

## THE EFFECT OF RECENT FIRE HISTORY ON THE ABUNDANCE AND VIABILITY OF LARGE SEEDS IN THE SOIL OF SCLEROPHYLL FOREST IN TASMANIA, AUSTRALIA

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(with two text-figures, two plates, eight tables and one appendix)

**Bezemer, N., Kirkpatrick, J.B. & Wood, J.A.** 2013 (17:xii): The effect of recent fire history on the abundance and viability of large seeds in the soil of sclerophyll forest in Tasmania, Australia. *Papers and Proceedings of the Royal Society of Tasmania* 147: 41–50. <https://doi.org/10.26749/rstpp.147.41> ISSN 0080-4703. School of Geography and Environmental Studies, University of Tasmania, Private Bag 78, Hobart, Tasmania 7001, Australia (NB\*, JBK); Royal Tasmanian Botanical Gardens, Queens Domain, Hobart, Tasmania 7000, Australia (JAW). \*Author for correspondence. Email address: nbezemer@gmail.com

There are few data on the effects of recent fire history on the composition of soil seed banks in sclerophyll forest communities. We predicted that the abundance and viability of soil-stored seeds would vary with fire history. Soils were sampled from areas with six different fire histories on Mt Nelson, Tasmania, Australia. Large seeds were extracted by hand separation and tested for viability. Responses to at least one of the two strongly-correlated components of fire history were detected in several taxa and for native and exotic seed. Native seeds, exotic seeds, *Astroloma humifusum* seed and *Exocarpos cupressiformis* seed were all more abundant in the soils of areas with one or less fires in the last 60 years than in the soils of areas burnt five times over the last 60 years. The viability of *A. humifusum* seeds decreased with fire frequency. These results support the hypothesis that frequent and recent fire can deplete the soil seed bank, and reduce soil seed viability, at least for some large-seeded species and species groups.

**Key Words:** eucalypt forest, fire frequency, fire history, seed abundance, seed viability, soil seed bank, time-since-fire, *Astroloma humifusum*, *Exocarpos cupressiformis*.

### INTRODUCTION

The long-term storage of seed in the soil (geospory) is an important life history strategy in plants (Fenner 1985, Bell 2001, Merritt & Rokich 2006). Soil seed banks provide a genetic reservoir, from which dormant seeds germinate simultaneously or intermittently once stimulated by environmental or disturbance cues (Merritt & Rokich 2006). Seed banks are in a constant state of flux, with predation, decay and senescence, movement of seeds within the soil and germination acting to remove the seeds that are periodically deposited (Harper 1977).

Fire seasonality and intensity have been shown to affect the emergence and survival of several scleromorphic shrub species (Knox & Clarke 2006). Responses to fire can be modified by other factors. For example, soil moisture, depth of seed placement in the soil, fire intensity and duration affect the germination of *Dodonea viscosa* (L.) Jacq. (Hodgkinson & Oxley 1990).

Fire may also alter seed bank composition by altering above-ground species composition. In dry sclerophyll forest near Sydney approximately 60% of floristic variation may be attributed to fire frequency (Morrison *et al.* 1995). Frequent fires may shift sclerophyllous communities towards resprouter dominance (Meney *et al.* 1994, Bell 2001), thus altering seed deposition and, consequently, the composition of the seed bank.

Seeds in the soil that do not germinate after the passage of fire are an important component of the residual seed bank (Auld & Denham 2006). Fire may prevent seed bank replenishment, thus depleting the residual store. In several genera of Ericaceae and Restionaceae, there was less viable seed in recently burnt sites than recently unburnt sites, with the total numbers of seeds in the soil varying from 9000 seeds/m<sup>2</sup> in unburnt sites to around 1500 seeds/m<sup>2</sup> in burnt sites (Meney *et al.* 1994). In heath communities,

fire can deplete the seedbank by half (Pierce & Cowling 1991). In the jarrah (*Eucalyptus marginata* Sm.) forest of southwestern Australia, the germinable soil seedbank was greater three years after fire than in soils from sites burned one and 13–22 years ago (Koch *et al.* 2009). This previous work suggests that fire history has a strong influence on the persistent soil seed store.

Germination after fire does not fully explain depletion of the seedbank, even in communities adapted to fire. In *Acacia suaveolens* (Sm.) Willd., maximum post-fire seed rain coincides with the maturation of post-fire germinants, at approximately two to three years (Auld 1986). Soil seed stores peak 10 years after a fire, after which stores decline in abundance and viability with loss of adult fecundity and decay. Soil seed stores of other species, such as *Grevillea barklyana* F. Meull. ex Benth., peak 16 years after fire (Vaughton 1998). Therefore, the magnitude of the soil seed store will be influenced by primary juvenile periods and patterns of post-fire fecundity, both of which can potentially be affected by fire regime.

Much of the above work was based on germination trials, which may not provide a complete representation of the soil seed bank, although being highly efficient in revealing the presence and abundance of most species. *Exocarpos cupressiformis* Labill. and *Astroloma humifusum* (Cav.) R.Br., for example, are conspicuous elements of dry sclerophyll communities that are rarely recorded in germination trials. For example, Penman *et al.* (2008) did not record their presence in the seed bank, as both species, although present in the vegetation, failed to respond to treatments. The cues used to stimulate the germination of seeds in *in situ* trials may be different to the ones that break the dormancy of particular species (Ooi *et al.* 2007).

The seed banks of scleromorphic communities are poorly known in Tasmania. Gilfedder & Kirkpatrick (1993) compiled a list of species observed in semi-natural

paddocks in the Tasmanian Midlands, and recorded those they germinated from the soil seed bank. Wilkinson & Jennings (1994) tested the regeneration capacity of *Acacia melanoxylon* R.Br. after fire in northwestern Tasmanian wet sclerophyll forests, and found that high intensity burning destroyed 67% of the viable seed in the uppermost part of the soil profile, and stimulated the germination of most of the remainder.

Although fire or fire-related cues are essential to break the dormancy of many species, fire also kills seeds in the soil, and temporarily prevents replenishment of the seed bank by killing adult and juvenile plants. We therefore test the hypothesis that the soil seed bank of geosporous species in dry sclerophyll forest is affected by variation in fire history. Our results are confined to large-seeded species to enable us to collect a number of samples sufficient to compare several fire histories. We use physical extraction and testing for viability, rather than germination trials, to ensure confidence in the completeness of the data for our subset of species.

## METHODS

### Study area

The study area is located on Mt Nelson, Hobart, Tasmania (147°19'E, 42°54'S) in the property of the University of Tasmania (fig. 1). The area includes a north–south gully occupied by *Eucalyptus globulus* Labill. wet forest with an understorey dominated by tall shrubs and small trees, such as *Beyeria viscosa* (Labill.) Miq., *Pomaderris apetala* Labill., *Bedfordia salicina* (Labill.) DC., *Exocarpos cupressiformis* and *Coprosma quadrifida* (Labill.) B.L.Rob., with occasional emergent *Acacia melanoxylon*. To the east of the gully is a large tract of *Allocasuarina verticillata* (Lam.) L.A.S. Johnson dry forest, which also occurs in two smaller patches in the western part of the reserve (fig. 1). Here, the understorey ranges from sparse to shrubby, with common species including *Bursaria spinosa* Cav., *Dodonea viscosa*, *Astroloma humifusum*, and *Lepidosperma laterale* R.Br. To the west of the gully is *Eucalyptus pulchella* Desf./ *E. viminalis* Labill. dry forest, which extends in a wide tract along much of the western border. *Bursaria spinosa* and *D. viscosa*, as well as native grasses, ericaceous shrubs and sedges, are typical components of the understorey. The southern and highest part of the reserve is comprised mostly of *E. pulchella*/ *E. globulus*/ *E. viminalis*/ *E. ovata* Labill. dry forest. The understorey is diverse, including most species already listed and additional species, notably *Epacris impressa* Labill., *Olearia ericoides* (Steetz) N.A.Wakef., *Ozothamnus ferrugineus* (Labill.) Sweet, *Lissanthe strigosa* (Sm.) R.Br., *Goodenia ovata* Sm. and *Pultenaea juniperina* Labill. Native grasses are prominent in the understorey. Small tracts of degraded *E. obliqua* L'Hér. dry forest and *E. ovata* dry forest occur along the southwestern perimeter (fig. 1).

### Field data collection

Across the University Reserve, six different fire histories were mapped from aerial photographs or satellite images dated 1946, 1957, 1967, 1975, 1980, 1984, 1989, 2001, 2004, 2008 and 2012 (table 1, fig. 2). An equal number of sites (10 per fire history; 60 in total) were selected from each fire history. Sites were chosen within five metres of a

mature *Acacia* tree to remove the current occurrence of the genus as a factor influencing seed distribution. For each site, vegetation type was recorded and plant species listed. Soil samples were collected from the uppermost 5 cm of soil using a metal ring with a diameter of 8 cm. The soil sample for each site was made up of nine sub-samples, with a total dry weight of c. 900 g/sample.

## Laboratory analyses

The soil samples were dried overnight and large seeds separated out by breaking up and passing the soil through a 1.7 mm sieve. As sifting did not remove all the soil, seeds were then separated by hand. To avoid measurement bias, each sample was identified by a number from 1 to 60, instead of the area from which it was collected.

Seeds were identified by JAW using the seed collections held at the Royal Tasmanian Botanical Gardens. Some seeds were identifiable only to genus level. The seeds of different taxa were described and photographed (appendix 1). The viability of each seed was determined using the cut test of Terry *et al.* (2003). Seeds in which the embryo appeared intact and healthy, and the endosperm clean and firm, were classed as viable.

## Statistical analyses

Minitab 16 (Minitab Inc. 2010) was used in all analyses. In vegetation in which structure and dominance can be strongly influenced by fire regime, floristic classifications can better reflect underlying environmental gradients, and can be a better integral of past vegetation conditions, than dominance/structural groups. For these reasons, floristic groups were generated from the above ground vegetation presence/absence data for each site. An agglomerative strategy using Euclidean distance and Ward's method was adopted. Five groups were selected as there was a marked difference in average distance values between five and four groups.

For taxa with sufficient seed-bank data, one-way ANOVA was used to determine whether the abundance of seed varied with the presence or absence of a species in the above-ground vegetation at each site. Areas with high fire frequency strongly tended to be those with a short time since the last fire. This strong inverse relationship between the two attributes of fire regime required two sets of models in which number of fires was the fixed variable in one set and time since fire was the fixed variable in the other set.

**TABLE 1**  
Known fire histories of the University Reserve

| Fire history                         | No. of fires | Time-since-fire (years) |
|--------------------------------------|--------------|-------------------------|
| No fire in last 50 years             | 0            | c. 60                   |
| Last fire 1967                       | 1            | 45                      |
| 1967, 1995                           | 2            | 17                      |
| 1967 <sup>1</sup> , 1995             | 3            | 17                      |
| 1967, 1995, 1998                     | 3            | 14                      |
| 1967 <sup>1</sup> , 1995, 1998, 2006 | 5            | 6                       |

<sup>1</sup> At least one low intensity fire between 1967 and 1995.

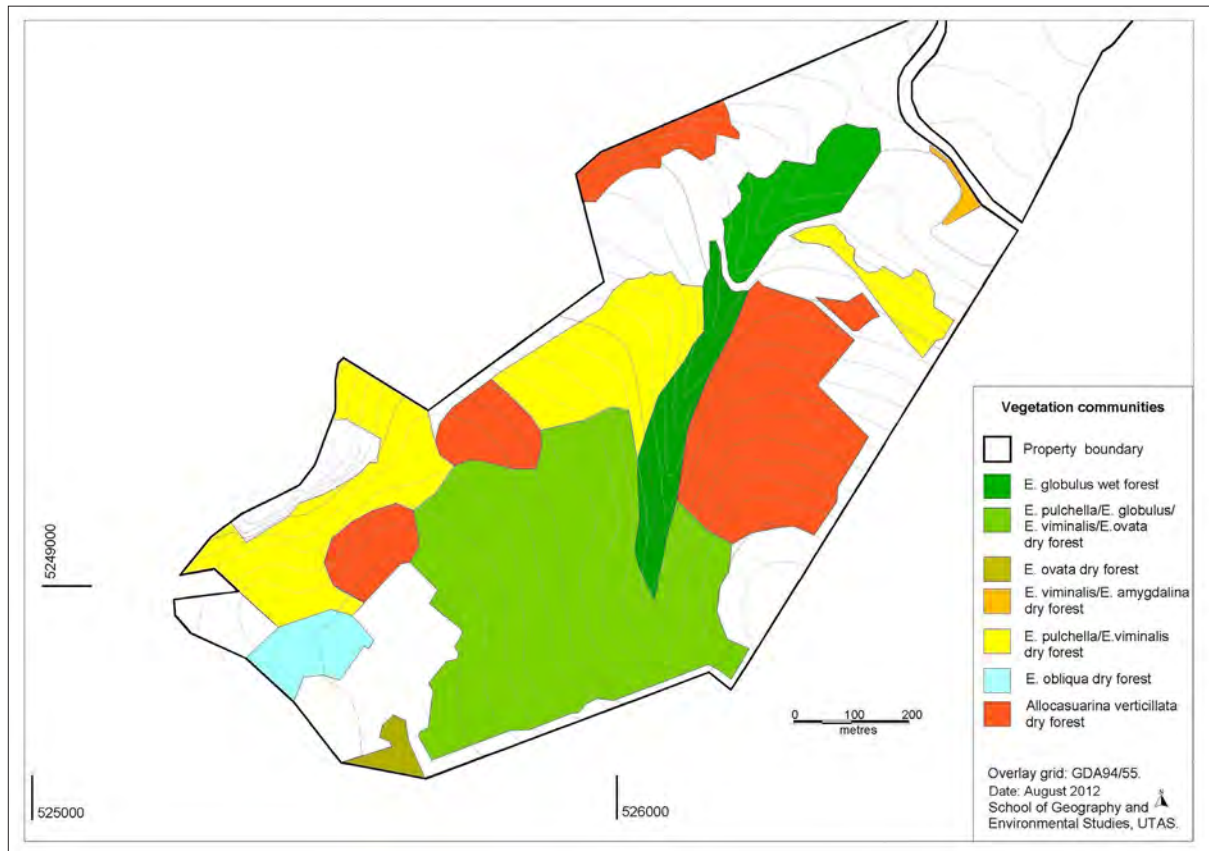


FIG. 1 — Vegetation types of the study area. Vegetation boundaries are based on the Biodiversity Management Plan (2012 draft) for the University Reserve. Base data from theLIST ([www.thelist.tas.gov.au](http://www.thelist.tas.gov.au)). © State of Tasmania



FIG. 2 — The recent fire history of the University Reserve, Tasmania (147°19'E, 42°54'S) and sample collection sites. Fire history boundaries are based on the Biodiversity Management Plan (2012 draft) for the University Reserve. Base data from theLIST ([www.thelist.tas.gov.au](http://www.thelist.tas.gov.au)). © State of Tasmania

In both sets, vegetation type (five categories, as described above) and floristic group were included as random factors. The response variables were soil seed abundance for *Acacia*, *Astroloma humifusum*, *Beyeria viscosa*, *Dodonea viscosa*, *Exocarpos cupressiformis*, *Lepidosperma laterale*, *Rubus fruticosus* (L.) sp. agg., total native seed and total exotic seed. Two sets of general linear models with the same predictors were constructed for seed viability for those of the above species and species aggregates for which there were sufficient data.

## RESULTS

Fourteen types of seed larger than 1.7 mm were found in the soil samples, 10 of which were identifiable to species or genus (appendix 1). Several of these taxa were too infrequent in the sample to analyse. The abundance of *Beyeria viscosa* seed in the soil was strongly related to its occurrence in the vegetation, whereas *Astroloma humifusum*, *Dodonea viscosa*, *Exocarpos cupressiformis*, *Lepidosperma laterale*, and *Rubus fruticosus* seed did not differ in abundance between sites in which they occurred and those in which they did not occur (table 2).

The number of fires between 1960 and 2012 was strongly related to the number of native and exotic seeds in the soil (table 3), seed number decreasing with the number of fires (table 4). *A. humifusum*, *E. cupressiformis* and *R. fruticosus* seed numbers also declined as the number of fires increased (tables 4 and 5). *E. cupressiformis*, as well as native and exotic seeds considered as a group, also had strong responses to time-since-fire (table 3). *D. viscosa*, *B. viscosa*, *Acacia* and *L. laterale* did not have a significant response to either number of fires or time-since-fire. While vegetation type was not significant in any of the models, floristic group affected the abundance of native, exotic, *D. viscosa* and *R. fruticosus* seeds in at least one of the analyses.

The seed viability of *A. humifusum* was related to the number of fires and time-since-fire (table 6). Native and *E. cupressiformis* seed viability was related to floristic group (table 5). Viability of native and *A. humifusum* seed was highest (46.8 and 53.3% respectively) in the area not burnt in the last 50 years and lowest (13.9 and 6.2%) in the area burnt in 1967+, 1995 and 1998 (tables 7 and 8).

## DISCUSSION

The 12 identified types of seed recovered from the soils of the study area (appendix 1) represented a small proportion of the 150 species of vascular plants recorded from the study area by one of us (JBK) and the 135 vascular plant species identified through germination trials in the soil seed bank of a grassy forest in southeastern Australia (Lunt 1997). Many species known to occur in the study area were not detected in the seed bank, despite having seeds > 1.7 mm in diameter. This result may indicate rarity of large seeds in the soil, or an insufficient sample size. Nevertheless, our procedures gave us confidence that our results reflected the reality of soil seed content for the subset of species with large seeds. We were able to count seeds of species, such as *Exocarpos cupressiformis*, that do not respond to normal germination trial procedures.

The distribution of the seed of *Astroloma humifusum*, *Dodonea viscosa*, *E. cupressiformis*, *L. laterale* and *Rubus*

*fruticosus* was independent of the presence of the species in the contemporary vegetation (table 2), suggesting, in combination with the tendency of some of them to accumulate soil seed with time elapsed since fire, that these species have a persistent soil seed store. Among the above species, *A. humifusum*, *E. cupressiformis* and *R. fruticosus* have fleshy fruits or arils, so may be widespread in the soil seed store because of bird dispersal. The positive relationship between *Beyeria viscosa* soil seed and its contemporary presence in the vegetation reflects its restricted distribution in the study area and its lack of attraction for birds and mammals. The species was only found in wet eucalypt forest that had not been burned since 1967, where it had a substantial seed store, with more than 60% viability. Many of the viable seeds had heavily weathered coats, suggesting that this species has a persistent seed store.

Previous Tasmanian soil seed bank studies (Gilfedder & Kirkpatrick 1993, Wilkinson & Jennings 1994) did not record *E. cupressiformis*, *A. humifusum* or *L. laterale*, the seeds of which were common in our samples. In contrast, *Acacia* species have been observed to have a soil seed store (Wilkinson & Jennings 1994), as in our study area.

There was a strong relationship between the least burned areas and the more mesic parts of the study area, although all fire histories had at least some wet and some dry forest. To the extent that was possible given this partial coincidence, we removed the effects of vegetation by making vegetation variables random within our models (tables 3 and 6). This modelling procedure accounts for the lack of statistical effect from the fire variables for seed numbers for several of our taxa and groups, despite the raw data (tables 4, 5, 7, 8) suggesting stronger patterns. For example, the low mean abundance of *A. humifusum* seed in the areas with the longest time elapsed since fire (table 5) may be largely an artefact of its inability to survive in wet eucalypt forest.

The lack of influence in the models of the vegetation types, while floristic groups were shown to have some influence, suggests that longer term influences, such as environment and the integral of fire history, have more effect on the soil seed store than the structural-dominance vegetation types present at a particular time.

After accounting for the vegetation effect, we were able to demonstrate some strong associations between frequent and recent fire and low numbers and low viability of soil-stored seed. Native seeds in the soil, predominantly comprised of *A. humifusum* and *E. cupressiformis*, declined with increasing number of fires and decreasing time-since-fire (tables 3, 4, 5). These results complement the findings of previous studies that show a depletion of the soil seed store by fire (e.g., Meney *et al.* 1994, Pierce & Cowling 1991, Wilkinson & Jennings 1994). Our results show that the number of large native seeds in the soil is markedly lower in 17-year-old-burn sites compared to 45-year-old burn sites. These findings are very different to those of Koch *et al.* (2009), who reported recovery of the soil seed store within three years after fire, and a decline thereafter.

One explanation for the associations observed in the present study is the breaking of dormancy by heat or the chemicals in smoke. Non-viable seed accumulates after most soil seed germinates. Heat-initiated germination has been observed for *Lepidosperma* (Penman *et al.* 2008) and *Acacia* (Fryer 2006). Several species of *Astroloma* also respond to smoke as a germination cue (Fryer 2006), although this response has not been confirmed for *A. humifusum*. Our viability data strongly suggest that germination of *A.*

**TABLE 2**  
Mean number of seeds  $\pm$  standard error (n) per 900 g (dry weight) soil at collection sites with and without plant taxa present in the above ground vegetation

| Species                         | Present            | Absent               | F value | P value |
|---------------------------------|--------------------|----------------------|---------|---------|
| <i>Astroloma humifusum</i>      | 7.9 $\pm$ 1.6 (26) | 7.2 $\pm$ 1.3 (34)   | 0.10    | 0.749   |
| <i>Beyeria viscosa</i>          | 2.5 $\pm$ 0.6 (25) | <0.1 $\pm$ 0.03 (35) | 21.98   | <0.001  |
| <i>Dodonea viscosa</i>          | 1.4 $\pm$ 0.5 (44) | 0.7 $\pm$ 0.3 (16)   | 0.70    | 0.405   |
| <i>Exocarpos cupressiformis</i> | 7.4 $\pm$ 3.6 (20) | 3.6 $\pm$ 1.8 (40)   | 1.17    | 0.285   |
| <i>Lepidosperma laterale</i>    | 0.4 $\pm$ 0.2 (28) | 1.0 $\pm$ 0.7 (32)   | 0.58    | 0.449   |
| <i>Rubus fruticosus</i>         | 0.0 $\pm$ 0.0 (57) | 0.7 $\pm$ 0.2 (3)    | 0.58    | 0.450   |

**TABLE 3**  
Results of general linear model analyses for seed number

| Response/fixed variable                | Fixed variable |                  | Random variables |       |                 |                  | R <sup>2</sup> (%) |
|--|----------------|------------------|------------------|-------|-----------------|------------------|--------------------|
|  | F              | P                | Vegetation type  |       | Floristic group |                  |                    |
|  |                |                  | F                | P     | F               | P                |                    |
| Native/fires <sup>1</sup>              | 6.01           | <b>0.001</b>     | 1.43             | 0.239 | 3.29            | <b>0.019</b>     | 59.26              |
| Native/tsf <sup>2</sup>                | 5.30           | <b>0.001</b>     | 0.91             | 0.464 | 4.23            | <b>0.005</b>     | 57.58              |
| Exotic/fires                           | 4.99           | <b>0.002</b>     | 0.72             | 0.583 | 2.05            | 0.103            | 45.82              |
| Exotic/tsf                             | 4.98           | <b>0.002</b>     | 0.91             | 0.464 | 2.89            | <b>0.032</b>     | 45.79              |
| <i>Acacia</i> spp./fires               | 0.88           | 0.485            | 0.32             | 0.865 | 0.83            | 0.511            | 18.18              |
| <i>Acacia</i> spp./tsf                 | 0.89           | 0.476            | 0.33             | 0.857 | 0.91            | 0.463            | 18.28              |
| <i>Astroloma humifusum</i> /fires      | 3.29           | <b>0.019</b>     | 2.16             | 0.088 | 0.79            | 0.541            | 33.16              |
| <i>Astroloma humifusum</i> /tsf        | 1.67           | 0.174            | 0.93             | 0.454 | 0.59            | 0.674            | 25.07              |
| <i>Beyeria viscosa</i> /fires          | 1.58           | 0.195            | 0.09             | 0.984 | 0.95            | 0.441            | 49.94              |
| <i>Beyeria viscosa</i> /tsf            | 1.56           | 0.201            | 0.07             | 0.991 | 0.94            | 0.451            | 49.84              |
| <i>Dodonea viscosa</i> /fires          | 1.96           | 0.115            | 1.05             | 0.392 | 3.44            | <b>0.015</b>     | 56.26              |
| <i>Dodonea viscosa</i> /tsf            | 1.91           | 0.125            | 1.18             | 0.332 | 6.29            | <b>&lt;0.001</b> | 56.07              |
| <i>Exocarpos cupressiformis</i> /fires | 6.21           | <b>&lt;0.001</b> | 0.07             | 0.992 | 1.69            | 0.168            | 52.16              |
| <i>Exocarpos cupressiformis</i> /tsf   | 6.21           | <b>&lt;0.001</b> | 0.08             | 0.989 | 1.89            | 0.128            | 52.17              |
| <i>Lepidosperma laterale</i> /fires    | 0.81           | 0.527            | 0.04             | 0.997 | 1.44            | 0.235            | 21.82              |
| <i>Lepidosperma laterale</i> /tsf      | 0.83           | 0.513            | 0.05             | 0.995 | 1.44            | 0.237            | 21.95              |
| <i>Rubus fruticosus</i> /fires         | 2.67           | <b>0.044</b>     | 1.05             | 0.394 | 2.03            | 0.105            | 48.72              |
| <i>Rubus fruticosus</i> /tsf           | 2.48           | 0.057            | 0.89             | 0.476 | 2.91            | <b>0.031</b>     | 48.04              |

<sup>1</sup> Fires = number of fires since 1960, <sup>2</sup> tsf = time since last fire.

**TABLE 4**  
Means and standard errors for seed number related to number of fires (1960–2012)

| No. of fires | n  | Native            | Exotic           | <i>A. humifusum</i> | <i>E. cupressiformis</i> | <i>R. fruticosus</i> |
|--------------|----|-------------------|------------------|---------------------|--------------------------|----------------------|
| 0            | 10 | 35.5 $\pm$ 9.1 A  | 12.2 $\pm$ 9.9 A | 3.4 $\pm$ 1.9 A     | 23.3 $\pm$ 7.7 A         | 1.2 $\pm$ 0.6 AB     |
| 1            | 10 | 22.3 $\pm$ 5.3 AB | 3.8 $\pm$ 1.4 A  | 11.5 $\pm$ 3.0 A    | 4.1 $\pm$ 1.9 B          | 2.4 $\pm$ 0.9 A      |
| 2            | 10 | 14.7 $\pm$ 2.0 B  | 0.7 $\pm$ 0.4 A  | 10.1 $\pm$ 2.1 A    | 1.2 $\pm$ 0.5 B          | 0.6 $\pm$ 0.3 AB     |
| 3            | 20 | 9.30 $\pm$ 1.8 B  | 0.5 $\pm$ 0.2 A  | 7.3 $\pm$ 1.8 A     | 0.4 $\pm$ 0.2 B          | 0.0 $\pm$ 0.0 B      |
| 5            | 10 | 6.10 $\pm$ 1.9 B  | 0.4 $\pm$ 0.2 A  | 5.4 $\pm$ 1.7 A     | 0.0 $\pm$ 0.0 B          | 0.1 $\pm$ 0.1 B      |

**TABLE 5**  
Means and standard errors for seed number related to time-since-fire

| Time-since-fire (years) | n  | Native        | Exotic       | <i>E. cupressiformis</i> |
|-------------------------|----|---------------|--------------|--------------------------|
| c. 60                   | 10 | 35.5 ± 9.1 A  | 12.2 ± 9.9 A | 23.3 ± 7.7 A             |
| 45                      | 10 | 22.3 ± 5.3 AB | 3.8 ± 1.4 A  | 4.1 ± 1.9 B              |
| 17                      | 20 | 12.1 ± 1.9 B  | 0.6 ± 0.2 A  | 0.7 ± 0.3 B              |
| 14                      | 10 | 9.0 ± 2.0 B   | 0.4 ± 0.3 A  | 0.6 ± 0.3 B              |
| 6                       | 20 | 6.1 ± 1.9 B   | 0.4 ± 0.2 A  | 0.0 ± 0.0 B              |

**TABLE 6**  
Results of general linear model analyses for the viability (%) of seed of selected species

| Response/fixed variable                | Fixed variable |              | Random variables |       |                 |                  | R <sup>2</sup> (%) |
|--|----------------|--------------|------------------|-------|-----------------|------------------|--------------------|
|  | F              | P            | Vegetation type  |       | Floristic group |                  |                    |
|  |                |              | F                | P     | F               | P                |                    |
| Native/fires <sup>1</sup>              | 1.33           | 0.275        | 0.17             | 0.953 | 5.81            | <b>0.001</b>     | 71.06              |
| Native/tsf <sup>2</sup>                | 1.33           | 0.275        | 0.19             | 0.942 | 6.46            | <b>&lt;0.001</b> | 71.02              |
| <i>Acacia</i> spp./fires               | 0.28           | 0.883        | 0.56             | 0.696 | 0.67            | 0.616            | 20.07              |
| <i>Acacia</i> spp./tsf                 | 0.82           | 0.554        | 0.59             | 0.671 | 0.72            | 0.584            | 20.37              |
| <i>Astroloma humifusum</i> /fires      | 3.48           | <b>0.016</b> | 0.28             | 0.889 | 2.01            | 0.109            | 30.58              |
| <i>Astroloma humifusum</i> /tsf        | 3.60           | <b>0.014</b> | 0.85             | 0.438 | 2.19            | 0.084            | 32.72              |
| <i>Exocarpos cupressiformis</i> /fires | 0.41           | 0.746        | 0.06             | 0.992 | 2.76            | <b>0.038</b>     | 69.78              |
| <i>Exocarpos cupressiformis</i> /tsf   | 0.41           | 0.746        | 0.06             | 0.993 | 2.76            | <b>0.038</b>     | 69.84              |

<sup>1</sup> Number of fires since 1960, <sup>2</sup> tsf = time since last fire.

**TABLE 7**  
Means and standard errors (n) of seed viability (%) related to number of fires (1960–2012)

| No. of fires | <i>A. humifusum</i> | <i>Acacia</i> spp. | <i>B. viscosa</i> | <i>D. viscosa</i> | <i>E. cupressiformis</i> | Natives            |
|--------------|---------------------|--------------------|-------------------|-------------------|--------------------------|--------------------|
| 0            | 53.3 ± 17.4 (7) A   | 81.9 ± 11.9 (4) A  | 60.9 ± 13.0 (9) A | 100.0 ± 0.0 (8) A | 31.7 ± 6.8 (10) A        | 46.8 ± 7.7 (10) A  |
| 1            | 24.0 ± 7.2 (10) AB  | 90.0 ± 10.0 (4) A  | 63.1 ± 15.0 (8) A | 74.1 ± 14.0 (7) A | 28.3 ± 10.0 (8) A        | 36.9 ± 6.6 (10) AB |
| 2            | 19.8 ± 5.2 (10) B   | 75.0 ± 25.0 (4) A  | –                 | 70.6 ± 16.1 (6) A | 28.6 ± 18.4 (7) A        | 33.0 ± 4.9 (10) AB |
| 3            | 13.7 ± 3.4 (16) B   | 66.7 ± 23.6 (4) A  | –                 | 100.0 ± 0.0 (4) A | 0.0 ± 0.0 (3) A          | 19.7 ± 6.0 (19) B  |
| 5            | 6.2 ± 6.2 (8) B     | 66.7 ± 33.3 (3) A  | –                 | 100.0 ± 0.0 (1) A | –                        | 13.9 ± 6.7 (8) B   |

**TABLE 8**  
Means and standard errors (n) of seed viability (%) related to time-since-fire (years)

| Time-since-fire | <i>A. humifusum</i> | <i>Acacia</i> spp. | <i>B. viscosa</i> | <i>D. viscosa</i>  | <i>E. cupressiformis</i> | Natives            |
|-----------------|---------------------|--------------------|-------------------|--------------------|--------------------------|--------------------|
| 50              | 53.3 ± 17.4 (7) A   | 81.9 ± 11.9 (4) A  | 60.9 ± 13.0 (9) A | 100.0 ± 0.0 (8) A  | 31.7 ± 6.8 (10) A        | 46.8 ± 7.7 (10) A  |
| 45              | 24.0 ± 7.2 (10) AB  | 90.0 ± 10.0 (4) A  | 63.1 ± 15.0 (8) A | 74.1 ± 14.0 (7) A  | 28.3 ± 10.0 (8) A        | 36.9 ± 6.6 (10) AB |
| 17              | 19.2 ± 3.7 (17) B   | 77.8 ± 16.5 (6) A  | –                 | 82.4 ± 10.4 (10) A | 28.6 ± 18.4 (7) A        | 31.6 ± 5.6 (19) AB |
| 14              | 10.2 ± 3.9 (9) B    | 50.0 ± 50.0 (2) A  | –                 | –                  | 0.0 ± 0.0 (3) A          | 10.5 ± 4.5 (10) B  |
| 6               | 6.2 ± 6.2 (8) B     | 66.7 ± 33.3 (3) A  | –                 | 100.0 ± 0.0 (1) A  | –                        | 13.9 ± 6.7 (8) B   |

*humifusum* is stimulated by fire. Hodgkinson & Oxley (1990) found that germinability in *D. viscosa* increased when placed in boiling water for five seconds, but seed was killed by slow burning litter fires when temperatures exceeded 80°C.

Species that do not germinate in response to fire, like *E. cupressiformis*, could lose soil seed through overheating. However, the effect of reduction in seed input consequent upon cessation of reproductive activity while individuals recover vegetatively from fire may be a more substantial influence on seed numbers. *Exocarpos cupressiformis* and *D. viscosa* are heavily grazed by macropods (JBK, personal observation), which may inhibit their establishment after fires create green pick. Infrequently burned areas have greater densities of these species than more frequently burned areas. Purdie & Slatyer (1976) note that post-burn populations of *A. humifusum* are smaller than pre-burn populations, therefore the decrease in seed numbers for this species may also be related to smaller population sizes in more frequently burnt areas. More frequent fires equate to shorter inter-fire intervals. Therefore, insufficient time to set seed may explain low seed abundance. To allow successful flowering and seed set, Benson (1985) recommends a minimum fire-free period of nine to 10 years for eucalypt-dominated scleromorph vegetation.

Bekker *et al.* (1998) found a strong negative correlation between seed longevity and the depth distribution of seeds, indicating that seed longevity is reduced in the surface layer. The heat associated with fire destroys organic matter (Humphreys & Craig 1981) and contributes to deterioration of porosity and increased erosivity (Certini 2005). Thus fire can be linked to soil compaction and reduced incorporation of seeds into the soil. This may partially explain the reduced viability in native and *A. humifusum* seeds in the areas burnt more frequently. That *Acacia* and *D. viscosa* were not affected in a similar manner may be explained by the dispersal of *Acacia* seeds into lower soil layers by ants, and by the small size of *D. viscosa* seeds, as smaller seeds are more likely to work their way down soil cracks (Bekker *et al.* 1998).

The conservation significance of the fire-related seed bank dynamics intimated by our data varies between the obligate seeder species and those with capacity for vegetative recovery from disturbance. As resprouters, as well as contributors to a persistent seed bank, species such as *E. cupressiformis* and *A. humifusum* are doubly buffered against disturbance or the lack thereof. Thus, *A. humifusum* can survive fire by resprouting, and survive elimination in the vegetation by light competition through its soil seed store, whereas the obligate seed regenerators *D. viscosa* and *B. viscosa* might be eliminated from an area if frequent fires exhaust their seed banks. Our data suggest that at least one major weed species, *R. fruticosus*, builds up its seed store as time elapses after fire. Such a mechanism may account for the prominence of exotic shrubs in long unburnt bush (Watson *et al.* 2009). There may thus be a tradeoff between maintaining obligate seeding natives and mitigating weed invasion. In the case of our study area, an interval between fires of less than 11 years is likely to lead to the elimination of *D. viscosa*, which takes this time after germination to release seed into the soil store (JBK, personal observation).

## CONCLUSION

Ours is the first study of the effects of fire history on the soil seed bank of large-seeded geosporous species in a Tasmanian scleromorph ecosystem. Out of six native large-seeded species the abundance of two species, *Astroloma humifusum* and *Exocarpos cupressiformis*, generally declined in the seedbank with more frequent and recent fire. This may be due to germination triggered by fire, selection against these species by fire, insufficient maturation periods between fire and reduced total seed output and population size due to repeated burning. A significant reduction in seed viability in natives and *A. humifusum* was also related to fire history, possibly reflecting loss of viable seed to germination.

## ACKNOWLEDGEMENTS

We thank Jon Marsden-Smedley for assistance with mapping.

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(accepted 5 November 2013)

## APPENDIX 1

### Characteristics of seed types

| Species                                   | Description   |
|---|---|
| <i>Exocarpos cupressiformis</i>           | ovoid and dark brown, with three suture lines on top  |
| <i>Dodonea viscosa</i>                    | globular, black and shiny, with a flattened rim (pl. 1F)  |
| <i>Astroloma humifusum</i>                | trigonal seeds contained within a woody, multi-chambered, ellipsoid capsule with longitudinal furrows (pl. 1D)              |
| <i>Lepidosperma laterale</i>              | ellipsoid with brown casing, white when casing removed, and with a capitate embryo (pl. 2F)                                 |
| <i>Beyeria viscosa</i>                    | oblong with a flat face at the attachment end (pl. 1E)  |
| <i>Acacia</i> spp.                        | seeds variably black, shiny, obovate or oblong (pl. 1A–C)   |
| <i>Rubus fruticosus</i>                   | triangular and flattened along radial axis, tan to light brown, with a reticulate surface                                   |
| <i>Passiflora tarminiana</i> <sup>1</sup> | cordiform, dark brown, with a pitted surface (pl. 2D)   |
| <i>Vicia</i> sp. <sup>1</sup>             | globular with a smooth speckled brown and green surface, and a distinctive hilum (pl. 2E)                                   |
| <i>Galium</i> sp. <sup>1</sup>            | spheroidal, dark brown, with finely netted ridges and a deeply depressed hilum (pl. 2C)                                     |
| <i>Plantago</i> sp. <sup>1</sup>          | elongate, with longitudinal faces and characteristic side-attachment (pl. 2A)   |
| <i>Cotoneaster</i> sp. <sup>1</sup>       | ovate, widest at the attachment end, with one flattened face, light brown to tan, with some retaining the peduncle (pl. 2B) |
| exotic seed 1 <sup>1</sup>                | variably spheroid, woody, with a single chamber   |
| exotic seed 2 <sup>1</sup>                | large, woody, with the two halves overlapping   |

<sup>1</sup> exotic taxon



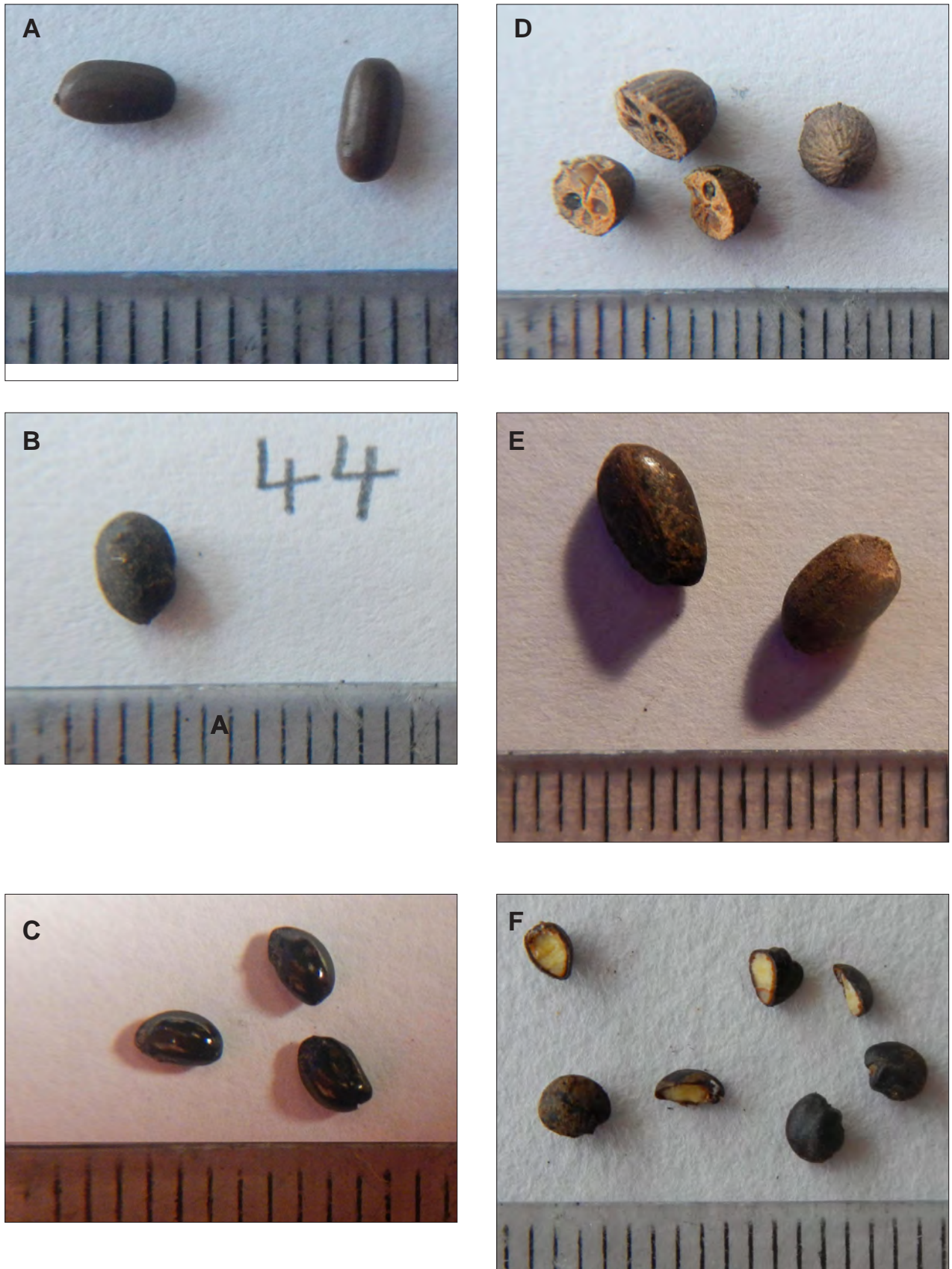


PLATE 1  
(A) *Acacia sp. 1*; (B) *Acacia sp. 2*; (C) *Acacia sp. 3*; (D) *Astroloma humifusum*; (E) *Beyeria viscosa*;  
(F) *Dodonea viscosa*. Scales in millimetres.

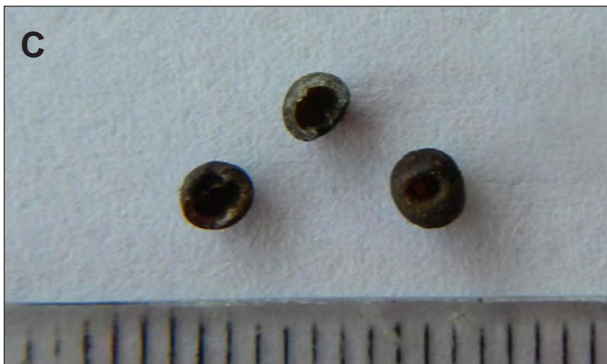
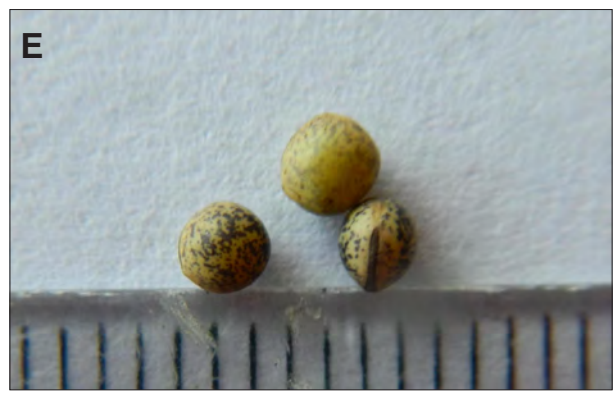
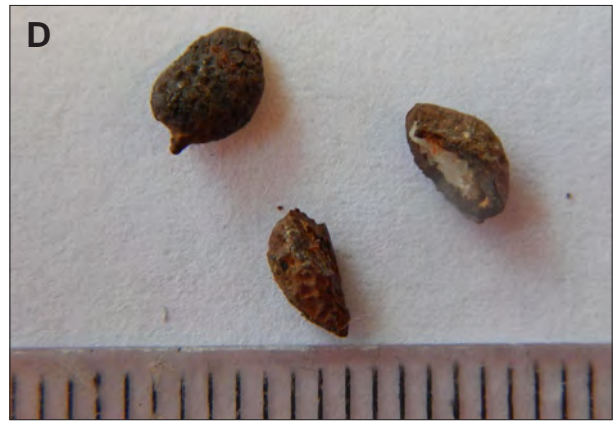


PLATE 2

(A) *Plantago lanceolata*; (B) *Cotoneaster sp.*; (C) *Galium sp.*; (D) *Passiflora tarminiana*; (E) *Vicia sp.*; (F) *Lepidosperma laterale*. Scales in millimetres.