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Review

A framework for testing the influence of Aboriginal burning on grassy ecosystems in lowland, mesic south–eastern Australia

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Abstract. The complex interactions among climate, soils, fire and humans in the biogeography of natural grasslands has long been debated in Australia. On the one hand, ecological models assume the primacy of climate and soils. On the other, Aboriginal burning is hypothesised to have altered the entire continent since before the last glacial maximum. The present paper develops a framework to test for the 'fingerprint' of Aboriginal burning in lowland, mesic grassy ecosystems of south-eastern Australia, using ecological theory, and the ethno-historical record. It is clear that fire-stick farming was used to promote staple roots in south-eastern Australia and, in some instances, it has been shown to influence grassland–woodland boundaries. The framework comprises the following three evidence lines: (1) archival benchmarking and palaeoecology; (2) phytoecology; and (3) ethnology and archaeology. That fire-stick farming was likely instrumental in grassland formation and maintenance must be supported by evidence that shows that 'natural' grasslands exist in climatically–edaphically unexpected places, that fine-scale patterns and dynamics are at least partly due to fire and that the fire regime has been influenced by Aboriginal burning. Application of the framework indicated that widespread Aboriginal burning for staple foods likely extended the area of temperate grasslands and influenced their structure and function.

Additional keywords: ethno-historical record, grassland–woodland boundaries.

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Introduction

Fire emerged following the appearance of the first terrestrial plants and led to the rise of fire-adapted biotas, including the highly flammable savannas where early humans began cooking food and, later, where hunter-gatherers routinely used 'fire-sticks' for other purposes (Bowman *et al*. 2009, 2011; Conedera *et al.* 2009). However, the historic influence of human fire on ecosystems globally is highly contested and our knowledge of regime diversity in time remains poor. Central to the debate about past fire regimes is how to isolate any human effect from 'natural' or background fire regimes driven by climate (Roos *et al*. 2014). Detecting the 'fingerprint' of human fire is no trivial matter and is critical for conserving ecosystems, understanding historical change, as well as protecting human health and property (Bowman *et al*. 2011; Coughlan and Petty 2012).

In Australia, there is a rich and complex literature on this issue. Much of the disagreement arises from differing perspectives, methods and spatio-temporal scales (spanning ecology, ethnography, anthropology, palaeoecology and palynology; e.g. Hope 1994; Bowman 1998; Jones 1999; Gott 2005; Gammage 2011; Cahir *et al.* 2016). For instance, whereas Mooney *et al*. (2012) concluded that there is little support in the palaeo-fire record for large-scale human impact on Australian fire regimes, Bowman (Bowman 1998; Bowman *et al*. 2012) noted a growing body of research supporting the view that Aboriginal burning was important for maintaining function in some ecosystems at the time of European arrival. To reconcile such apparently conflicting ideas and improve our understanding of human–fire relationships (Swetnam *et al*. 1999; Roos *et al*. 2014), we need an interdisciplinary approach that links the social and physical aspects of fire ecology (Coughlan and Petty 2012; Bowman *et al*. 2015). In the present paper, I propose a framework that allows this reconciliation.

Jones (1969) famously coined the phrase 'fire-stick farming', arguing that Aboriginal burning widely reported at the time of European arrival was part of a continuum going back to the earliest inhabitants, and that the whole continent was burnt to boost food supply and population. According to some advocates, one outcome of such wide-spread burning was the vast swaths of open grassy woodlands and grasslands, often described as 'park-like' by early European pioneers (e.g. Ryan *et al*. 1995). The view that Aborigines literally transformed Australia with fire is today so pervasive that it is more-or-less accepted popularly and in ethnographic disciplines (e.g. Gott 1982, 1999, 2005; Horton 1982; Flannery 1994; Jackson 1999; Hope 1999; Gammage 2011; Cane 2013). However, this view has been widely contested (e.g. Benson and Redpath 1997). In contrast, 'deep time' disciplines such as palaeoecology and palynology, reliant on proxies in natural archives (e.g. pollen grains, minerals, macrofossils), tend to be more equivocal on fire-stick farming (Clark 1983; Kershaw *et al*. 1994; Dodson and Mooney 2002; Mooney *et al*. 2012).

Much of the debate revolves around the veracity of the ethno-historical record, interpreting the ecological effects of fire through the imprecise nature of the language used, the prejudice and agenda of observers, and the devastating impacts of colonisation on traditional society (Clark 1983; Benson and Redpath 1997; Fensham 1997; Bowman 1998; Cahir *et al.* 2016). Many scholars have taken the view that details of these regimes are unquantifiable and probably unknowable (Clark 1983; Fensham 1989; Morgan 1994; Lunt 1994, 1995, 1998; Benson and Redpath 1997; Bowman 1998). Thus, because it is so difficult to study historic fire regimes, especially in south-eastern Australia where Aboriginal burning has long ceased, the ecological orthodoxy is that fire plays a secondary, even minor role in grassy ecosystems, compared with primary drivers of climate and soils (Patton 1930; Clark 1983; Benson 1994; Foreman 1996; Lunt 1997; Kirkpatrick *et al*. 1995; Lunt *et al*. 2012; Morgan *et al*. in press). While there may be conjecture as to whether or not Aboriginal burning helped maintain open woodlands and grasslands across the lowland plains of Victoria (Clark 1983; Lunt 1998), there appears to be little disagreement among ecologists that climate and soils are more important than fire in driving the distribution of Australian vegetation overall (Lunt *et al*. 2012; Williams *et al*. 2015).

However, Jones (1999) concluded that given the prevalence of Aboriginal burning in pre-European ecosystems, we should not rule out a more prominent role for fire in grassy ecosystems. This cautionary approach highlights the likelihood of complex, heterogeneous historical relationships among soils, climate, fire and humans, from broad to fine spatio-temporal scales. This requires multi-disciplinary collaboration, multiple lines of evidence and new methods (Jones 1999; Lunt 2002; Swetnam *et al*. 1999; Coughlan and Petty 2012; Roos *et al*. 2014).

The aim of the present paper is to (1) identify the ecological basis for the potential impact of fire-stick farming (*sensu* Jones 1969), and (2) develop a framework based on hypotheses that could be used to test for the 'fingerprint' of fire-stick farming in lowland, mesic grassy ecosystems of south-eastern Australia. Application of the multiple lines of evidence in the framework will improve our understanding of the complex processes that influence grassland–woodland biogeography in south-eastern Australia.

The study system

Study area

Mesic grasslands of south-eastern Australia occupy the productive lowland plains, inland slopes and tablelands. Annual precipitation is 400–1000 mm; moisture availability is high in winter–spring, moderate in summer, and most plant growth occurs in spring (Hutchinson *et al*. 2005; Lunt *et al*. 2012). This region includes the Tasmanian lowlands, the Victorian lowlands (except the north-west), the Southern Tablelands and inland slopes of New South Wales and the Australian Capital Territory, and parts of the Mount Lofty Ranges in South Australia. It broadly corresponds with the Köppen Temperate zone, namely, mild to warm summer (no dry season) and cold winter (Stern *et al*. 2000). Six discretely different nationally 'endangered' temperate and southern semi-arid grasslands, all being associated with characteristic sub-bioregions, are currently recognised (Morgan *et al*. in press; Fig. 1).

Grassland definition

Mesic grasslands are dominated by perennial native C_3 or C_4 tussock grasses (comprising a single species or multiple genera of the family Poaceae). There are few or no shrubs, and trees are also sparse (<5%) or absent. A variety of sub-dominant grasses and many other herbaceous plants, mostly perennial forbs and monocots, occupy the inter-tussock spaces. Common interstitial families in these grasslands include Poaceae, Asteraceae, Fabaceae, Liliaceae and Cyperaceae. Almost all mesic grasslands tend to be dominated or co-dominated by kangaroo grass (*Themeda triandra*), but often other genera such as *Austrostipa, Rytidosperma* and *Poa* are also abundant. In the historic record, this vegetation was often referred to as a 'plain' or 'open plain', often explicitly described as 'treeless' or 'without timber', bordering areas described as 'timbered', 'wooded' or 'forest'. Because these grasslands occupy fertile, lowland plains and lower slopes so widely affected by European land use, today only a tiny fraction persists as isolated refugia in relictual landscapes (Morgan *et al*. in press).

The role of fire in grassy-biome dynamics

The vegetation state 'realised' in any one location is the product of multiple processes and interactions at various spatial and temporal scales, often giving rise to complex and unpredictable patterns (Grime 1977, 1979; Southwood 1988; Westoby *et al*. 1989; McIntyre and Lavorel 2007; Bowman *et al*. 2015). Evidence of non-linear thresholds and tipping-point interactions among climate, resource availability and disturbance regimes, operating at various spatio-temporal scales, is especially important (House *et al*. 2003). For instance, African savannas switch from being 'climate-dependent' to 'disturbance-dependent' ecosystems above rainfall of 650–700 mm per year (Sankaran *et al*. 2005, 2008). Global models of fire-dependent C_4 grassy ecosystems show greatest extent in the tropics and southern hemisphere, including much of Australia's eastern seaboard, which has the climate potential to support woodlands and forest, and is regulated by 'bottom-up' and 'top-down' controls on structure and composition (Jones 1999; Bond *et al*. 2003, 2005; Waldram *et al*. 2008; Leonard *et al*. 2010; Lunt *et al*. 2012; Fensham *et al*. 2015). Thus, altering the 'top-down' controls, such as fire regime, drives a response in the structure and composition of the grassy sward, affecting grassland–woodland boundaries, and the extent of woody cover (south-eastern Australian examples: Fensham and Kirkpatrick 1992; Foreman 1996; Hadden 1998; Lunt 1998; Lunt and Morgan 1999; Franco and Morgan 2007; Price and Morgan 2009; Lunt *et al*. 2010, 2012; Williams *et al*. 2015; Kirkpatrick *et al*. 2016).

Although little is known of original fire regimes, especially in south-eastern Australia, where the impact of colonisation was catastrophic (Christie 1979; Broome 2005), there is much anthropological evidence that Aborigines manipulated fire

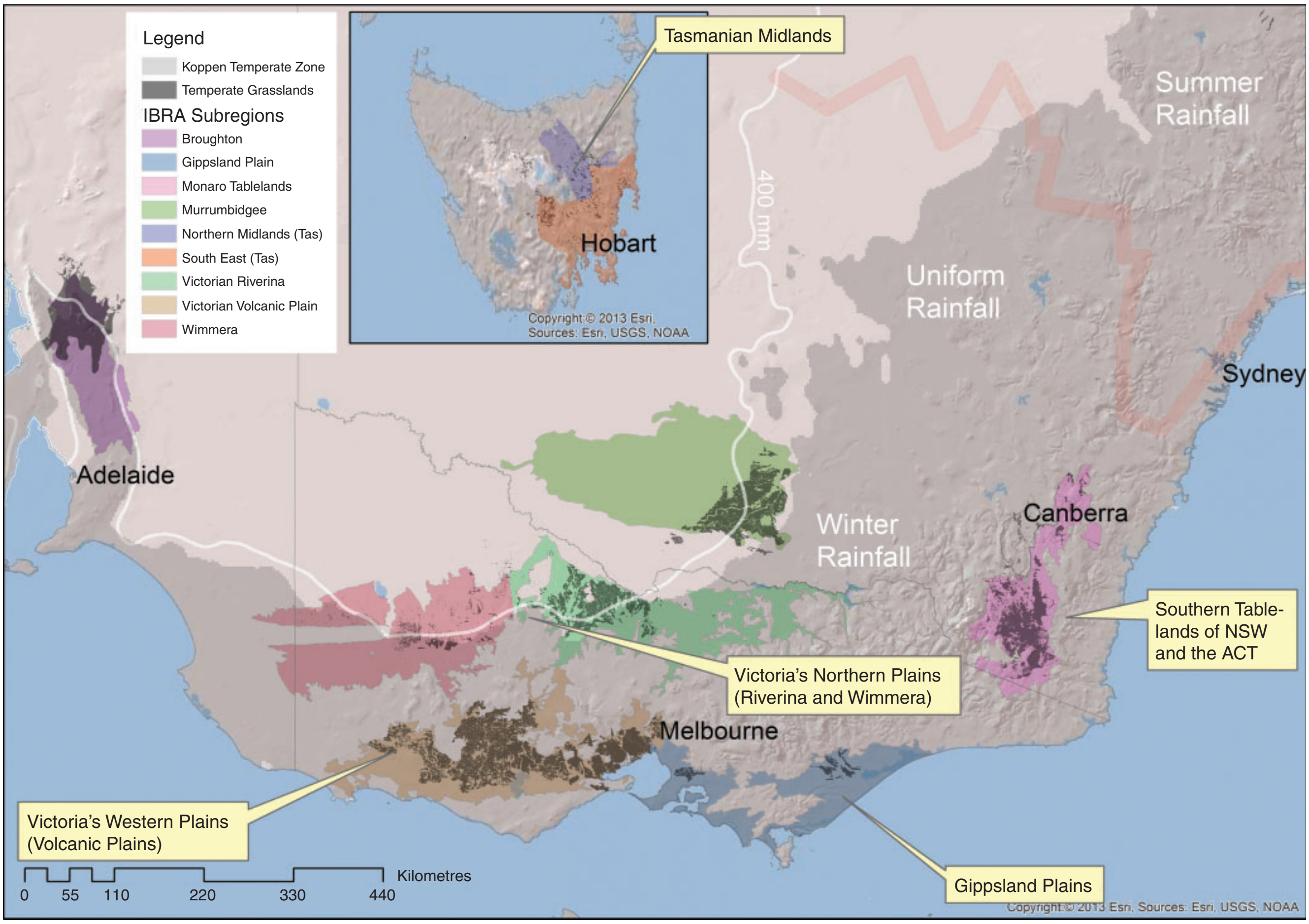

Fig. 1. Distribution of mesic tussock grasslands of south-eastern Australia. Call-outs indicate locations of case studies and key nationally listed grassland ecological communities; pale red line indicates boundary between dominant summer rainfall and uniform/winter-dominant rainfall.

regimes in grassy ecosystems for food/hunting (Clark 1983; Hallam 1989; Bowman 1998; Gammage 2011). For instance, Gott (2005) posed a direct link between Aboriginal burning to promote areas for staple roots (the 'yam fields' of Williams *et al*. 2015) and broader ecosystem changes. However, estimating the extent and trajectories of such change is complex, and highly contested (Bowman *et al*. 2012). Both biophysical/ecological models and anthropological/historical records can be used to shed light on such problems (Swetnam *et al*. 1999), although even in well studied ecosystems such as grasslands, our knowledge of change is often partial because of a limited range of research approaches (Lunt 2002) and archival information (Clark 1983).

Contrary to popular views of universal burning (e.g. Gammage 2011), it makes sense that the effect of Aboriginal burning on ecosystem dynamics will be context/ecosystem dependent. For instance, Aborigines were unlikely to have deliberately burnt areas that provided little in the way of food plants or did not assist with hunting (such as wet sclerophyll forests; Gott 2005; also see Prober *et al.* 2016).

Adding to the evidence problem is that ecological and socio-anthropological schema look at the world differently. The main concern appears to be how historic records are used to construct grand narratives. First, the accounts contain no detailed information on burning regimes, such as fire season, frequency or intensity (Clark 1983; Lunt 1998). Second, there appears to be a lack of records directly describing the purpose and practice of burning from primary sources. And third, there are questions around whether traditional society had been significantly disrupted well before the first explorers arrived. Thus, in the absence of primary information, rather than dismiss the issue or succumb to supposition, the challenge is to build confidence around a body of inferential tests.

A framework for testing the influence of Aboriginal burning on grassy ecosystems in lowland, mesic south-eastern Australia

The 'fingerprint' of human influence can only be inferred when 'natural' processes can be discounted (Kohen 1995), and a plausible (alternative) mechanism of human agency established. Given the widespread historic references to Aboriginal burning, and the well established narratives in the ethno-historical literature, especially in the more productive landscapes first exploited by Europeans, it is difficult to explain why this sort of approach has not been used to test the fire-stick farming hypothesis more broadly.

Over much of the continent, where ever traditional Aboriginal society has long ceased, the consequences of fire-stick farming can be deduced only by inference, with confidence increasing in proportion to the number of evidence lines available. It would be necessary to accept at least one hypothesis from multiple-evidence types (described below) to conclude that fire-stick farming was instrumental in grassland formation or maintenance. First, it must be demonstrated that 'natural' grasslands exist or existed in regions where, climatically, trees would be expected (>400 mm per year in lowland south-eastern Australia; Fensham *et al*. 2015). Second, the fine-scale distribution and dynamics of grasslands must be partly due to fire. And third, fire must have been partly due to targeted, purposeful and frequent (often annual) Aboriginal burning (Fig. 2).

Under this framework, nine tests are proposed across the three evidence lines, as follows:

Archival benchmarking and palaeoecology:

(1) Corroborated historic records of grasslands in areas where trees are expected (>400 mm per year);
(2) Historic grassland patches have a lower density of tree cover and support grassland remnants;
(3) Stable presence of *Themeda* (C_4) grasslands in at least the latter Holocene;

Phytoecology:

(4) Grassland–woodland boundaries not aligned to soil patterns;
(5) Negligible floristic divergence between grasslands and grassy woodlands (ground layer);
(6) Loss of diversity and woody invasion following cessation of burning;
(7) Diversity recovery and inhibited woody invasion with re-introduction of fire;

Ethnology and archaeology:

(8) Grassland distribution linked to patterns of Aboriginal habitation; and
(9) Historic records of targeted, purposeful and frequent use of fire by Aborigines.

Rationale for hypotheses

(1) Corroborated historic records of grasslands in areas where trees are expected (>400 mm per year)

Several studies and reviews have mentioned the accurate designation of grassland–woodland boundaries in historic plans dating from the first decades of colonisation (Fensham 1989; Foreman 1996; Lunt 1997; Lunt *et al*. 2012; Williams *et al*. 2015). These surveys were critical for exploitation of the rich pastoral lands and the economic development of the colony (Boyce 2011). In areas of southern Australia receiving >400 mm per year, woody cover is predicted to be higher on clay-rich soils (cf. sandy soils) on the basis of the 'inverse texture effect' (Fensham *et al*. 2015), and the absence of trees needs to be explained by processes other than seasonal drought stress. Such grasslands are also unexpected here in the sense of being outside areas previously mapped (examples for Victoria include Woodgate and Black 1988; Foreman 1996; 'ecological vegetation classes' in Parkes *et al*. 2003). Within applicable bioregions, mesic grasslands derived by fire-stick farming would be ecologically distinct from semi-arid grasslands because of the operation of a different combination of 'top-down' and 'bottom-up' processes.

(2) Historic grassland areas have lower density of tree cover and support grassland remnants

Perhaps one reason why so few grassland remnants have been picked up east of the Campaspe River in the Victorian Riverina, for instance, is because no one has looked. It was presumed they were either never there or have long since disappeared. The mapping of historic grasslands establishes a spatial framework to systematically assess for remnants, and searches in the Victorian Riverina have been surprisingly productive. Dozens of often high-quality sites, closely matching the historic map, have been discovered across the region, mostly on roadsides and other public land (P. Foreman unpubl. data).

A second expected feature of historic grasslands is a lower tree cover. In contrast to unfragmented landscapes, given the intensity of land use in the lowlands, tree cover today is generally much diminished (e.g. Woodgate and Black 1988). Thus, woody-plant encroachment or canopy densification is only possible over a small percentage of the landscape (Lunt *et al*. 2010). Patterns of change can be readily interpreted by comparing the historic grasslands with historic aerial photographs (~1940s) and contemporary imagery. Supplemented with field assessment, historic imagery is especially useful for tracking changes in large, old remnant trees and the original grassland–woodland boundaries (Fig. 3).

(3) Stable presence of Themeda *(C_4) grasslands in at least the latter Holocene*

There is a long history of palaeoecological studies in Australia using archival proxies such as carbonised particles, pollen and radiocarbon dating, to make inferences about changes in vegetation, fire, climate and human interactions in 'deep time' (e.g. Kershaw *et al*. 1994; Moss *et al*. 2007). However, most have focussed at a scale of thousands of years and tended to be equivocal on issues such as the human use of fire, and more recently, century-scale change (Lunt 2002). Stable carbon-isotope analysis of soil organic matter (SOM) has been used to demonstrate recent woody encroachment and Holocene vegetation dynamics in montane eastern Australia, and elsewhere (McPherson *et al*. 1993; Connin *et al*. 1997; Butler *et al*. 2014).

Although occurring within the temperate zone, the (C_4) *Themeda*-dominated mesic grasslands of south-eastern Australia have important functional similarities to those where stable carbon-isotope analysis has been used elsewhere. It is hypothesised that (C_3) eucalypts and grasses have encroached *Themeda*-dominated grasslands formerly maintained by frequent fire, at least on some soil types and locations. If this is correct, there should be a discrepancy between the $\delta^{13}C$ values of the C_3 plants thought to have invaded *Themeda*-dominated grasslands, and the associated SOM, which should still have a C_4-like value. And, if woody plant species have been only recently cleared, the $\delta^{13}C$ values of the associated SOM in the

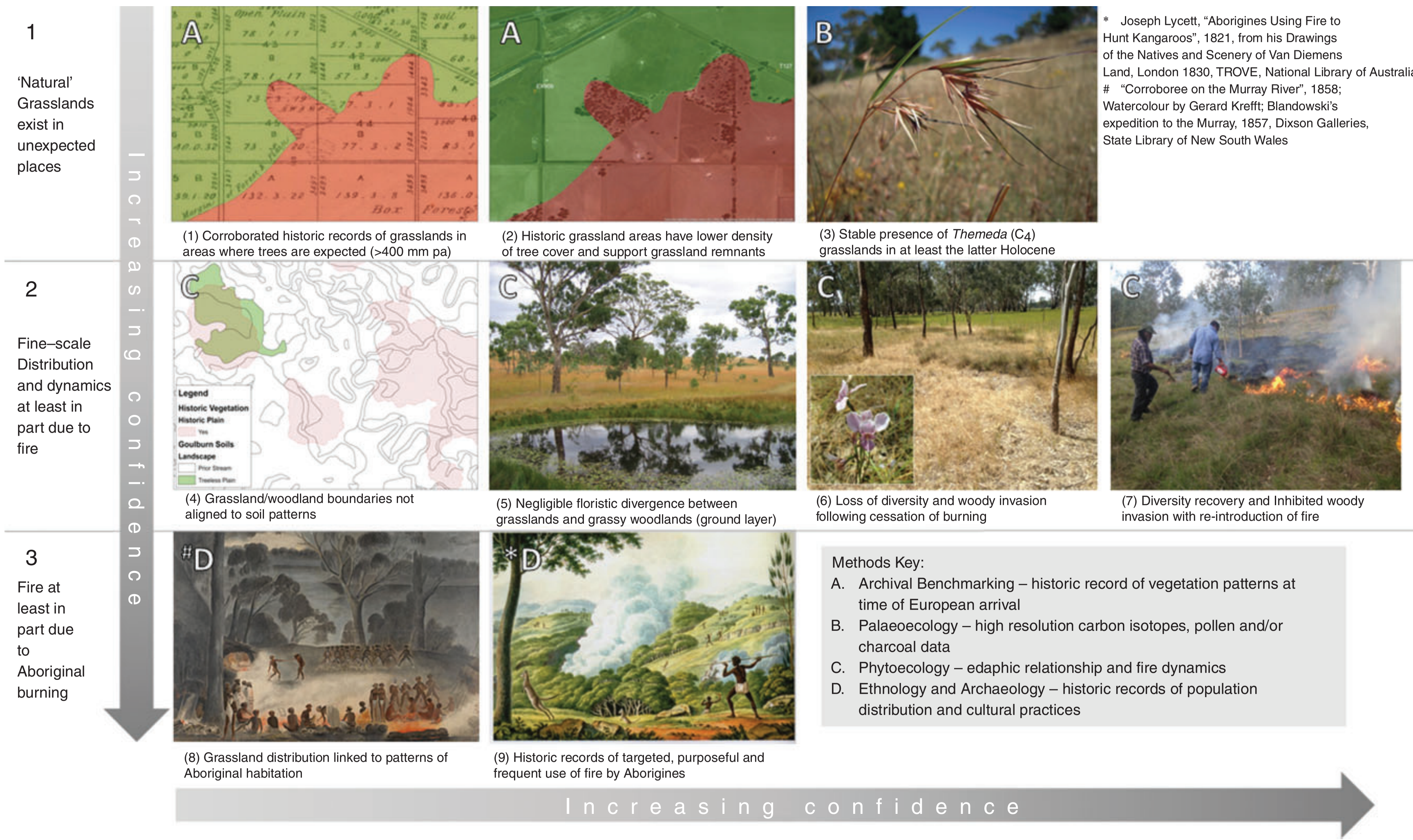

Fig. 2. A framework for testing the influence of Aboriginal burning on grassland–woodland boundaries in lowland, mesic grassy ecosystems of south-eastern Australia. The schematic shows nine hypotheses structured around the following three key evidence lines: (1) archival benchmarking and palaeoecology; (2) phytoecology; and (3) ethnology and archaeology. It would be necessary to accept at least one hypothesis from multiple evidence types to conclude that fire-stick farming was instrumental in grassland formation or maintenance. First, it must be demonstrated that 'natural' grasslands exist or existed in regions where, climatically, trees would be expected (>400 mm per year in lowland south-eastern Australia; Fensham *et al.* 2015). Second, the fine-scale distribution and dynamics of grasslands must be partly due to fire. And third, fire must have been partly due to targeted, purposeful and frequent Aboriginal burning.

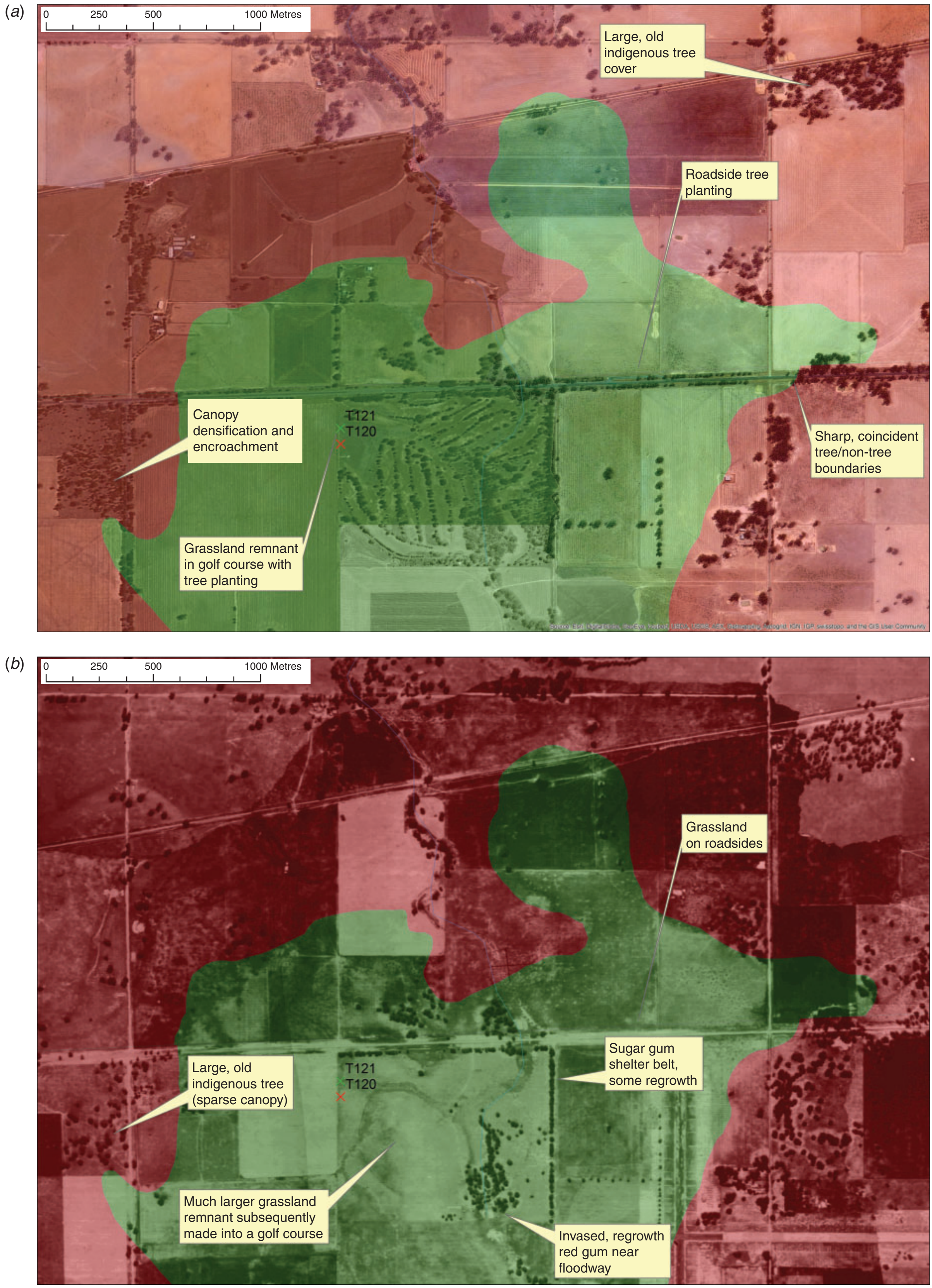

Fig. 3. Historic treeless plain east of Murchison in central Victoria, showing century-scale changes in tree cover: (*a*) contemporary imagery and (*b*) 1946 photomosaic (Murchison 799B3) courtesy of State Government of Victoria.

best *Themeda*-dominated grassland should bear a C_3-like isotope signature.

(4) Grassland–woodland boundaries not aligned to soil patterns

It is widely believed that temperate grasslands are associated with clay soils not subject to inundation. Plants with deep roots, it is argued, struggle to establish or persist because of a combination of slow water percolation and poor aeration when wet, excessive moisture loss during summer, or root shearing in self-mulching, cracking-clay soils (Patton 1930; Geraghty 1971; Foreman 1996; Lunt 1997; TSSC 2012; Morgan *et al*. in press). If this is true, historic grassland–woodland boundaries would be closely aligned with patterns of clay-rich soils. However, clays support more woody biomass than do non-clay soils over ~20% of the continent (>400 mm per year in the south) where droughts are less severe or frequent and where clays have superior moisture-holding capacity and fertility (Fensham *et al*. 2015).

Cold-air drainage, frequent frost and even snow, prohibiting tree encroachment, have been discounted on the lowland plains of the south-eastern mainland, and, in Tasmania, low temperature has been cited as a secondary cause of treelessness, mostly at high elevation (≥800 m asl) (Kirkpatrick *et al*. 1988; Fensham and Kirkpatrick 1992; Kirkpatrick 1999; Benson 1994; Lunt 1997). Where water-logging has been linked to treelessness on the lowland plains, it is more likely that the original vegetation was a herbaceous wetland of seasonally inundated, poorly drained clay depressions (Boulton and Brock 1999). Although Australian ecosystems have evolved with native grazers, very high densities of marsupial herbivores can drive complex interactions, cause serious degradation, and are also likely to have influenced grassland distribution (Cheal 1986; Barker and Caughley 1992; Fensham and Kirkpatrick 1992; Kirkpatrick 2004; Fletcher 2006; Roberts 2009; Leonard *et al*. 2010; Ingram and Kirkpatrick 2013; Hazeldine and Kirkpatrick 2015).

Putative explanations of treelessness in temperate grasslands comprise a diverse mix of both (1) ‘bottom-up’ processes (seasonal droughting, severe drought, difficulties in seedling establishment in heavy soils, waterlogging) and (2) ‘top-down’ processes (frost and snow damage and low temperature, grazing, dense grass sward competition, frequent fire) operating at various spatio-temporal scales (Fensham 1989; Fensham and Kirkpatrick 1992; Lunt 1997; Fensham and Fairfax 2007; Sinclair and Atchison 2012). A nested, two-scale treelessness model is proposed on the basis of the Pleistocene or Holocene relict hypotheses developed for montane grasslands in south-eastern Queensland and Tasmania (Ellis 1985; Fensham and Fairfax 1996, 2006; Bowman *et al*. 2013). Under this model, grasslands represent small to large patches in a woodland–forest matrix, resulting from the dynamic interplay of (1) broad-scale, rare or infrequent disturbances (extreme drought, frost, storms/tornados, wildfire) and (2) frequent, fine-scale disturbances (Aboriginal burning, native herbivore grazing, dense grass sward competition), mediated by soil and terrain (Fig. 4).

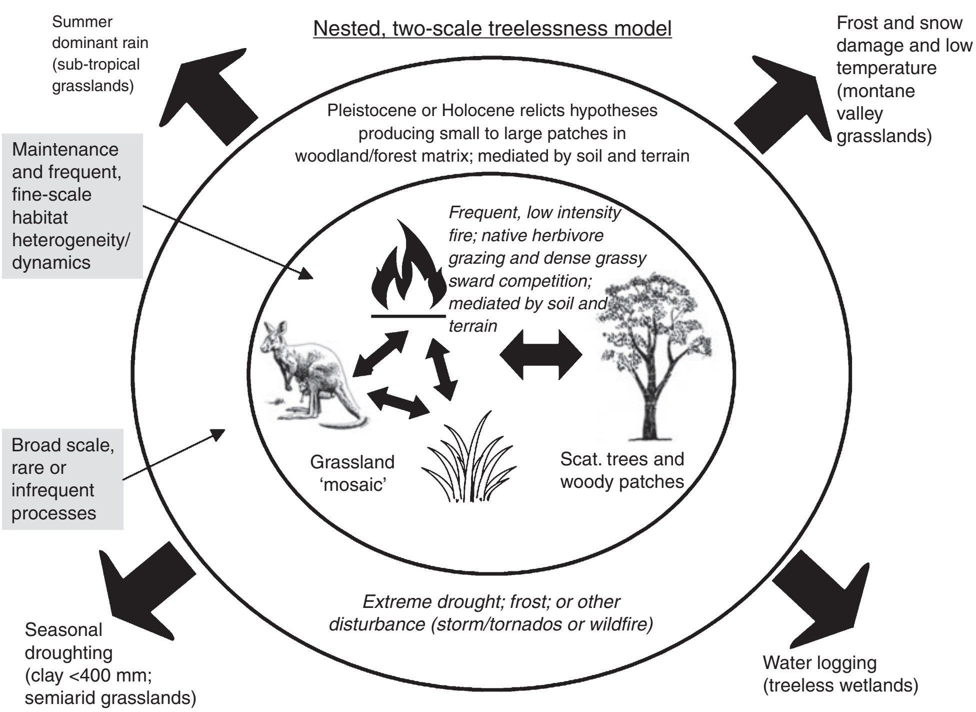

Fig. 4. Nested, two-scale treelessness model in lowland, south-eastern Australian mesic grassy ecosystems. Rare or infrequent disturbance created open patches in the woodland–forest matrix (extreme drought, frost, or other disturbance, such as storm/tornado or wildfire), which was maintained as a dynamic, fine-scale habitat mosaic by the interplay of frequent, low-intensity fire (Aboriginal burning), native herbivore grazing and dense grass sward competition. Woody-plant presence would be mediated by patchy spatio-temporal recruitment opportunities, most likely where fire frequency and grazing pressure were moderate (e.g. rocky/stony rise fire refugia and were grass swards were also less dense and vigorous).

Thus, historic grassland composite maps are a kind of archival benchmark, where a mix of soil textures could reflect an overriding influence of disturbance.

Because the lowland plains of south-eastern Australia are productive agricultural landscapes, they are often data-rich. For instance, detailed, high-resolution soil maps were produced for irrigation expansion in the Victorian Riverina and Gippsland (e.g. Skene 1971; Skene and Walbran 1948). In semi-arid regions, such as the north-western Victorian Riverina, it is expected that historic grasslands would be closely associated with mapped patterns of non-inundated, clay-rich soils more prone to seasonal drought-stress (e.g. Foreman 1996), whereas in mesic regions, this association is expected to be decoupled, with grasslands widely associated with a mix of soils, and often widespread on non-inundated, non-clay soils. It is suggested that this switch would be evidence of a transition from treelessness mostly driven by 'bottom-up' processes in semi-arid regions, to grasslands in mesic regions where 'top-down' processes are more influential.

(5) Negligible floristic divergence between grasslands and grassy woodlands (ground layer)

Both the Pleistocene and Holocene relict hypotheses developed for the montane grassy balds of south-eastern Queensland (Fensham and Fairfax 1996) would be applicable to mesic grasslands of south-eastern Australia. Thus, in areas where fire has been excluded or greatly contained over the past two centuries, there have been reports of woody-plant encroachment because of prolific woody-species seed production and the competitive suppression of grasses under intense stock grazing (Bragg and Hulbert 1976; Lunt 1998; Briggs *et al*. 2002, 2005; Hoch *et al*. 2002; Franco and Morgan 2007; Lunt *et al*. 2010, 2012).

Given any mesic grasslands derived by Aboriginal burning would have been initiated very recently in an evolutionary sense, there would have been insufficient time for a distinct grassland flora to have segregated from the surrounding woodland matrix (from which they were derived; see Fig. 4). In other words, grasslands and woodlands in such regions would share a relatively cosmopolitan flora compared with regions where the grassland–woodland boundary has been driven by much more long-standing (albeit dynamic) climatic–edaphic processes, where resource partitioning would have resulted in a level of floristic divergence. This is certainly the case for the 'derived' montane grassy balds where the dominant ground-stratum species in grassland and forest were quite similar and very few grassland species were not recorded in grassy forests (Butler *et al*. 2006, 2014). Several researchers have noted the floristic similarities of grasslands and open woodlands in western Victoria and Gippsland, where few species are known to be restricted to grasslands (Willis 1964; Lunt 1997; Williams *et al*. 2015). In contrast, in northern Victoria, Foreman (1996) found that semi-arid grasslands and the better-quality woodlands, typically with a well developed shrub layer, were broadly floristically distinct. Thus, if this hypothesis is correct, it is expected the herbaceous flora of carefully selected, least-modified remnant pairs of grassland and woodland in mesic regions would show negligible divergence.

(6) Loss of diversity and woody invasion following cessation of burning

The spatio-temporal heterogeneity of treelessness mechanisms is especially important when describing ecosystem structure and function, and how a particular system might have responded to the cessation of Aboriginal burning and other post-European changes. If frequent fire were a primary agent of treelessness on at least some soil types, an increase in tree establishment would be expected. However, this can be tested only at sites where other causes of tree encroachment (herbivores and dense grassy sward competition) are absent. The 'reference grasslands' of McIntyre and Lavorel (2007) may be suitable candidates where ever it can be established that they were grasslands historically.

The majority of the best roadside remnants are characterised by the absence of frequent disturbance (Lunt 1998), including the active suppression of fire. One of the rare exceptions is the serendipitous coincidence of frequent fuel hazard reduction and conservation on roadsides of Victoria's Volcanic Plains (Williams *et al*. 2015). Should these practices cease, it is clear that these *Themeda*-dominated remnants, with a long fire history, would rapidly deteriorate (Lunt and Morgan 1999). Controlled experiments have shown that annual burning maximises species richness in *Themeda*-dominated grasslands in part by optimising the regenerative opportunities of perennial forbs (especially geophytes) that have deeper rootstocks better protected from the intense heat of summer fires (Morgan 2001; Lunt *et al*. 2012). Plant population extinction rates have been shown to be greatest in western Victoria where fire frequency has declined in recent decades (Williams *et al*. 2005), a pattern likely to be more widespread in south-eastern Australia.

This hypothesis can best be tested by comparing the floristics and structure of least-modified, frequently burnt and long-unburnt grassland pairs selected on the basis of historic vegetation patterns. In practice, the best prospects for sampling will be from western Victoria, although localised opportunities exist where ever recent control burns are known.

(7) Diversity recovery and inhibited woody invasion with re-introduction of fire

The key mechanism of treelessness in grasslands driven by fire is the mortality of tree seedlings 'within the flame zone' because of the intense heat of summer or early autumn fires (Fensham and Kirkpatrick 1992). The regeneration of the dominant trees in the lowland plains of south-eastern Australia is strongly episodic, with dense and widespread regeneration cohorts being triggered by major floods delivering ample summer soil moisture and reduced grass competition as a result of preceding drought (Lunt *et al*. 2010). Given these seedlings establish under favourable climate–edaphic conditions that promote an erect, single-stemmed habit with little lignotuber development (Carr *et al*. 1984), they tend to be more vulnerable to fire mortality until flame height is exceeded (perhaps within 3–5 years). Thus, frequent burning has the potential of greatly reducing or even eliminating tree encroachment, provided cohorts do not establish and mature during an extended absence of fire.

Because it is well recognised that many grassland forbs are poor dispersers, it is not surprising that re-colonisation following local extinctions are unlikely, given the sparse, relictual distribution of remnants (Morgan 1995; Foreman 1996; McIntyre *et al*. 1995). In studying patterns of plant functional traits and local extinctions to disturbance and environmental gradients, Williams *et al*. (2006) found that most lifeforms, but especially rosetted perennial forbs and geophytes, were much more vulnerable to extinction where reduction in fire frequency was greatest. Although the effect of reviving frequent fire in long-unburnt mesic grasslands has not been well studied (Prober and Thiele 2005), it is clear that the return of fire will not quickly, or at all, reverse the degradation caused by frequent fire hiatus. Although the return of frequent fire will reduce biomass, and can also reduce the abundance of exotic annual grasses (Foreman 1996; Morgan 2001; Prober and Thiele 2005), the recovery of perennial forbs is very slow because of poor dispersal, and rare, climatically cued, recruitment pulses (Williams *et al*. 2015). Restoration of even the better, long-unburnt mesic grasslands will not be achieved simply or quickly by reinstating frequent fire. The best results will most likely be achieved if coupled with other interventions that can, over time frames of decades rather than years, restore some functional integrity.

This hypothesis can best be tested by comparing the floristics and structure of least-modified, long-unburnt grasslands where frequent fire has been recently re-introduced at one of the sites. Again, in practice, the best prospects for sampling will be from western Victoria.

(8) Grassland distribution linked to patterns of Aboriginal habitation

Given fire-managed mesic grasslands are thought to have been the major source of staple roots for Aborigines, ethnologists and anthropologists have proposed a direct link between fire management and Aboriginal population distribution and abundance. Hence, historic mesic grassland patterns are likely to be non-random and closely linked to proxies of human habitation. Although anthropologists generally agree that, so as to exploit a wide variety of resources, Aboriginal people were highly mobile within their clan or language territories, they tended to concentrate around active river valleys, flood plains, wetlands and coastal areas that were richest in food resources (Christie 1979; Lourandos 1980; Broome 2005). It is argued that it was socioeconomic evolution, driving population growth and sedentism, in part due to technology change, that helped stabilise and control staple resources, including the availability of tuberous roots (Lourandos 1983).

Furthermore, if Gott's (1982) view is correct, namely that combined with gathering and digging, Aboriginal burning resembled a form of 'agriculture' that changed the vegetation on the plains to ensure the supply of staple food plants, it is likely that evidence of this would be visible in the historical vegetation patterns, including woody cover. If woody plants were eliminated, or at least greatly reduced, in areas managed in this intensive way, and if this represented a significant on-going investment for a sparse human population, such 'yam fields' and/or hunting grounds would have been clustered around habitation areas. If this is true, historic grasslands would be proximal to major river valleys, flood plains, wetlands and coastal areas, and broad patterns of woody cover would be 'variegated' (60–90%) or 'fragmented' (10–60%) rather than 'relictual' (<10%; McIntyre and Hobbs 1999). In regions where woody vegetation is expected, a spatial association between 'plains' as a key source of staple food and human habitation infers a motivation and the opportunity for direct agency through fire.

(9) Historic records of targeted, purposeful and frequent use of fire by Aborigines

The documentary archives, especially the diaries and journals of the explorers and pioneering pastoralists, the first Europeans to see these landscapes, are replete with Aboriginal fire observations (Gammage 2011; Cahir *et al.* 2016). Using new, web-based IT tools to place these records accurately in space and time throughout a region (Bickford and Mackey 2004; Silcock 2014), a more detailed picture of Aboriginal burning activity and background wildfire can be developed. These data can then be compared against the historic vegetation maps and the fire-stick farming hypothesis.

Assessing the value of the framework

Case studies

Below I introduce case studies that provide an excellent template for illustrating and testing the framework. They represent a cross-section of temperate grasslands over a wide climate–edaphic range, where there is some data/knowledge about medium-term dynamics/change, and where Aboriginal burning was likely mentioned in the ethno-historical record.

Victoria's northern plains (Riverina and Wimmera)

It is generally believed that grassland in the Victorian Riverina is a semi-arid system driven by climate–edaphic relationships (Foreman 1996; McDougall 2008), where *Themeda* is virtually absent (DSE 2004; TSSC 2012). However, recent research has provided evidence of grasslands in mesic areas previously thought to support treed vegetation (P. Foreman unpubl. data; Fig. 5). The boundaries between treed and treeless grassy 'plains' or 'open plains' were frequently sharp, and often recorded by the early surveyors with some precision (Fig. 6). The location and nature of these 'plains' has often been well corroborated by other sources, notably the journals of the first explorers (Andrews 1981; Mitchell 2011), pioneering pastoralists (Hawdon 1952; Walker 1965; Bride 1969; Mollison 1980) and others (Howitt 1972; Clark 1988).

Importantly, not only are these grasslands *Themeda*-dominated, but they also lack the characteristic chenopods and annual forbs, and appear to be functionally different from what is currently accepted for northern plains grasslands (DSE 2004; TSSC 2012). They are patchily distributed over complex patterns of prior streams, river valleys and floodplains, and are apparently not associated with particular soils. Fire-induced treelessness is implicated in many places because trees and shrubs have invaded in the long-absence of fire, and the lack of biomass regulation has reduced diversity by competitive exclusion. In contrast to studies in forested regions (e.g. Tasmanian highland grasslands; Bowman *et al*. 2013), such dynamics are restricted in this overwhelmingly agricultural region, requiring careful, targeted sampling for testing under this framework. As is the case across

(*a*)

(*b*)

Fig. 5. (*a*) *Themeda*-dominated grassland on a disused rail side north of Wangaratta in the Victorian Riverina. A site with very high species richness, including many tuberous perennial forbs such as wedge diuris (*Diuris dendrobioides*, insert), owing to frequent burning (among other things). (*b*) Another rail-side grassland near Benalla, also supporting significant geophytes such as purple diuris (*Diuris punctata* var. *punctata*, insert), but deteriorating and threatened by tree invasion because of a lack of burning (among other things). Photographs: P. Foreman.

(*a*)

(*b*)

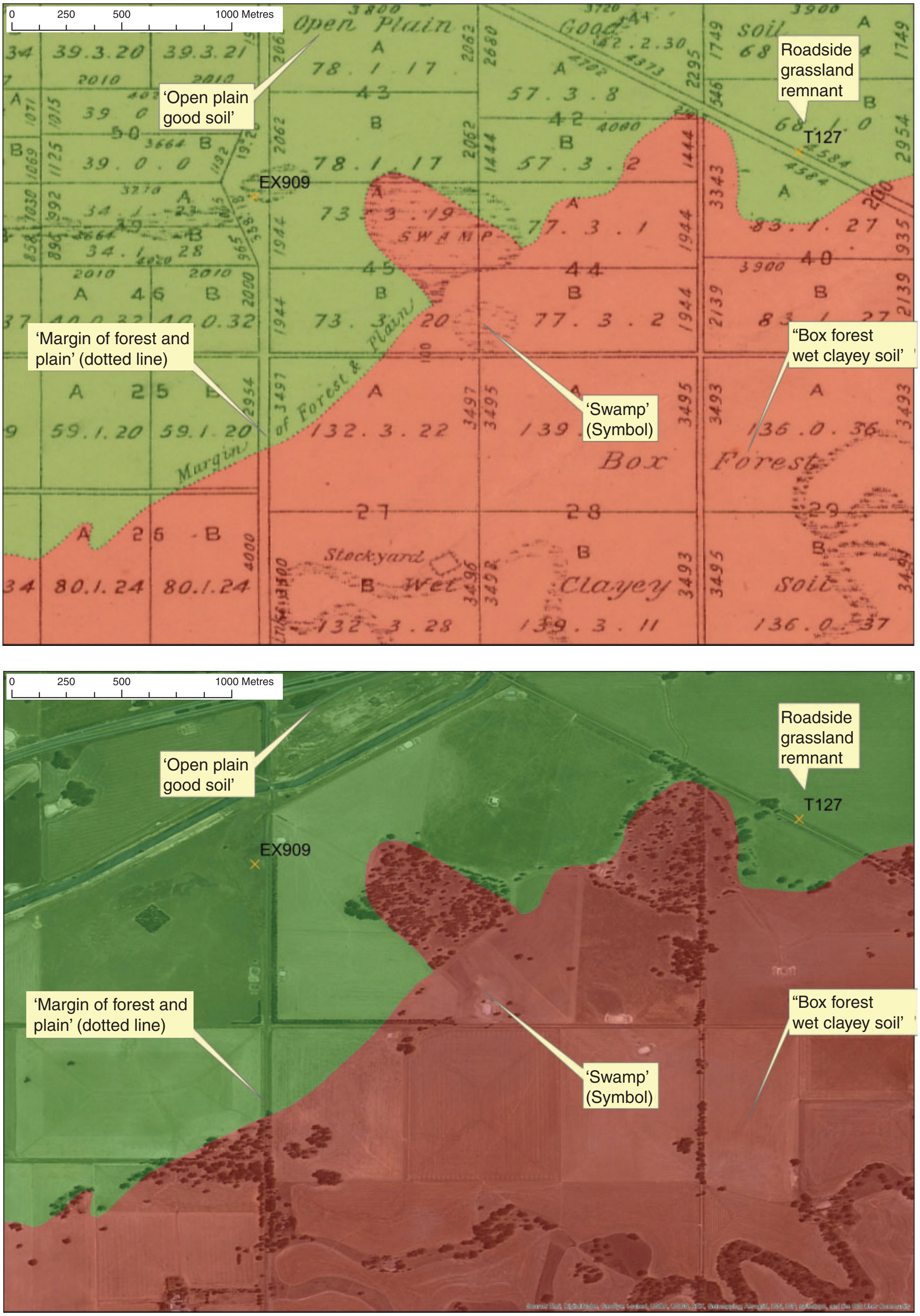

Fig. 6. (*a*) Parishes of Dargalong and Molka, Murray District, surveyed by John Downey, Contract Surveyor, July 1863, showing the precise 'margin of forest and plain' separating 'open plain' from 'box forest'. (*b*) Historic boundary overlayed with current vegetation patterns, showing trees more-or-less south of the line and the two crosses indicate *Themeda*-dominated grassland remnants along roadsides. Photomosaic courtesy of State Government of Victoria.

(a)

(b)

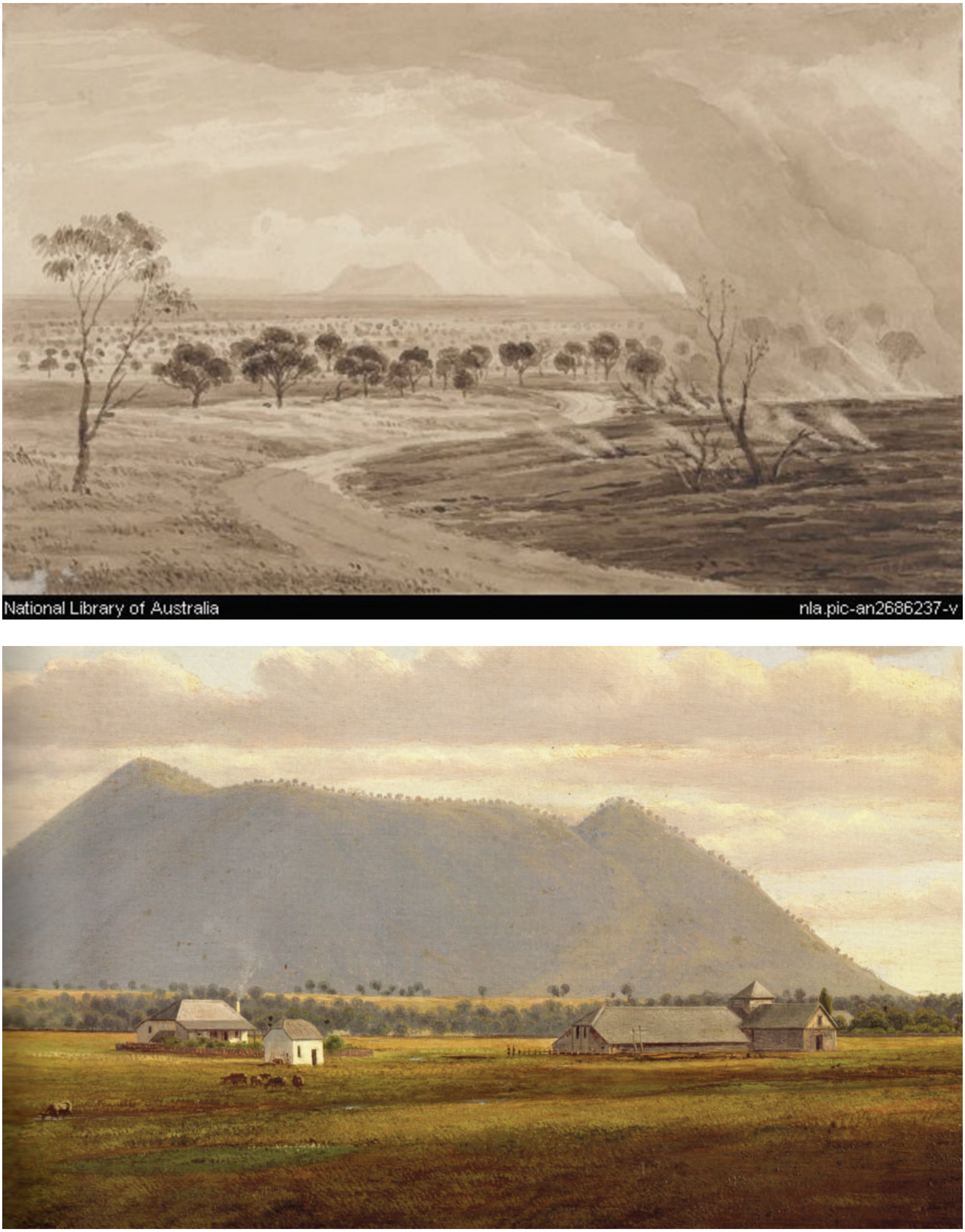

Fig. 7. (*a*) Duncan E. Cooper 'A bush fire, Mount Elephant, Victoria' [sepia wash ~1845]. Source: National Library of Australia http://nla.gov.au/nla.obj-134422839. (*b*) Eugene von Guerard [Larra 1857]. Source: Pullin (2011).

much of lowland south-eastern Australia, there is also a clear historic record of Aboriginal burning in Victoria's northern plains at the time of European arrival, which undoubtedly had an impact on vegetation (e.g. Hodgkinson 1856; Curr 1965; Mollison 1980 and others cited in Cahir *et al.* 2016).

Victoria's western plains (volcanic plains)

The vast, undulating volcanic plain extending west from Melbourne lies well within the temperate zone, receiving 500–1000 mm of rain per year (Stuwe and Parsons 1977; Stuwe 1986). The region is famously known for its vast treeless grassy plains, central to the establishment of early Melbourne, and popularly believed to be the product of Aboriginal burning on the basis of early accounts (Flinders 1966; Batman 1983; Boyce 2011). Ecologists tend to associate these natural grasslands with cracking-clay vertisols on basalt and alluvium, implying treelessness is predominantly controlled by climate–edaphic constraints (Morgan *et al*. in press).

However, finer-scale historical studies have shown that these now critically endangered grasslands were apparently not mostly treeless as they mostly appear today (e.g. Sinclair and Atchison 2012). Annotations from historic plans abound with references to trees and wooded vegetation; phrases such as 'lightly wooded', 'thinly timbered' and 'scattered sheoak' are particularly common. Nearly half of the ~2,570 annotations collated from the newer volcanics (41%) explicitly cite abundant trees such as eucalypts (e.g. river red gum (*Eucalyptus camaldulensis*), blackwood (*Acacia melanoxylon*), honeysuckle (*Banksia marginata*) and oak (drooping she-oak (*Allocasuarina verticillata*) and buloke (*Allocasuarina luehmannii*)); S. Sinclair, unpubl. data). The accounts of early explorers portray a clear impression of a variegated landscape, with and without trees (e.g. Andrews 1981).

These data are also well corroborated with pastoral-era accounts, including early landscape paintings by Eugene von Guerard and Fiery Creek pastoralist, Duncan E. Cooper. Although Cooper was an amateur, both artists are acclaimed for their insightful, detailed portrayal of landscapes (Brown 1987; Pullin 2011). Their paintings featuring Mount Elephant, the prominent scoria cone near Derrinallum, show typical volcanic plain landscape, gently undulating and covered with grass, but with numerous trees scattered in the foreground, the background, and over Mount Elephant itself (Fig. 7).

A reconstruction of pre-colonial vegetation patterns on the Werribee Plains shows a fragmented mix of wooded vegetation types in a matrix of treeless grassland, where the absence of trees is attributed to a mix of explanations including Aboriginal burning (Sinclair and Atchison 2012). There is also evidence from century-scale change studies in related systems nearby, that the absence of disturbance, especially the cessation of Aboriginal burning, can trigger a rapid shift from open grassy woodland dominated by drooping she-oak, eucalypts and honeysuckle (with very few shrubs), to closed scrub dominated by wattles (Lunt 1998). In today's highly disturbed, relictual landscapes, dispersal limitations severely constrain such dynamics even on protected tenures. Hence, there is sufficient basis to suspect a role for Aboriginal burning in influencing vegetation patterns, possibly over very large areas.

Other regions

Furthermore, there is support for similar patterns in other regions. In the Gippsland plains, a reconstruction of grassland distribution using soil correlations and historic plan annotations has revealed anomalies that imply multiple explanations of treelessness including fire (Lunt 1997). Again, we know fire was frequently used in this landscape at the time of European arrival, where early observers believed it had the capacity to mediate tree encroachment (see Howitt 1888; Brodribb 1978). In the Southern Tablelands of New South Wales and the Australian Capital Territory, we see similar grasslands, but at a higher elevation and occupying a greater range of parent rocks and terrain, where treelessness has principally been attributed to cracking-clay soils and cold-air drainage (Cambage 1909; Benson 1994). However, early accounts of Aboriginal burning (patchy, low-intensity fires in autumn and spring; Havard 1936; Flood 1980) suggest an influence of fire despite non-permanent occupation of montane areas (as reported elsewhere, such as in Fensham and Fairfax 1996; Bowman *et al*. 2013).

The Tasmanian Midlands was a natural north–south transport route for the Van Diemen's Land penal colony and the setting of numerous early accounts of 'park-like' and 'naturally cleared' landscapes (Meehan 1812, cited in Fensham 1989; Gammage 2008; Boyce 2011). However, reconstructed vegetation patterns again reveal a variegated tree cover, with forest and woodland (most frequently 'open' or 'thinly') dominated by eucalypts (*E. amygdalina*, *E. viminalis*, *E. ovata*), honeysuckle and wattles (*A. melanoxylon*, *A. dealbata*), interspersed with patches of treeless vegetation (Fensham 1989). Regional phytoecological and palynological data suggest that floristic patterns are most closely related to soil moisture, driven by complex terrain and substrate patterns, with treelessness being caused by dense grass swards and probably also frost, waterlogging, herbivory (including marsupials), and drought as well as fire (Fensham 1989; Fensham and Kirkpatrick 1992; Leonard *et al*. 2010; Ingram and Kirkpatrick 2013; Kirkpatrick *et al*. 2016; Romanin *et al*. 2016). Mostly on the basis of the historic record, others have argued that grasslands were more extensive historically and that the influence of Aboriginal burning has been understated (Gammage 2008).

Although the precise distribution of grasslands owing to Aboriginal burning will probably never be known, in all of these regions, it should be possible to determine which areas are more likely to bear the 'fingerprint' of fire-stick farming with application of the framework.

Conclusions

In linking what we already know about the vital role of frequent fire in maintaining the diversity of *Themeda* grasslands with patterns of century-scale and Holocene change, Lunt (1998) mused: '*it is difficult to conceive of alternative processes which might have acted across broad areas*'. In many ways, Aboriginal burning could be a 'missing link' of south-eastern Australian mesic grassland biogeography. It accords well with contemporary ecological research, patterns of century-scale change, and with interpretations from the historic record of Aboriginal practices before European arrival. The framework outlined in the present paper used appropriate, multiple lines of evidence, and can be applied readily in multiple sites in south-eastern Australia. It has great potential to test the hypothesis that widespread Aboriginal burning for food production had substantial effects on the dynamics of the region's temperate grassy ecosystems. It is hoped the framework will also help broaden the range of research approaches, and structure and integrate the disparate evidence lines to allow for rigorous testing. In this way, it should be possible to build confidence around the fire-stick farming hypothesis, shed light on the finer-scale influence of Aboriginal burning on these ecosystems, and to advance our understanding of grassland distribution, dynamics and conservation.

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