

## Dynamics of the overstorey and species richness in Australian heathlands

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### Abstract

We studied the impact of overstorey shrubs on understorey richness in three study areas in south-western Australian heathlands. In unburnt heathlands, understorey richness varied inversely with shade cast by the overstorey and was greatest in open sites with no overstorey. Burning increased species richness by as much as 50%. In post-burn sites, understorey richness relative to open sites was significantly lower under sprouting shrubs than under the skeletons of non-sprouters. Sprouters had half the number of species of open sites whereas non-sprouters had the same, or slightly more species at the southern and northern sandplain heath site. However, in burnt *Banksia* woodlands near Perth, understorey richness was significantly reduced relative to open sites. Understorey composition differed among open, sprouter and non-sprouter sites with most species preferring open and non-sprouter sites. We develop a simple model to explore factors influencing understorey diversity. The model predicts that the magnitude and sign of overstorey effects on understorey diversity is strongly influenced by the proportion of species with dormant propagules, since they can survive shading by transient canopies, and by the strength of competitive interactions in the understorey assemblage. We conclude that understorey/overstorey interactions are important for conservation management of these heathlands, and perhaps other vegetation types. However an overstorey may suppress or promote understorey richness, depending on local species traits, and management of overstorey shrubs should vary accordingly.

### Introduction

Patterns of species richness have been studied in relation to diverse gradients and at scales from the local to the global (Rosenzweig, 1995; Huston, 1994). At a local scale, plant species richness peaks at intermediate levels of stand biomass in many plant communities from many parts of the world (Begon *et al.*, 1996); at a landscape scale, tree species richness increases linearly with the joint availability of energy and water (Currie & Paquin, 1987; Currie, 1991). These and other general patterns of species richness have been used for predicting biodiversity responses to environmental change. They have also been the subject of theoretical and experimental tests of underlying mechanisms that produce these patterns (eg. Tilman, 1988; Tilman, 1994; Oksanen, 1996; Turner *et al.*, 1996). Among the least explored patterns is that between different layers of vertically stratified plant communities. Species richness of understorey layers can be influenced by the properties of overstorey layers. For example, where most species are light-demanding, understorey species richness

would be expected to decline with increasing shade cast by the overstorey. Specht & Morgan (1981) showed a remarkably close correlation between understorey species richness and overstorey cover for a diverse range of Australian plant communities. Understorey richness declined in a consistent way with increasing canopy shading over continent-wide samples of vegetation (Specht & Specht, 1989). The relationship does not seem to have been studied on other continents though it seems likely that different patterns would occur in other regions, such as tropical forest belts, where a larger pool of shade-tolerant species occurs in the flora.

In this study, we explore the influence of life history properties of overstorey species on understorey species richness. From Specht & Morgan's (1981) relationships, one would predict that the amount of shade cast by an overstorey is the single most important factor determining understorey richness. However overstorey plants are not permanent. Tree deaths cause gaps where well lit conditions permit colonisation by seedlings of both canopy and understorey species. Rapid turnover of trees has been shown to correlate with tree species

richness for a large sample of diverse tropical forests (Philips *et al.*, 1994). For understorey species, high turnover of canopy plants should promote species richness in floras with many shade-intolerant species. Long-lived canopy species should reduce understorey richness whereas short-lived species should increase it. Differences in the lifespan of canopy species within a forest would promote biotic heterogeneity.

#### *Understorey/overstorey interactions in heathlands*

We explored the effects of life histories of overstorey species on understorey diversity in Australian heathlands. The south-western Australian heathlands, together with fynbos shrublands of South Africa, are among the richest temperate floras on earth and processes determining this richness are of considerable interest (Cowling *et al.*, 1996). Heathlands are fire-prone shrublands which are very convenient for studying overstorey/understorey interactions. Overstorey species can easily be classed as long-lived or transient based on disturbance response. Long-lived overstorey species sprout after fire, occupying the same space for many fire intervals. Transient overstorey species are killed by fire (non-sprouters, "seeders") but regenerate from seeds stored in canopy or soil seedbanks (Whelan, 1995; Bond & van Wilgen, 1996). Their lifespan is determined by the length of the fire interval which ranges from ca. 5-30 years in Australian heathlands (Bradstock *et al.*, 1995). The overstorey in Australian and South African heathlands is commonly formed by members of the Proteaceae. These are 1-4 m tall, often broad-leaved shrubs that form a discontinuous layer shading a species-rich understorey of fine-leaved shrubs, graminoids (sedges, grasses, Restionaceae) and other herbs (Cowling *et al.*, 1997; Lamont & Groom, 1998). Fires kill the canopy and also trigger understorey species recruitment. Because fire stimulates recruitment, you can count the full array of understorey species, including those that exist only as dormant propagules in undisturbed vegetation, by censusing communities shortly after a fire (Cowling *et al.*, 1997; Bell *et al.*, Taylor, 1993).

There is a large literature on how the fire regime directly influences survival and regeneration of species (Noble & Slatyer, 1980; Whelan, 1995; Enright *et al.*, 1996; Bond & van Wilgen, 1996). Recent studies have begun to explore indirect effects of burns through changes to species interac-

tions, especially between the overstorey and understorey, in South African fynbos (Cowling & Gxaba, 1990; Yeaton & Bond, 1991; Vlok & Yeaton, 1999) and Australian heathland (Keith & Bradstock, 1994; Bradstock *et al.*, 1995). All of these studies showed significant effects of the overstorey on understorey richness and composition. The effects were dynamic, meaning that fire-induced changes in the populations of overstorey species would initiate changes in the diversity and composition of the understorey. However the direction of change differed. Vlok & Yeaton (1999) reported positive effects of a transient overstorey on understorey richness and Cowling & Gxaba (1990) and Keith & Bradstock (1994) reported negative effects. Since the abundance of overstorey shrubs can be readily manipulated by the fire regime, these studies have led to changes in fire management for conservation purposes aimed, especially in Australia, at promoting understorey diversity by reducing the overstorey effect (Bradstock *et al.*, 1995).

We sampled understorey species in a number of South-western Australian shrubland communities to test for canopy effects on community richness. We compared species richness under the crowns of sprouters and non-sprouters to test the prediction that richness would be higher under transient species and to determine the sign of overstorey effects. After first reporting results of the study, we develop a simple model of species interactions that might help explain the diversity of patterns observed in our, and other, studies.

#### **Study area**

We sampled three study areas during the flowering season in spring (October, 1996). The three areas cover the geographic range of heathlands with one at Eneabba in the northern sandplain heaths, one at Hopetoun in the southern sandplain heaths and one at Perth in the central area of the South-Western Botanical province. We sampled stands that had been burnt 1 to 4 years previously so as to include the full diversity of species in an area, including species which survive as dormant seedbanks under an overstorey. Dormancy in fire-prone shrublands is common but fire stimulates germination and heathlands reach the same or slightly higher species richness in the first year or so after a fire (Wark *et al.*, 1987; Keith & Bradstock, 1994). Where possible, we matched burnt and unburnt sites to indicate the

proportion of “ghost” species (species which persist, after shoot death, either in dormant soil seed-banks or vegetative storage organs).

#### *Eneabba*

The Eneabba study area was beside the Brand Highway 23.2 km south of Eneabba (29°49'E, 115°16' S). The study area was a flat sandy plain bisected by a road. The shrubland last burnt about 15 years ago on the eastern side of the road. The western side had burnt in February 1995 in a lightning fire, about two years before our study. The vegetation was a species rich heathland 1-2 m tall. Taller shrubs (overstorey species), included *Banksia grossa*, *B. lanata*, *B. candolleana*, *B. attenuata*, *B. menziesii*, *Hakea trifurcata* and others. The density of the overstorey varied from sparse over most of the area to moderately dense in parts.

#### *Hopetoun*

This study area was in the southern sandplain heaths on the south coast of South-western Australia a few kilometres east of the village of Hopetoun (33°57'E, 120°07'S). We sampled an area that had been burnt ca. 4 years prior to our study in October 1996. Slopes were level to gently undulating and soils were deep sands. Overstorey density was patchy. The vegetation is rich in understorey species. Common overstorey species included *Banksia speciosa*, *Adenanthos cuneatus*, *Conospermum teretifolium*.

#### *Perth*

This site was on the Swan Coastal Plain in Kensington Park, a suburb of Perth. It is one of numerous fragments of *Banksia* woodlands left in the city and suburbs. Part of the area had been burnt in a low intensity fire about one year before our study. The vegetation was a *Banksia* woodland characteristic of the Swan Coastal Plain (Dodd & Griffin, 1989). The *Banksia* species were 4-6m tall, sprout after fires, and form a relatively sparse canopy. We studied the effects of *Adenanthos cygnorum* on understorey richness. This is a non-sprouting overstorey species up to 4 m tall which casts a dense shade. The Swan coastal plain is undergoing rapid urbanisation and has been heavily impacted by human settlement. Unlike the northern and southern sandplains, few non-sprouting overstorey (and understorey) species occur in this community, possibly because of frequent anthropogenic fires in the past (Lamont, unpublished).

## Methods

### *Sampling procedure*

We studied the effects of different crown types by sampling species in paired quadrats beneath an overstorey plant and in an adjacent site with no overstorey shrubs present (“open” sites). The open site quadrats were placed in a fixed direction and distance (< 2 m) from the overstorey sites to avoid sampling bias. The paired quadrats were close enough to minimise any possible micro-site differences, other than those caused by the presence of a canopy species. We recorded all species rooted in a quadrat. The growth form of each species was recorded as shrub, graminoid or forb (non-graminoid herb). We selected one to three overstorey species at each study area representing short-lived (non-sprouting) or long-lived (sprouting) lifespans. In burnt sites, we determined the pre-burn position of non-sprouting canopies from the burnt skeleton. In most cases, we sampled beneath 15 shrubs of each overstorey species using 0.5 x 0.5 m quadrats paired with 15 quadrats of the same size in open positions. In the Perth study area, we laid out transects 0.3 m wide and of length equal to the broadest diameter of the overstorey shrub, *Adenanthos cygnorum*, so as to include more species. Transects of equal dimensions were established in adjacent open sites. The overstorey species used at each study area and their characteristics are shown in Table 1. We recorded shade cast by each species with a camera with automatic focus (28 mm lens). This was placed on the ground facing upwards midway between the plant stem and the edge of the canopy. The photographic slides were scanned and imported into a computer. Percentage plant cover and percentage sky were calculated using the program MULTISPEC. We also measured percentage light transmitted through a canopy by recording light intensity outside, and beneath, canopies using a LiCor meter with a 4Pi PAR sensor placed at the same location as the camera.

### *Analyses*

We used ANOVA, and parametric or non-parametric two-sample tests to compare patterns of species richness and growth-form richness under different canopy types. Parametric tests were only applied where data met requirements of equality of

Table 1. Characteristics of overstorey species in each study area. FS is fire survival mode: S = sprouter (persistent), NS = non-sprouter (transient). FPC is % foliage projective cover. The number of overstorey plants sampled, n+, and paired sites with no overstorey present, n-, is also indicated.

Study area	Stand age (y)	Species	FS	FPC	n+	-
Eneabba	2 + 15	<i>Banksia grossa</i>	S	74	15	15
	2 + 15	<i>B. candolleana</i>	S	84	15	15
	2 + 15	<i>B. lanata</i>	NS	82	15	15
Hopetoun	5	<i>Adenanthos cuneatus</i>	S	83	15	15
	5	<i>Conospermum teretifolium</i>	S	73	15	15
	5	<i>B.speciosa</i>	NS	79	15	15
Perth	1 + 10	<i>A. cygnorum</i>	NS	83	10	10

variances (t test) and homogeneity of variances (ANOVA). We also compared the total species list across all sample sites of each overstorey type. We used the software package STATISTICA for statistical analyses.

We analysed the effects of different overstoreys on species composition by comparing the number of indicator and exclusive species under each overstorey species with open sites. Indicator species were defined as those that occurred more often under either closed, or open, sites. We used  $P < 10$  (Fisher's Exact Test) as the threshold for indicators.

Exclusive species occurred only under either closed or open sites for a given data set. Most were single occurrences. We tested the null hypothesis of equal proportions of indicator and exclusive species under overstorey versus open sites using Chi-square tests.

## Results

### *Burnt vs unburnt species richness*

Unburnt stands give an indication of equilibrium values for understorey richness in relation to overstorey type. Unburnt stands on similar slopes and soils and close to burnt stands were only available at Eneabba and Perth. Understorey richness at Eneabba varied in proportion to the light passing through the different canopies (*B. grossa* – 15%, mean richness,  $s = 5.3$  per  $0.25 \text{ m}^2$ ; *B. candolleana* – 4%, mean  $s = 4.0$ ; *B. lanata* – 2%, mean  $s = 3.1$ ). Understorey richness in unburnt open sites was at least double that of shaded sites (Table 2). At Perth, open stands had nearly three times as many species as under the non-sprouting overstorey species, *Adenanthos cygnorum*. This species casts a dense shade (10% of open light).

Burnt sites at Eneabba had higher understorey richness than unburnt sites under all canopy types (Table 2) indicating the presence of many "ghost" species in mature vegetation. The difference in richness between unburnt and burnt stands was greatest under *B. lanata*, a non-sprouter, where there were six times more species in the burnt site. Burning caused a two-fold increase or less under sprouter canopies and in open sites. Burnt open sites at Perth also had slightly more species than unburnt open sites (Table 2).

### *Overstorey effects in burnt communities*

Patterns of mean species richness per quadrat in relation to canopy type for burnt sites are shown in Table 2. In all three study areas species richness increased after fire. Species richness under sprouters was significantly lower than under the skeletons of non-sprouters or open sites in both the northern and southern sandplain sample areas. In both areas, non-sprouter sites had slightly, but not significantly, more species than open sites. Though species richness was proportional to overstorey foliage densities in unburnt stands, the pattern was not evident in stands recovering from burning. Instead, richness under the canopy skeleton was proportional to the richness of the adjacent open site for each species at both Eneabba and Hopetoun. Initial species richness after a fire therefore appears to depend on the size of the local propagule pool more than the former degree of shading.

The effects of overstorey shading in Perth was opposite to the pattern in southern and northern sandplain heaths. Although *Adenanthos cygnorum* is a non-sprouter, species richness under burnt plants was half that of open sites. This overstorey species casts dense shade similar to *B. lanata* at Eneabba (Table 1) but the latter had high richness in burnt sites. We discuss this anomalous pattern further below.

Table 2. Effects of overstorey type on understorey species richness at three study areas in south-western Australian heathlands. Values are mean number of species counted in  $0.5 \times 0.5$  m quadrats centred under the respective overstorey shrub species or adjacent areas with no overstorey ( $n=15$  in each type). Standard deviations are given in parentheses. Sprouters are persistent, and non-sprouters transient, occupants of a site.

Overstorey	Species	UNBURNT Overstorey		BURNT Overstorey	
		with	without	with	without
<b>Eneabba 1</b>					
Sprouter	<i>B. grossa</i>	5.3 (2.31)	10.7 (2.79)	7.8 (2.40)	13.9 (2.25)
Sprouter	<i>B. candolleana</i>	4.0 (1.41)	9.6 (2.32)	10.1 (2.76)	17.6 (3.36)
Non-sprouter	<i>B. lanata</i>	3.1 (1.33)	7.3 (1.45)	18.5 (2.77)	16.0 (3.05)
<b>Hopetoun 2</b>					
Sprouter	<i>A. cuneata</i>	-	-	8.1 (2.61)	14.3 (3.59)
Sprouter	<i>C. teretifolium</i>	-	-	5.9 (1.94)	13.7 (2.74)
Non-sprouter	<i>B. speciosa</i>	-	-	14.7 (3.59)	14.0 (3.17)
<b>Perth 3</b>					
Non-sprouter	<i>A. cygnorum</i>	5.5 (2.42)	14.5 (5.11)	9.6 (3.89)	18.5 (2.91)

1. ANOVA for the burnt Eneabba sites showed significant species, cover, and interaction effects (df 1, 84, species:  $F = 33.2$ ,  $P < 0.001$ , presence/absence of overstorey  $F = 43.2$ ,  $P < 0.001$ , interaction  $F = 29.3$ ,  $P < 0.001$ ).
2. ANOVA for the Hopetoun sprouter species showed no significant differences between the two species but a significant overstorey effect (df 1, 56, species:  $F = 3.8$ ,  $P < 0.10 > 0.05$ , presence/absence of overstorey  $F = < 92.8$ ,  $P < 0.001$ , interaction  $F = 1.2$ ,  $P > 0.05$ ). Species richness was significantly different among sites with sprouter or non-sprouter overstoreys (df 1, 70,  $F = 515$ ,  $P < 0.001$ ).
3. ANOVA for the Perth study area showed significant differences between burnt unburnt comparisons and overstorey presence/absence but no significant interaction effects (df 1, 46, burnt unburnt  $F = 15.8$ ,  $P < 0.001$ , presence/absence of an overstorey  $F = 65.2$ ,  $P < 0.001$ , interaction  $F = 0.03$ ,  $P > 0.05$ ).

### Cumulative species counts and heterogeneity

Cumulative counts of all species encountered under the different canopy types are listed in Table 3. For both burnt and unburnt sprouters, total species richness beneath the canopy was much less than in the open. However, under burnt non-sprouters (*B. lanata*, *B. speciosa*), species richness was greater than open sites in both the northern and southern sandplain study areas. The Perth study area was again different with more species in the open sites.

Turnover of species between plots can be estimated as the ratio of total species count (Table 3) to mean species richness (Table 2) and is a measure of patchiness or community "heterogeneity" (Collins, 1992; Schilke *et al.*, 1997). If turnover rates are equal, then the ratios should be equal. In unburnt sites, species turnover was greater when an overstorey was present (overstorey present, mean ratio = 6.75,  $sd = 0.55$ , absent, mean = 5.34,  $sd = 0.48$ ,  $df = 6$ ,  $P < 0.01$ , paired t test). The same trend occurred in burnt vegetation (overstorey present, mean ratio = 4.6,  $sd = 1.15$ , absent mean =

Table 3. Total species richness in sites with and without an overstorey present at three study areas in south-western Australian heathlands. Values are total species counts from 15 samples in each microsite type.

Species	Study area	UNBURNT Overstorey		BURNT Overstorey	
		present	absent	present	absent
<b>Sprouters</b>					
<i>Banksia grossa</i>	Eneabba	37	56	53	66
<i>B. candolleana</i>	Eneabba	25	50	45	73
<i>A. cuneatus</i>	Hopetoun	-	-	34	50
<i>C. teretifolium</i>	Hopetoun	-	-	32	51
<b>Non-sprouters</b>					
<i>B. lanata</i>	Eneabba	23	44	59	58
<i>B. speciosa</i>	Hopetoun	-	-	60	51
<i>A. cygnorum</i>	Perth	35	71	41	60

3.81,  $sd = 0.49$ ,  $P < 0.05$ , paired t test). Sprouters had higher turnover rates than non-sprouters (mean sprouter ratio = 5.2,  $sd = 1.18$ , mean non-sprouter = 3.8,  $sd = 0.58$ ,  $df = 5$ ,  $0.05 < P < 0.10$ , Mann Whitney). Thus, species turnover was greater underneath overstorey plants than in the open and also greater under long-lived than under transient canopies. In general, the difference between turnover values under and outside the canopy is greater for sprouters than seeders.

#### Compositional change

The number of indicator species and exclusive species indicate the extent to which overstorey species alter understorey composition. Few species were indicators of sprouter sites but many were indicators of open sites (Table 4). There were also more exclusive species in open sites than under sprouting shrubs (Table 4). This suggests that a long-lived overstorey causes an attrition of understorey species and that few, if any, prefer shade. Indicator species for the Eneabba study area in the northern sandplains are shown in Table 5 and for Hopetoun in the southern sandplain heaths in Table 6. There were no species with statistically significant preferences for sprouter overstorey sites.

In contrast to the sprouters, non-sprouters had negligible effects on species composition in both the northern and southern sandplain study areas. The number of indicator species was small and similar in both open and overstorey sites. The number of species exclusive to either open or

closed sites was also very similar for the non-sprouter species at both Eneabba and Hopetoun. *Adenanthos cygnorum*, in the Perth study area, had effects more like a sprouting overstorey species. It supported no indicator species compared with seven in open sites. Six exclusive species were recorded under *Adenanthos* compared with 25 exclusive species in open sites.

#### Discussion

We set out to study the dynamic interactions between overstorey shading and understorey species richness. Following Specht & Specht (1989), one would predict that shading by an overstorey layer is the single most important factor influencing the species richness of understorey layers in heathland plant communities. For unburnt stands at Eneabba and Perth, our data provide some support for this prediction, even at the scale of understorey plants growing under a single overstorey shrub. Species richness beneath overstorey shrubs decreased in proportion to the shade cast. This result indicates a shade-intolerant flora as does the scarcity of any shade loving (indicator) species (Tables 4,5,6). In South African fynbos, Cowling & Gxaba (1990) reported an increase in bird-dispersed, shade-tolerant species under non-sprouting shrubs. However most of these species were seedlings of shade-tolerant forest precursors (Manders *et al.*, 1992). Most fynbos species appear to be intolerant of shade. In both heathland

Table 4. The distribution of indicator and exclusive species under burnt overstorey shrubs versus open sites in western Australian heathlands. Indicator species had a significant preference for sites either with or without an overstorey (Fisher's Exact test,  $P < 0.10$ ). Exclusive species occurred only in open or in overstorey sites. Significant differences ( $P < 0.05$ ) between open and overstorey counts are indicated by bold lettering (test = chi square).

Overstorey type	Species	Number of indicators		Number of exclusives	
		present	absent	present	absent
<b>Eneabba</b>					
Sprouter	<i>B. grossa</i>	1	6	20	33
Sprouter	<i>B. candolleana</i>	<b>2</b>	<b>11</b>	7	19
Sprouter	<i>grossa</i> + <i>candolleana</i>	<b>1</b>	<b>13</b>	<b>19</b>	<b>44</b>
Non-sprouter	<i>B. lanata</i>	2	2	15	16
<b>Hopetoun</b>					
Sprouter	<i>A. cuneata</i>	0	5	4	11
Sprouter	<i>C. teretifolia</i>	<b>1</b>	<b>14</b>	<b>0</b>	<b>10</b>
Sprouter	<i>cuneata</i> + <i>teretifolia</i>	<b>0</b>	<b>11</b>	<b>3</b>	<b>23</b>
Non-sprouter	<i>B. speciosa</i>	4	6	15	20
<b>Perth</b>					
Non-sprouter	<i>A. cygnorum</i>	0	7	6	<b>25</b>

Table 5. Indicator species for different microsites in burnt (2 year post-burn) Eneabba heathland. Number of occurrences is indicated for each canopy type (+) and its open pairs (-). Overstorey species are *Banksia grossa* (sprouter), *B. candolleana* (candoll, sprouter), *B. lanata* (non-sprouter). Significant differences ( $P < 0.05$ ) are indicated in **bold** lettering (Fisher's exact test).

Indicator species	Sprouter				Non-sprouter <i>lanata</i> canopy	
	<i>grossa</i> canopy +	-	+	<i>candolleana</i> canopy -	+	-
<b>Indicators of open sites</b>						
<i>Laxmannia sessiliflora</i>	<b>2</b>	<b>11</b>	<b>1</b>	<b>13</b>	11	12
<i>Johnsonia pubescens</i>	<b>5</b>	<b>13</b>	<b>2</b>	<b>11</b>	8	10
<i>Schoenus pleisomoneus</i>	1	3	<b>0</b>	7	9	11
<i>Stylidium diuroides</i>	0	3	<b>1</b>	7	11	8
<i>Stylidium repens</i>	<b>1</b>	7	1	5	<b>1</b>	7
<i>Melaleuca trichophylla</i>	<b>2</b>	<b>8</b>	<b>0</b>	<b>6</b>	3	2
<i>Drosera erythrorhiza</i>	1	5	1	6	3	1
<i>Austrostipa ?acroclitata</i>	0	2	1	6	<b>1</b>	7
<i>Tripterococcus brunonis</i>	-	-	<b>0</b>	<b>5</b>	4	6
<i>Anigozanthos humilis</i>	0	1	<b>0</b>	<b>6</b>	4	3
<i>Pileanthus filifolius</i>	<b>0</b>	<b>10</b>	0	2	-	-
<i>Schoenus curvifolia</i>	<b>0</b>	<b>5</b>	-	-	3	1
<b>canopy indicators</b>						
<i>Gompholobium knightianum</i>	-	-	9	2	4	1

Table 6. Indicator species for different microsites in burnt (4 year post-burn) Hopetoun heathland. Number of occurrences is indicated for each canopy type (+) and its open pairs (-). Overstorey species are *Adenanthos cuneata* (Adenan, sprouter), *Conospermum teretifolium* (Cono, sprouter), *B. speciosa* (Banksia, non-sprouter). Significant differences ( $P < 0.05$ ) are indicated in **bold** lettering (Fisher's exact test).

Indicator species	Sprouter			Non-sprouter <i>Banksia</i> canopy		
	<i>Adenan</i> canopy +	-	+	<i>Cono</i> canopy -	+	-
<b>Indicators of open sites</b>						
<i>Conostylis vaginata</i>	<b>2</b>	<b>12</b>	<b>1</b>	<b>10</b>	7	11
<i>Lechenaultia tubiflora</i>	<b>1</b>	<b>8</b>	<b>1</b>	<b>9</b>	9	8.5
<i>Hibbertia sp.</i>	<b>1</b>	<b>8</b>	<b>3</b>	<b>9</b>	8	8.5
<i>Laxmannia sessiliflora</i>	<b>0</b>	<b>8</b>	2	2	3	5
<i>Drosera parvula</i>	1	5	<b>0</b>	<b>5</b>	3	5
<i>Melaleuca sp.</i>	1	6	1	3	0	4.5
<i>Lysinema ciliatum</i>	0	4	1	6	2	5
<i>Schoenus curvifolia</i>	9	9	<b>1</b>	7	2	8
<i>Andersonia lehmanniana</i>	0	2	<b>0</b>	<b>6</b>	2	4
<i>Oligarrhena micrantha</i>	0	2	<b>0</b>	<b>5</b>	0	3.5

types, understorey communities are therefore partly patterned by the density and shading properties of overstorey species creating intra-community heterogeneity (Collins, 1992; Ne'eman *et al.*, 1992; Schwilk *et al.*, 1997; Vlok & Yeaton, 1999).

The pattern of low diversity under taller shrubs does not necessarily persist after a disturbance. An apparently barren understorey may still contain species persisting in a dormant state. There is little information on seed or vegetative dormancy for the many species encountered in this study or, in

general, in the species-rich south-western kwongan. Ghost species are generally members of two life history groups highlighted by Pate & Hopper (1993). These are obligate non-sprouter species with dormant seeds in the soil and fire ephemerals. Fire ephemerals appear briefly after a burn while obligate non-sprouters live longer but eventually senesce and die. In contrast to these groups, many understorey species have propagules which persist for only a short time in the seed bank (Meney *et al.*, 1994). Such species do not persist as "ghosts".

The repeated suppression of understorey by persistent sprouter overstorey species would lead to under-representation of these species under sprouters in comparison with non-sprouters and open areas. Members of the Epacridaceae are often non sprouters with short-lived seeds (Meney *et al.*, 1994). It may be significant that four of the 12 species which were indicators of open sites at Hopetoun (Table 6) were non sprouters from this family.

Detailed information on the vital attributes of species is useful in predicting likely responses to changes in fire regimes or overstorey shading. However, where such information is limited, we can estimate the frequency of "ghost" species in a community from the difference in species number between unburnt and burnt sites. For the Eneabba study area, a burn increased the total species count by 18% for open sites next to *B. grossa*, 32% for *B. lanata* and 46% for *B. candolleana* (Table 2). Thus "ghost" species contribute between one fifth and nearly half of the species in post-burn communities. The situation in the Perth study area was completely different. Here the total species count in burnt sites (60 spp.) was less than in unburnt sites (71 spp) indicating few or no "ghost" species in this community. Here burnt *A. cygnorum* shrubs left distinct gaps in the heath community. These were colonised mostly by opportunistic, invasive weedy species such as *Briza minor*, *Ehrharta calycina*, *Gladiolus caryophyllaceus*, *Romulea rosea* and *Arctotheca calendula*. These species were rare in intact heath but seem to be far better at dispersing into gaps than native species.

Recovery of understorey diversity after an overstorey plant dies depends primarily on the presence of "ghost" species. The presence of "ghosts" depends on whether their dormant propagules can out-live the overstorey plant that casts the shade. Our study confirmed that the life history of the overstorey species had a significant effect on post-burn richness. In northern and southern sandplain heaths, understorey richness under sprouters was only 53% of open sites in contrast to non-sprouters which had equivalent (108%) richness to open sites. The implication is that these heathlands would maintain their diversity under non-sprouter canopies but could lose up to half their species should sprouters come to dominate the overstorey. Our results are probably an underestimate of potential species losses because we ignored edge effects and the potential spill-over of species from

open sites to shaded patches. Our study is the first to report differences between sprouting and non-sprouting overstoreys on understorey richness in Australian or South African heathlands. However similar patterns have been reported for some Florida communities where rosemary scrub (dominated by the non-sprouting *Ceratiola ericoides*) is more species rich than sprouter dominated scrub-by flatwoods (Menges & Hawkes, 1998).

At Eneabba and Hopetoun, understorey richness under non-sprouters was equivalent to open sites, a surprising result given the pervasive effect of shading on species loss between burns. This result contradicts patterns reported by Cowling & Gxaba (1990) for South African fynbos or Keith & Bradstock (1994) for eastern Australian heathlands. At our Perth study area we found a pattern more consistent with these studies since the non-sprouter canopy significantly depressed diversity.

#### *A simple model of overstorey/understorey interactions*

To help explore these conflicting results and their implications for conservation management, we develop a simple model to explore the mechanisms of understorey/overstorey interaction. For a given community, we express the number of understorey species that are intolerant of shading as  $S_i$  and the number of species that can persist in the shade as "ghosts" (ie. with soil-stored seedbanks or dormant underground storage organs), as  $S_g$ . The effect of overstorey shading on the shade intolerant species can be expressed as  $B_i = S_i (1-F)$  where  $B_i$  is the number of understorey species observed under a mature canopy and  $F$  is a measure of shading ranging from 0 with no overstorey shading to 1 with complete shading.

Species that can persist as "ghosts" still need enough time and resources to reproduce so they can produce the "ghost" propagules. Sprouter crowns develop rapidly from old rootstocks after a fire and are likely to smother understorey species before they can flower and set seed. The overstorey effect on "ghost" species can be expressed as  $B_g = aS_g$  where  $B_g$  is the number of "ghost" species present and  $a$  is a measure of overstorey suppression (effectively the proportion of "ghost" species that survive from canopy closure to the next burn in the form of dormant soil seedbanks or dormant storage organs). The value of  $a$  ranges from 1, with all species surviving, to 0, with none surviving. It will vary with the rate of canopy development so that  $a_s$ , the proportion sur-



viving under sprouters will be less than  $a_{ns}$ , the proportion under non-sprouter canopies. Non-sprouters recover from burns as seedlings and canopy development is therefore much slower than sprouters.

The effect of an overstorey on total understorey species,  $B_{tot}$ , is the sum of the effects on shade intolerant and “ghost” species:

$$1) B_{tot} = S_i (1-F) + a S_g$$

In a post-burn census, more species will occur under non-sprouters (sub-script ns) than sprouters (sub-script s) if:

$$2) S_i (1-F_{ns}) + a_{ns} S_g > S_i (1-F_s) + a_s S_g$$

which, by algebraic manipulation, reduces to

$$3) a_{ns} > a_s + (S_i/S_g)(F_{ns} - F_s)$$

If a sprouter casts denser or similar shade to a non-sprouter ( $F_s \geq F_{ns}$ ), the expression on the right is 0 or  $< 0$ . This means that the non-sprouter will always have more species present because the proportion of “ghost” species surviving under non-sprouters,  $a_{ns}$ , is always greater than under sprouters,  $a_s$ . Canopy shading ( $F$ ) was similar for sprouters and non-sprouters in the northern and southern sandplain heaths (Table 1) but sprouters had far fewer species (Table 2), consistent with model predictions.

If a sprouter casts much less shade than the non-sprouter, ( $F_s \ll F_{ns}$ ), then the effect on understorey richness depends on the relative impact on the understorey,  $a$ , of the two canopy life history types **and** the relative number of “ghost” species since:  $a_{ns} > a_s + S_i/S_g$ . If there are no, or few, “ghost” species at a site, then, from equation 1, the number of understorey species collapses to being a simple function of canopy shading independent of life history type. This seems to be the situation in our Perth study area. In contrast to the sandplain heaths, total species counts were greater in unburnt than in burnt sites indicating few, if any, “ghost” species. Canopy shade was very dense under *Adenanthos cygnorum* compared with the light shade cast by the *Banksia* species forming the woodland canopy and understorey richness was significantly depressed by the non-sprouter.

A similar approach can be used to estimate how the presence of an overstorey affects understorey richness relative to open sites. The species pool is again divided into shade intolerant species and

species that can persist as “ghosts”. For a non-sprouting overstorey, for example, species richness will be greater than open sites if:

$$4) S_i (1-F_{ns}) + a_{ns} S_g > a_o S_i + a_o S_g$$

where  $a_o$  is the proportion of species surviving competition from dominant species in open sites ranging from 1 with no competitive effect (all species surviving) to 0 with intense competition among understorey species. In other words, species compete with each other in the absence of an overstorey and this causes a reduction in species richness of magnitude  $a_o$ . By algebraic manipulation, this means that a non-sprouter will have more species than an open site if:

$$5) a_{ns} > a_o(S_i - S_g)/S_g - S_i(1-F_{ns})/S_g$$

If the overstorey casts dense shade ( $F_{ns}$  approaches 1), then:

$$a_{ns} > a_o(B_{tot})/S_g$$

and non-sprouters will have higher numbers of understorey species than open sites whenever  $a_{ns}/a_o > (S_i + S_g)/S_g$ . Higher richness under an overstorey than in the open is clearly unlikely if ghost species form a small proportion of the species pool. However if ghost species are common, and competition among species in open sites is significant ( $a_o$  is small relative to  $a_{ns}$ ), the model predicts equal or higher richness under the overstorey. In both our northern and southern sandplain heath sites, understorey richness equalled, or slightly exceeded, richness in adjacent open sites. At Eneabba, burnt sites had up to 50% more species than unburnt sites indicating a significant pool of “ghost” species. According to our model, this is a necessary, but not sufficient, requirement and there must also be significant competitive suppression taking place in “open” sites to account for the high relative richness under an overstorey. An alternative possibility is that there were significant edge effects with seeds spilling over from open to overstorey sites. However edge effects would not explain why sprouters had fewer species than non-sprouters. In Cape fynbos, Vlok & Yeaton (1999) argued that vigorously sprouting graminoid plants (including clonal Restionaceae) suppress diversity in open sites but are shaded out under transient overstorey shrubs. Our study areas lacked this growth form but clonally spreading shrubs were

present in open communities and may behave in a similar way suppressing understorey species in open sites but being themselves suppressed under overstorey shrubs. In fact, *Banksia candolleana* (Eneabba site) and *Conospermum teretifolium* (Hopetoun site) are both low growing proteoids that could be considered understorey competitors rather than overstorey shrubs.

The model we have developed is a simplification of a complex set of interactions. It describes a snapshot view of understorey/overstorey relationships at a single point in post-burn succession. A more complete analysis should take into account the dynamics of the pool of "ghost" species through post-burn succession, alternative expressions for canopy shading effects, and how  $a$ , the coefficient measuring crown suppression effects, changes through time. We have also not considered post-burn dispersal into overstorey sites. We note earlier that invasive alien weeds were common at our Perth study site, dispersing into burnt gaps created by the death of *A. cygnorum* shrubs. Native species at this site appeared to have very limited post-burn dispersal ability.

Though the model could have added realism, it is useful in succinctly showing why overstorey effects might vary in different communities. Key factors for understorey assemblages are differences in the proportions of "ghost" species and in the importance of competitive effects; and for overstorey species, differences in canopy shading and life history type (sprouter vs non-sprouter). One prediction, for example, is that eastern Australian heathlands are likely to have few "ghost" species since they show significant understorey suppression (Keith & Bradstock, 1994).

## Conclusions

Interaction between layers of a community produces very general relationships between overstorey shading and understorey species richness in Australian vegetation (Specht & Specht, 1989). These relationships are important for conservation management in heathlands because of the magnitude of the overstorey effect and because the overstorey is strongly influenced by the disturbance regime. In our sandplain heath sites, for example, a switch from non-sprouter to sprouter dominance could potentially halve the diversity of these heathlands. We know little about the kinds of fire

regimes that promote sprouter overstorey species but far more about non-sprouters (Whelan, 1995; Enright *et al.*, 1996; Bond & van Wilgen, 1996). We suggest that more attention be given to sprouter demography because of the large potential effect on species richness of a switch to a sprouter-dominated overstorey. In eastern Australia, the assumed negative effects of overstorey/understorey interactions on species richness have already led to changes in fire policy in conservation areas (Bradstock *et al.*, 1995). To reduce overstorey impacts, shorter fire frequencies have been recommended (Keith & Bradstock, 1994; Bradstock *et al.*, 1995). In South African fynbos, Cowling & Gxaba (1990), following similar reasoning, argued that fire regimes should allow for periodic recruitment failures of protea shrubs to promote understorey richness. However Vlok & Yeaton (1999), noting positive effects on community richness, proposed fire regimes that maintained a vigorous proteoid overstorey and argued that the loss of the overstorey would cause significant loss of fynbos species. Our results suggest that non-sprouter overstoreys can have neutral, or even slightly positive, effects in some areas and negative effects in others. The model we have developed suggests that the variable pattern is probably explained, in part, by variation in the number of "ghost" species in different areas. It would be unwise to promote general fire policy changes for managing understorey/overstorey interactions until the nature of the interaction is determined for a particular area. We have shown that an overstorey could promote, or deplete, community richness depending on local circumstances.

Taking a broader view, it is interesting to note that the peculiar conditions that led to the evolution of a temporary overstorey cover (non-sprouting life histories) may have contributed to the high levels of species richness for which these heathlands are renowned. Overstorey/understorey interactions deserve wider attention in these and other vegetation types for the role they may play in structuring plant communities.

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