

Viewpoint

# Using a Multi-Century Post-Fire Chronosequence to Develop Criteria to Distinguish Prior and Bowman's (2020) Post-Fire Obligate Coloniser and Fire-Intolerant Flora

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**Abstract:** Prior and Bowman added a new dimension to existing frameworks of post-fire responses of woody plants, by including the trait of colonisation ability (C) for those taxa which neither resprout ( $R_{f-}$ ) nor produce seedlings ( $S_{f-}$ ) after fire. Specifically, they recognised distinctions between: (i) post-fire obligate colonisers, being species that neither resprout nor produce seedlings from persistent seed banks post-fire but are able to colonise burnt areas through dispersal from unburnt populations, and (ii) fire-intolerant, which are unable to recover after fire by either resprouting, seeding or colonisation. We use data on temporal and spatial patterns of colonisation of  $R_{f-}S_{f-}$  mistletoes from a chronosequence study with an exceptionally long span of times since fire as a practical example of the delineation of post-fire obligate coloniser and fire-intolerant species. We propose that when a population of a species is burnt, if the species is unable to regularly colonise and reach reproductive maturity in burnt areas spatially distant from fire edges within plausible and regularly-occurring maximum fire-return intervals for the now-burnt community type, it would be classified as fire-intolerant. In our examples, *Lysiana* meets the criteria for fire-intolerant in obligate-seeder eucalypt woodland, while *Amyema* is classed as a post-fire obligate coloniser.

**Keywords:** fire-response trait; obligate seeder; temperate eucalypt woodland; mistletoe; resprouter

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Prior and Bowman [1] added a new dimension to existing frameworks of post-fire responses of woody plants [2,3]. Building on Pausas and Keeley's [2] post-fire coloniser strategy for those taxa which neither resprout ( $R_{f-}$ ) nor produce seedlings ( $S_{f-}$ ) after a fire, Prior and Bowman [1] included colonisation ability (C) as a trait. Specifically, Prior and Bowman [1] recognised distinctions between: (i) post-fire obligate colonisers ( $R_{f-}S_{f-}C+$ ; using the notation of [1]), being species that neither resprout nor produce seedlings from persistent seed banks post-fire but can colonise burnt areas through dispersal from unburnt populations; and (ii) fire-intolerant ( $R_{f-}S_{f-}C-$ ), which are unable to recover after a fire by either resprouting, seeding or colonisation. We agree this is an important conceptual advance in understanding and predicting the impact of fire on ecosystems, which is particularly timely given the recent extensive penetration of fire into ecosystems which rarely burn [4,5], and contain floras that lack mechanisms to persist after burning at the individual and/or population level (i.e., not  $R_{f+}S_{f-}$ ,  $R_{f+}S_{f+}$ ,  $R_{f-}S_{f+}$ ) [3,6].

Prior and Bowman [1] illustrate fire-intolerant species through examples of several Australian conifers. However, they do not proffer any examples of post-fire obligate colonisers. Practical application of the novel Prior and Bowman [1] classification could be improved by operational criteria to distinguish

between post-fire obligate colonisers and fire-intolerant species beyond the binary and unquantified notion of being able or unable to readily colonise burnt areas after a fire. We suggest that  $R_f-S_f-$  species that reproduce by seed and/or vegetative spread can colonise otherwise suitable burnt areas if there is sufficient time without fire and unburnt populations are not separated from burnt populations by insurmountable dispersal barriers. Colonisation is thus inherently defined by spatial and temporal criteria. We use data on temporal and spatial patterns of colonisation of  $R_f-S_f-$  species from a chronosequence study with an exceptionally long span of times since fire [7] as a practical example of the delineation of post-fire obligate colonisers and fire-intolerant species.

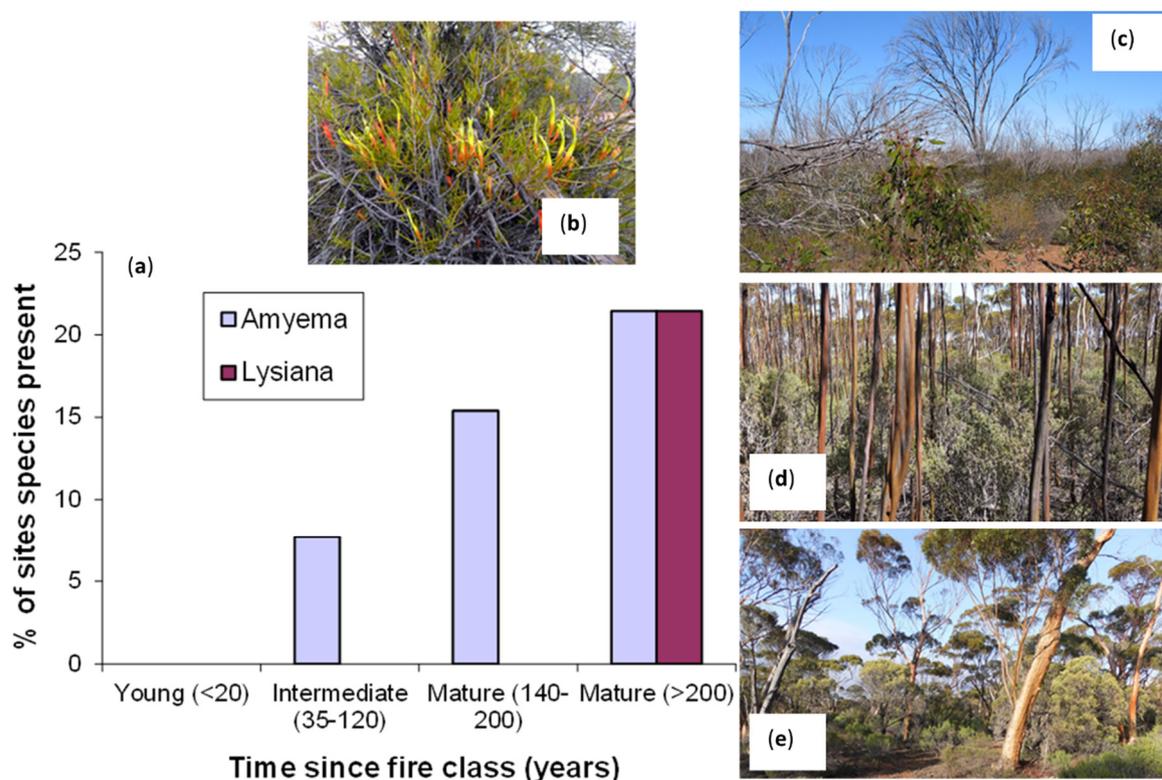
Obligate-seeder eucalypt woodlands of semi-arid south-western Australia have historically burnt infrequently despite regular severe fire weather, with mature woodlands having low flammability due primarily to discontinuous distribution of litter and vegetation [8,9]. Plant richness in obligate-seeder eucalypt woodlands shows a 'U'-shaped response to time since fire, with increased rates of occurrence in long-unburnt woodlands of a range of non-woody species and a small number of woody species without traits enabling persistence as individuals or populations through fire ( $R_f-S_f-$ ) [7,10]. Using data from the 72 50 × 50 m plots distributed across a ~400-year time since fire chronosequence of Gosper and co-workers [7,11], we examine the spatial and temporal patterns of colonisation by exemplar  $R_f-S_f-$  taxa, the mistletoes *Amyema miquelii* and *Lysiana casuarinae*. Both stem parasitic mistletoes are killed by fire and lack persistent seed banks, have fleshy fruits adapted to endozoochorous dispersal by birds, and have typical local hosts of canopy *Eucalyptus* and understorey *Acacia* and *Exocarpos*, respectively [3,12,13].

*Lysiana* was absent from all sites <200 years post-fire but was present at ~20% of sites unburnt for >200 years (Figure 1). *Amyema* was absent from young (<35 years since fire; delineation of 'young' and 'intermediate' age classes follows [7]) sites, and then showed an increasing frequency of occurrence with time since fire thereafter. *Amyema* occurrences at intermediate-aged (35–120 years) sites were relatively close (<200 m) to long-unburnt woodlands. This spatial pattern of occurrence raises the prospect that colonisation was initially facilitated by proximity to the fire edge (and presumably extant individuals, although we have no data on distance to extant individuals), perhaps due to short-distance seed dispersal [14]. Either dispersal (associated with often large fire size combined with disperser behaviour [14–16]) or recruitment (associated with changes in post-fire obligate-seeder host stature and community structure in regenerating woodlands [9,17]) limitations are plausible in explaining mistletoe absence from young and most intermediate-aged woodlands. If recruitment opportunities are the limiting factor, then post-fire mistletoe recolonisation, even after a crown fire, may be much more rapid in ecosystems dominated by epicormically-resprouting hosts.

These examples suggest that both spatial and temporal processes are important and should be considered in the criteria informing colonisation ability. Furthermore, the time-period that species have to recolonise burnt areas before the next fire and the spatial distances over which recolonisation needs to occur will vary between ecosystems in relation to their fire regime. Thus, an individual species may be able to reliably recolonise after fires in one community type but not another. The continuum of responses in colonisation ability between populations within species and between species is not dissimilar to continuous variation in resprouting and seeding ability [3,18]. In studies and databases aggregating plant fire-response traits in binary categories, we note the importance of explicitly defining the criteria used and having database functionality to capture data at a population and fire event level.

We propose that when a population of a species is burnt, if the species is unable to regularly colonise and reach reproductive maturity in burnt areas spatially distant (>~100 metres) from fire edges within plausible and regularly-occurring maximum fire-return intervals for the now-burnt community type, it would be classified as fire-intolerant. In our examples, both mistletoes can recolonise burnt woodlands if given enough time. However, analysis of recent fire regimes in obligate-seeder woodlands show that there is little prospect of burnt woodlands eluding fire for the >200 years required for recolonisation of *Lysiana* [8]. *Lysiana*, therefore, would be classified as fire-intolerant ( $R_f-S_f-C-$ ) in obligate-seeder woodlands. *Amyema* was able to recolonise at around the modelled

maximum fire return interval for regenerating obligate-seeder woodlands of just beyond 100 years [8]. Thus, this species could be classed as a post-fire obligate coloniser ( $R_f-S_f-C+$ ), noting that the marginal spatial and temporal capacity to recolonise burnt areas according to our definition suggests that populations will become increasingly restricted to fire refugia such as around salt lakes [8] as fires continue to erode the extent of mature obligate-seeder eucalypt woodlands [17,19,20].



**Figure 1.** (a) Occurrence of two mistletoes unable to resprout or recruit from persistent seed banks after a fire in plots in time since fire chronosequence in obligate-seeder eucalypt woodlands. Plot time since fire follows Gosper and co-workers [7], using the conservative model 2 method; (b) *Lysiana casuarinae* on a host *Exocarpos*; (c–e) obligate-seeder eucalypt woodland at (c) young (<20 years); (d) intermediate (35–120); and (e) mature (>200 years) stages of post-fire succession. Photos: Carl Gosper.

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