

Influence of fire-age mosaics on macrolichens and bryophytes in southwestern Australia

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ABSTRACT

Lichens and bryophytes are important groups of organisms in almost all natural ecosystems in that they contribute to carbon and nitrogen cycles, and the formation, stability and infiltration properties of soils. Few Australian studies include the response of these organisms to fire at landscape scales. Here we report on the response of cryptogams to post-fire age and its heterogeneity (i.e., a mosaic of fire ages compared to a single fire age) across jarrah forest blocks in southwestern Australia. Three vegetation units were sampled within each of two adjoining forest blocks of 5000 and 6700 ha. Samples were collected in 2005 and 2010, 2.5 and 7.5 years after wildfire in the northern forest block. The other forest block was burned to produce mosaics of fire ages that differed in structure between sampling in 2005 and 2010. The northern block was sampled in two sub-blocks, each with two replicate sample grids of the three vegetation units (12 sample grids), whereas the mosaics were similarly sampled (six sample grids) in the southern block. Each sample grid consisted of four 2 × 50 m plots within which the presence–absence of species within the total area sampled (400 m²) was recorded. Sixty-seven species were recorded from 36 samples: 40 macrolichens, 20 mosses and seven liverworts. We examined effects of vegetation unit, fire age and heterogeneity on the composition of cryptogam assemblages using Per MANOVA. Cryptogam assemblage composition and richness were associated with vegetation units within jarrah forests and they varied with time since fire. Lichen and bryophyte richness was greatest in landscapes composed of a mosaic of post-fire seral stages and least in pyrically homogenous landscapes 2.5 years after fire. The influence of fire age on cryptogam species richness and assemblage compositions in the deliberately created mosaics is a practical demonstration of the ability of such a landscape to conserve long unburned patches and provide a range of seral stages to maintain cryptogam diversity.

KEYWORDS: assemblage composition, cryptogam, fire heterogeneity, landscape, lichens, liverworts, mosses, patch, refuges, seral stages

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INTRODUCTION

Bryophytes (mosses and liverworts) and lichens, collectively referred to as cryptogams, are susceptible to fire because their preferred habitat is potentially vulnerable to the flame zone and are known to be fire sensitive (Kantvilas *et al.* 2015). However, they persist in Australian ecosystems subjected to periodic fire events. Southwestern Australia contains large areas of flammable native vegetation which, combined with its Mediterranean-type climate of hot dry summers, makes it one of the most fire-prone regions in the world (Burrows & McCaw 2013). The region is also recognised as a biodiversity hotspot (Hopper & Gioia 2004, Rix *et al.* 2015) where fire plays a key role as a selection process (Burrows & Wardell-Johnson 2003, Hopper 2003, He *et al.* 2011), in redistributing nutrient resources (Hingston *et al.* 1989), and competition between plant species (Pekin *et al.* 2012a, b). The coarse filter of periodic fires in these ecosystems from pre-human to more recent times is

likely to have pre-conditioned the biota to persist despite recurrent fire intervals varying from short (less than 5 years) to long (at least 30 years). This conditioning has probably contributed to the observed resilience of the south-west ecosystems to fire (Burrows & Wardell-Johnson 2003, Wittkuhn *et al.* 2011).

Pre-European fire regimes practised by indigenous Australians were characterised by frequent low-intensity fires in the drier parts of the jarrah forest and forest margins (Hallam 1975, Burrows *et al.* 1995, Abbott 2003). Regular and frequent introduction of low-intensity burning, where there are patches of regenerating vegetation that will not carry fire, is likely to have developed a mosaic of vegetation at different seral stages from recently burnt patches to long unburnt patches. These mosaics may have limited the spread and intensity of fires under severe burning conditions.

Since the 1960s prescribed fires have been used extensively as a management practice to reduce fuel load to protect State forest, reserves, and adjoining private property from high intensity fires and more recently to maintain species diversity (Burrows & McCaw 2013). The

premise that mosaics of varying fire ages might lessen fire spread prompted the Department of Biodiversity, Conservation and Attractions to investigate if employing frequent applications of fire across an entire forest block would emulate the outcomes of the Aboriginal style of burning, including if this would help limit the spread of intense bushfires (cf. Boer *et al.* 2009). The deliberate fire management strategy of patch mosaic burning is postulated to promote biodiversity by providing a range of habitats with different fire histories, qualities, and seral stages at a given scale (Parr & Andersen 2006, Burrows 2008, Stein *et al.* 2014). Such mosaics provide refuges during and after fires, retain propagule sources, and provide stepping-stones for recolonization after fire (Robinson *et al.* 2013). The study was designed with an integrated, multi-disciplinary approach, and included a secondary objective to determine if the mosaic pattern of fire maximized species diversity of vertebrates, invertebrates, fungi, plants and cryptogams at the scale of a whole forest block.

Lichens and bryophytes have a wide range of vital ecosystem functions. These functions include soil formation, soil stabilisation and reducing soil erosion (Cornelissen *et al.* 2007), filtering water (Rieley *et al.* 1979), mobilising minerals and nutrients (Van Heerwaarden *et al.* 2003), extracting and fixing nitrogen from the atmosphere (Kershaw 1985), and providing cover and forage for invertebrates and other small animals (Asplund & Wardle 2016, Glime 2017). In sclerophyll forests, their habitat includes soil, rock, bark, leaves, logs and tree trunks and, where there is a relatively cool microclimate with adequate humidity, leaves and branches of understorey shrubs.

Processes that influence how an ecosystem responds to disturbance include the fundamental processes of species dispersal, colonization, and establishment (Mittelbach & Schemske 2015). A fire has the potential to remove or modify the condition of the habitat and to impact cryptogams through direct exposure of the organisms to flame and heat. Following fire, recolonization of cryptogams relies on the fallout of airborne propagules from unburnt source areas (e.g., for lichens Nascimbene *et al.* 2017, and for bryophytes Hutsemekers *et al.* 2008, Baker *et al.* 2013, Barbé 2016), and 'chance' for suitable conditions in the burnt area (e.g., for lichens Werth *et al.* 2006, and for bryophytes Smith & Stark 2014).

The severity of impact and recovery time is linked to fire intensity and scale (Pharo *et al.* 2013). Low-intensity fires leave unburnt patches with cryptogams (Hylander & Johnson 2010 for bryophytes; Ray *et al.* 2015 for lichens) and provide both unaffected and new habitats for species that prefer early to late successional periods. By comparison, intense fires denude the landscape of cryptogam species (Pharo *et al.* 2013 for bryophytes; Ray *et al.* 2015 for substrate specialized lichens). For many species, suitable conditions enabling recolonization are likely only after the vascular flora has at least partially recovered to particular seral stages (Turner *et al.* 2011 for bryophytes; Kantvilas & Jarman 2012 for bryophytes and lichens).

This study investigates the response of cryptogams to fire, particularly species richness and assemblages in a landscape comprising a diversity of post-fire seral stages

including long unburnt refuges compared to one of a uniform seral stage recovering from an intense fire. We assessed variation in species richness and assemblages with time since the last fire, and across land systems that are surrogates for broad vegetation units (Mattiske & Havel 1998, 2000). Four hypotheses were tested within measurement grids for each of mosses, liverworts and macrolichens: (i) species assemblages (i.e., richness and composition) are not affected by vegetation type; (ii) species assemblages are not affected by fire age or (iii) heterogeneity in fire age; and (iv) species assemblages do not predict fire age or heterogeneity in fire age.

METHODS

Study area

The study was conducted across London (34°48'S, 116°55'E) and Surprise forest blocks 30 km northeast of Walpole, covering ~5000 and ~6700 ha respectively,

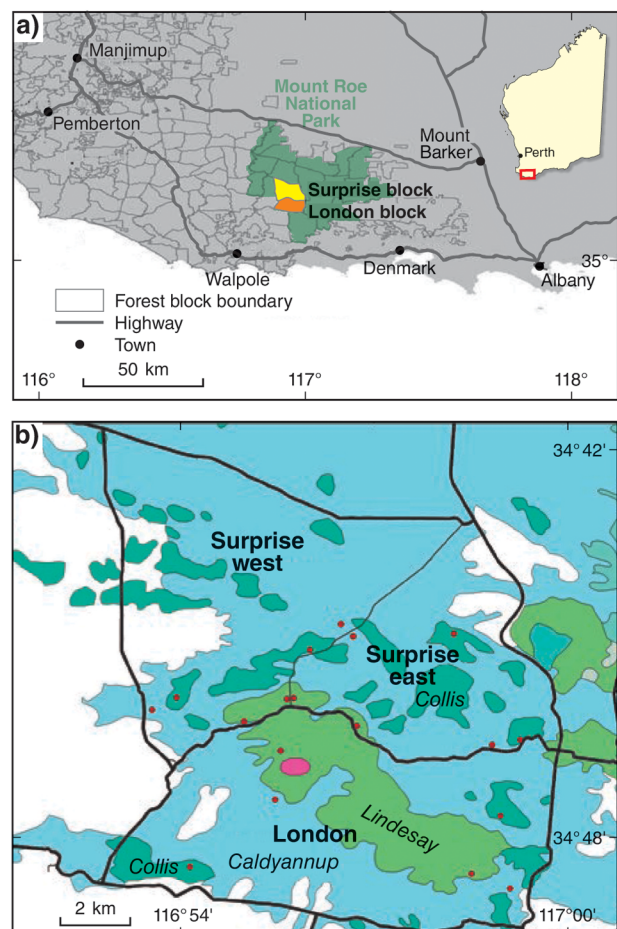


Figure 1. a) Location of the study area at London and Surprise forest blocks, south-west Western Australia; b) Location of sample grids (●) within London and Surprise forest blocks, and vegetation units. Bold lines are forest block boundaries along tracks; Sampled vegetation units of Mattiske and Havel (1998) in London and Surprise blocks denoted thus: Collis (■); Lindesay (■), (■); and Caldyannup (■). White areas are un-sampled minor vegetation units in London and Surprise.

within Mount Roe National Park in the south-west of Western Australia (Figure 1a). The region experiences a Mediterranean-type climate with cool wet winters and warm dry summers (Gentilli 1989). Mean annual rainfall is ~1100 mm, most of which falls over the winter months. Mean monthly temperatures range from 15°C to 26.7°C (Bureau of Meteorology 2016).

The soils and landforms of the study area are derived from granitic gneiss (Churchward *et al.* 1988). Landforms are sharply delineated and form a catena of well-drained ridge and hillslope units, respectively named Collis and Lindsay, and poorly drained swampy slopes, plains and drainage floors named Caldyannup (Churchward *et al.* 1988; Figure 1b). Vegetation on the Collis and Lindsay landform units is mostly open eucalypt forests to 30 m dominated by jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) with a dense, shrubby understory to two metres tall. The presence of stumps and stump coppice indicated some areas of Collis and Lindsay vegetation were subject to a light and selective jarrah harvest probably during the 1960s (Heberle 1997). Vegetation associated with the Caldyannup landform consists mostly of a variety of reed-dominated seasonal wetlands and heathlands of myrtaceous shrubs to 2 m (Mattiske & Havel 2000).

Fire treatments

The Surprise and London forests blocks are similar, forming a continuum of land systems and vegetation associations, but differed in the fire regimes imposed on them. Prior to the study London block was burnt by low-intensity spring fires in 1994 and 2002. Before 1994, fires within this block were six to nine years apart in spring (Wittkuhn & Hamilton 2010). Further prescribed burns introduced into London block in 2002, 2004, 2006 and 2008 were an attempt to create a fine-scale mosaic of different seral stages since the last fire (Table 1, Figure 2). By 2010, there were patches of vegetation from a few to several hundred hectares ranging from relatively recently burnt to long unburnt (Burrows & Middleton 2016). Thus, sampling London block in spring 2005 and spring 2010 incorporated different fire-age mosaic configurations.

Fire intensity across London block varied from low, with scorch height less than six metres, to high with full canopy scorch. Intensity was further indicated by the removal of different layers of fuel (Gould *et al.* 2007). Landsat imagery with a pixel resolution of 30 m before and after burn applications was used to map the extent and location of different categories of fire treatment (Figure 2). The extent of burnt patches and loss of vegetation cover were determined from Normalised Difference Vegetation Index (NDVI; Li *et al.* 2001). Field data (e.g., canopy scorch, tree mortality, defoliation heights, fuels consumption, ash cover) helped test these indices across a variety of vegetation to check their accuracy.

Surprise block, which adjoins London block, was burnt by a single fire event by an intense bushfire in March 2003 (Wittkuhn & Hamilton 2010) and had no further fire until spring 2011 when a prescribed burn covered its eastern portion. The 2003 fire was intense enough to cause spalling of exposed granite and complete combustion of crown foliage. Previous fires on Surprise

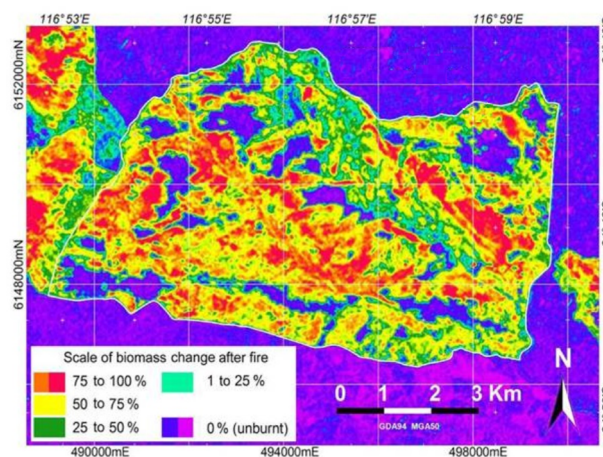


Figure 2. Mapping of burn severity using NDVI classifications in London forest from 2003 satellite imagery following a prescribed fire in spring 2002 (Source: Department of Conservation and Land Management). Note: two unburnt vegetation categories have different reflectances.

were mostly in spring at intervals of six to nine years. Prior to the March 2003 fire two areas within Surprise, affecting only one Lindsay grid, had fires less than five years apart (Wittkuhn & Hamilton 2010). Thus, sampling Surprise block in spring 2005 and spring 2010 covered two homogenous areas with fire ages of 2.5 and 7.5 years, respectively.

Sample grids

A network of sample grids was established as part of a broader fire ecology study (Burrows & Wardell-Johnson 2004, Burrows & Middleton 2016). The network consisted of 18 two hectare (200 m x 100 m) biodiversity sample grids (McCaw *et al.* 2011) established in the three major land systems described above in both London (six grids: 3 vegetation units x 2 replicate grids) and Surprise blocks (Figure 1b). Surprise block had east and west sub-blocks to accommodate planned fire regimes imposed later than the present study (2 x 6 grids: two sub-blocks x three vegetation units x two replicate grids). The initial placement of grids targeted each of the three main vegetation units (Collis, Lindsay, and Caldyannup) within areas of at least 10 ha, and maximum fire age contrasts within London forest block. Although the vegetation units are not of equal extent in the two forest blocks (Figure 1b), each vegetation unit was equally represented in samples from London forest block and Surprise east and west sub-blocks (Table 2).

Species list

An initial survey of lichen and bryophytes was conducted in 2005 to compile a list of species, collect vouchers, and to provide experience for field and lab identification for mosses, liverworts, and macrolichens. This involved collecting specimens along the perimeter of each of the two-hectare grids. The area within the grids was not searched to preserve the integrity of the cryptogam flora for periodic sampling following fire treatments.

Cryptogam response

In 2005, four larger plots (2 × 50 m and a minimum of 50 m apart) were established around the perimeter of the one hectare central part of the sample grids. These two-metre-wide transects were used because they were easily scanned by a single surveyor (R J Cranfield) and their start and finish were defined by permanent pegs established as part of the broader biodiversity survey. Previous sampling in jarrah forest (Cranfield *et al.* 2011) and sampling in the initial survey described above indicated these four 100 m² plots would provide sufficient sampling intensity at the local scale. The presence or absence of each species was noted within the combined area of the four plots. The same experienced surveyor who assessed the grids in 2005 reassessed them in 2010. Time taken to survey plots was flexible and depended on richness and abundance of species. Time available to sample individual plots was not limited. Bryophytes and lichens were sampled at the same time. New or unknown species were collected for further investigation and identification in the laboratory. A conservative approach to field identification was taken with the collection of vouchers and later identification in the laboratory against voucher specimens, catalogued specimens in the Western Australian Herbarium (PERTH), and taxonomic literature. Laboratory identifications of species were by R J Cranfield in consultation with C Cargill and J Elix for some specimens of lichens and liverworts. The primary taxonomic literature used for species identifications included: Catcheside (1980), Buck *et al.* (2002), McCarthy (2006) for mosses; Scott (1985), Glenny & Malcolm (2005) for liverworts; George (1992), Grgurinovic (1994), Lumbsch *et al.* (2001), McCarthy (2001), McCarthy & Malcolm (2004), McCarthy & Mallett (2004), McCarthy (2009) for macrolichens. Vouchers of all collected species are lodged in the Western Australian Herbarium, (PERTH).

Frequency of substrates

Twenty plots of one square metre were established at 10 m intervals along two sides of the central hectare of each grid and the presence or absence of habitat substrates on each plot noted in 2010. The substrates investigated were wood, bark, termite mound, soil, rock, organic matter (other than wood or bark), and charcoal.

Analysis

Before analysis, the data were arranged into a repeated measures design of two forest blocks sampled in spring

2005 and 2010. Fire heterogeneity was confounded with forest block, and fire age was confounded with the year of a sample in Surprise block yielding four unreplicated fire-age heterogeneity categories (Tables 1 & 2). Data used was species presence–absence on grids in the combined four 100 m² plots. Data were analysed using the permutational multivariate analysis of variance (PerMANOVA) with forest block (confounded with fire age and heterogeneity), vegetation unit, sample grid nested in block by vegetation unit, and year of sample (confounded with time since fire in Surprise block), as main effects (Anderson *et al.* 2008, Clarke & Gorley 2006). PerMANOVA is analogous to a conventional multivariate analysis of variance (MANOVA), where presence or absence of a species is treated as an individual attribute of a sample grid, but significance values in PerMANOVA are determined by randomisation resulting in Pseudo-*F* and P_{Perm} estimates. In contrast to conventional MANOVA, the only underlying assumption is that sample grids are interchangeable (i.e., they have the same species composition) if the null hypothesis is true (Anderson *et al.* 2008). For all PerMANOVA analyses, Type III sums of squares were used with unrestricted permutation of the raw data for 9999 permutations. Specifically, we tested the hypotheses that time since last fire (determined by the year of sampling for Surprise block), fire heterogeneity (forest block), and vegetation unit had no effect on the species assemblage. We analysed mosses, liverworts and lichens separately. Where significant main effects were detected, we conducted pairwise tests using PerMANOVA to identify which vegetation units, fire heterogeneity, or fire ages were significantly different.

Because the effects of fire heterogeneity and forest block were confounded we attempted to isolate forest block effects due to habitat substrates (both utilized and unutilized) using data from London and Surprise blocks collected in 2010. By 2010, 7.5 years after fire in Surprise, fire effects on substrate availability were assumed to be minimal, thus revealing forest block effects on substrate availability. Counts of substrate frequencies were normalized and a PerMANOVA was conducted on the Euclidean distance between grids for substrate composition to determine the effects vegetation unit and forest block (Anderson & Robinson 2003).

Where vegetation unit had a significant effect on the composition of assemblages we calculated the frequency of grids where each species was found in the combined forest (Collis and Lindesay) and Caldyanup vegetation

Table 1. Years when cryptogams sampled in relation to preceding fire regimes on London and Surprise forest blocks.

Forest block	Older pre-sample fires	Younger pre-sample fires	Sample 2005	Additional fires	Sample 2010
London	Spring fires at intervals of 6 to 9 years leaving unburnt patches	Spring 1994, Spring 2002, Autumn 2004, all leaving unburnt patches	Samples from a mosaic of fire ages	Autumn 2006, Summer 2008, both leaving unburnt patches	2005 grids resampled. Samples from a mosaic of fire ages
Surprise	Spring fires at intervals of 6 to 9 years leaving unburnt patches	Intense wildfire March (Autumn) 2003 leaving few if any unburnt patches	All samples taken from areas intensely burnt in March 2003	No further fires	2005 grids resampled. All samples taken from areas intensely burnt in March 2003

Table 2. Time since fire in the sampled grids and forest blocks. The design can be considered as a repeated measures design (the same grids sampled in 2005 and 2010), with fire-age heterogeneity confounded with forest block (London presented heterogeneity within and between measurement grids in fire age, and Surprise homogeneity of extensive and intensive wildfire).

Forest block	Vegetation unit	Fire ages within sample grids in sample year 2005		Fire ages within sample grids in sample year 2010	
		Replicate grid A	Replicate grid B	Replicate grid A	Replicate grid B
London	Collis	≥20	≥20, 3	≥25, 4.5	≥25, 8, 4.5
	Lindesay	≥20	3	≥25, 4.5, 2	4.5
	Caldyannup	3	3	8, 2	8, 2
Surprise east	Collis	2.5	2.5	7.5	7.5
	Lindesay	2.5	2.5	7.5	7.5
	Caldyannup	2.5	2.5	7.5	7.5
Surprise west	Collis	2.5	2.5	7.5	7.5
	Lindesay	2.5	2.5	7.5	7.5
	Caldyannup	2.5	2.5	7.5	7.5

units. The small size of the data set allowed Fisher's exact tests (1-tail) to be conducted on the raw presence-absence data to determine the independence of this categorization from vegetation unit. Indicator values were calculated (as per Turner *et al.* 2011 to overcome differences in sample sizes) for the vegetation categories of each species where significant dependence was detected.

We categorized the combined forest (Collis and Lindesay) vegetation units by the fire-age heterogeneity categories defined by forest block and year of sampling and determined indicator values. We selected grids on London where some area of age ≥ 20 years was present (6 sample grids: Table 2) and pooled the two years of data (2005 and 2010) from London into one fire-age category defined by having at least some area of age ≥ 20 years. Sparse replication rendered a similar analysis for Caldyanup vegetation unit as impractical.

RESULTS

Species richness

Sixty-seven species of cryptogams were recorded from all sampling grids within London and Surprise blocks

comprising 40 lichen, 20 moss, and seven liverwort species. More species of lichen were detected in Lindesay and Caldyanup vegetation units in 2010 than in 2005 (Table 3, Appendix).

We compared species richness of Surprise block (single fire age) with that of London block (mosaic of fire ages). Surprise east and west forest sub-blocks each contained a total of 10 species of lichen and bryophytes 2.5 years after the intense bushfire, which was about one-third of that found for the same sampling effort for the London mosaic containing fire ages of 3 and ≥20 years (Figure 3a). Fewer species were found on Surprise east and west in 2010, 7.5 years after the fire, than on London block sampled in 2010 with comparable sampling efforts (Figure 3a). At the sample grid scale, species richness increased in Surprise block between 2005 and 2010, whereas species richness per grid in London remained stable during that period (Figure 3b). Paired *t*-tests (1 tail) revealed significant differences between 2005 and 2010 in number of species per grid on Surprise east ($t_{(5)} = -14.16$, $P \geq 0.001$) and Surprise west ($t_{(5)} = -4.49$, $P = 0.003$), but not London ($t_{(5)} = -1.25$, $P = 0.13$). Within 7.5 years after fire in Surprise, average richness on grids was similar between London and Surprise blocks (Figure 3b).

Table 3. The number of lichen, moss and liverwort species for the three vegetation units Collis, Lindesay and Caldyanup from the 2005 and 2010 assessments.

	2005			2010			Total
	Collis	Lindesay	Caldyanup	Collis	Lindesay	Caldyanup	
Number of grids sampled	6	6	6	6	6	6	2 × 18
Lichen	17	8	8	18	17	16	40
Moss	10	9	6	11	11	7	20
Liverwort	5	3	4	4	4	4	7
Total	32	20	18	33	32	27	67

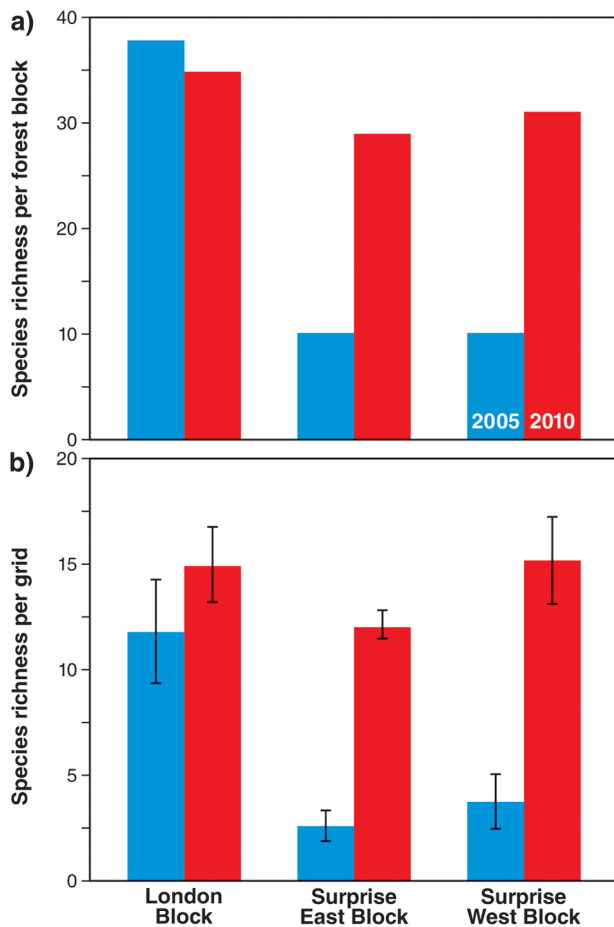


Figure 3. Comparisons of cryptogam species in London, Surprise east and Surprise west forest blocks for 2005 and 2010 measurements. Sampling intensity for each category in both sets of measurements were equivalent: **a)** Total number of cryptogam species (note that fire ages in London are mixed for both years); **b)** Average number of cryptogam species per sample grid. In London mosaics fire ages range from 3 to ≥ 20 in 2005 and 2 to ≥ 25 years in 2010. In Surprise, fire ages were 2.5 years in 2005 and 7.5 years in 2010. Thin bars indicate \pm standard error of the mean.

Substrate availability

By 2010 there was no significant difference between London and Surprise blocks in the composition of available habitat types. There were differences in habitat composition according to vegetation unit (Pseudo- $F = 5.65$, $P_{\text{Perm}} = 0.0001$) and each vegetation unit showed a unique composition of habitat types. Pairwise comparisons were as follows: Collis and Lindsay, $t = 1.618$, $P_{\text{Perm}} = 0.03$; Collis and Caldyanup, $t = 2.858$, $P_{\text{Perm}} = 0.0002$; Lindsay and Caldyanup, $t = 2.44$, $P_{\text{Perm}} = 0.0003$. Exposed rock is virtually absent within the Caldyanup units, whereas both bark cover and rock are more prevalent in Collis units than Caldyanup and Lindsay units. Wood, bark and charcoal were least abundant in Caldyanup units (Figure 4).

Vegetation and fire influences

Vegetation unit had a significant effect on assemblages of mosses, liverworts, and macrolichens (Table 4).

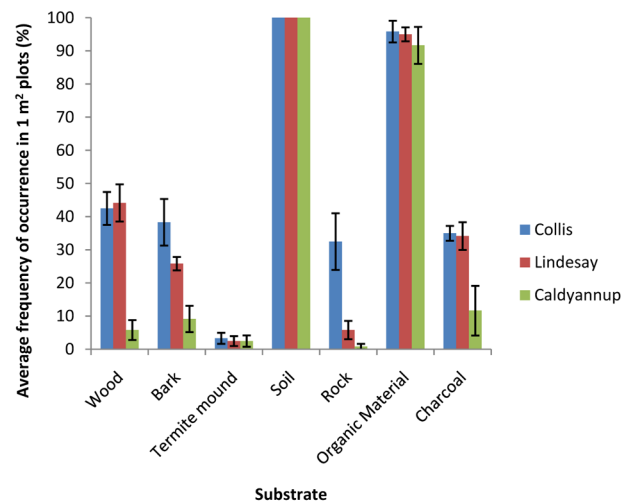


Figure 4. Habitat composition by vegetation unit for London and Surprise forest blocks in 2010. Thin bars indicate \pm standard error of the mean.

Differences between assemblages among vegetation types are summarised in Table 5. Collis and Lindsay vegetation units were indistinguishable from each other in species assemblage. Both Collis and Lindsay had different species assemblages of mosses, liverworts, and macrolichens to Caldyanup units (Table 5). Forest block (confounded with fire heterogeneity) had a significant effect on moss and macrolichen but not liverwort assemblages (Table 4). Year of sampling (delimiting fire age in Surprise block) had a significant effect on assemblages of all three life forms. Block by year interaction had a significant effect on assemblages of all three life forms. Differences in assemblages among forest block and year of sampling combinations which define the four fire treatments are summarised in Table 5. On Surprise block fire ages of 2.5 and 7.5 years consistently differed in species assemblages for all three life forms. On London block mosaic fire treatment categories London mosaic 2005 and London mosaic 2010 were indistinguishable in species assemblage for liverworts, but not mosses and lichens. Comparing London and Surprise blocks within sample years, fire treatment categories Surprise age 2.5 and London Mosaic 2005 were different in assemblages of mosses and lichens and indistinguishable for liverworts. Fire treatment categories Surprise age 7.5 and London mosaic 2010 were indistinguishable in species assemblage for mosses and lichens and different for liverworts.

Species assemblage predicts vegetation unit and fire age?

The frequencies of some species is dependent on the vegetation unit (Tables 6), fire age, or fire-age heterogeneity (Table 7). There were three species with a preference for Caldyanup and two species which preferred forest vegetation units (Table 6). Five species were early colonizers after the wildfire in the forest vegetation units (Table 7). Of these, the liverwort *Cephaloziella exiliflora* and the moss *Campylopus introflexus* had their greatest abundance on older seral stages. Seven

Table 4. Effects of forest block (London and Surprise, which is confounded with fire heterogeneity treatments), vegetation unit (Collis, Lindesay, and Caldyannup), sample grid (nested within forest block and vegetation unit), and year of measurement (2005 and 2010) on moss, liverwort, and macrolichen assemblages based on Bray-Curtis similarity matrices analysed by PerMANOVA. Degrees of freedom (df) define the effective rather than nominal sample sizes for effects and their interactions.

Effect	df	Mosses	Liverworts	Macrolichens
		Pseudo-F, P_{PERM}	Pseudo-F, P_{PERM}	Pseudo-F, P_{PERM}
Block	1	2.862, 0.03	3.611, 0.06	4.893, 0.005
Vegetation unit	2	3.528, 0.003	5.111, 0.009	2.684, 0.02
Block x Veg	1	2.023, 0.06	1.882, 0.17	1.752, 0.10
Grid(Block x Veg)	13	1.222, 0.26	2.232, 0.03	0.828, 0.72
Year	1	5.002, 0.003	9.506, 0.0009	21.459, 0.0001
Block x Year	1	5.172, 0.002	4.528, 0.02	5.342, 0.008
Veg x Year	2	0.522, 0.82	4.849, 0.006	1.502, 0.19
Block x Veg x Year	2	1.896, 0.09	Excluded	1.115, 0.35
Residual	11, 13, 11	-	-	-

Table 5. Pairwise comparisons of assemblages based on a Bray-Curtis similarity matrices analysed by pairwise PerMANOVA with forest block (London and Surprise, which is confounded with fire heterogeneity treatments), vegetation unit (Collis, Lindesay, and Caldyannup), sample grid (nested within forest block and vegetation unit), and year of measurement (2005 and 2010) as effects.

Assemblages compared	Mosses	Liverworts	Macrolichens
	t, P_{PERM}	t, P_{PERM}	t, P_{PERM}
Collis, Lindesay	1.329, 0.15	0.653, 0.65	1.208, 0.22
Collis, Caldyannup	2.332, 0.004	3.033, 0.005	2.029, 0.01
Lindesay, Caldyannup	2.141, 0.003	2.262, 0.03	1.496, 0.03
London 2005 (Multiple age mosaic), London Mosaic 2010 (Multiple age mosaic)	1.766, 0.04	1.795, 0.14	1.676, 0.02
London Mosaic 2005 (Multiple age mosaic), Surprise 2005 (Age 2.5)	2.369, 0.004	1.633, 0.09	3.104, 0.002
London Mosaic 2010 (Multiple age mosaic), Surprise 2010 (Age 7.5)	0.381, 0.92	2.566, 0.009	0.757, 0.77
Surprise 2005 (Age 2.5), Surprise 2010 (Age 7.5)	2.990, 0.0004	3.127, 0.002	6.478, 0.0001

Table 6. Indicator species for Caldyannup and forest (Collis and Lindesay) vegetation units. Western Australian Herbarium (PERTH) specimen numbers are provided for vouchers of unnamed or unidentified species.

Species	Life form	Frequency of grids with occurrence (%)		Fishers exact probability of observed or more extreme (1-tail)	Indicator value	
		Caldyannup	Forest		Caldyannup	Forest
		N = 12	N = 24			
<i>Campylopus bicolor</i>	Moss	83	46	0.034	74	41
<i>Geobelobryum unguiculatum</i>	Liverwort	67	17	0.005	73	18
<i>Leptogium</i> sp. (PERTH 06896111)	Macrolichen	50	13	0.022	65	16
<i>Sematophyllum subhumile</i> var. <i>contiguum</i>	Moss	0	33	0.024	0	67
<i>Cephaloziella exiliflora</i>	Liverwort	17	67	0.006	18	73

Table 7. Frequency of early colonizers of forest (Collis and Lindesay) vegetation units on Surprise block, and fire-age indicator species within Collis and Lindesay units. London grids include some fire areas ≥ 20 years as well as areas ranging from 2 to 8 years since fire. Early colonizers marked ^a, species most strongly indicative of fire age 7.5 years marked ^b, and species most strongly indicative of sites containing some fire areas ≥ 20 years marked ^c. Western Australian Herbarium (PERTH) specimen numbers are provided for vouchers of unnamed or unidentified species.

Species	Life form	Frequency of Collis and Lindesay grids with occurrence (%)			Fishers exact probability of observed or more extreme (2 tail, $\alpha = 0.05$)	Indicator value		
		Age 2.5 N = 8	Age 7.5 N = 8	London grids which include some area of age ≥ 20 N = 6		Age 2.5	Age 7.5	London with some area of age ≥ 20
<i>Funaria hygrometrica</i> ^a	Moss	100	100	83	ns	–	–	–
<i>Campylopus bicolor</i> ^a	Moss	25	63	67	ns	–	–	–
<i>Barbula calycina</i> ^a	Moss	25	75	50	ns	–	–	–
<i>Cephaloziella exiliflora</i> ^a	Liverwort	13	100	100	0.0002	9	74	74
<i>Campylopus introflexus</i> ^a	Moss	13	100	100	0.0002	9	74	74
<i>Thysanothecium scutellatum</i>	Macrolichen	0	100	100	0.000006	0	75	75
<i>Cladia aggregata</i>	Macrolichen	0	100	83	0.00002	0	77	64
<i>Cladia schizopora</i>	Macrolichen	0	75	50	0.008	0	68	45
“Grey green slick” PERTH 06320082 ^b	Macrolichen	0	63	17	0.011	0	71	19
<i>Diploschistes scruposus</i> ^b	Macrolichen	0	88	33	0.0008	0	80	30
<i>Hypocenomyce foveata</i>	Macrolichen	0	63	67	0.011	0	55	59
<i>Cladonia rigida</i> ^c	Macrolichen	0	63	100	0.0004	0	50	81

macrolichen species that are relatively common on older seral stages remained absent 2.5 years after fire. The unidentified lichen “Grey green slick” and *Diploschistes scruposus* had high indicator values for a fire age of 7.5 years whereas *Cladonia rigida* had a high indicator value for grids containing some areas with a fire age ≥ 20 years.

Thirty-three percent of the total cryptogam flora collected was only from London block, which includes areas of mixed fire ages and long unburned substrates. Nine percent of the total flora was found only on Surprise block areas burnt 7.5 years beforehand, and six percent of the total flora was exclusive to Surprise block in areas with a fire age of 2.5 years.

DISCUSSION

Fire age affects species richness and composition

Vascular and woody vegetation composition in the study area is known have a long-term resilience to a variety of fire histories (Wittkuhn *et al.* 2011, Pekin *et al.* 2012b). However, within these habitats severe and extensive wildfires have reduced cryptogam species richness and altered species assemblages of mosses and lichens compared to mosaic fire areas. Changes in species composition and an increase in species richness with time since wildfire are consistent with outcomes reported elsewhere for both eucalypt (Pharo & Beattie 1997, Pharo *et al.* 2013, Kantvilas *et al.* 2015) and other forests (Esposito *et al.* 1999, Ray *et al.* 2015).

Time since fire is likely to contribute to species turnover from early to late-successional species due to

changes in habitat suitability and differences among species in habitat requirements (Duncan & Dalton 1982, Esposito *et al.* 1999, Turner *et al.* 2011, Kantvilas & Jarman 2012). This has different consequences where there have been many fire ages rather than a single fire event. The frequent introduction of fire to London forest maintained a range of post-fire succession stages with variations in fire intensity, ages and spatial scales within grids (metres and tens of metres), as well as between grids (hundreds of metres to kilometres). Whereas the composition of liverwort assemblages did not change over time in the mosaics, likely due to the range of refuge habitats maintained (Hylander & Johnson 2010), moss and macrolichen assemblages in the shifting mosaics did change. We have insufficient data to explore the mechanism for this observed difference; however, the development of lichen communities is not neutral with respect to habitat age (Gjerde *et al.* 2012, Nascimbene *et al.* 2017), and the proportions of different fire ages on sample grids within the mosaic varied between 2005 and 2010.

Following the single high-intensity fire event in Surprise block, species showed a successional trend from one seral stage to the next. Early colonists were followed by a period when early and late-successional species tended to coexist. At 7.5 years post-fire in Surprise block, assemblages of mosses and macrolichens but not liverworts were similar to those in London block where there were fire ages ranging from two to ≥ 25 years. Cranfield *et al.* (2011) found sites subjected to controlled fuel reduction fires and timber harvesting in comparable jarrah forest sites had low cryptogam species richness at

one to four years after fire. Richness gradually increased until about 10 years after fire. Beyond 10 years after fires, species richness reduced again until species richness was lower than sites only one to four years after fire. They attributed this later reduction of species richness to ground-inhabiting species being covered by leaf litter, and the subsequent loss of substrates suitable for primary colonizers. Both processes affect the availability of suitable habitat with time since fire. The return within 7.5 years of species richness after the severe fire in Surprise block to levels approaching those of the mosaic with ages two to ≥ 25 years might indicate that dispersal or habitat limitation are not operating for most species in the jarrah forest cryptogam flora. We consider the disturbance due to light and selective timber harvesting in the 1960s in the study area was probably small compared to the effects of repeated fire cycles between then and sampling in 2005 and 2010.

London fire mosaic and the 'storage' effect

Responses of cryptogam community composition to fire age in boreal forests in North America are detectable decades and centuries beyond the fire-age range of the present study, whereas species richness in those same communities remained stable in a space-for-time study (Boudreault *et al.* 2002). Distributions of slowly dispersing cryptogams in contemporary landscapes may reflect historic linkages to source populations of propagules rather than contemporary linkages, thereby concealing an extinction debt (Johansson *et al.* 2013). The imperative to preserve cryptogam species diversity by maintaining a range of fire ages linked to landscape level suggested by Boudreault *et al.* (2002) is equally applicable to jarrah forest where fire return intervals are shorter. Long fire return intervals in jarrah forest allow build-up of fuels permitting intense and extensive fire events due to the inevitability of ignition and difficulties of fire suppression with heavy fuel loads (McCaw 2013). In that case, the 'storage effect', whereby long unburned patches accumulate the most species or provide unique habitats for some species (Roxburgh *et al.* 2004, Fenton and Bergeron 2008), becomes tenuous.

The consequences of the intense bushfire in Surprise forest was immolation of cryptogam biomass, loss of organic habitat substrates for cryptogams, and loss of habitat from spalling of rock surfaces, all leading to a likely protracted loss of some species from assemblages (Kantvilas & Jarman 2012). The London forest block mosaic exhibited no loss in cryptogam richness per grid over time, was richest when comparing equivalent sampling intensity, and maintained the majority of species exclusive to any fire-age treatment. The conservation of the variety and availability of substrates, including newly available and particularly those long undisturbed by fire such as retained bark and the unburnt surfaces of large coarse woody debris, appeared to be the mechanism for maximizing cryptogam diversity at the forest block scale. We suggest that the fire-age mosaic effect on cryptogam species richness and assemblages within London block is a practical and successful demonstration of how to conserve long unburned patches and maximize cryptogam richness at the forest block scale without elevating the risk of high-intensity fire.

Species assemblage predicts fire age

The presence of some species is dependent on fire-age heterogeneity or vegetation type. Landscape-scale prioritization of cryptogam species conservation based on a mosaic of fire ages within vegetation units has the ability to conserve cryptogam species at risk of reduction at a local and landscape scale. Many species were seldom collected and hence of little predictive value in this study. These species may be of highest concern for fire managers because their scarcity in regional sources of propagules makes them vulnerable to their loss from the landscape where fires are frequent, or severe and extensive (See also Table 3 in Hylander & Johnson 2010). One species, *Cladonia rigida*, was common to grids containing burnt areas ≥ 20 years old, although this species was also present on some grids by 7.5 years after the fire. For many species, recolonization rate compared to fire frequency remains unknown (Wills *et al.* in press), requiring further research at the species and landscape level.

The effects of vegetation type

Cryptogams have the ability to colonize a wide range of substrates. Whereas some are substrate specific, many are able to share a range of substrates (Turner & Pharo 2005, Pharo *et al.* 2013). There is considerable variation in the ability of substrates provided by vascular and woody plants to host cryptogams (Pharo *et al.* 2013). Substrate availability was variable in the London and Surprise blocks as each of the vegetation units had a unique combination of substrates. Caldyanup vegetation unit had the fewest wood, bark, charcoal and rock substrates, which may predispose this unit to be the least rich in cryptogams. Caldyanup grids also differed in moss, liverwort, and lichen assemblages from Lindesay and Collis units. Elsewhere, vegetation type differentiates the community composition of cryptogams (e.g., McMullan-Fisher *et al.* 2010, Ardelean *et al.* 2015). However, other factors potentially correlate with vegetation type (humidity, edaphic characteristics, and substrate availability) and may contribute to substrate use and species assemblages. From our limited data, we were unable to identify any mechanism that allows vegetation type to affect species assemblage and richness.

CONCLUSIONS

In the studied jarrah forest frequent introduction of fire maintained habitats with a mixture of fire ages at both local and landscape scales. This, in turn, maintained cryptogam diversity at those scales. Intense and extensive fire jeopardised some species, resulting in their absence more than 7.5 years post-fire. The recovery of cryptogams is favoured by low-intensity fire as this produces a mosaic of small patches including unburnt areas or in which the heat intensity is low enough to be non-lethal to in-situ propagules.

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APPENDIX

Species of bryophytes and lichens collected from London and Surprise forest blocks in 2005 and 2010 with number of sample grids where they were present. Western Australian Herbarium (PERTH) specimen numbers are provided for vouchers of unnamed or unidentified species.

Taxon	Life form	London 2005 and 2010	Surprise 2005	Surprise 2010	Total number of samples where present N = 36
		Fire age mosaics N = 12	Fire age 2.5 N = 12	Fire age 7.5 N = 12	
<i>Funaria hygrometrica</i>	Moss	9	11	12	32
<i>Campylopus introflexus</i>	Moss	10	3	12	25
<i>Campylopus bicolor</i>	Moss	8	4	9	21
<i>Barbula calycina</i>	Moss	4	3	7	14
<i>Othodontium lineare</i>	Moss	3	0	5	8
<i>Sematophyllum subhumile</i> var. <i>contiguum</i>	Moss	4	0	4	8
<i>Rosulabryum capillare</i>	Moss	3	0	3	6
<i>Fissidens tenellus</i> var. <i>tenellus</i>	Moss	2	0	3	5
<i>Hypnum cupressiforme</i>	Moss	1	0	3	4
<i>Ceratodon purpureus</i> subsp. <i>convolutus</i>	Moss	1	1	0	2
<i>Dicranella dietrichiae</i>	Moss	2	0	0	2
<i>Didymodon torquatus</i>	Moss	2	0	0	2
<i>Pleurophascum occidentale</i>	Moss	2	0	0	2
<i>Triquetrella papillata</i>	Moss	0	0	2	2
<i>Dicranoloma billarderi</i>	Moss	0	1	0	1
<i>Rosulabryum campylothecium</i>	Moss	1	0	0	1
<i>Sematophyllum homomallum</i>	Moss	1	0	0	1
<i>Syntrichia antarctica</i>	Moss	1	0	0	1
<i>Thuidopsis sparsa</i>	Moss	0	0	1	1
<i>Zygodon menziesii</i>	Moss	0	1	0	1
<i>Cephaloziella exiliflora</i>	Liverwort	7	1	10	18
<i>Geobelobryum unguiculatum</i>	Liverwort	5	4	3	12
<i>Lethocolea pansa</i>	Liverwort	7	3	1	11
<i>Chiloscyphus semiteres</i>	Liverwort	3	0	3	6
<i>Kurzia compacta</i>	Liverwort	3	2	0	5
<i>Astrella drummonii</i>	Liverwort	0	1	0	1
<i>Riccardia crassa</i>	Liverwort	1	0	0	1
<i>Cladia aggregata</i>	Lichen	9	0	11	20
<i>Thysanothecium scutellatum</i>	Lichen	8	0	12	20
<i>Cladonia rigida</i>	Lichen	7	0	8	15
<i>Cladia schizopora</i>	Lichen	5	0	9	14
<i>Diploschistes scruposus</i>	Lichen	2	0	8	10
<i>Hypocenomyce foveata</i>	Lichen	4	0	6	10
<i>Leptogium</i> sp. (PERTH 06896111)	Lichen	3	0	6	9
<i>Usnea inermis</i>	Lichen	4	0	3	7
“Grey green slick” PERTH 06320082	Lichen	2	0	5	7
<i>Imshaugia aleurites</i>	Lichen	3	0	3	6
<i>Ochrolechia subpalleescens</i>	Lichen	4	1	0	5
<i>Cladonia krempelhuberi</i>	Lichen	2	0	3	5
<i>Cladonia</i> sp. London	Lichen	2	0	1	3
<i>Ramboldia stuartii</i>	Lichen	2	0	1	3
<i>Pannoparmelia wilsonii</i>	Lichen	1	1	1	3
<i>Cladonia sulcata</i>	Lichen	1	0	2	3
<i>Buellia dissa</i>	Lichen	2	0	0	2
<i>Hypocenomyce scalaris</i>	Lichen	2	0	0	2
<i>Rhizocarpon</i> sp. grey (PERTH 06324452)	Lichen	2	0	0	2
<i>Notocladonia cochleata</i>	Lichen	1	1	0	2
<i>Glonium circumserpens</i>	Lichen	1	0	1	2

Taxon	Life form	London 2005 and 2010	Surprise 2005	Surprise 2010	Total number of samples where present N = 36
		Fire age mosaics N = 12	Fire age 2.5 N = 12	Fire age 7.5 N = 12	
<i>Ochrolechia</i> sp. tan doughnuts (PERTH 06319300)	Lichen	1	0	1	2
<i>Ochrolechia subrhodotropa</i>	Lichen	1	0	1	2
<i>Amandinea punctata</i>	Lichen	1	0	0	1
<i>Calicium abietinum</i>	Lichen	1	0	0	1
<i>Cladia inflata</i>	Lichen	1	0	0	1
<i>Cladonia cervicornis</i> var. <i>verticellata</i>	Lichen	1	0	0	1
<i>Cladonia ochrochlora</i>	Lichen	1	0	0	1
<i>Cladonia scabriuscula</i>	Lichen	1	0	0	1
<i>Dictyographa</i> sp. brown lips (PERTH 06322301)	Lichen	1	0	0	1
<i>Diploschistes euganeus</i>	Lichen	1	0	0	1
<i>Diploschistes sticticus</i>	Lichen	1	0	0	1
<i>Halegrapha mucronata</i>	Lichen	1	0	0	1
<i>Hypogymnia pulverata</i>	Lichen	1	0	0	1
<i>Pannaria elixii</i>	Lichen	1	0	0	1
<i>Hypogymnia subphysodes</i> var. <i>subphysodes</i>	Lichen	0	1	0	1
<i>Ainoa mooreana</i>	Lichen	0	0	1	1
<i>Caloplaca marina</i>	Lichen	0	0	1	1
<i>Cladonia</i> sp. golden coral (PERTH 07320388)	Lichen	0	0	1	1
<i>Tephromela alectoronica</i>	Lichen	0	0	1	1