Title

The influence of fine-scale topography on the impacts of Holocene fire in a Tasmanian montane landscape.

Haidee Cadd[1,2]*

haidee.cadd@adelaide.edu.au

Michael-Shawn Fletcher[1]

msfl@unimelb.edu.au

Michela Mariani[1,4]

Michela.Mariani@nottingham.ac.uk

Hendrik Heijnis[3]

hhx@ansto.gov.au

Patricia S Gadd[3]

psp@ansto.gov.au

[1] School of Geography, University of Melbourne, Parkville, Victoria, 3052, Australia

[2] Department of Earth Sciences, University of Adelaide, South Australia, 5005, Australia

[3] Australian Nuclear Science and Technology Organisation, Locked Bag 2001, Kirrawee DC NSW, Australia 2232.

[4] School of Geography, University of Nottingham, Nottingham, UK

*Corresponding author

Acknowledgments

We acknowledge that our work was conducted on Tasmanian Aboriginal lands and thank the Tasmanian Aboriginal community for their ongoing support of our research. Financial support for this project comes from the Australian Research Council (award: DI110100019 and IN140100050) and Australia Institute of Nuclear Science and Engineering (award: ALNGRA13529). We thank Simon Connor, Scott Nichols and Alexa Benson for their assistance in the field.

Abstract

Tasmania's montane temperate rainforests contain some of Australia's most ancient and endemic flora. Recent landscape-scale fires have impacted a significant portion of these rainforest ecosystems. The complex and rugged topography of Tasmania results in a highly variable influence of fire across the landscape, rendering predictions of ecosystem response to fire difficult. We assess the role of topographic variation in buffering the influence of fire in these endemic rainforest communities. We developed a new 14,000 year (14 ka) palaeoecological dataset from Lake Perry, southern Tasmania and compared it to neighbouring Lake Osborne (<250 m distant; Fletcher et al., 2014, 2018) to examine how topographic variations influence fire and vegetation dynamics through time. Repeated fire events during the Holocene cause a decline in montane rainforest taxa at both sites; however in the absence of fire, rainforest taxa are able to recover. Montane temperate rainforest taxa persist at Lake Perry until European settlement, whilst these taxa are driven locally extinct and replaced by *Eucalyptus* species at Lake Osborne after 2.5 ka. Contiguous topographic fire refugia within the Lake Perry catchment provide areas of favourable microclimates that discourage fire spread and support the recovery of these montane temperate rainforests.

KEYWORDS

Athrotaxis; *Nothofagus gunnii,* charcoal, rainforest; topography

Introduction

Fire is a key ecological and evolutionary agent that has shaped the vegetation landscape of Australia (Bowman, 2000; Keeley *et al.*, 2011; Hill *et al.*, 2016; Hill, 2017). While fire is of central importance in the regeneration and maintenance of many Australian species (so-called pyrophytic) (Williams and Woinarski, 1997; Keeley *et al.*, 2011), some species are extremely fire-sensitive (pyrophobic) and often experience widespread mortality and regeneration failure following fire (Kirkpatrick and Dickinson, 1984; Cullen and Kirkpatrick, 1988; Bowman, 2000; Holz *et al.*, 2015).

In the mountainous landscape of western Tasmania, pyrophobic plant communities are often juxtaposed against pyrophytic plant communities (Jackson, 1968; Brown and Podger, 1982; Bowman, 2000; Harris and Kitchener, 2005). Topographic position and its influence over fire occurrence and frequency is the best predictor of modern vegetation distribution in this landscape (Wood et al., 2011). Despite this, little is known about how topography interacts with long-term changes in climate and fire to buffer or expose fire sensitive vegetation to burning. This is a critical knowledge gap that negates effective and informed management of these critically endangered fire sensitive plant communities in the face of a rapidly changing climate and increasing fire activity (DPIPWE, 2002; Mariani and Fletcher, 2016; Bowman *et al.*, 2017; Harris *et al.*, 2018; Mariani *et al.*, 2018). Here, we assess the role of topography in the long-term fire ecology of threatened, fire sensitive, *Athrotaxis*-dominant montane rainforest, using a 14 kyr pollen, charcoal and geochemical analysis of a lake sediment core from southern Tasmania.

Conifer-dominant montane rainforests in Tasmania are presently restricted to topographic fire refugia in the mountainous region of western Tasmania. The limited work on the fire ecology of canopy dominants, *Athrotaxis* (Cupressaceae) and *N. gunnii,* indicate that they (1) suffer very high (almost complete) mortality from fire, (2) display limited post-fire regeneration from seed, (3) have poor dispersal abilities and (4) slow growth to maturation rates (Kirkpatrick and Dickinson, 1984; Cullen, 1987, 1991; Holz *et al.*, 2015). These life history traits confer a vulnerability on montane rain forests to changes in climate and fire regime (Pearson *et al.*, 2014; Enright *et al.*, 2015; Landesmann and Morales, 2018). The high mortality and limited recovery following fire leads to post-fire recovery times in excess of 800 years (Fletcher *et al.*, 2014). Recovery can be further compounded by the potential displacement by faster growing and well-dispersed species, such as *Eucalyptus,* following fire. The rapid post-fire recovery of *Eucalyptus* and their ability to propagate fire can increase the likelihood of fires recurring (Brooks *et al.*, 2004). Once established, the positive relationship between *Eucalyptus*, altered vegetation structure, microclimate and fire can alter the prevailing fire regime of a site.

The great longevity of these montane rainforest canopy dominants, along with poor dispersal and slow growth to maturation can increase the time lag between species distributions and their geographic climate envelopes (Loehle, 2018), thus increasing extinction risks (Talluto *et al.*, 2017). Mariani et al., (*In Press*) demonstrate that changing climates in Tasmania's montane rainforest ecosystems induced a disequilibrium between climate and vegetation that resulted in reduced resilience, and increased extinction risk, of this forest type to fire. Critically, what is unknown is to what extent topographic complexity creates spatial buffering (ie. refugia) for this forest type via its influence over microclimate, irrespective of macroscale climatic changes (*sensu* Lenoir et al., 2013).

Landscape-scale analyses indicate that that steep south facing slopes act as topographic fire refugia (TFR), by creating microclimates that discourage fire spread and as a geographic barriers to wind-driven fire (predominantly northwest in Tasmania) (Wood et al., 2011). The influence of TFRs over microclimate and fire spread is further enhanced by a negative feedback between fire, low rainforest fuel flammability and high sub-canopy humidity within rainforest vegetation (Kirkpatrick and Dickinson, 1984; Wood and Bowman, 2012). This internal fire-retardant buffering against fire is scale dependent, with small patches of vegetation and scattered individual rainforest trees suffering high fire induced mortality irrespective of topographic setting (Pappas, 2010; Baker *et al.*, 2012). Pappas (2010) identified a threshold of forest patch size for temperate rainforest above which the negative feedback between vegetation and fire is initiated, suggesting that large TFR could act to buffer against the effects of changes in macroclimate in the Tasmanian landscape.

In this paper, we present a detailed reconstruction of ecosystem change from high-resolution pollen, charcoal and µXRF scanning geochemistry datasets over the last 14 ka from a subalpine lake, Lake Perry, in southern Tasmania, Australia. To assess whether local-scale topographic heterogeneity influences the response of montane rainforest to fire we compare our Lake Perry dataset the existing dataset from neighbouring Lake Osborne where Fletcher et al. (2014, 2018) found that coniferous montane rainforest suffered localised extinction after successive fire events during the Holocene. The present-day vegetation around Lake Perry is dominated by pyrophytic sclerophyll vegetation, with several *Athrotaxis selaginoides* (Cupressaceae) stags on the steep east-facing slopes of the catchment, and scattered living individuals bordering the lake shore. The catchment size, lake area and geology of these two catchments is virtually identical, however, the local-scale topography of the two lake catchments displays differences. We hypothesise that the larger area of TFR in the Lake Perry catchment will have buffered the effects of fire on montane rainforest species at that site relative to Lake Osborne. Thus, we expect that, despite similar fire histories, the vegetation history at these adjacent sites will differ with respect to the response of montane rainforest to fire.

Study Site

The Hartz Mountains are a north-south trending mountain range in southern Tasmania, situated on the margin of the super humid western and subhumid eastern climate zones of Tasmania (Figure 1). Lake Perry (43°12'48", 146°45'16"E) is the northern most basin in a series of small moraine-bound subalpine (>900 masl) lakes that dot the ridge of the Hartz Mountains. Lake Perry lies 230 m NE of Lake Osborne (43°12'53", 146°45'30"E), a small moraine bound lake that has a similar lake surface area and catchment size (Fletcher et al., 2014, 2018). Average annual precipitation at Keogh's Pimple climate station (43°12′0″S, 146°46′12″ E; 831 m a.s.l; 1.9 km northeast of Lake Perry) is 971.2 mm per annum (BOM and

BOM, 2018). The geology of the Hartz Mountains is composed of quartz dominated Permian sandstone capped by outcrops of erosion resistant Jurassic dolerite. The overall topography of the Lake Perry and Lake Osborne catchments is similar, being dominated by steep (>30º) N-NE facing slopes (Figure 5, Figure S2 in Appendix S1). Lake Perry hosts a taller and steeper moraine along its northern edge that produces a large continuous section of south facing slope.

Vegetation cover and soil development on the Hartz Mountains, and within the Lake Perry catchment, is generally low, with a substantial amount of exposed dolerite bedrock. The vegetation of the Hartz Mountains includes areas of alpine communities, sub-alpine woodlands, scrub heath, temperate rainforest and wet *Eucalyptus* forest. Dominant species of the Lake Perry catchment include *Eucalyptus coccifera*, *Eucalyptus vernicosa*, *Nothofagus cunninghamii*, *Eucryphia milliganii*, *Gahnia grandis,* Proteaceae (including *Bellendena montana, Hakea lissosperma, Orites revoluta, O. acicularis*, and *Telopea truncata*) and Ericaceae (including *Richea scoparia, R. pandanifolia, Epacris serpyllifolia* and *Monotoca*) shrub species. Individuals of *A. selaginoides* grow intermittently along the lake shore and *A. selaginoides* stags dot the southwest facing slopes of the catchment.

Materials and Methods

Lake Osborne

Proxy and chronological information for Lake Osborne can be found in Fletcher et al., (2014, 2018) (Table 1).

Lake Perry

2.1 Core collection and chronology

An entire sediment sequence was retrieved from the deepest part of Lake Perry (23 m) using a rod-in-rod Livingston Piston Corer. Two surface cores that captured the sediment-water interface were retrieved from Lake Perry using a 6-cm polycarbonate tube attached to a Universal Gravity Corer (http://www.aquaticresearch.com/universal_core_head.htm).

Eighteen samples were submitted for radiocarbon analysis from Lake Perry. Four samples were analysed at the ANU Radiocarbon Dating Laboratory and 14 samples were analysed at Direct AMS radiocarbon dating services, Bothell, WA. Radiocarbon dates were calibrated to calendar years before present (cal. yr BP; AD 1950) using the Southern Hemisphere calibration curve (Hogg *et al.*, 2013). Age-depth modelling of the composite cores from Lake Perry were performed using the Bacon package (Blaauw and Christen, 2011) in R (R Core Team, 2017).

2.2 Palynology

Pollen, spores and microscopic charcoal were processed using standard protocols (Fægri and Iverson, 1989). A total of 300 pollen grains of terrestrial origin (excluding terrestrial fern spores) form the base pollen sum. Percentages of aquatic taxa and ferns are based on a super-sum inclusive of these and the terrestrial pollen sum. Fossil pollen data were divided into assemblage zones with the aid of stratigraphically constrained cluster analysis (CONISS; Grimm, 1987). Patterns of vegetation community change were estimated using a principal curve (PrC) on untransformed percentage pollen data in *analogue v. 0.17-0* (Simpson and Oksanen, 2014) in R (R Core Team, 2017).The PrC is a one-dimensional curve fitted through the pollen data that minimises the distance between the curve and the response values of each species observation (Simpson and Oksanen, 2014). Microscopic charcoal accumulation rates (CHAR) were based on concentrations (calculated via the addition of a *Lycopodium* sp. spike), with the deposition time (yr cm^{-1}) calculated from the age-depth model.

2.3 Macroscopic charcoal analysis

Macroscopic charcoal content of contiguous sediment samples (1.25 cc) were analysed using standard protocols (Whitlock & Larsen, 2002). Samples were immersed in bleach for approximately 7 days, sieved using 125 µm and 250 µm mesh sieves and tallied under a dissecting microscope. Macroscopic charcoal accumulation rates (CHAR; fragments cm^{-2} $year^{-1}$) were calculated using charcoal counts and deposition time (yr cm^{-1}) calculated from the age-depth model. Time series analysis of macroscopic charcoal data was conducted in CHARanalysis (Higuera *et al.*, 2009). Charcoal counts were interpolated to the median samples resolution (10 cal. yrs). Charcoal peaks (C_{peak}) were identified as the ratio between charcoal accumulation rates and the background charcoal determined from the 95^{th} percentile threshold of noise distribution from a locally fitted mean Gaussian model. 'High-impact' fires (*sensu* Fletcher et al. 2014) have been identified as macroscopic charcoal peaks occurring in association with a change in pollen and/or the geochemical composition of the sediment.

2.4 Geochemical analysis

Non-destructive elemental analyses of the Lake Perry core were conducted at 1 mm intervals using the µXRF X-ray fluorescence core scanner at the Australian Nuclear Science and Technology Organisation (ANSTO). Raw elemental data were normalised by total counts per second (cps) and transformed by centre-log-ratio (clr) in the *compositions* package (van den Boogaart and Tolosana-Delgado, 2008) in R (R Core Team, 2017) to avoid spurious patterns and relationships resulting from the closed sum effect (Pawlowsky-Glahn and Egozcue, 2006; Croudace and Rothwell, 2015). A PrC was performed on untransformed µXRF elemental profiles normalised to cps from Lake Perry in *analogue v. 0.17-0* (Simpson and Oksanen, 2014) in R (R Core Team, 2017).

2.6 Topography

We used structure from motion photogrammetry to develop a high-resolution topographic map of the Lake Perry and Lake Osborne catchments using an unmanned aerial vehicle (UAV). Images were imported into Pix4D for matching and point-cloud generation from which a digital terrain model (DTM) was developed with a pixel resolution of 8.52 cm/pixel that was subsequently resampled to 1 m resolution. ArcMap 10.33 was then used to extract slope and aspect data from the DTM. We identified areas within the catchment that have a southerly aspect (between 90-270°) and a slope greater than 15°, following the work of Wood et al. (2011), who identified these parameters as important predictors of rainforest distribution in southwest Tasmania. Pixels with a south facing aspect and >15º slope were considered to be Topographic Fire Refugia (TFR) and mapped for the Lake Perry and Lake Osborne catchments. Hotspot analysis was undertaken in ArcMap 10.3 to highlight areas with high density of TFR pixels using a 10 m resolution fishnet. Contiguity analysis was also performed: pixels surrounded by more than 1 TFR pixels on all sides were considered 'core' TFR as they are afforded greater buffering from the edge pixels (Wu and Murray, 2008).

Results

Lake Osborne

Proxy results for Lake Osborne can be found in Fletcher et al., (2014, 2018) (Table 1).

Lake Perry

3.1 Core collection and chronology

Four sediment profiles were retrieved from the deepest part of Lake Perry (TAS1303): SC1 (212 cm), BL1 (134 cm), LCA drives 1 - 4 (398.5 cm) and LCB drives 1 - 4 (373 cm). All cores consisted of homogenous orange/brown organic sediment that graded to inorganic grey clay sediment towards the base of drive 4 in LCA and LCB. SC1, BL1 and LCA were used for µXRF scanning and destructive analysis for this study. Stratigraphic core correlation of SC1, BL1 and LCA cores was achieved using µXRF scanning geochemical profiles, macroscopic charcoal values and corroborated using radiometric dating.

Radiometric analyses were performed on SC1, BL1 and LCA (See Table S1 in Appendix S1). A maximum radiocarbon age of 14,816 cal. yr BP was obtained for Lake Perry at a depth of 415 cm. The top (0 - 0.5 cm) bulk sediment sample of BL1 returned a radiocarbon age of 1337 ^{14}C yr BP. Due to this anomalously old age and a collection of radiocarbon ages of ~3000 cal yr BP in the upper 20 cm of SC1 and BL1 (See Table S1, Figure S1 in Appendix S1) it was inferred that a portion of the bulk sediment carbon of the Lake Perry sediments had been derived from older carbon stored within the catchment. A paired bulk sediment and macrofossil radiocarbon sample (155 cm) returned similar radiocarbon ages (5913 ± 32, 5806 ± 36 ^{14}C yr BP respectively). The paired radiocarbon samples returning similar ages indicates that there was no significant portion of stored carbon entering the system at this point. The store of ‘old’ carbon in the catchment after ca. 5.9 ka, immediately following a high-impact fire event, may be a result of highly recalcitrant charcoal remaining within the catchment and erosion of this highly weathered, fine recalcitrant carbon entering the sediments over time.

To account for the stored carbon entering the system, an age offset of 1337 ^{14}C BP (taken from the top 0.5 cm sample) was incorporated into the age-depth model for depths above 155 cm. The selected age model was compared to the nearby Lake Osborne, with similar sedimentation history, climate forcing and catchment characteristics, to validate the choice of age model. The selected age-depth model, a non-reservoir age-depth model for Lake Perry and Lake Osborne age-depth model are presented in Appendix S1, Figure S1.

3.2 Palynology

A total of 183 samples from Lake Perry were analysed for pollen, spores and microscopic charcoal from cores SC1, BL1, LCA3 and LCA4. The Pollen PrC explained 82% of the variance within the pollen spectra. Low values are associated with montane rainforest taxa and high stability of vegetation (Figure 3).

Three main pollen zones were identified for Lake Perry (Figure 2). Zone 1 (14.2 – 11.7 ka) represents the late glacial period, dominated by *Eucalyptus* sp. (18 - 30%), Asteraceae (5 - 13%) and Poaceae (15 - 21%). The high late glacial *Eucalyptus* values may reflect either extra-local long-distance pollen transport from downslope or the presence of cool climate *Eucalyptus* (eg. *E. vernicosa*) within the local catchment (Fletcher and Thomas, 2007). A rapid transition from a cool climate late glacial assemblage to a montane rainforest assemblage occurs at ca.11.7 ka, concurrent with the beginning of the Holocene epoch.

Zone 2 (11.7 – 8.1 ka) is dominated by the montane rainforest species *N. gunnii* (5 – 27%), lowland rainforest species *N. cunninghamii* (24 – 39%), *P. aspleniifolius* (4 – 18%) and *Eucryphia* species (4 - 17%). Zone 3 (8.1 ka – present) is divided into three subzones. Subzone 3a (8.1 – 5.8 ka) is dominated by Cupressaceae (5 – 23%), *N. cunninghamii* (22 – 38%), *P. aspleniifolius* (12 – 27%) and *Eucryphia* species (4 – 20%). Subzone 3b (5.8 – 2.3 ka) is dominated by *N. cunninghamii* (18 – 43%), *P. aspleniifolius* (11 – 26%) and *Eucryphia* species (7 – 23%), with a notable increase in Cupressaceae (4 – 21%) at the end of the subzone. Subzone 3c (2.3 ka – present) is dominated by Cupressaceae (2 – 22%), *N. cunninghamii* (22 – 44%), *P. aspleniifolius* (11 – 28%) and *Eucryphia* species (5 – 19%), with slight increases in *Eucalyptus* sp. (3 – 13%). and Proteaceae (0 – 3%) at the end of the subzone.

3.3 Macroscopic charcoal

A total of 1,099 samples from Lake Perry cores SC1, BL1, LCA2, LCA3 and LCA4 were analysed for macroscopic charcoal. Macroscopic charcoal values were low throughout the late glacial, with background charcoal increases occurring after 11.7 ka (Figure S4 in Appendix S1). High impact fire events occur at Lake Perry at ca. 8.2, 7.8, 5.9, 4.9, 2.5 and 0.15 ka (AD 1890) ka (Figure 3).

3.4 Geochemical analysis

Scanned elemental profiles were obtained for cores SC1, BL1 and LCA 1 – 4. The µXRF PrC explained 99% of the variance and is strongly correlated with Fe, Rb, Ti, K, Ca, V, Mn, Cr and Si (minerogenic/detrital elements) (Table S2 in Appendix S1). Increases in geochemical PrC occur following macroscopic charcoal peaks (Figure 3).

3.5 Topography

The area (ca. 0.24 km^2) and overall topography of the Lake Perry and Lake Osborne are very similar. Both catchments are steep (up to 90%) and mostly facing NE-N (Figure 5). The NE facing slopes of Lake Osborne are characterised by more gentle slopes (<30%), with the rest of the catchment comprised of mixed aspects, dominated by E and SE facing slopes (Figure 5). Identification of TFR within each catchment (Figure 5) demonstrates that, while both catchments have a broadly similar total TFR area, the TFR in Lake Perry is notably contiguous, while TFR within the Lake Osborne catchment is distinctly fragmentary.

Discussion

4.1 Post-glacial environmental history

Our data indicate a tight coupling of late glacial and Holocene vegetation change between Lakes Perry and Osborne. An initial cool climate assemblage, composed of grass, herb and *Eucalyptus* (Figure 2; Fletcher et al., 2018), dominates at both sites during the late glacial. The high minerogenic input into Lake Perry at this time (geochemical PrC; Fig. X) is consistent with an influx of detrital material from a sparsely vegetated catchment. The beginning of the Holocene is marked by a synchronous colonisation of the Lake Perry and Lake Osborne catchments by montane rainforest species, *Nothofagus gunnii* and Cupressaceae (Figure 4). This pollen assemblage is akin to the hyper fire-sensitive plant community Cupressaceae – *N. gunnii* short montane rainforest (*sensu* Harris and Kitchener, 2005) that is presently found in high-altitude topographic fire refugia across southern and western Tasmania (Kirkpatrick and Harwood, 1980; Harris and Kitchener, 2005). This pollen assemblage dominates a number of southern Tasmanian upper tree line sites at this time (Macphail, 1979; Macphail and Colhoun, 1985; Fletcher *et al.*, 2018), reflecting the regional upslope expansion of montane rainforest in response to postglacial climate change and low fire activity across the region.

The early Holocene dominance by *N. gunnii, N. cunninghamii, P. aspleniifolius* and Cupressaceae of the pollen spectra at Lake Perry (Figure 2), Lake Osborne (Fletcher *et al.*, 2018) and other southern Tasmanian sites (Macphail, 1979; Macphail and Colhoun, 1985) indicate the persistence of a cool, humid climate across southern Tasmania between ca. 11.7 – 8.2 ka. This period was characterised by low fire activity and persistence of Cupressaceae – *N. gunnii* montane temperate rainforest between at Lakes Perry and Osborne (Figure 3 & 4) (no charcoal data is available for other sites). The persistence of virtually undisturbed (by fire) rainforest for nearly 4 ka fostered the development of organic rich soil profiles, which develop under rainforest in the cool and humid climates of western and southern Tasmania (Bowman and Jackson, 1981; Pemberton, 1988). These organic soils likely blanketed the catchments of Lakes Perry and Osborne, capturing weathered materials and resulting in a reduction of minerogenic input into the lake basins (Figure 3).

Fire is the key driver of vegetation changes within the montane rainforest communities at both Lake Osborne and Lake Perry during the Holocene. The mid-Holocene is characterised by a series of high-impact fire events at both lakes (hereon "high-impact" fire events are charcoal peaks associated with shifts in pollen and or geochemistry; sensu Fletcher et al., 2014). These high-impact fire events are associated with a reduction in one or both montane rainforest canopy dominants and increased deposition of detrital elements into the lake following the destruction of the catchment vegetation and underlying organic soil (Figure 3 and 4; Fletcher et al., 2018, 2014). Erosion of organic soil profiles by heavy rains following fires is common in the wetter parts of Tasmania (Pemberton, 1988; Bridle, Cullen and Russell, 2003). At Lake Perry, the high magnitude of the initial geochemical PrC peaks at 8.2 and 7.8 ka likely reflects substantial catchment disturbance by fire and the subsequent erosion of the soil profiles that developed under the stable forest vegetation system between ca. 11.7 – 8.2 ka.

These high-impact fires at ca. 8.2 and 7.8 ka occurred at both Lakes Perry and Osborne and as associated with declines in montane rainforest (Cupressaceae and *N. gunnii*) at both sites. Whilst montane rainforest suffers declines at both sites, the fire event at ca. 7.8 ka is associated with the local extinction of *N. gunni* at Lake Perry. In contrast this species recovers from this fire and persists for another 2000 years at Lake Osborne (Figure 4). The divergent response of the vegetation to fire at these proximal sites likely reflects the non-uniform intensity and impact of fires that burn across landscapes (e.g. Chafer et al., 2004). While charcoal data is lacking from other sites across southern Tasmania, localised extinctions of *N. gunnii* occur across number of southwest Tasmanian sites through the mid- to late Holocene (Macphail, 1979; Macphail and Colhoun, 1985; Fletcher *et al.*, 2018). These localised extinctions likely reflect the impact of fire on montane rainforest across this region and is consistent with the hyper fire sensitivity of *N. gunnii* (Kirkpatrick and Harwood, 1980; Fletcher *et al.*, 2014, 2018). The limited recovery ability and lack of recolonisation seen at Lake Perry, even across relatively small distance from the Lake Osborne catchment, (<250 m distant) further emphasise the limited dispersal ability of these species.

Despite experiencing the same incidence of fire, the post-fire recovery of montane rainforest becomes increasingly dissimilar between Lakes Perry and Osborne after ca. 6 ka (Figure 4). This period is marked by shift toward a more variable climate in Tasmania following the onset and amplification of ENSO variability in the tropical Pacific (Fletcher and Moreno, 2012; Mariani and Fletcher, 2017). After the fire-driven destruction of the extant coniferous forests at both sites at 5.9 ka, partial recovery of Cupressaceae forests occur at Lake Osborne while no apparent recovery occurs within the Lake Perry catchment over the next 3 ka (Figure 4). Despite recurrent and broadly synchronous fires, Cupressaceae persisted at both Lake Osborne and Lake Perry into the late Holocene (Figure 3, 4), until a high-impact fire at ca. 2.5 ka caused the localised extinction of this taxon from Lake Osborne. At Lake Perry, Cupressaceae recovers until a high-impact fire during the post-British colonisation period causes substantial declines (Figure 4), a recurrent trend across the landscape during this time (Cullen, 1991; Holz *et al.*, 2015).

4.2 Fire, climate, topography and montane rainforest

We observe two clear phases of fire recovery of montane rainforest in our study area: an early to mid-Holocene high resilience phase and a mid to late-Holocene low resilience phase. Fires in the early to mid-Holocene are followed by recovery of one or both montane rainforest canopy dominants at both sites. This dynamic recovery reflects a degree of resilience to fire that is not apparent at either site in the mid to late Holocene or in the modern landscape (Cullen, 1991; Holz *et al.*, 2015). Fletcher et al., (2018) argue that the onset of ENSO variability after ca. 6 ka resulted in a climate less conducive to post-fire recovery, growth and reproduction, while simultaneously increasing the occurrence of fire in Tasmania's montane rainforest. In addition, Mariani et al., (*In press*) use species distribution modelling and palaeoecology (including Lake Osborne) to argue that a shift in climate after ca. 4 ka resulted in a disequilibrium between montane rainforest and climate across much of its range. Critically, post-fire recovery did not occur in areas of climate-vegetation disequilibrium, supporting the notion that regional climate is a key component that influences the resilience of this system to fire.

An apparent slowing down of the post-fire rate of recovery of Cupressaceae after ca. 6 ka occurs at Lake Perry and Lake Osborne (Figure 3, 4). Whilst this slowed recovery is consistent with a variable climate regime inhibiting the recovery, fecundity and efficacy of growth in these long-lived species, Cupressaceae continues to recover from fire throughout this period at Lake Perry (Figure 3, 4). Indeed, Cupressaceae recovers following a high impact fire at ca. 2.5 ka, a period associated with localised fire-driven extinction of montane rainforest across southern and western Tasmania (Mariani et al., *In press*). Notwithstanding the potential that the fire at ca. 2.5 ka at Lake Perry was of insufficient intensity to result in the localised extinction of Cupressaceae (albeit it is associated with a clear peak in detrital inputs that mirrors previous high-impact fires), our data suggests that (macro)climate alone is an insufficient predictor of montane rainforest resilience to fire.

Topographic complexity within a landscape offers protection from fire at a range of spatial scales by influencing local microclimates (such as reduced solar radiation) and fire occurrence (Krawchuk *et al.*, 2016). Topographic fire refugia (TFR) are an expression of the modification of the microclimate and act to buffer intensity and spread of fire (Lenoir *et al.*, 2013; Krawchuk *et al.*, 2016). Our fine-scale topographic data reveals a clear difference in the local-scale topography between Lake Osborne and Lake Perry catchments. This topographic variation provides a potential mechanism for the persistence of Cupressaceae at Lake Perry, despite a fire history similar to Lake Osborne and a pervasive macroclimate inhospitable to post-fire recovery of this taxon (Figure 3, 4). In Tasmania, slope and aspect are significant predictors of rainforest distribution (Wood et al., 2011). While the overall aspect of both catchments is predominantly north facing, the catchment of Lake Perry hosts a larger contiguous proportion of steep (>15°) south facing slopes (i.e. TFR) than Lake Osborne (Figure 5c).

Spatial contiguity within a landscape plays a significant role in buffering ecosystems from pressures such as land use change, biodiversity loss and disturbance (Diamond and Wright, 1991; Williams and ReVelle, 1996; Haddad *et al.*, 2015). Increased contiguity of temperate rainforest buffers the effects of fire by increasing the subcanopy humidity and reducing the flammability between edge and core areas of forests (Didham and Lawton, 1999; Wood and Bowman, 2012; Cawson *et al.*, 2017; Landesmann and Morales, 2018). Thus, we contend that the increased size and contiguity of the TFR area and core within the Lake Perry catchment afforded greater protection for montane rainforest from fire. This protection provided a proximal recolonisation source of Cupressaceae within the Lake Perry catchment that fostered increased recovery. In contrast, the relatively more open Lake Osborne catchment, with limited areas core TFR, was more susceptible to the influence of fire. In addition, the steady increase in *Eucalyptus* species within the Lake Osborne catchment after 3 ka (Figure 4) would have altered the catchment vegetation structure, reduced canopy humidity and increased the flammability of vegetation, increasing exposure to fire. This biological interaction with microclimate and topography apparently increased the vulnerability of montane temperate rainforest and reduced probability of recovery that led to the eventual localised extinction of rainforest from that catchment.

Conclusions

Climate amelioration at the onset of the Holocene sees the upslope migration of forest taxa within the Lake Perry and Lake Osborne catchments. The Cupressaceae – *N. gunnii* forest association remain stable for the next 4000 years, during a period of low fire activity. The climate driven vegetation patterns persist through the late glacial and early Holocene until 8.2 ka, when the vegetation system switches to one governed by fire.

High-impact fires occur synchronously across both catchments during the Holocene in response to regional macroclimate drivers, resulting in the reduction of one or both montane rainforest canopy dominants. The catchment scale extinction of *N. gunnii* at Lake Perry in the early Holocene and Cupressaceae at Lake Osborne in the late Holocene emphasise the variable impacts of fire across the landscape. In addition, the lack of recolonisation of the adjacent catchments by these species over a 2,000-year period highlights the extremely limited dispersal ability of these species.

Persistence of montane rainforest at Lake Perry until 1890 AD occurs as a result of topographic variations that create rainforest dominated, super-humid and non-flammable patches that buffer the effects of marcoclimate and fire within the landscape (i.e. areas of SW facing slopes). The presence of *Eucalyptus* species further alter the microclimate characteristics and may have engineered fire-regime changes, contributing to the vulnerability of these systems. Topographic fire refugia contribute to the recovery of fire-sensitive rainforests by providing proximal re-colonisation sources to burnt patches. We suggest that conservation efforts in this topographically diverse, flammable landscape should prioritise these locations as potential arks against the future extinction of these endemic species.

References

Baker, P. J., Simkin, R., Pappas, N., *et al.* (2012) 'Fire on the mountain: A multi-scale, multiproxy assessment of the resilience of cool temperate rainforest to fire in Victoria's Central Highlands', *Terra Australis*, 34(24), pp. 375–391.

Blaauw, M. and Christen, J. A. (2011) 'Flexible paleoclimate age-depth models using an autoregressive gamma process', *Bayesian Analysis*, 6(3), pp. 457–474. doi: 10.1214/11-BA618.

BOM and BOM, (Australian Bureau of Meterology) (2018) *Climate statistics for Australian locations*. Available at: http://www.bom.gov.au/climate/averages/tables/cw_040209.shtml (Accessed: 24 January 2018).

van den Boogaart, K. G. and Tolosana-Delgado, R. (2008) '"compositions": A unified R package to analyze compositional data', *Computers and Geosciences*, 34(4), pp. 320–338. doi: 10.1016/j.cageo.2006.11.017.

Bowman, D. M. J. S. (2000) *Australian Rainforests: Islands of Green in a Land of Fire*. New York: Cambridge University Press. doi: 10.1111/j.1745-7939.2001.tb01610.x.

Bowman, D. M. J. S., Williamson, G. J., Abatzoglou, J. T., *et al.* (2017) 'Human exposure and sensitivity to globally extreme wildfire events', *Nature Ecology and Evolution*. Macmillan Publishers Limited, part of Springer Nature., 1(3), pp. 1–6. doi: 10.1038/s41559-016-0058.

Bowman, D. M. J. S. and Jackson, W. D. (1981) 'Vegetation succession in southwest Tasmania', *Search*, 12(10), pp. 358–362.

Bridle, K., Cullen, P. and Russell, M. (2003) *Peatland hydrology, fire management and Holocene fire regimes in southwest Tasmanian blanket bogs*, *Nature Conservation Branch of the Department of Primary Industries, Water and Environment*. Hobart, Tasmania.

Brooks, M. L., Antonio, C. M. D., Richardson, D. M., *et al.* (2004) 'Effects of Invasive Alien Plants on Fire Regimes', *BioScience*, 54(7), pp. 677–689. doi: https://doi.org/10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2.

Brown, M. J. and Podger, F. D. (1982) 'Floristics and fire regimes of a vegetation sequence from sedgeland-heath to rainforest at bathurst harbour, Tasmania', *Australian Journal of Botany*, 30(6), pp. 659–676. doi: 10.1071/BT9820659.

Cawson, J. G., Duff, T. J., Tolhurst, K. G., *et al.* (2017) 'Fuel moisture in Mountain Ash forests with contrasting fire histories', *Forest Ecology and Management*, 400, pp. 568–577. doi: 10.1016/j.foreco.2017.06.046.

Chafer, C. J., Noonan, M. and Macnaught, E. (2004) 'The post-fire measurement of fire severity and intensity in the Christmas 2001 Sydney wildfires', *International Journal of Wildland Fire*, 13(2), p. 227. doi: 10.1071/WF03041.

Croudace, I. W. and Rothwell, R. G. (2015) *Micro-XRF Studies of Sediment Cores: Applications of a non-destructive tool for the environmental sciences*, *Developments in Paleoenvironmental Research*. Dordrecht: Springer. doi: 10.1007/978-94-017-9849-5.

Cullen, P. (1991) 'Regeneration of Athrotaxis selaginoides and other rainforest tree species on landslide faces in Tasmania', in Banks, M. . and Royal Society of Tasmania (eds) *Aspects of Tasmanian Botany : A Tribute to Winifred Curtis*. Hobart: Royal Society of Tasmania, pp. 191–200.

Cullen, P. J. (1987) 'Regeneration patterns in populations of Athrotaxis selaginoides D. Don. from Tasmania', *Journal of Biogeography*, 14(1), pp. 39–51.

Cullen, P. J. and Kirkpatrick, J. B. (1988) 'The ecology of Athrotaxis D. Don (Taxodiaceae). I. Stand structure and regeneration of A. cupressoides', *Australian Journal of Botany*, 36(5), pp. 547–560. doi: 10.1071/BT9880547.

Diamond, J. T. and Wright, J. R. (1991) 'An implicit enumeration technique for the land acquisition problem', *Civil Engineering Systems*, 8(2), pp. 101–114. doi: 10.1080/02630259108970613.

Didham, R. K. and Lawton, J. H. (1999) 'Edge Structure Determines the Magnitude of Changes in Microclimate and Vegetation Structure in Tropical Forest Fragments', *Biotropica*, 31(1), pp. 17–30. doi: 10.2307/2663956.

DPIPWE (2002) *Schedule 3A of the Nature Conservation Act*. Available at: https://www.legislation.tas.gov.au/view/html/inforce/current/act-2002-063.

Enright, N. J., Fontaine, J. B., Bowman, D. M. J. S., *et al.* (2015) 'Interval squeeze: Altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes', *Frontiers in Ecology and the Environment*, 13(5), pp. 265–272. doi: 10.1890/140231.

Fægri, K. and Iverson, J. (1989) *Textbook of Pollen Analysis*, *Textbook of pollen analysis.* New York: Wiley.

Fletcher, M.-S., Bowman, D. M. J. S., Whitlock, C., *et al.* (2018) 'The changing role of fire in conifer-dominated temperate rainforest through the last 14,000 years', *Quaternary Science Reviews*. Elsevier Ltd, 182, pp. 37–47. doi: 10.1016/j.quascirev.2017.12.023.

Fletcher, M. S., Wolfe, B. B., Whitlock, C., *et al.* (2014) 'The legacy of mid-holocene fire on a Tasmanian montane landscape', *Journal of Biogeography*, 41(3), pp. 476–488. doi: 10.1111/jbi.12229.

Fletcher, M. S. and Moreno, P. I. (2012) 'Have the Southern Westerlies changed in a zonally symmetric manner over the last 14,000 years? A hemisphere-wide take on a controversial problem', *Quaternary International*, 253, pp. 32–46. doi: 10.1016/j.quaint.2011.04.042.

Fletcher, M. S. and Thomas, I. (2007) 'Modern pollen-vegetation relationships in western Tasmania, Australia', *Review of Palaeobotany and Palynology*, 146(1–4), pp. 146–168. doi: 10.1016/j.revpalbo.2007.03.002.

Grimm, E. C. (1987) 'CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares', *Computers and Geosciences*, 13(1), pp. 13–35. doi: 10.1016/0098-3004(87)90022-7.

Haddad, N. M., Brudvig, L. A., Clobert, J., *et al.* (2015) 'Habitat fragmentation and its lasting impact on Earth's ecosystems', *Science Advances*, 1(2), pp. 1–9. doi: 10.1126/sciadv.1500052.

Harris, R. M. B., Beaumont, L. J., Vance, T. R., *et al.* (2018) 'Biological responses to the press and pulse of climate trends and extreme events', *Nature Climate Change*. Springer US, 8(7), pp. 579–587. doi: 10.1038/s41558-018-0187-9.

Harris, S. and Kitchener, A. (2005) *From Forest to Fjaeldmark: Descriptions of Tasmania's Vegetation*. Hobart: Department of Primary Industries, Water and Environment. doi: 10.1111/j.1442-9993.2006.01716.x.

Higuera, P. E., Brubaker, L. B., Anderson, P. M., *et al.* (2009) 'Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska', *Ecological Monographs*, 79(2), pp. 201–219. doi: 10.1890/07-2019.1.

Hill, R. S., Beer, Y. K., Hill, K. E., *et al.* (2016) 'Evolution of the eucalypts - An interpretation from the macrofossil record', *Australian Journal of Botany*, 64(8), pp. 600–608. doi: 10.1071/BT16117.

Hill, R. S. (2017) *History of the Australian Vegetation: Cretaceous to Recent*. Edited by R. S.

Hill. Adelaide: University of Adelaide Press. doi: http://dx.doi.org/10.1017/9781922064356.

Hogg, A. G., Hua, Q., Blackwell, P. G., *et al.* (2013) 'SHCal13 southern hemisphere calibration, 0 - 50,000 cal BP', *Radiocarbon*, 55(4), pp. 1889–1903.

Holz, A., Wood, S. W., Veblen, T. T., *et al.* (2015) 'Effects of high-severity fire drove the population collapse of the subalpine Tasmanian endemic conifer Athrotaxis cupressoides', *Global Change Biology*, 21(1), pp. 445–458. doi: 10.1111/gcb.12674.

Jackson, W. D. (1968) 'Fire, air, water and earth - an elemental ecology of Tasmania', *Proceedings of the Ecological Society of Australia*, 3, pp. 9–16.

Keeley, J. E., Pausas, J. G., Rundel, P. W., *et al.* (2011) 'Fire as an evolutionary pressure shaping plant traits', *Trends in Plant Science*, pp. 406–411. doi: 10.1016/j.tplants.2011.04.002.

Kirkpatrick, J. B. and Harwood, C. E. (1980) 'Vegetation of infrequently burned Tasmanian mountain region', *Proceedings of the Royal Society of Victoria*, 91, pp. 79–107.

Kirkpatrick, J. B. J. and Dickinson, K. J. M. (1984) 'The Impact of Fire on Tasmanian Alpine Vegetation and Soils', *Australian Journal of Botany*, 32(6), p. 613. doi: 10.1071/BT9840613.

Krawchuk, M. A., Haire, S. L., Coop, J., *et al.* (2016) 'Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America', *Ecosphere*, 7(12), pp. 1–18. doi: 10.1002/ecs2.1632.

Landesmann, J. B. and Morales, J. M. (2018) 'The importance of fire refugia in the recolonization of a fire-sensitive conifer in northern Patagonia', *Plant Ecology*. Springer Netherlands, 219(4), pp. 455–466. doi: 10.1007/s11258-018-0808-4.

Lenoir, J., Graae, B. J., Aarrestad, P. A., *et al.* (2013) 'Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe', *Global Change Biology*, 19(5), pp. 1470–1481. doi: 10.1111/gcb.12129.

Loehle, C. (2018) 'Disequilibrium and relaxation times for species responses to climate change', *Ecological Modelling*. Elsevier, 384(June), pp. 23–29. doi: 10.1016/j.ecolmodel.2018.06.004.

Macphail, M. K. (1979) 'Vegetation and climates in southern Tasmania since the last glaciation', *Quaternary Research*, 11(3), pp. 306–341. doi: 10.1016/0033-5894(79)90078-4.

Macphail, M. K. and Colhoun, E. A. (1985) 'Late Last Glacial vegetation, climates and fire activity in Southwest Tasmania', *Search*, 16, pp. 43–45.

Mariani, M., Holz, A., Veblen, T. T., *et al.* (2018) 'Climate Change Amplifications of Climate-Fire Teleconnections in the Southern Hemisphere', *Geophysical Research Letters*, 45(10), pp. 5071–5081. doi: 10.1029/2018GL078294.

Mariani, M., Fletcher, M. S., Haberle, S., *et al.* (no date) 'Climate change reduces resilience to fire in subalpine rainforests', *Global Change Biology*.

Mariani, M. and Fletcher, M. S. (2016) 'The Southern Annular Mode determines interannual and centennial-scale fire activity in temperate southwest Tasmania, Australia', *Geophysical Research Letters*, 43(4), pp. 1702–1709. doi: 10.1002/2016GL068082.

Mariani, M. and Fletcher, M. S. (2017) 'Long-term climate dynamics in the extra-tropics of the South Pacific revealed from sedimentary charcoal analysis', *Quaternary Science Reviews*. Elsevier Ltd, 173, pp. 181–192. doi: 10.1016/j.quascirev.2017.08.007.

Pappas, N. (2010) *The impacts of the 2009 bushfires on cool temperate rainforest in the Central Highlands of Victoria*. Monash University.

Pawlowsky-Glahn, V. and Egozcue, J. J. (2006) ‘Compositional data and their analysis: an introduction’, *Geological Society, London, Special Publications*, 264(1), pp. 1–10. doi: 10.1144/GSL.SP.2006.264.01.01.

Pearson, R. G., Stanton, J. C., Shoemaker, K. T., *et al.* (2014) ‘Life history and spatial traits predict extinction risk due to climate change’, *Nature Climate Change Change*, 4(February), pp. 217–221. doi: 10.1038/NCLIMATE2113.

Pemberton, M. (1988) ‘Soil erosion between Birchs Inlet and Elliott Bay, southwesternTasmania’, *Papers and Proceedings of the Royal Society of Tasmania*, 122, pp. 109–114.

R Core Team (2017) ‘R: A Language and Environment for Statistical Computing’, *R Foundation for Statistical Computing, Vienna, Austria*, p. {ISBN} 3-900051-07-0. doi: http://www.R-project.org/.

Simpson, G. L. and Oksanen, J. (2014) ‘analogue: Analogue and weighted averaging methods for palaeoecology’.

Talluto, M. V., Boulangeat, I., Vissault, S., *et al.* (2017) ‘Extinction debt and colonization credit delay range shifts of eastern North American trees’, *Nature Ecology & Evolution*, 1(June), p. 0182. doi: 10.1038/s41559-017-0182.

Whitlock, C. and Larsen, C. (2002) ‘Charcoal as a fire proxy’, in *Tracking Environmental Change Using Lake Sediments*. Dordrecht: Springer, pp. 75–97.

Williams, J. C. and ReVelle, C. S. (1996) ‘A 0-1 programming approach to delineating protected reserves’, *Environment and Planning B: Planning and Design*, 23(5), pp. 607–624.

Williams, J. E. and Woinarski, J. (1997) *Eucalypt ecology : individuals to ecosystems*. Cambridge University Press.

Wood, S. W. and Bowman, D. M. J. S. (2012) ‘Alternative stable states and the role of fire-vegetation-soil feedbacks in the temperate wilderness of southwest Tasmania’, *Landscape Ecology*, 27(1), pp. 13–28. doi: 10.1007/s10980-011-9677-0.

Wood, S. W., Murphy, B. P. and Bowman, D. M. J. S. (2011) ‘Firescape ecology: How topography determines the contrasting distribution of fire and rain forest in the south-west of the Tasmanian Wilderness World Heritage Area’, *Journal of Biogeography*, 38(9), pp. 1807–1820. doi: 10.1111/j.1365-2699.2011.02524.x.

Wu, X. and Murray, A. T. (2008) ‘A new approach to quantifying spatial contiguity using graph theory and spatial interaction’, *International Journal of Geographical Information Science*, 22(4), pp. 387–407. doi: 10.1080/13658810701405615.

Table 1. Summary of the proxies and the source of each proxy discussed in this study.

Proxies	Lake Osborne	Lake Perry
Chronology	Fletcher et. al., (2014, 2018)	This Study
Macroscopic Charcoal	Fletcher et. al., (2014, 2018)	This Study
Palynology & microscopic charcoal	Fletcher et. al., (2014, 2018)	This Study
Geochemical (ITRAX)	Fletcher et. al., (2014)	This Study
Topography	This Study	This Study

List of figure captions

Figure 1. Map of Tasmania with average annual rainfall shown in blue shading. Solid line indicates 1250 mm rainfall contour. Location of the Hartz Mountains is shown by the red star. On the right a satellite image of Lake Perry and Lake Osborne.

Figure 2.Pollen stratigraphy of selected pollen spectra from Lake Perry. Pollen data is expressed as percentages and grouped by montane rainforest taxa, temperate rainforest taxa, sclerophyllous taxa, herbs and shrubs and wetland species. Microscopic charcoal is presented as particles per $cm^{-2}yr^{-1}$ x 10^3. CONISS cluster analysis represents the significant cluster groups and subzones of the terrestrial pollen types. Solid lines represent breaks between Zone 1, 2 and 3 while dashed lines separate subzones of Zone 3.

Figure 3. Summary plot of Lake Perry data including: Macroscopic charcoal peaks (Cpeak cm-2 yr-1) in black, pollen spectra principle curve (PrC), Nothofagus gunnii percentage, Cupressaceae percentage and geochemical principle curve (PrC). Dashed orange lines indicate high-impact fire events identified at Lake Perry.

Figure 4. Comparison plot between Lake Perry and Lake Osborne Macroscopic charcoal peaks (Cpeak cm-2 yr-1) in black, montane rainforest (N. gunnii in light green and Cupressaceae in dark green) pollen spectra and Eucalyptus pollen percentages in olive green. Orange lines show timing of high-impact fire events identified at Lake Perry.

Figure 5. Topographic maps of the Lake Osborne and Lake Perry catchments. **a**) High-resolution aspect map created from the digital terrain model. **b**) High-resolution slope map created from the digitail terrain model. **c**) Topographic fire refugia (TFR) within the Lake Perry and Lake Osborne catchments. Green pixels indicate south facing aspects with a slope >15° that provide the highest topographic protection. Darker green TFR core pixels are those that have at least one TFR pixel on each side.