

RESEARCH ARTICLE

CRYPTOGAM RECOLONIZATION AFTER WILDFIRE: LEADERS AND LAGGARDS IN ASSEMBLAGES?

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ABSTRACT

Cryptogams (restricted here to mosses, liverworts, and lichens) have no particular fire-adapted survival strategies and rely on airborne spores or propagules to disperse to new habitats. Following fire, recolonization by cryptogams relies on the propagule sources in regional or local remnant unburned areas and for suitable conditions in the burned area. We used species occurrences on a fire-age (i.e., time since burn) mosaic in jarrah (*Eucalyptus marginata* Donn ex Sm.) forest near Walpole in southwestern Australia to predict recolonization of cryptogam species in an adjacent forest block. The frequency of a species' occurrence in a fire mosaic predicted the frequency of occurrence in the adjacent forest block that was subjected to an intense wildfire 7.5 years previously. The residuals from a 1:1 prediction were normally distributed when the total lichen and bryophyte flora were considered. Frequencies of species occurrence in the mosaic of fire ages and after recolonization of the wildfire were similar. We interpreted this to indicate that the composition of regional sources of propagules dominated assembly of cryptogam communities after severe fire, rather than community assembly resulting from filtering of species by dispersal ability or

RESUMEN

Las criptógamas (restringidas aquí a algunos musgos, hepáticas y líquenes) no tienen estrategias de supervivencia y adaptación al fuego particulares, dependiendo de esporas liberadas en el aire o propágulos para dispersarse en nuevos hábitats. Después de un fuego, la recolonización con criptógamas depende de las fuentes de propágulos en áreas remanentes sin quemar (locales o regionales) y de condiciones favorables en áreas quemadas. Utilizamos la ocurrencia de especies en un mosaico de edades de fuego (i.e., tiempo pasado desde la quema) en bosques de jarrah (*Eucalyptus marginata* Donn ex Sm.) cerca de Walpole en el sudoeste de Australia, para predecir la recolonización de especies criptógamas en un bloque de bosque adyacente. La frecuencia de la ocurrencia de una especie en un mosaico de fuego predijo la frecuencia de ocurrencia en un bloque adyacente de bosque que fue afectado por un fuego intenso 7,5 años antes. Los residuales de una predicción 1:1 presentaron una distribución normal cuando se consideraron el total de los líquenes y de la flora briófitas. Las frecuencias de ocurrencia de especies en el mosaico de edades de fuego y en el de la recolonización después del fuego fueron similares. Interpretamos esto para indicar que la composición de fuentes de propágulos regionales dominaron el ensamble de comunidades de criptógamas luego de fuegos severos, más que el ensamble de comunidades resultantes que dominan por su habilidad de dispersión o de há-

habitat suitability. We inferred that ecological requirements favored or disfavored recolonization by some components of the cryptogam flora. The residuals from the predicted frequency of colonizing species of liverworts positively correlated with the number of types of organic substrate they colonized. Lichens and mosses tended to have different preferences for substrates. The fire mosaic and the wildfire block 7.5 years after fire had similar compositions of substrates, so this could not account for differences in species frequency between the fire mosaic and the wildfire block. Differences at phylum level and substrate preferences affect the ability some species to recolonize after fire.

Wildfires have the potential to denude areas of cryptogam species. Regional and landscape-scale mosaics of fire-ages reduce fuel biomass to mitigate intensity and spread of fires while retaining sources of cryptogam propagules and allowing opportunities for recolonization after fires.

bitats adecuados. Inferimos que los requerimientos ecológicos favorecen o no la recolonización, basándonos en algunos componentes de la flora criptógama. Los residuales de las especies colonizadoras de hepáticas se correlacionaron positivamente con la cantidad de tipos de sustratos orgánicos que las mismas colonizaron. Los líquenes y musgos tendieron a tener diferentes preferencias para los sustratos. El mosaico de fuego y el bloque de incendios de 7,5 años luego del fuego tuvieron composiciones de sustratos similares, por lo que esto no puede tenerse en cuenta para diferenciar la frecuencia de especies entre el mosaico de fuego y el bloque de incendios. Diferencias a nivel de tipo biológico y preferencias de sustrato afectan la habilidad de algunas especies para recolonizar después del fuego.

Los incendios naturales tienen el potencial de denudar áreas de especies criptógamas. Mosaicos de diferentes edades de incendios a nivel regional y de paisaje reducen la biomasa combustible para mitigar la intensidad y la propagación de fuegos, mientras que retienen fuentes de propágulos de criptógamas y crean oportunidades para su recolonización después del fuego.

Keywords: assemblages, Australia, *Eucalyptus marginata*, fire-age, lichens, liverworts, mosaic, mosses, recolonization, substrates, time since burn

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INTRODUCTION

How a eucalypt forest ecosystem responds to disturbance depends on the fundamental processes of dispersal, colonization, and establishment of biota (Mittelbach and Schemske 2015). A fire has the potential to remove or modify the condition of the habitat and to impact the bryophyte (mosses and liverworts) and lichen flora (collectively termed cryptog-

ams) through direct exposure of the organisms to flame and heat. Cryptogams have no particular fire-adapted survival strategies and rely on airborne spores or propagules to disperse to new habitat (e.g., Flø and Hågvar 2013, Nascimbene *et al.* 2017). The bank of bryophyte diaspores in the soil, originating from fallout or *in situ* production, represents a source of latent propagules awaiting suitable conditions for germination and growth (Biggs and Wit-

tkuhn 2006, Iglesias *et al.* 2015, Glime 2017). Although bryophyte diaspores in the soil may survive fire (Smith *et al.* 2014), the extent of this strategy in eucalypt forest is unknown. There is some evidence that cryptogam spores and propagules can be carried by animals to habitats preferred by cryptogams (Rudolphi 2009, Zona 2013, Lewis *et al.* 2014, Barbé *et al.* 2016a). Cryptogam zoochory in eucalypt forest is largely unknown. Following fire, recolonization by cryptogams relies on regional sources of propagules, and sources in local remnant unburned areas (Hutsemekers *et al.* 2008; Baker *et al.* 2013; Gjerde *et al.* 2015, Barbé *et al.* 2016b, 2017). There also needs to be suitable conditions in the burned area to allow recolonization (Werth *et al.* 2006, Smith and Stark 2014, Singh *et al.* 2015).

The severity of impact and recovery time from fire is linked to fire intensity and scale (Pharo *et al.* 2013, Barbé *et al.* 2016b). Low-intensity fires leave unburned patches in which cryptogam species remain present (Hylander and Johnson 2010, Pharo *et al.* 2013, Barbé *et al.* 2017). Low-intensity fires potentially provide both unaffected and new habitat in which species that prefer any early to late successional periods are accommodated. Intense fires in eucalypt forests in which the crown is consumed leave burned areas denuded of cryptogam species (Pharo *et al.* 2013). In that case, the extent to which habitat and dispersal limitation governs recovery of cryptogam assemblages after an intense fire is not clear.

Several mechanisms can lead to differences in colonization rates between species. Cryptogams vary between species in their propensity for sexual versus asexual reproduction and this can affect the potential for long-distance versus short-distance dispersal through the differences in dispersal ability of sexual and asexual or vegetative propagules (Singh *et al.* 2015, Laenen *et al.* 2016, Nascimbene *et al.* 2017). Species-specific characteristics of propagule size and ornamentation are also im-

portant modifiers of airborne dispersal ability (Virtanen 2014, Zanatta *et al.* 2016). While some cryptogams are suited to conditions immediately after fire (Duncan and Dalton 1982, Ryömä and Laaka-Lindberg 2005), suitable conditions for many species are likely to occur only after the vascular flora has at least partially recovered (Turner and Pharo 2005, Turner *et al.* 2011, Kantvilas and Jarman 2012).

Different species have different responses to post-fire conditions. Patch mosaic burning is postulated to promote biodiversity by providing a range of habitat patches with different fire histories and habitat qualities at a given scale (Parr and Andersen 2006, Burrows 2008, Stein *et al.* 2014). There is a potential to maximize the geometric mean abundance for the maximum number of species across taxa by selecting an optimal proportion of fire-ages at a landscape scale (Di Stefano *et al.* 2013), although it is probably difficult for managers of fire to achieve this in a dynamic mosaic. Fire-prone landscapes can be considered as dynamic mosaics, at various scales, of more or less temporary refuges that act as sources of propagules and stepping stones for colonizing habitat denuded of species after fires (Robinson *et al.* 2013). The rate at which species that are vulnerable to fire can move through the dynamic landscape is critical to their survival.

Local abundance of organisms is often highly correlated with regional abundance (e.g., Löbel *et al.* 2006). The relationship may be causal, in which the abundance of propagules reaching and colonizing a site is related to the abundance of regional propagule sources (Lönnel *et al.* 2014). The relationship may also depend on local conditions that support particular community compositions as influenced by a hierarchy of regional to local conditions replicated across landscapes (Medina *et al.* 2014).

In our study, we used least squares regression and species occurrences on a fire-age (i.e., time since burn) mosaic generated in jarrah (*Eucalyptus marginata* Donn ex Sm.) forest

near Walpole in southwestern Australia (Burrows and Middleton 2016) to predict recolonization of cryptogam species in an adjacent forest block 7.5 years after a severe and extensive wildfire. Where there are dispersal or habitat filters operating between source populations and recolonization of the burned areas on both forest blocks, we might expect significant kurtosis or skewness in the distribution of residuals arising from the regression using species abundances on the mosaic as the predictor of colonization after the wildfire. This could arise, in part, due to the presence of populations on the mosaic block unaffected by fire and not subject to dispersal and establishment constraints. We tested three hypotheses: (1) that deviation from prediction is related to the number of substrates colonized by a species; (2) that deviation from normality in the relationship between species occurrences on the two forest blocks arises from phylum-level differences in substrate preferences; and (3) that there are different responses to the same substrates at the phylum level.

METHODS

Study Area

The study was conducted in London and Surprise forest blocks 30 km northeast of Walpole in southwestern Australia (Figure 1). 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 material (Churchward *et al.* 1988). Landforms are sharply delineated and form catenae of the well-drained ridge and hillslope units (named Collis and Lindsay, respectively) and poorly drained swampy slopes, plains, and drainage floors named Caldyanup (Churchward *et al.*

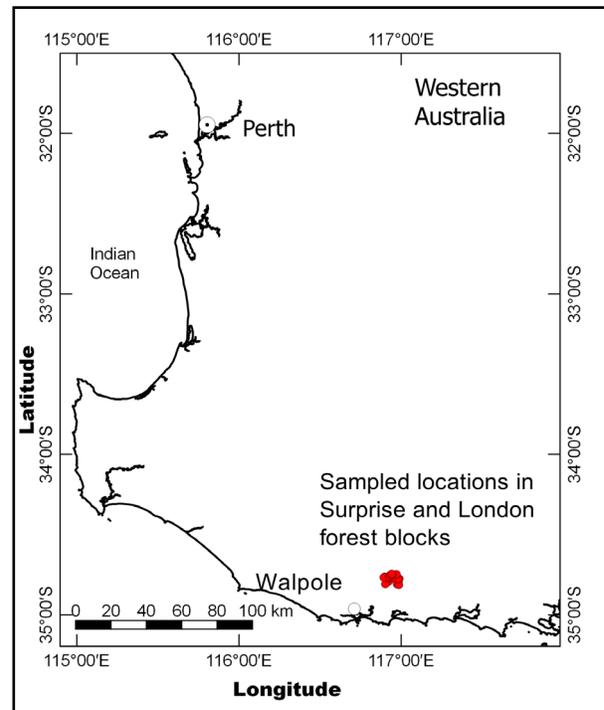


Figure 1. Location of study area at London and Surprise forest blocks, southwest Western Australia.

1988; Mattiske and Havel 1998, 2000; Figure 2). Vegetation on the Collis and Lindsay landform units is mostly comprised of open eucalypt forests to 30 m, dominated by jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla* [Lindl.] K.D.Hill & L.A.S. Johnson), with a dense shrubby understory to 2 m tall. Vegetation associated with the Caldyanup unit is comprised of a variety of reed-dominated seasonal wetlands and heathlands of myrtaceous shrubs to 2 m.

Fire Treatments

Investigation of cryptogam recolonization after fires was part of a broader fire ecology study (Burrows and Wardell-Johnson 2004, Burrows and Middleton 2016) that opportunistically used the contrasting fire regimes of the adjacent London and Surprise forest blocks. The fire history of the two forest blocks was well understood. Forest blocks of about 5000 ha to 8000 ha are the usual spatial unit of fire management in Western Australian forests. A

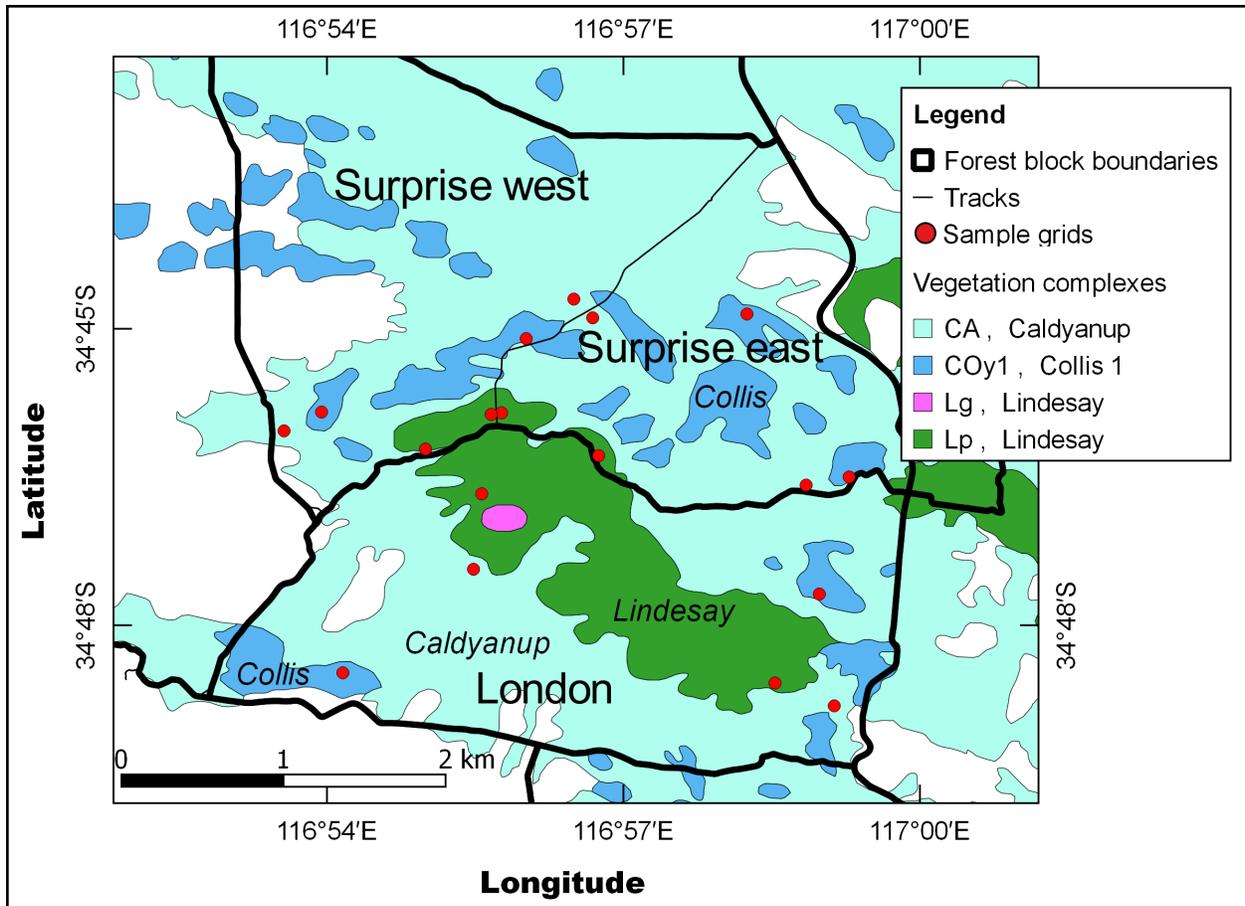


Figure 2. The spatial relationship between Surprise east and Surprise west sub-blocks, and London forest block. White areas are vegetation units not sampled. Names of the particular Caldyanup, Collis and Lindesay vegetation units sampled are specified in the legend according to nomenclature of Mattiske and Havel (1998).

natural wildfire completely burned Surprise forest block (~6700 ha) in 2003, while London forest block (~5000 ha) was burned by managed fuel reduction fires in 1994 and 2002. Surprise and London forest blocks differed in their initial and subsequently managed fire regimes. London burned in a managed low-intensity fire in spring 1994, prior to the study. Further prescribed fire was introduced into the London block about every three years over the period 2002 to 2012 in an attempt to create a fine-scale mosaic of patches of vegetation at different ages (seral stages). By 2010, patches of vegetation from a few to several hundred hectares ranged from relatively recently burned to long unburned (Burrows and Middleton 2016). Heterogeneity in fire-ages oc-

curred at scales within sample grids (meters to tens of meters) and between sample grids (hundreds of meters to kilometers). Thus, sampling London block in spring 2005 and spring 2010 effectively sampled different fire-age mosaic configurations.

Surprise forest block, which adjoins London to the north, burned in a single fire event by an intense wildfire in March 2003 (Wittkuhn and Hamilton 2010). The same fire consumed forest blocks to the west, north, and east. The intensity of the 2003 fire caused spalling of exposed granite and complete combustion of crown foliage. No further fire occurred in Surprise forest block during the measurement period of this study.

Fires on London block prior to 1994 occurred in spring at intervals of six to nine years (Wittkuhn and Hamilton 2010). Fires on Surprise block previous to 2003 occurred mostly in spring at intervals of six to nine years. Wildfires at an interval of fewer than five years burned two areas of Surprise, affecting only one Lindesay grid prior to the March 2003 fire (Wittkuhn and Hamilton 2010).

Sample Design

We established 18 2 ha ($200\text{ m} \times 100\text{ m}$) grids for sampling multiple taxa (McCaw *et al.* 2011) in 2005 in the three major land systems described above in both London (6 grids: 3 vegetation units \times 2 replicate grids) and Surprise blocks (Figure 2). We divided Surprise block into Surprise east and Surprise west sub-blocks to accommodate planned fire regimes imposed later than the present study (2×6 grids: 2 sub-blocks \times 3 vegetation units \times 2 replicate grids). The initial placement of grids targeted each of the three main vegetation units (Collis, Lindesay, and Caldyanup) within areas of at least 10 ha, and maximum fire-age contrasts within the London forest block. While the vegetation units were not of equal extent in the two forest blocks (Figure 2), each vegetation unit was equally represented in samples from London forest block and Surprise east and Surprise west sub-blocks.

Cryptogam Samples

Previous experiences of monitoring lichens and bryophytes in jarrah forest (Cranfield *et al.* 2011) guided the sampling intensity adopted. We established four plots of 50 m long \times 2 m wide (100 m^2), 50 m apart around the perimeter of the one-hectare central part of the grid (Figure 3). A single assessor (R. Cranfield, Manjimup Research Centre, Western Australia, Australia) noted the presence or absence of each species within each grid in the combined plot area within grids. We reas-

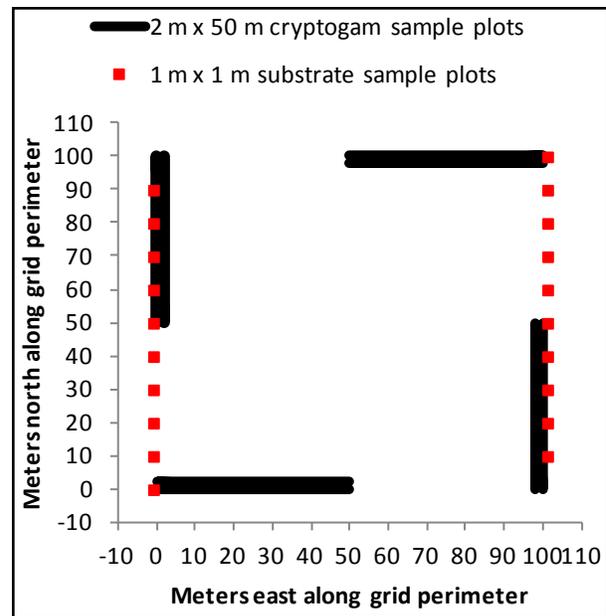


Figure 3. Arrangement of plots within central 1 ha of sample grids. Cryptogams were sampled for presence-absence in the combined area of four $2\text{ m} \times 50\text{ m}$ plots on each grid. Substrates were sampled for frequency of $1\text{ m} \times 1\text{ m}$ plots on which they occurred out of 20 plots on each grid. Plots were so dispersed to minimize disturbance from concurrent sampling on the grids for other biota.

sessed the same grids in 2010 the same way. New or unknown species were collected for further investigation and identification. A conservative approach to field identification was taken; vouchers were collected and later identified in the laboratory against voucher specimens, specimens held in the Western Australian Herbarium (PERTH in Perth, Australia), and taxonomic literature. Literature consulted for identifying species including the following primary texts: Catcheside (1980), Buck *et al.* (2002), and McCarthy (2006) for mosses; Scott (1985) and Glenny and Malcolm (2005) for liverworts; and George (1992), Grgurinovic (1994), Lumbsch *et al.* (2001), McCarthy (2001), McCarthy and Malcolm (2004), McCarthy and Mallett (2004), and McCarthy (2009) for macro-lichens. Vouchers of all collected species were lodged in the Western Australian Herbarium, Perth, Australia.

Frequency of Substrates

Twenty plots of 1 m² were established at intervals of 10 m along two sides of the central hectare of each grid (Figure 3) in 2010 and the presence or absence of habitat substrates on each plot recorded. We assessed wood (uncharred wood surfaces), bark (uncharred bark surfaces), soil, stone, organic matter (uncharred organic matter other than wood or bark), and charcoal. The frequency of substrates on a sample grid was approximated as the frequency of plots on the grid in which a substrate occurred.

Species Richness

We tallied the number of species from all grids to derive the total species richness of combined London and Surprise blocks. We tallied the number of species from London and Surprise east and Surprise west sub-blocks separately and for each year to derive the species richness of each forest block or sub-block for each year. We tallied numbers of species within grids, within years, and within forest blocks and calculated average richness per sample grid for each forest block and year.

Analysis

We calculated the species frequency of occurrence for the London mosaic from 2005 and 2010 data (2 years × 6 grids), and for Surprise from 2010 data for only 7.5 yr after fire

(1 year × 12 grids). Assumptions underlying the use of London block as a contributor and predictor are developed below. We assumed a local and regional structure of propagule sources available to the forest blocks at the landscape scale (Table 1). We assumed that the same regional source of propagules was common to both forest blocks. (A common regional source would contribute to a correlation between London and Surprise in the frequency of species occurrences.) Making no assumption of dependence, we tested for correlation in the frequency of species occurrence between London and Surprise blocks. We then assumed that London block was one of, but not the only, source area for propagules for Surprise block. We assumed asymmetry in dispersal between the two forest blocks due to the denudation of Surprise by the wildfire and retention of unburned source areas within London (allowing assumption of the partial dependence of frequency in Surprise on frequency in London with London as a source of propagules for Surprise). Note that propagules from London mosaics in both 2005 and 2010 could contribute to colonization of Surprise by 2010. We used the frequency of occurrence of a species in London in 2005 and 2010 as the predictor of its frequency of occurrence on Surprise east and Surprise west in 2010 in a least-squares regression. We explored the strength of these assumptions by testing the hypothesis that the regression slope does not differ from zero using an *F*-test of regression coefficients, from the *R*² of the actual regression, and test-

Table 1. Summary of assumed sources of cryptogam propagules for London and Surprise forest blocks.

Propagule source	London, fire-age mosaic	Surprise, recovering from intense fire
Regional source of airborne propagules	Similar to that of Surprise with a diverse fire-age composition, and relatively species rich	Similar to that of London (and including London) with a diverse fire-age composition, and relatively species rich
Local source of airborne propagules	London, a diverse fire-age composition, species rich	Surprise, mainly a single fire-age, species poor
Local fire refugia	Many	Few or none
Local soil bank	Assumed relatively rich	Assumed depleted by fire

ing the slope of the regression against 1:1 prediction using a *t*-test (Zar 1974: 208). We ranked residuals derived from the 1:1 prediction and identified them by taxon to visually present patterns of residual sign and magnitude relating to taxa. We assumed equal dispersal and establishment ability among species and higher taxa and tested this assumption as follows: we generated summary statistics for residuals from the 1:1 prediction including kurtosis and skewness, and performed a Jarque-Bera test for normality in distribution of the residuals from the regression (Jarque and Bera 1987) while interpolating the effects of small sample sizes on the χ^2 approximation of α (MathWorks 2017). In addition, local propagule sources were available to London forest block from unburned areas within the mosaic of fire-ages but there were no unburned areas within Surprise block grids. Based on Smith *et al.* (2014), we assumed that the intensity of the fire on Surprise block depleted the contribution from the local soil bank. Recolonization of soil at an accelerated rate compared to denser inorganic substrates, which might tend to indicate survival of propagules in soil interstices and violation of this assumption, was tested using a Fisher's exact test comparing the proportion present of all species capable of colonizing soil with the proportion present of all species capable of colonizing stone and charcoal substrates 2.5 yr after wildfire.

We performed a PerMANOVA on a resemblance matrix derived from simple matching, with species as samples and the substrates from which they had been collected as variables, to detect systematic differences between bryophytes and lichens in the array of substrates from which they were recovered. Presence-absence in the swamp (Caldyanup) or forest (Collis and Lindesay) vegetation units were also used as variables. The types of substrates considered are the same as those previously mentioned, above. PerMANOVA is analogous to a conventional multivariate analysis of variance (MANOVA), in which each

substrate value is treated as an individual attribute of a species, but significance values are determined by randomization. In contrast to conventional MANOVA, the only underlying assumption is that species are interchangeable (i.e., they have the same substrate preferences) if the null hypothesis is true (Anderson *et al.* 2008). We summarized differences between the bryophytes and lichens visually by using an ordination derived by principal coordinates analysis (PCO; Anderson and Robinson 2003).

To explore which substrates had a greater facility for colonization, we used Welch's *t*-tests to compare average residuals from the 1:1 prediction of species colonizing Caldyanup, forest (Collis or Lindesay), and the above substrates on Surprise block with species not colonizing the substrates or vegetation types.

To examine whether substrate specialization affected colonization ability, we tested for correlation between the number of substrates colonized and deviation from the 1:1 prediction for species of mosses, liverworts, and lichens.

To test whether deviation from normality in the distribution of the residual from the 1:1 prediction was characteristic of substrate preference or life form, we classified species as lichens or mosses, as occurring on soil or organic matter (most species occurring on one or the other occurred on both), or only on other substrates (wood, bark, stone, or charcoal). We then generated summary statistics for the categorized residuals from the 1:1 prediction and tested for deviation from normality as above.

RESULTS

Species Richness

We recorded a total of 67 species of lichen and bryophytes from all 18 sampling grids within London and Surprise from two sampling years: 40 lichens, 20 mosses, and 7 liverworts. Surprise east and Surprise west sub-blocks each supported 10 species of lichen

and bryophytes in 2005, 2.5 yr after the intense bushfire, which was about one-quarter of that observed for London (38 species) in 2005 with a mosaic of mixed fire-ages. In 2010, 35 species were observed in London block while Surprise east and Surprise west sub-blocks supported 29 and 31 species, respectively. Species richness per grid increased in Surprise forest block and, by 2010, 7.5 yr after fire, average species richness per grid was similar between London and Surprise forest blocks (Figure 4).

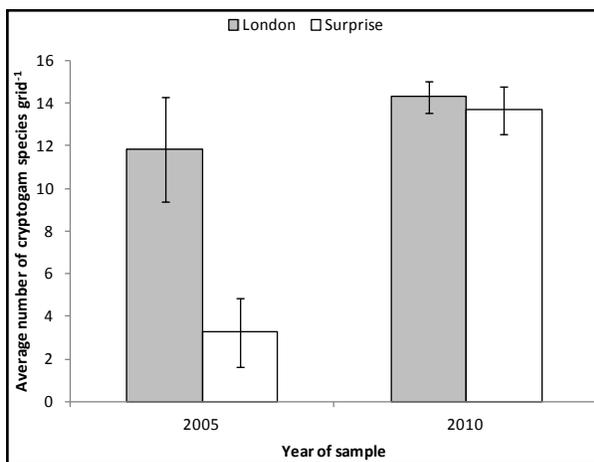


Figure 4. Average number of cryptogam species per sample grid in London (gray bars) and Surprise (white bars) forest blocks for 2005 and 2010 measurements. Fire-ages in London forest block ranged from 3 yr to ≥ 20 yr in 2005 and 2 yr to ≥ 25 yr in 2010. Fire-age in Surprise forest block was 2.5 yr in 2005 and 7.5 yr in 2010. Error bars are \pm SE.

Thirty-three percent of the total flora collected was exclusive to London forest block where mixed fire-ages including long unburned substrates were present. Nine percent of the total flora was exclusive to Surprise forest block 7.5 yr after fire, and six percent of the total flora was exclusive to Surprise forest block 2.5 yr after fire (Table 2).

Frequency of Species Occurrence

We found that, 2.5 yr after fire, the proportion of species present on soils, of all species able to colonize soils, was not significantly different from those able to colonize stone or charcoal, of all species able to colonize stone or charcoal, using a Fisher's exact test. From this, we infer that soil was not more liable than other inorganic substrates to have harbored propagules that survived the intense fire *in situ* and contributed to recolonization.

The frequency of species occurrences in London and Surprise forest blocks strongly correlated ($R = 0.84$, $P_{(2 \text{ tail})} \leq 0.001$). The frequency of species occurrences in London predicted the frequency of species occurrences in Surprise ($R^2 = 0.71$, $F = 155.5$, $P \leq 0.001$; Figure 5). The slope of the regression ($b = 1.158$) did not significantly differ from the 1:1 prediction. The distribution of residuals arising from the 1:1 prediction, when considering all cryptogams, was not significantly different from normal when using the Jarque-Bera test and interpolating the effects of small sample sizes (Table 3). Bryophyte (combined mosses and liverworts) residuals were normally distributed. Moss residuals were non-normal and platykurtic (more species with more variation from predicted frequencies in Surprise forest block than normal expectations). We interpreted this to indicate that dispersal or habitat limitation was more variable between species than expected for mosses. Lichen residuals were non-normally distributed and right skewed (more species with frequencies in Surprise block greater than predicted than normal expectations). We interpreted this to indicate that lichens tended to be slightly better dispersers or that substrates favored lichens more than bryophytes. We did not test for normality in liverwort residuals due to the small sample size. The majority of liverworts appeared less frequently in Surprise than predicted from their frequency in London (Figure 6). The four species with the most negative residuals

Table 2. The number of occurrences of species exclusive to London or Surprise forest block, or fire-ages. PERTH herbarium specimen numbers are provided for unidentified or un-named material. Fire-ages in London forest block ranged from 2 yr to ≥ 25 yr. Fire-age in Surprise forest block was 2.5 yr in 2005 and 7.5 yr in 2010.

Species	Life form	Forest block		
		London	Surprise	
		2005	2010	
<i>Dicranella dietrichiae</i> (Müll. Hal.) A.Jaeger	Moss	2	0	0
<i>Didymodon torquatus</i> (Taylor) Catches.	Moss	2	0	0
<i>Pleurophascum occidentale</i> R.E.Wyatt & A.H.Stoneb.	Moss	2	0	0
<i>Buellia dissa</i> (Stirt.) Zahlbr.	Lichen	2	0	0
<i>Hypocenomyce scalaris</i> (Ach.) M. Choisy	Lichen	2	0	0
<i>Rhizocarpon</i> sp. grey (PERTH 06324452)	Lichen	2	0	0
<i>Rosulabryum campylothecium</i> (Taylor) J.R.Spence	Moss	1	0	0
<i>Sematophyllum homomallum</i> (Hampe) Broth.	Moss	1	0	0
<i>Syntrichia antarctica</i> (Hampe) R.H.Zander	Moss	1	0	0
<i>Riccardia crassa</i> (Schwägr.) Carrington & Pearson	Liverwort	1	0	0
<i>Amandinea punctata</i> (Hoffm.) Coppins & Scheid.	Lichen	1	0	0
<i>Calicium abietinum</i> Pers.	Lichen	1	0	0
<i>Cladia inflata</i> (F.Wilson) D.J.Galloway	Lichen	1	0	0
<i>Cladonia cervicornis</i> var. <i>verticellata</i> (Hoffm.) Ahti.	Lichen	1	0	0
<i>Cladonia ochrochlora</i> Flörke	Lichen	1	0	0
<i>Cladonia scabriuscula</i> (Delise) Nyl.	Lichen	1	0	0
<i>Dictyographa</i> sp. brown lips (PERTH 06322301)	Lichen	1	0	0
<i>Diploschistes euganeus</i> (A. Massal.) J.Steiner	Lichen	1	0	0
<i>Diploschistes sticticus</i> (Korb.) Müll.Arg.	Lichen	1	0	0
<i>Halegrapha mucronata</i> (Stirt.) Lücking	Lichen	1	0	0
<i>Hypogymnia pulverata</i> (Nyl.) Elix	Lichen	1	0	0
<i>Pannaria elixii</i> P.M. Jørg. & D.J.Galloway	Lichen	1	0	0
<i>Dicranoloma billarderi</i> (Brid.) Paris	Moss	0	1	0
<i>Zygodon menziesii</i> (Schwagr.) Arn.	Moss	0	1	0
<i>Astellia drummonii</i> (Taylor) R.M.Schust. ex D.G.Long	Liverwort	0	1	0
<i>Hypogymnia subphysodes</i> (Kremp.) Filson var. <i>subphysodes</i>	Lichen	0	1	0
<i>Triquetrella papillata</i> (Hook.f. & Wilson) Broth.	Moss	0	0	2
<i>Thuidopsis sparsa</i> (Hook.f. & Wilson) Broth.	Moss	0	0	1
<i>Ainoa mooreana</i> (Carroll) Lumbsch & I. Schmitt	Lichen	0	0	1
<i>Caloplaca marina</i> (Wedd.) Zahlbr.	Lichen	0	0	1
<i>Cladonia</i> sp. golden coral (PERTH 07320388)	Lichen	0	0	1
<i>Tephromela alectoronica</i> Kalb	Lichen	0	0	1
Number of species exclusive to forest block and fire-age		22	4	6
Percentage of total species collected		33	6	9

from the 1:1 prediction (less frequent than expected) were the liverworts *Lethocolea pansa* (Taylor) G.A.M.Scott & K.G.Beckm., *Geobryum unguiculatum* (Hook.f. & Taylor) Grolle, *Kurzia compacta* (Stephani) Grolle, and the lichen *Ochrolechia subpallenscens*

Verseghy. The four species with the most positive residuals from the 1:1 prediction (more frequent than expected) were the three lichens including unidentified “grey green slick” (PERTH 06320082), *Thysanothecium scutellatum* (Fr.) D.J.Galloway, *Diploschistes scrupo-*

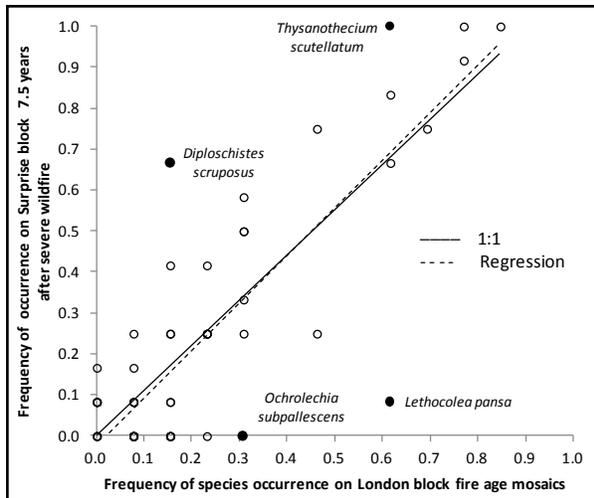


Figure 5. Frequency of grids with cryptogam species occurrence on Surprise forest block 7.5 yr after fire plotted against frequency of grids with species occurrence on London forest block fire-age mosaic. Each data point represents one species; species with the most extreme residual from a 1:1 prediction are labeled. Some data points overlap due to the limited number of grids sampled. For regression: $y = 1.158x - 0.023$, $R^2 = 0.71$. For test of regression coefficients: $F = 155.5$, $P \leq 0.001$.

sus (Schreb.) Norman, and the moss *Barbula calycina* Schwägr.

From PerMANOVA, lichens were different from both mosses and liverworts in their preferences for substrates (lichens, mosses: $t = 2.804$, $P_{\text{Perm}} = 0.001$; lichens, liverworts: $t = 2.231$, $P_{\text{Perm}} = 0.003$). Mosses and liverworts were not different in their preferences. Preference for soil and organic matter as substrates tended to distinguish between bryophytes and lichens (Figure 7).

London and Surprise forest blocks showed no differences in frequency of respective substrate types. Soil and organic matter were the most common substrates, while stone substrates were least common (Figure 8). Species differed in their ability to colonize depending on the substrate colonized. Species able to colonize Caldyanup grids, stone, or organic material other than wood or bark were more frequent than predicted in Surprise block 7.5 yr after wildfire compared to species not found on these substrates (Table 4).

Table 3. Summary statistics of the distribution of residuals from a 1:1 prediction of frequency of grids in Surprise 7.5 yr after fire carrying a particular species from frequency of grids in London 2005 and 2010 mosaics carrying them. Mean = mean of the residual frequency of grids from the 1:1 prediction. RMSE = root mean square error, or the standard deviation of residuals from the 1:1 prediction. Jarque-Bera (*JB*) statistic and probability describe significance of deviation from a normal distribution, ns = not significant.

Group	Mean	RMSE	Skewness	Kurtosis	<i>JB</i> statistic	<i>P</i>
Cryptogams (lichens, liverworts, and mosses)	0.008	0.16	0.17	1.95	3.43	ns
Bryophytes (liverworts and mosses)	-0.004	0.17	-0.86	1.77	5.01	ns
Liverworts	-0.12	0.24	-0.57	0.86		
Mosses	0.03	0.13	0.15	-1.07	13.91	≤ 0.01
Lichens	0.02	0.16	1.15	2.05	10.39	≤ 0.02
Mosses on soil or organic matter	0.27	0.20	-0.006	-0.79	9.59	< 0.02
Lichens on soil or organic matter	0.28	0.25	1.2	0.82	5.73	< 0.03
Lichens not on soil or organic matter	-0.03	0.21	1.19	2.64	5.78	< 0.03

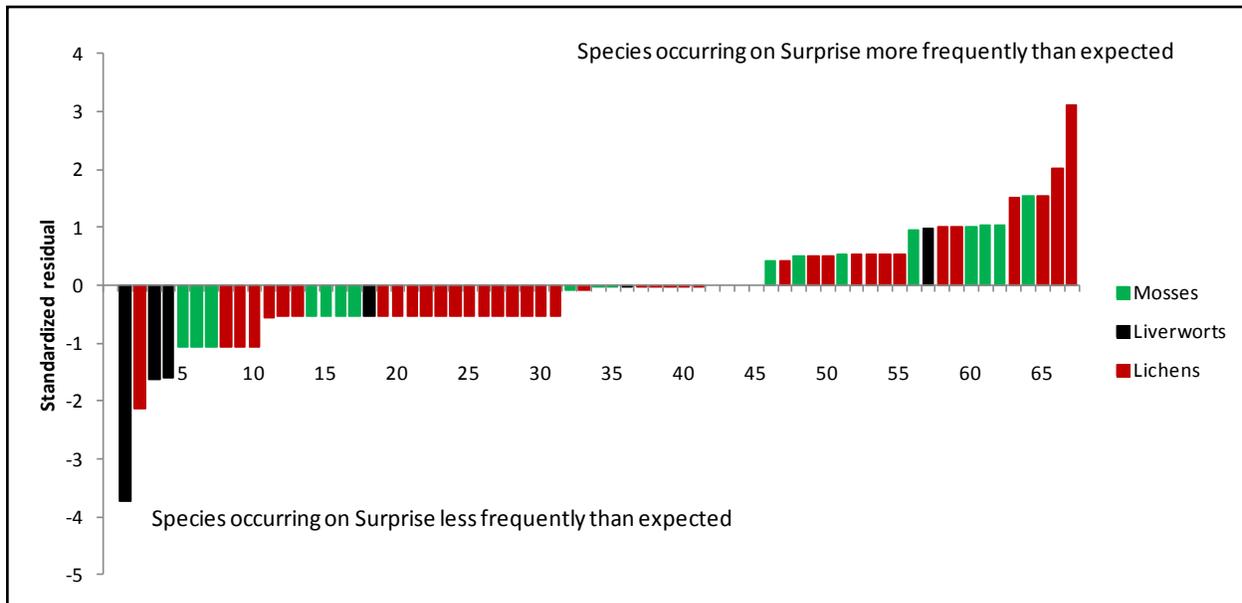


Figure 6. Residuals from the 1:1 prediction of frequency of grids with species occurrence on Surprise forest block using the frequency of grids carrying the species on London forest block fire-age mosaic as a predictor. Residuals are arranged in rank order as indicated on the horizontal axis and identified by taxon with color.

Liverworts, but not mosses or lichens, showed a positive correlation between residuals from the 1:1 prediction from London and the number of types of organic substrates colonized (organic matter, wood, and bark; $P_{(1 \text{ tail})} < 0.005$). Liverwort residuals were also positively correlated with the total number of types of substrates colonized ($P_{(1 \text{ tail})} < 0.05$; Table 5).

When mosses and lichens were compared with respect to substrate preferences, mosses on soil and organic matter had a platykurtic distribution of residuals, while lichens on the same substrates had a right-skewed and platykurtic distribution of residuals (Table 3). Lichens on bark, wood, stone, or charcoal substrates had a right-skewed and mesokurtic distribution of residuals. Right skewness indicates more positive residuals than normal expectations (dispersal or habitat limitation were weaker than expected and species tended to be better colonists than predicted), and a platykurtic distribution means more species with more variation from normal expectations (dispersal or habitat limitation were more variable than

expected and there were more better and worse colonists than predicted). Thus, both phylum level characteristics and species substrate preferences affected colonization ability of some species after wildfire as reflected in the distributions of residuals.

DISCUSSION

The frequency of occurrence in a fire mosaic predicted the frequency of occurrence in an adjacent forest block 7.5 yr after severe wildfire. In particular, the residuals from the 1:1 prediction considering the total flora were normally distributed. We interpreted this to indicate that, by 7.5 yr after wildfire, the availability of propagules from regional source populations dominated the assembly of cryptogam communities, rather than filtering by dispersal ability or habitat suitability. This concurs with observations on the assembly of bryophyte communities on slag heaps for which both maximum similarity in flora and the highest number of nearest sources of re-

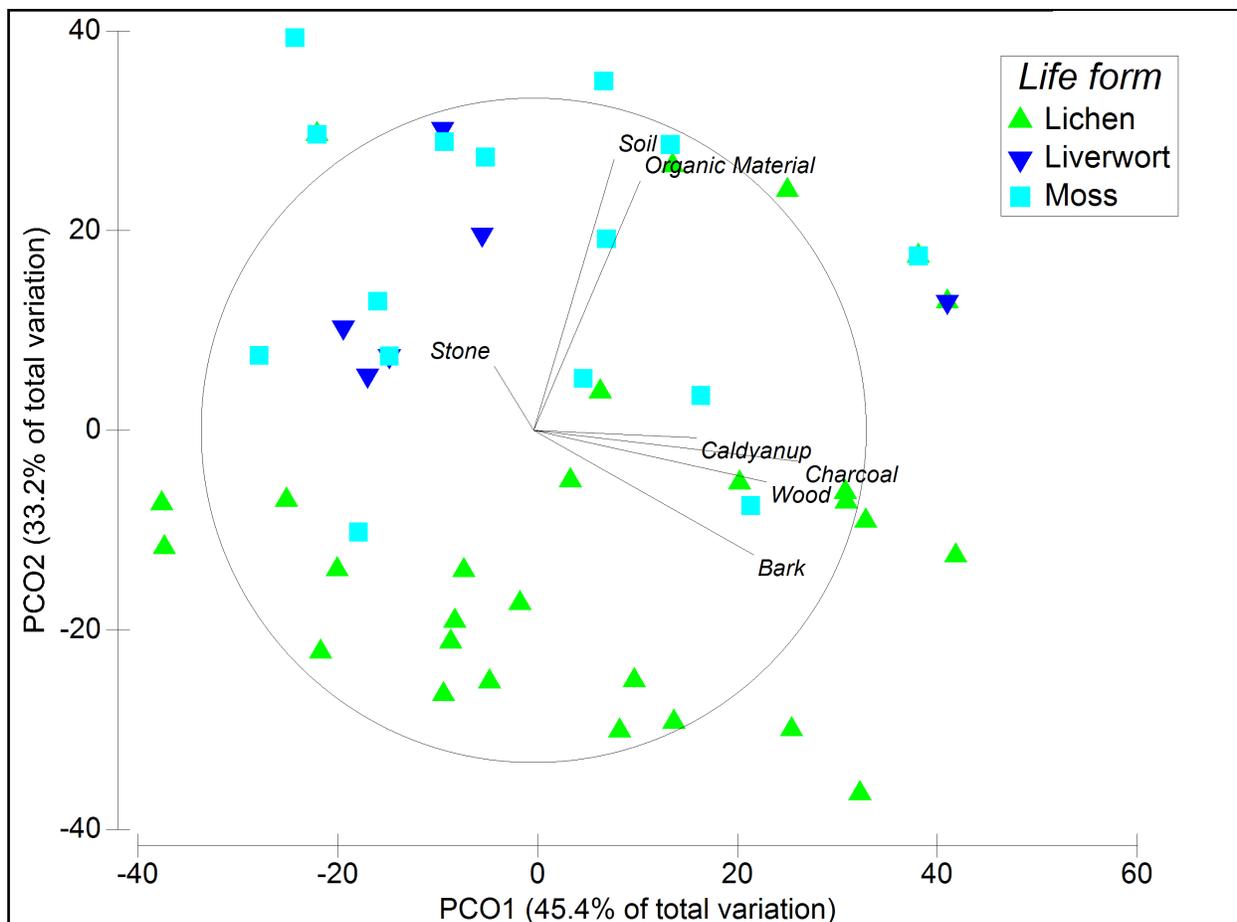


Figure 7. Principal coordinates analysis ordination of a resemblance matrix based on simple matching of cryptogam species according to substrates that they are capable of colonizing and their presence-absence in forest (Collis and Lindsay) and swamp (Caldyanup) vegetation units. Overlying vectors are Spearman correlations of variables with the principal coordinate axes PCO1 and PCO2.

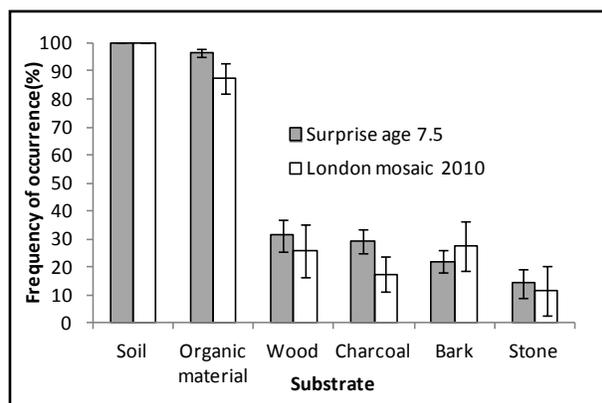


Figure 8. Frequency of encounter of substrates in 1 m² plots on Surprise 7.5yr after fire and London fire-age mosaic 2010. There are no differences between Surprise and London forest blocks using *t*-tests for each substrate.

cruitment were within 10 km of the sampled site (Hutsemekers *et al.* 2008). The observations accord with the dominance of long-distance dispersal in the assembly of lichen communities (Gjerde *et al.* 2015). Our observations also conform to the distance effects on the composition of propagule fallout and establishment in boreal forests after patchy fires (Barbé *et al.* 2016b).

Exceptions to the regional dominance of assembly occur at phylum and species levels. We inferred that ecological requirements favored or disfavored some components of the cryptogam flora. These exceptions relate to differences in habitat preferences of phyla and species.

Table 4. Comparison of means of residuals from the 1:1 prediction for species colonizing substrates on Surprise block 7.5 yr after wildfire and species not colonizing those substrates. Probability ($P_{(1 \text{ tail})}$) of Welch's t statistic (t stat) generated assuming unequal variances and using the listed degrees of freedom (df). Ability to colonize a substrate is assumed to enhance colonization so 1 tail probability is used. Where $P_{(1 \text{ tail})} \leq 0.05$, mean residual for colonists is \geq mean residual for non-colonists; ns = no significant difference between mean of residuals for colonists and non-colonists. Note that species included are only those for which substrate preferences are known (61 species).

Substrate	Mean of residual frequency of grids for non-colonists	Non-colonists (n)	Mean of residual for colonists	Colonists (n)	df	t stat	$P_{(1 \text{ tail})}$
Caldyanup	-0.215	28	0.26	33	49	-1.94	0.03
Collis or Lindesay	-0.130	10	0.07	51	41	-1.03	ns
Wood	-0.178	28	0.22	33	49	-1.52	ns
Bark	-0.034	34	0.13	27	58	-0.64	ns
Organic material not wood or bark	-0.167	31	0.25	30	56	-1.65	0.05
Soil	-0.033	37	0.15	24	49	-0.69	ns
Stone	-0.127	42	0.41	19	30	-1.82	0.04
Charcoal	-0.010	35	0.11	26	54	-0.44	ns

Table 5. The correlation between the numbers of substrates colonized by species of a taxon and the residuals from a 1:1 prediction of their frequency in Surprise age 7.5 yr from frequency in London 2005 and 2010. Cell values are correlation coefficient R. Significant correlations are followed by level of significance (1 tail, positive correlations expected). Organic substrates are wood, bark, and organic matter other than wood or bark. Mineral substrates are stone, soil, and charcoal.

Life form	Correlation with number of substrates colonized		
	Organic	Mineral (including charcoal)	Total
Moss	0.18	0.17	0.22
Liverwort	0.90, $P < 0.005$	0.34	0.74, $P < 0.05$
Lichen	0.11	0.13	0.14

For liverwort species, but not lichens or mosses, deviation from predicted frequencies correlated with the number of types of organic substrates colonized. Habitat specialization affected colonization ability for liverworts. Species colonizing the most organic substrate types were more frequent than predicted, while species colonizing no or few organic substrates were less frequent than expected. While the

presence of too few liverworts prevented meaningful tests for normality in residuals, we documented lower than expected liverwort species frequencies in Surprise forest block.

Elsewhere, geographical range sizes in liverworts show differences according to whether or not vegetative propagules are produced, indicating that lack of vegetative reproduction limits dispersal ability particularly for

long-distance dispersal (Laenen *et al.* 2016). On the other hand, liverworts require moist habitat and removal of biomass cover by fire results in greater exposure of habitat. Liverworts appear to be particularly sensitive to disturbance by fire in both boreal (Paquette *et al.* 2016, Barbé *et al.* 2017) and wet eucalypt forest (Kantvilas *et al.* 2015). Liverworts are abundant in wet eucalypt forest where fires are infrequent and recover greatest species richness in these forests decades after disturbance by silviculture or fire (Turner *et al.* 2011). Later seral stages of wet eucalypt forests would have the greatest diversity of organic substrates for liverworts and tend to accommodate substrate specialization.

We found lichens and mosses contravened normality in the distribution of residuals. That is, variations from predictions are expected for cryptogams, yet the variations observed were exceptional for lichens and mosses. Lichens tended to be right skewed in their distribution of residuals. More lichen species were more frequent colonists than expected. Mosses had a platykurtic distribution of residuals. More moss species were more or less frequent colonists than expected. We interpreted this to indicate weaker than expected dispersal or habitat limitations in lichens, and more variable than expected dispersal or habitat limitations in mosses.

London and Surprise forest blocks had similar frequencies of available substrates on the sample grids, so this is not a mechanism accounting for differences between phyla in colonization of Surprise forest block. Species able to colonize Caldyanup vegetation units, stone, or organic substrates had a greater propensity for colonization than species not colonizing these substrates. Mosses and lichens showed differences in preferred substrates, and we suggest that these differences in substrate preferences resulted in differences in the distribution of residuals according to both substrate and phylum. Habitat limitation differs between phyla because of differences in spe-

cies-level tendencies for substrate preference between phyla, and some substrates are more readily colonized than others (*cf.* Kumar *et al.* 2017).

Assembly of lichen floras on forelands of retreating glaciers was affected by dispersal ability and ecological characteristics of lichen species (Nascimbene *et al.* 2017). Similar mechanisms differentiating recolonization ability might operate for some species in lichen recolonization after an intense fire. The presence of habitat preferences among mosses is well known from bryophyte succession after disturbance (e.g., Duncan and Dalton 1982, Esposito *et al.* 1999, Kantvilas and Jarman 2012). This leads to differences in the composition of established flora from source and propagule fallout compositions (Barbé *et al.* 2016b) as habitats change with the progression of seral stages.

A third of all species collected in our study remained absent from Surprise block 7.5 yr after severe fire. Cryptogam species differ in their relative ability to disperse and establish after fire. Some species and taxa are leaders in dispersing and establishing (Jackson 1971, Esposito *et al.* 1999, Ryömä and Laaka-Lindberg 2005, Kantvilas and Jarman 2012), while others are laggards (Turner *et al.* 2011, Paquette *et al.* 2016), or transiently present (Turner *et al.* 2011, Kantvilas and Jarman 2012). Retaining unburned patches that serve as source populations of laggards and regionally rare species is vital. 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 in which the rate of landscape-change (in this case, governed by fire return intervals) exceeds dispersal capabilities (Johansson *et al.* 2013). Long undisturbed patches that accumulate uncommon species and those with specialized habitat requirements provide a “storage” effect (Roxburgh *et al.* 2004), enabling the regional persistence of those components of the flora

(Fenton and Bergeron 2008). We suggest that some species, being more scarce than expected in the early recolonization of Surprise forest block, demonstrates the benefits of fire-age mosaics including long-unburned patches and diverse seral stages in providing and maintaining a regional source of propagules (*cf.* Barbé *et al.* 2017).

The potential for severe and extensive fires is likely to increase in the southwestern Australian forested landscape in response to a drying and warming climate trend, and a growing urban and wildland interface where human-caused ignitions become increasingly

likely (Enright and Fontaine 2014). Meta-population dynamics demonstrated for fauna after a recent extensive and severe fire in moist karri and jarrah forest in southwestern Australia (Bain *et al.* 2016) provide an indicator that some elements of cryptogam floras are also likely to have suffered long-term depletion in those forests. Managed reintroduction of fire to reduce fuel loads in landscapes subject to previous intense fires depends on a comprehensive disposition of sources of cryptogam propagules to promote their retention in fire-age mosaics that include long-unburned patches.

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