The role of species composition in the emergence of alternate vegetation states in a temperate rainforest system

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Abstract
Context Forest systems are dynamic and can alternate between alternative stable states in response to climate, disturbance and internal abiotic and biotic conditions. Switching between states depends on the crossing of critical thresholds and the establishment of feedbacks that drive (and maintain) changes in ecosystem functioning. The nature of these thresholds and the workings of these feedbacks have been well-researched, however, the factors that instigate movement toward and across a threshold remain poorly understood.

Objectives In this paper, we explore the role of species composition in initiating ecosystem state change in a temperate landscape mosaic of fire-prone and fire-sensitive vegetation systems.

Methods We construct two 12-kyr palaeoecological records from two proximal (230 m apart) sites in Tasmania, Australia, and apply the Alternative Stable States model as a framework to investigate ecosystem feedbacks and resilience threshold dynamics.

Results Our results indicate that, in this system, invasion by pyrogenic Eucalyptus species is a key factor in breaking down negative (stabilising) feedbacks that maintain pyrophobic sub-alpine rainforest.

Conclusions We conclude that the emergence of an alternative stable pyrogenic state in these relic rainforest systems depends on the extent of pyrophytic species within the system. These findings are critical for understanding resilience in forest ecosystems under future climate and land management changes and are relevant to fire-adapted cool-temperate ecosystems globally.

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Keywords  Alternative stable states · Critical transitions · *Eucalyptus* · Rainforest · Resilience · Tasmania

**Introduction**

Critical transitions, or catastrophic regime shifts between ecosystem states are of profound importance, given that they are often sudden, unpredicted and can substantially alter important ecosystem functions and services (Folke et al. 2004). Critical transitions between alternative stable ecosystem states occur when an ecosystem has multiple potential stable states that are separated by unstable equilibria (Scheffer et al. 2001; Iglesias and Whitlock 2020). The emergence of alternative stable ecosystem states is induced by feedbacks between the state of the system and limiting environmental factors, such as climate, disturbance, soil moisture conditions or nutrient loading (Borgogno et al. 2007). A considerable body of literature focusses on the feedback loops that hold an ecosystem in a stable state (Warman and Moles 2009; Wood and Bowman 2012), and on the various thresholds that must be crossed to tip an ecosystem into a new state (Scheffer and Carpenter 2003; Scheffer et al. 2012). In contrast, comparatively little attention has been paid to the factors required to initiate a switch between stable states. Once an environmental and/or disturbance threshold has been crossed, factors such as the presence or absence of species can initiate a positive feedback switch that modifies the local environment in such a way that favours the new community/species (Wilson and Agnew 1992; Borgogno et al. 2007).

Where multiple (alternative) stable states exist, a change in environmental conditions can influence ecosystem dynamics and increase the response time of an ecosystem to repeated disturbance events (Scheffer et al. 2009, 2012). Conceptually, this critical slowing down of recovery time is a product of a shallowing basin of attraction that brings the system closer to a critical threshold (or bifurcation point), which increases the potential of a switch between alternate stable states in response to further environmental change, perturbation(s) and/or internal ecosystem dynamics (Scheffer et al. 2009; Enright et al. 2015; Iglesias and Whitlock 2020). A shift between alternative states occurs when species required for the self-maintenance of one state are removed and new species arrive that initiate a switch to an alternative state. If the new species assemblage is capable of self-maintenance for more than one generation, a switch to a new stable state has occurred (Connell and Sousa 1983; Petraitis and Latham 1999; Scheffer et al. 2001; Scheffer and Carpenter 2003). Thus, it can be postulated that in the absence of species that initiate a feedback switch, that either crossing a critical environmental and/or disturbance (e.g. fire, moisture, edaphic etc.) threshold alone will be insufficient to drive a critical transition between alternative stable states (Wilson and Agnew 1992; Borgogno et al. 2007), that no threshold is present or that the alternate basin of attraction does not exist (i.e. has not yet emerged).

Transitions between pyrophobic and pyrophytic vegetation states can be spatially and temporally abrupt and are often viewed through the alternative stable states model (Warman and Moles 2009; Odion et al. 2010; Wood and Bowman 2012). These antagonistic vegetation states are maintained by clear and directly opposing feedback mechanisms: pyrophobic species tend to have low flammability and can reproduce in the absence of fire, while pyrophytic species often promote fire and reproduction is often stimulated by (or even dependent on) fire (Fig. 1). Transitions between pyrophobic and pyrophytic vegetation states mainly occur when moisture or fire thresholds are crossed that interrupt the internal feedbacks in each state (e.g. burning of rainforest can facilitate the establishment of fire-promoting species that increase the probability of subsequent burning) (Warman and Moles 2009). Importantly, conceptual models of pyrophytic–pyrophobic vegetation systems principally focus on thresholds of environmental change and/or disturbance frequency, and the presence or absence of species capable of initiating a positive feedback switch is often overlooked (Warman and Moles 2009; Wood and Bowman 2012; Bowman et al. 2015). Here, we aim to identify what role species composition plays in the initiation and maintenance of a switch from a pyrophobic to pyrophytic vegetation state.

Understanding the factors involved in both the maintenance of alternative stable states and the initiation of a switch between potential states is critical for sustainable, effective and efficient
ecosystem management. For example, attempts to mitigate against the potential loss of vulnerable ecosystems to climate-driven wildfires comes at an enormous financial cost (Cochrane 2003; Gill et al. 2013) and the relative lack of understanding of how post-fire changes in species composition either facilitate or mitigate ecosystem state shifts exposes a critical knowledge gap in this endeavour (Bowman et al. 2015; Holz et al. 2015). Given the long generational times in many terrestrial ecosystems, gathering sufficient temporal data to understand the cumulative impact of repeated disturbance, interrogate notions of stability, and assess the factors involved in critical transitions is challenging (Petraitis and Dudgeon 2004; Fletcher et al. 2014). It is here that palaeoecological data represents a powerful means of understanding long-term ecosystem dynamics (Willis and Birks 2006). In this paper, we use high-resolution palaeoecological data from two sediment sequences to investigate the roles of climatic change, disturbance, and species composition in the transition between pyrophytic and pyrophobic vegetation states in a cool temperate forest system.

We exploit a unique natural experiment by analysing archives of long-term vegetation and fire changes stored in the sediments of two small and adjacent lakes (230 m apart) within a temperate forest landscape in Tasmania, Australia. Tasmania’s south and west are home to the largest remaining tracts of cool temperate rainforest in Australia. While this perennially wet landscape is ideal for the development of temperate rainforest (Jackson 1968), a landscape-scale decoupling of vegetation and climate has resulted in the predominance of pyrogenic vegetation as a result of the long-term (≥40,000–year) application of fire by Indigenous people (Fletcher and Thomas 2010; Mariani et al. 2017). As a result, rainforest is currently restricted to major low-altitude water courses and tiny topographic fire refugia, which, in this topographically complex landscape, are steep south-facing mountain slopes (Wood et al. 2011). Catastrophic wildfires have threatened these vegetation systems in recent years.

Fig. 1 Conceptual model of the feedbacks within pyrophobic and pyrophytic vegetation states, based on Wood and Bowman (2012). Grey shading and dashed lines indicate the hypothesised role of species capable of initiating a positive feedback switch between vegetation states (sensu Wilson and Agnew 1992). Thresholds of moisture and fire are drawn from Warman and Moles (2009).
(particularly the 2016 and 2019 fire seasons) and an understanding the potential feedbacks between climate, vegetation composition and fire in these rainforest systems is critical for their long-term survival. These forests house endangered subalpine endemics such as Nothofagus gunnii and Athrotaxis spp.—the latter of which has experienced more than 30% range contraction driven by fire-regime changes since the removal of Indigenous fire management by the British in the late 1700s (Cullen 1987, 1991; Holz et al. 2015).

The extreme flammability of Eucalyptus species and their ability to alter local fire regimes by initiating a positive feedback switch is well known (Wilson and Agnew 1992; Williams and Woinarski 1997; Bowman 2000). Many Eucalyptus species maintain physiological traits that facilitate recovery from fire, such as reserve (lignotuber) and epicormic budding, heat-tolerant bark, post-fire seed germination and rapid, light-tolerant seedling growth (Gill 1975). Eucalyptus communities can also actively encourage higher fire frequencies by increasing fine-fuel loads, decreasing sub-canopy humidity, and supporting the proliferation of flammable understorey species (Brooks et al. 2004; Bowman 2000). In Tasmania, a synergistic relationship between climate and the extreme pyrophytic nature of Eucalyptus is implicated in the conversion of rainforest communities to eucalypt forest (Gilbert 1959; Jackson 1968). Recurrent infrequent fires and associated post-fire increases in Eucalyptus and other fire-promoting species are thought to facilitate critical transitions between rainforest and Eucalyptus ecosystem states (Fletcher et al. 2014; Beck et al. 2017; Cadd et al. 2019), yet this relationship has not yet been tested. Following shifts from rainforest to fire, positive feedbacks between Eucalyptus and fire are then able to maintain the new ecosystem state by altering local fire regimes (Fletcher et al. 2014).

Our study lakes are located in the south of the cool temperate island of Tasmania, Australia, a mountainous and topographically complex area that is bistable between pyrophobic rainforest and pyrophytic Eucalyptus forest. We use sedimentary charcoal to reconstruct past fires and pollen for past vegetation change over the last 12,000 years (12 ka). Tasmanian forest systems have a high biomass and fires in these systems are climate-limited, with fires occurring during anomalously dry phases. Fires in the study area are linked to El Niño-Southern Oscillation (ENSO), with an intensification of ENSO after 6 ka increasing both the likelihood and occurrence of fire in the region (Fletcher et al. 2014; Mariani and Fletcher 2016; Mariani et al. 2016; Beck et al. 2017), while also decreasing the ability of some forest types to recover post-fire (Mariani et al. 2019a, b). Here, we use a proxy dataset for changes in the frequency of El Niño events, binned to the number of events per year (Moy et al. 2002), to depict the long-term hydroclimatic trajectory over the region. We predict that repeated burning of rainforest in response to the onset of an increasingly variable climate through the last 6 kyrs will only result in a critical transition between pyrophobic and pyrophytic vegetation states if species are present that can initiate a positive feedback (such as Eucalyptus). Thus, in the absence of these species, rainforest will recover in the prolonged absence of fire, irrespective of past wildfire history.

Methods

Core collection and chronology

This paper focusses on two previously published high-resolution pollen, spore and charcoal records from the Southern Ranges in southern Tasmania, Australia: a 14,000 year (14 kyr) record from Lake Perry (43° 12′ 48″ S, 146° 45′ 16″ E; 931 masl) (Cadd et al. 2019); and a 14 kyr record from Lake Osborne (43° 12′ 53″ S, 146° 45′ 30″ E, 924 masl) (Fletcher et al. 2014, 2018). These neighbouring lakes are 230 m apart and are situated on the Hartz Range, part of a series of ranges collectively known as the Southern Ranges. The Southern Ranges were an early Holocene (ca. 10–8 ka) refugium for fire-sensitive montane rainforest—an ecosystem dominated by Athrotaxis selaginoides (Cupressaceae) and Nothofagus gunnii (Nothofagaceae), two long-lived (> 500 years) and slow-growing species endemic to Tasmania (Macphail 1979; Macphail and Colhoun 1985; Fletcher et al. 2018). Today, these ranges host some of the most extensive areas of intact montane rainforest remaining in the region. Current rainfall over the Hartz range is 971.2 mm p/a, while temperatures range from 17.6 to 1.3 °C. The current vegetation of the Hartz Range is diverse and includes areas of alpine communities, sub-alpine woodlands, scrub heath and wet Eucalyptus forest, with rainforest presently restricted to areas

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afforded protection from fire by the complex topography.

Palynology and charcoal analysis

Full details of sample resolution and chronology of the Lake Osborne and Lake Perry are contained within their respective publications (Fletcher et al. 2014, 2018; Cadd et al. 2019). Pollen, spores and microscopic charcoal were isolated from a set volume of sediment using standard techniques (Faegri and Iversen 1989). Macroscopic charcoal (> 125 μm) was isolated from a set volume of sediment in contiguous subsamples at both sites using standard techniques (Whitlock and Larsen 2001). Both sediment sequences are anchored in time using radiometric dating techniques and statistical modelling. To interpolate estimated ages (and associated errors) for each subsample analysed we used standard analytical and modelling techniques in the software package *clam* v2.3.2 for R (Blaauw 2010; Blaauw and Christen 2011).

Statistical analyses

Patterns of vegetation change at both sites were interrogated using detrended correspondence analysis (DCA) in PC-ORD 6.08 (McCune and Mefford 2011). A DCA was performed on a combined dataset of terrestrial pollen types from both lakes, with the primary ordination axes from each site extracted for further analysis. The time series plots of DCA axis 1 of each record were divided into three periods corresponding to the geological subdivision of the Holocene epoch: early Holocene 12–8 ka; mid Holocene 6–4 ka; and late Holocene 4 ka-present. We then created frequency distribution plots of the DCA axis 1 scores for each time slice at each site to understand how the dominant compositional trend compared at each site through time. We focussed on the Holocene epoch only (ca. < 12 ka), as this represents the time of establishment of essentially modern climate and vegetation composition at the sites following the end of the Last Ice Age (Fletcher et al. 2018; Cadd et al. 2019).

To test for the relationship between fire-driven shifts in montane rainforest and *Eucalyptus* pollen, we employed a two-step analytical procedure:

Step 1: Regime shift detection: the Sequential *T* test Analysis of Regime Shifts algorithm (STARS) (Rodionov 2004) was combined with classical multivariate techniques to identify statistically significant changes in the mean of the palaeoecological time series employed in this study. The algorithm was applied on a composite montane rainforest curve (comprised of Cupressaceae and *N. gunnii*), which was sorted into 5-sample bins, standardized by the mean and passed through a red noise filter (subsample size = 3). The significance value (*p*) was set to 0.001. Fire-driven regime shifts were identified as significant negative shifts in montane rainforest that occurred synchronously with charcoal peaks (see Online Resource Figure S1).

Step 2: Superposed Epoch Analysis (SEA) in R v.3.0.3 was used to identify a relationship between fire-driven shifts in montane rainforest and *Eucalyptus* pollen. To satisfy the requirements of even age steps and stationarity for the SEA, the eucalypt curves were first interpolated to 60-year age bins in both records (the median combined age interval) and the interpolated datasets were differenced (Diggle 1990) prior to running the SEA. This analysis assesses the significance of the departure from the mean for a given set of key event years and lagged years (Lough and Fritts 1987). Using the STARS-identified fire-driven montane rainforest shifts as event years (regime shifts), we tested for lagged correlation between these pollen-inferred regime shifts and *Eucalyptus* pollen. Significance was set to *p* < 0.01 in the SEA.

Results

Palynology and charcoal analysis

The full pollen and charcoal sequences can be seen in the respective publications for Lakes Osborne (Fletcher et al. 2014, 2018) and Perry (Cadd et al. 2019). Here, we present combined montane rainforest, *Eucalyptus*, macroscopic and microscopic charcoal curves for each site (Fig. 2).

Statistical analyses

The DCA biplot shows correlations between pollen taxa and the ordination axis for both Lake Perry and Lake Osborne (Online Resource Figure S2). The ordination space is organised into 4 time periods: Late Glacial 14.5–12 ka; early Holocene 12–8 ka; mid
Holocene 6–4 ka; and late Holocene 4 ka—present (Online Resource S2). Axis 1 explains 59.4% of the variation in the dataset and is strongly correlated with *N. gunnii* (negative), *Eucalyptus*, Restionaceae and *Allocasurina* (positive). Axis 2 explains 8.5% of the variance and displays a strong negative correlation with Cupressaceae. Long-term vegetation development at both sites follows the same trajectory in the ordination space between ca. 14.5–6 ka, with a clear separation of the two sites commencing at ca. 6 ka and culminating in distinct populations within the ordination space after ca. 2.6 ka (Fig. S2), with Lake Osborne pollen spectra at this time notably higher in *Eucalyptus* than Lake Perry (Fig. 2). This is evident in the frequency distribution plots of the DCA axis 1 scores over the Holocene (Figs. 3, 5), which shows overlapping populations between 12 and 8 ka, separation of the sites between 8 and 4 ka and discrete populations after 4 ka.

The STARS algorithm identified 4 negative montane rainforest shifts at Lake Perry and 4 at Lake Osborne. Visual inspection identified that all shifts at both Lake Osborne and Lake Perry correspond to charcoal peaks (Online Resource Figure S1). These shifts were interpreted as fire-driven montane rainforest shifts and were used as event years in the SEA. The results of the SEA indicate a significant positive departure of *Eucalyptus* with fire-driven montane rainforest shifts at 0-lag (i.e. 0–60 years following charcoal peaks) at Lake Osborne, while no statistically significant relationship between fire-driven montane rainforest shifts and *Eucalyptus* was observed at Lake Perry (Fig. 4).

**Discussion**

Temperate rainforest and *Eucalyptus* forest as alternative stable states

The catchments of Lakes Perry and Osborne occupy the same biophysical environment and are remarkably similar in elevation, size and overall topographic context. Establishment of montane rainforest dominated by *Nothofagus gunnii* and Cupressaceae occurred at these adjacent sites between ca. 12–8 ka in the absence of fire. Montane rainforest dominated across several nearby sites through this period.
and, collectively, indicates a stable cool and humid climate regime and low fire activity across southern Tasmania at this time (Fletcher et al. 2018). The absence of fire during this rainforest-dominated period at both Lake Osborne and Lake Perry is consistent with the stabilising feedbacks proposed for rainforest vegetation in the alternative stable states model put forward by Wood and Bowman (2012): low fuel flammability and high sub-canopy humidity of pyrophobic rainforest inhibits the occurrence of fire and allows the establishment and dominance of pyrophobic rainforest (Fig. 1).

The series of fires at both lakes between ca. 8–2.5 ka (Fig. 2) facilitated the establishment of discrete vegetation states after 2.5 ka: pyrophytic eucalypt-dominant vegetation became established at Lake Osborne, while pyrophobic (montane rainforest) vegetation persisted within the catchment of Lake Perry (Figs. 2, 3). The juxtaposition of pyrophobic rainforest and pyrophytic eucalypt forest at these adjacent sites for ca. 2.5 kyr implies that these vegetation states are stable alternatives within this landscape. The pyrophytic vegetation state is maintained by a positive feedback between fire and the

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establishment of flammable fire-promoted species (Warman and Moles 2009; Wood and Bowman 2012). The vegetation shift at Lake Osborne is accompanied by a clear shift in the charcoal signature deposited within that lake (from macroscopic to microscopic dominance; Fig. 2). While shifts in charcoal size fractions are often interpreted as changes in local versus distant source area (Whitlock and Larsen 2001), this change in charcoal signature also reflects a change in fuel biomass (see also Mariani et al. 2019a, b). Rainforests have a high woody biomass and fires within rainforest vegetation are infrequent and high intensity (Murphy et al. 2013), usually resulting in substantial tree mortality and consumption (Hill 1982). In contrast, the eucalypt associations on the Hartz Mountains are comparatively sparse. Further, Eucalyptus foliage is highly flammable, burns rapidly and, in the case of resprouting species such as E. coccifera found in the study area today, usually only the leaf matter is consumed (Bowman 1998, 2000). We contend that establishment of the pyrophytic vegetation state caused a shift from a low-frequency, high-intensity rainforest fire regime to a higher-frequency, lower-intensity eucalypt fire regime that is reflected by the higher microscopic charcoal content following this switch (Fletcher et al. 2014). Indeed, a similar shift in charcoal particle size following the initial burning and deforestation of New Zealand rainforest (which was replaced by lower-biomass grass- and scrublands) following the arrival of Maori (McWethy et al. 2010) lends support to this inference.

The role of climate in initiating vegetation state switches

While the influence of the long-term shift in climatic variability through the Holocene over Tasmanian climate and fire regimes is well described (Fletcher and Moreno 2012; Fletcher et al. 2015; Beck et al. 2017; Mariani and Fletcher 2017), comparatively little is known about how this shift influenced the terrestrial ecology within this landscape. Montane rainforest appears to have dominated much of the Southern Ranges of Tasmania through the early Holocene (ca. 12–8 ka). The overall lack of charcoal peaks at our sites through this period is consistent with a stable cool and humid climate regime conducive for rainforest development and prohibitive to fire (Macphail 1979; Macphail and Colhoun 1985; Fletcher et al. 2018) (Fig. 2). In contrast, there is a marked increase in fire activity in the Southern Ranges through the last ca. 8 kyrs. Repeated fires during this period, several of which were synchronous at both sites (Fig. 2), occurred in response to an increasingly variable rainfall regime, driven principally by an increase in the frequency and amplitude of ENSO variability in the tropical Pacific (Fig. 3) (Fletcher et al. 2014; Rees et al. 2015; Beck et al. 2017; Mariani and Fletcher 2017; Fletcher et al. 2018). Importantly, we observe a divergence in the developmental trajectories of the vegetation within our adjacent study catchments in response to this repeated disturbance. Repeated fires over the last ca. 8 kyrs led to the emergence and subsequent establishment and spread of a pyrophytic vegetation state at Lake Osborne, while montane rainforest persisted at Lake Perry (Figs. 2, 3, 4, 5).

The role of species composition (i.e. Eucalyptus) in initiating vegetation state switches

Theory predicts that the emergence of an alternative stable state can be induced by feedbacks between an ecosystem state and limiting factors, such as precipitation and fire (Borgogno et al. 2007; Iglesias and Whitlock 2020). The frequency distribution plots of the individual site ordination axis scores (DCA 1), split into ca. 12–8 ka; 8–4 ka; and < 4 ka intervals (Figs. 3, 5), allow a conceptualisation of the initial emergence of an alternate basin of attraction after ca. 8 ka and the subsequent establishment of an alternate basin of attraction after ca. 4 ka (Figs. 3, 5). The transition from pyrophobic rainforest to pyrophytic eucalypt forest at Lake Osborne, in contrast to the maintenance of pyrophobic rainforest at Lake Perry, offers a critical insight into the factors leading to the emergence of an alternative stable pyrophytic state within this system. We detect a significant difference in the relationship between Eucalyptus pollen and fire-driven shifts in montane rainforest between our two study sites: Lake Osborne (the pyrophytic site) displays a significant increase in Eucalyptus pollen synchronous with fire-driven reductions in montane rainforest, while no relationship is evident between Eucalyptus and fire-driven reductions in montane rainforest at Lake Perry (the pyrophobic site). Our results indicate that a positive feedback between century-scale rainfall deficits, coupled with repeated fire and pyrophytic species invasion and
spread (here, *Eucalyptus*), led to the emergence and subsequent establishment of an alternate pyrophytic vegetation state. Without a sufficient degree of pyrophytic species invasion, the shifts in moisture and fire occurrence experienced at both sites appear to be insufficient to have driven a switch between pyrophobic and pyrophytic vegetation states at Lake Perry. It is probable that a threshold for the degree of species invasion must be breached before its presence can drive a system toward an alternate stable state, however whether this threshold relates to the species’ relative proportions or patch size/s within the landscape (see also Van Nes et al. 2018) is impossible to determine from our data. Nonetheless, our results indicate that a crucial component of a switch between pyrophobic and pyrophytic vegetation states in this landscape is the post-fire establishment of *Eucalyptus*. The implication of this result for all pyrophobic-pyrophytic vegetation transitions is that it is critically important that post-fire species composition be considered when assessing the potential for recovery of pyrophobic vegetation from fire. A case-in-point are assertions that the large-scale fire damage to conifer-dominant rainforest across Tasmania in response to changes in fire use following British invasion are irreversible (Holz et al. 2015). Previous research (Fletcher et al. 2014; Cadd et al. 2019) indicates that Tasmanian montane rainforest systems require substantial (ca. 1 ka) fire-free periods to recover post-fire, however our data indicates that recovery also hinges on the post-fire species composition (specifically the proportion of eucalypts in the forest system). Thus, attempts to mitigate the effects of future fire and conserve these ecosystems must bear these critical factors in mind.

**Conclusions**

Despite overall similar vegetation histories during the early Holocene, the vegetation trajectories of our two study sites experience a marked divergence after 6 ka.
The increased importance of *Eucalyptus* species within the Lake Osborne catchment precipitated a positive feedback switch that resulted in the emergence of an alternate stable pyrophytic state. The greater extent of *Eucalyptus* led to a shift in fire regime from low-frequency/high-intensity to a higher-frequency/lower-intensity regime that precluded the reestablishment of pyrophobic rainforest. We conclude that in this fire-prevalent landscape, the greater incidence of *Eucalyptus* species initiates a feedback switch that drives transitions between pyrophobic and pyrophytic vegetation states. Without sufficient cover of *Eucalyptus* species, crossing thresholds of moisture deficit and fire disturbance alone are inadequate to cause a switch to an alternate stable state.

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