularity on fire regime (disturbance frequency) but also the possible interactive effects of landscape and climate on the regeneration niche.

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Appendix

Congeneric comparisons of species for habitat differences and fire response syndrome (as per Table 4). (I, II, killed by fire; V, VII, resprouts). ^a Species recorded outside quadrat samples

Family and genus	Form	Outcrop habitat	Trait	Overlapping habitat	Trait	Forest habitat	Trait
Asteraceae							
<i>Brachycome</i>	Herb	<i>stuartii</i>	II	–		<i>microcarpa</i>	II
<i>Olearia</i>	Shrub			<i>gravis</i>	II	sp. aff. <i>elliptica</i>	V
				<i>ramosissima</i>	II	–	
				<i>microphylla</i>	II?	–	
<i>Ozothamnus</i>	Shrub	<i>obcordatus</i>	II	–		<i>diosmifolius</i> ^a	V
Casuarinaceae							
<i>Allocasuarina</i>	Tree			<i>inopholia</i> ^a	I	<i>torulosa</i>	VI
Dilleniaceae							
<i>Hibbertia</i>	Shrub	sp. nov.	II	<i>acicularis</i>	V	<i>cistoidea</i>	V
		–		sp. B	II	<i>obtusifolia</i>	V
		–		–		<i>riparia</i>	V
		–		–		<i>serpyllifolia</i>	V
		–		–		<i>vestita</i>	V
Epacridaceae							
<i>Brachyloma</i>	Shrub	<i>saxicola</i>	II	–		<i>daphnoides</i>	V
<i>Leucopogon</i>	Shrub	<i>biflorus</i>	II	<i>attenuatus</i>	?	<i>lanceolatus</i>	V
		<i>neo-anglicus</i>	II	<i>melaleuroides</i>	V	<i>microphyllus</i>	V/II
		–		<i>muticus</i>	II	<i>virgatus</i>	V
<i>Melichrus</i>	Shrub	<i>erubescens</i>	II	<i>urceolatus</i>	V	<i>procumbens</i>	V
Fabaceae							
<i>Bossiaea</i>	Shrub	–		<i>rhombofolia</i>	II	<i>obcordata</i>	V
		–		–		<i>scortechinii</i>	V
<i>Daviesia</i>	Shrub	<i>acicularis</i>	II	<i>umbellulata</i>	II	<i>latifolia</i>	V/II
		–		–		<i>mimosoides</i>	V
<i>Dillwynia</i>	Shrub	–		<i>sericea</i>	II?	<i>phyllicoides</i>	V
		–		<i>sieberi</i>	II	–	
<i>Hovea</i>	Shrub	<i>granitica</i>	II	<i>apiculata</i>	II	<i>heterophylla</i>	V
<i>Mirbelia</i>	Shrub	–		<i>speciosa</i>	II	<i>rubiifolia</i>	V
		–		<i>pungens</i>	II	–	
<i>Podolobium</i>	Shrub	<i>arborescens</i> ^a	II/V	–		<i>ilicifolium</i> ^a	V
Haloragaceae							
<i>Gonocarpus</i>	Herb	–		<i>teucroides</i>	II	<i>micranthus</i>	III
		–		–		<i>tetragynus</i>	V
Lamiaceae							
<i>Prostanthera</i>	Shrub	<i>staurophylla</i>	II	<i>saxicola</i>	II?	–	
				<i>scutellaroides</i> ^a	II		
Lobeliaceae							
<i>Isotoma</i>	Herb	–		<i>anethifolius</i>	II	<i>fluviatilis</i>	V
Mimosaceae							
<i>Acacia</i>	Shrub	<i>granitica</i>	II	<i>burbridgeae</i>	II	<i>betchei</i>	II
		<i>latisejala</i>	II	<i>hispidula</i>	II	<i>buxifolia</i>	V
		<i>viscidula</i>	II	<i>penninervis</i>	V	<i>fimbriata</i>	II
		<i>williamsiana</i> ^a	II	<i>torringtonensis</i>	II	<i>gunnii</i>	V
		–		<i>venulosa</i>	II	<i>juncifolia</i>	V
		–		–		<i>longifolia</i>	II
		–		–		<i>neriifolia</i>	V
		–		–		<i>pruinosa</i>	?
		–		–		<i>ulicifolia</i>	V/II
Myrtaceae							
<i>Callistemon</i>	Shrub	<i>Sp. Nov.</i>	I	–		<i>linearis</i>	V
		–		–		<i>pityoides</i>	V
		–		–		<i>sieberi</i>	V
		–		–		<i>aff. flavovirens</i>	V

Appendix Continued

Family and genus	Form	Outcrop habitat	Trait	Overlapping habitat	Trait	Forest habitat	Trait
<i>Eucalyptus</i>	Tree	–		<i>dealbata</i>	VI	<i>andrewsii</i>	VI
		–		<i>prava</i>	VI	<i>brunnea</i>	VI
		–		–		<i>caleyi</i>	VI
		–		–		<i>caliginosa</i>	VI
		–		–		<i>laevopinea</i>	VI
		–		–		<i>subtilior</i>	VI
<i>Leptospermum</i>	Shrub	<i>novae-angliae</i>	V	<i>trinervium</i>	V	<i>polygalifolium</i>	V
		–		<i>brevipes</i>	V	–	
Poaceae							
<i>Aristida</i>	Grass	–		<i>jerichoensis</i>	V	<i>ramosa</i>	V
<i>Danthonia</i>	Grass	<i>longifolia</i>	V	–		<i>linkii</i>	V
		<i>monticola</i>	V	–		<i>racemosa</i>	V
<i>Digitaria</i>	Grass	–		<i>breviglumis</i>	V	<i>diffusa</i>	V
		–		–		<i>ramularis</i>	V
Polygalaceae							
<i>Comesperma</i>	Shrub	–		<i>ericinum</i>	II	<i>defoliatum</i>	V
Proteaceae							
<i>Grevillea</i>	Shrub	<i>beadleana</i>	II	–		<i>viridiflava</i>	V
		–		–		<i>tritemata</i>	V?
<i>Hakea</i>	Shrub	<i>macrorrhyncha</i>	I	–		<i>laevipes</i>	V
<i>Persoonia</i>	Shrub	<i>terminalis</i>	II	<i>cornifolia</i>	V	<i>sericea</i>	V
		–		–		<i>tenuifolia</i>	V
Rhamnaceae							
<i>Cryptandra</i>	Shrub	<i>amara</i>	II	–		<i>scotechinii</i>	V
		<i>lanosifolia</i> ^a	II	–		–	
Rutaceae							
<i>Boronia</i>	Shrub	<i>bipinnata</i> ^a	II	<i>granitica</i>	II	<i>algida</i>	V
		–		–		<i>microphylla</i>	V
		–		–		<i>polygalifolia</i>	V
		–		–		<i>whitei</i> ^a	V
<i>Zieria</i>	Shrub	<i>laevigata</i>	II	<i>aspalathoides</i>	II	<i>cytisoides</i> ^a	V
		<i>nivea</i>	II	–		–	
Sapindaceae							
<i>Dodonaea</i>	Shrub	<i>hirsuta</i>	II	<i>viscosa</i>	V	<i>triquetra</i>	V
Stylidiaceae							
<i>Stylidium</i>	Herb	–		<i>laricifolium</i>	III	<i>graminifolium</i>	V

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