Quaternary Science Reviews 182 (2018) 37–47

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

The changing role of fire in conifer-dominated temperate rainforest through the last 14,000 years

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A R T I C L E I N F O

Article history:
Received 25 September 2017
Received in revised form
21 December 2017
Accepted 27 December 2017

Keywords:
Pollen
Charcoal
Rainforest
Tasmania
El Niño-Southern Oscillation (ENSO)
Superposed epoch analysis (SEA)

A B S T R A C T

Climate, fire and vegetation dynamics are often tightly coupled through time. Here, we use a 14 kyr sedimentary charcoal and pollen record from Lake Osborne, Tasmania, Australia, to explore how this relationship changes under varying climatic regimes within a temperate rainforest ecosystem. Superposed epoch analysis reveals a significant relationship between fire and vegetation change throughout the Holocene at our site. Our data indicates an initial resilience of the rainforest system to fire under a stable cool and humid climate regime between ca. 12–9 ka. In contrast, fires that occurred after 6 ka, under an increasingly variable climate regime wrought by the onset of the El Niño-Southern Oscillation (ENSO), resulted in a series of changes within the local rainforest vegetation that culminated in the replacement of rainforest by fire-promoted Eucalypt forest. We suggest that an increasingly variable ENSO-influenced climate regime inhibited rainforest recovery from fire because of slower growth, reduced fecundity and increased fire frequency, thus contributing to the eventual collapse of the rainforest system.

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1. Introduction

Fire is a key Earth System process, exerting an influence over global vegetation dynamics, biogeochemical cycles and climate (Bond et al., 2005; Scott et al., 2013). Future climate projections suggest an increase in fire activity in many regions (Moritz et al., 2012), a regime shift that may already be underway in some places (Bowman et al., 2017; Mariani and Fletcher, 2016). This projected increase, combined with changed fire use as Europeans (and other colonists over the last millennia) spread across the globe, presents a serious threat to fire-intolerant ecosystems over much of the Earth (Bowman et al., 2009). A further threat to many of these ecosystems comes from the combined effects of shortening the fire return interval and a shift to increasingly inhospitable conditions for plant growth and recovery as the climate system rapidly changes (Enright et al., 2015). Thus, to successfully manage natural systems into the future, it is important that we understand how fire influences the Earth System at multiple scales of space and time. High-resolution palaeoecological data are an important source of ecological information at temporal scales unavailable to direct observation (Froyd and Willis, 2008; Willis and Birks, 2006). Here, we use sedimentary pollen and charcoal to assess how a shift toward an increasingly variable climate through the Holocene influenced the vegetation-fire dynamic of a temperate rainforest refugium in Tasmania, Australia.

Wet temperate forests are dominated by long-lived tree species and are often characterised by long fire-return-intervals (Fletcher et al., 2014). Thus, the utility of traditional ecological observations to inform our understanding of ecosystem dynamics in these systems is limited. Archives of pollen and charcoal stored in sediments is often the only means of understanding the long-term drivers and consequences of fire regime changes in temperate forest ecosystems (Froyd and Willis, 2008; Willis et al., 2010). This is particularly the case for Southern Hemisphere temperate rainforests, which are dominated by long-lived (>1000 years) conifer species that are very intolerant to fire, such as *Fitzroya cupressoides* (Cupressaceae) in Chile (Lara et al., 1999), and *Athrotaxis cupressoides* and *A. selagnioides* (Cupressaceae) (Cullen, 1987, 1991; Holz et al., 2015) and *Lagarostrobos franklinii* (Podocarpaceae) in Tasmania (Gibson and Brown, 1991). The modern distributions of these conifers

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https://doi.org/10.1016/j.quascirev.2017.12.023
0277-3791/© 2017 Published by Elsevier Ltd.

have been negatively impacted by fire in recent centuries, for instance, in Tasmania, *Athrotaxis* species have suffered a fire-driven range contraction of more than 30% in the post-British invasion period that commenced in 1803 (Cullen, 1987, 1991). Increased fire activity combined with the influence of climate change over the recruitment, growth and recovery of fire-intolerant tree species: so-called "interval-squeeze" (Enright et al., 2015) render these endemic conifers vulnerable to extinction. Hence, there is a pressing need to understand the long-term fire ecology of conifer-dominated rainforest systems if we are to sustainably manage them into the future.

The "interval-squeeze" hypothesis predicts that the shift toward a drier and more variable climate regime, forecast for many regions in to the future, will increase woody plant extinction risk and change ecosystem function and structure (Enright et al., 2015). This effect is manifested principally through a shortening of the fire-return-interval (i.e. more frequent disturbance) and a reduced ability of particularly fire-intolerant woody species to recruit, grow and survive under altered climate conditions (Enright et al., 2015). A 6.5 kyr pollen and charcoal record from a small lake located in subalpine Tasmania demonstrates that repeated burning of conifer-dominant rainforest over successive millennia can result in the localised extinction of rainforest in favour of fire-promoting Eucalypt-vegetation (Fletcher et al., 2014). Fires in this system occurred in response to negative moisture anomalies resulting from an increase in the frequency of El Niño events through time (Fletcher et al., 2014) following the onset of increased ENSO variability after ca. 6 ka (Moy et al., 2002). The authors cite several successive post-fire changes in the local catchment through the past 6.5 kyrs, such as localised species extinction, soil nutrient leaching and reduced catchment soil cover, as being instrumental in the eventual collapse of the rainforest system. Critically, they do not consider the potential influence of long-term climate change over fire frequency and the ability of fire-intolerant rainforest trees to recover and regrow under increasingly inhospitable climate (*sensu* Enright et al., 2015).

We build on the study by Fletcher et al. (2014) to examine early-Holocene fire-vegetation-climate dynamics based on sedimentary pollen and charcoal records from a small lake, Lake Osborne, within the Southern Ranges of Tasmania (Fig. 1). Palynological evidence from the Southern Ranges indicates that the region served as a refugium for fire-intolerant rainforest during the early Holocene (ca. 12–9 ka) (Macphail, 1979; Macphail and Colhoun, 1985) when pollen and charcoal evidence indicates that relatively dry conditions and increased fire activity drove a reduction of regional rainforest cover over the main areas of rainforest habitat in Tasmania (Mariani et al., 2017; Mariani and Fletcher, 2017; Stahle et al., 2016, 2017). The study of Fletcher et al. (2014) showed a regime of infrequent burning (>1000 year fire return interval) between ca. 6–3 ka that culminated in the localised removal of rainforest at the expense of fire-promoted Eucalypt forest after ca. 2.6 ka (Fletcher et al., 2014). In this paper, we extend the existing 6 kyr high-resolution pollen and charcoal records from this site back to ca. 14 kyrs with the analysis of charcoal and pollen from new sediment cores. We hypothesise (1) that the Southern Ranges acted as refugium for coniferous rainforest during the early Holocene when less variable and humid conditions negated the occurrence of fire; and (2) that the onset of an ENSO-driven climate regime after 6 ka promoted burning of rainforest and reduced the ability of forest to recover from fire.

2. Climate, fire and vegetation in Tasmania

2.1. Climate

Tasmania is a cool temperate continental island located between 41 and 44°S, around 300 km off the coast of mainland Australia (Fig. 1a). The island is bisected by north-west/south-east trending mountain ranges that intercept the prevalent mid-latitude westerlies and produce a steep orographic precipitation gradient. Mean annual temperature varies from 5–7 °C (winter) to 14–16 °C (summer) and annual precipitation values exceed 3000 mm in the west and less than 600 mm in the east. Rainfall amount in the west (east) is positively (negatively) correlated to changes in the strength of westerly airflow over the island (Hendon et al., 2007; Hill et al., 2009). Inter-annual rainfall variability is significantly correlated with ENSO in the north and east, and with the Southern Annular Mode (SAM) in the west (Fig. 1) (Hill et al., 2009; Mariani and Fletcher, 2016; Mariani et al., 2016). Importantly, both modes exert an influence over most of the island during extreme events, particularly ENSO, which can cause island-wide rainfall deficits during particularly strong El Niño events (Hill et al., 2009; Nicholls and Lucas, 2007). During the Holocene, an initial insolation-driven warming trend (Berger, 1978; Stahle et al., 2017) was concomitant with a reduction in westerly airflow, producing a warm and dry climate in the west and a warm-humid climate in the east between ca. 12–9 ka (Fletcher and Moreno, 2012; Jones et al., 2017; Mariani and Fletcher, 2017). This trend reversed after ca. 8 ka and a generally cooler and wetter climate prevailed in the west until ca. 6 ka, while the east experienced a drying trend (Fletcher and Moreno, 2012; Jones et al., 2017; Mariani and Fletcher, 2017). The intensification of ENSO after ca. 6 ka drove an increase in climatic variability across Tasmania (Fletcher and Moreno, 2012; Jones et al., 2017; Mariani and Fletcher, 2017), with phases of increased frequency/magnitude of El Niño events, which starve eastern Australia of rainfall, associated with an island-wide moisture reduction (e.g. between ca. 4–3 ka) (Jones et al., 2017; Mariani and Fletcher, 2017).

2.2. Fire and vegetation

Fires are ubiquitous across Tasmania and have shaped the vegetation landscape since at least the arrival of people after ca. 40 ka (Bowman, 2000; Fletcher and Thomas, 2010b). The north, east and southeast are dominated by *Eucalyptus* forests that promote high fire frequencies under the relatively dry climate (Jackson, 1999). While cool temperate rainforest is the climate potential vegetation in the west, the landscape has been dominated by fire-promoted treeless vegetation (moorland) since the Late Glacial due to the disruption regional climate-driven vegetation dynamics by anthropogenic burning (Fletcher and Thomas, 2010b; Mariani et al., 2017). Rainforest is now restricted to isolated pockets afforded protection from fire by topography or by natural fire breaks (Wood and Bowman, 2012; Wood et al., 2011). Fires are climate (moisture)-limited in Tasmania (McWethy et al., 2013) and recent fire activity is tightly coupled to ENSO in the north, east and southeast and SAM in the west and southwest (Mariani and Fletcher, 2016; Mariani et al., 2016; Styger and Kirkpatrick, 2015). While people are the most likely ignition source in Tasmania (Bowman and Brown, 1986), long-term (centennial to multi-millennial scale) fire activity in Tasmania appears to be tightly coupled with climate (Fletcher et al., 2015; Fletcher and Moreno, 2011; Mariani and Fletcher, 2017; Rees et al., 2015). Put simply, phases of decreased westerly air flow (between ca. 12–9 ka) bring less (more) moisture and increased (decreased) burning in the west (east), with the opposite trend effect resulting from increased westerly airflow over the island (between ca. 8–6 ka). Following the onset of ENSO at ca. 6 ka, fire activity has progressively increased in the west with marked peaks in fire occurring synchronously in at sites located across both west and east (between 4 and 3 ka) (Beck et al., 2017; Fletcher et al., 2015; Jones et al., 2017; Mariani and Fletcher, 2017).

The vegetation response to these long-term changes in fire

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