RESEARCH ARTICLE

Long-term stability of temperate Australian wet forest-moorland mosaics despite recurrent fires associated with late Holocene climate change

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Abstract

Context The primary factors(s) responsible for the maintenance of Alternative biome states (ABS) in world forest biomes remains unclear and debatable, partly due to insufficient long-term ecological data from suitable ecosystem sites. The occurrence of moorland in southern and western Tasmanian wet temperate forest presents a suitable setting to test for ABS and understand the main stabilizing factors of ABS.

Objectives We use a palaeoecological approach to test for ABS and identify the degree of vegetation change and the effect of climate change and fire occurrence associated with ABS in southern Tasmania.

Methods Sediment sequence from sink-hole lake in a forest and nearby pond in southern Tasmania were analysed for pollen and charcoal to reconstruct histories of forest, moorland and fire in the Tasmanian Wilderness World Heritage Area (TWWHA). Reconstructions were compared to palaeoclimate record.

Results Moorland and forest in southern Tasmania have occupied the same habitat for at least the last 2600 years, and neither past climate change nor fire occurrence affected the stability of the vegetation mosaic. We suspect that localized environmental settings, such as topography and edaphic conditions are the primary stabilizing factors of the forest-moorland mosaics.

Conclusions The observed stable vegetation mosaics in our study is contrary to the dominant ecological paradigm of landscape dynamics currently used to manage the TWWHA, and there is a need to refine the ecological basis of fire management in the area. Similar targeted palaeoecological studies are needed to fully understand the underlying factors responsible for the persistence of treeless vegetation in world forest biomes.

Keywords Tasmania · Temperate forest · Sedgeland · Alternative biome states · Tasmanian Wilderness World Heritage Area

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Introduction

The occurrence and persistence of treeless ecosystems in environments climatically suitable for forest development has long puzzled ecologists (Bowman 2000; Oliveras and Malhi 2016; Bowman and Perry 2017; Langan et al. 2017; Pausas and Bond 2020) and has led to the refining of biome definition to be based on plant growth habits in some cases rather than solely climatic zones (Moncrieff et al. 2016). The co-existence of structurally and floristically different ecosystems (e.g., forest and savanna) in the same environment are referred to as alternative biome states (ABS) and many propositions have been put forward to explain the origin and maintenance of this apparent ecological paradox (Pausas and Bond 2020). The persistence of open, and often herbaceous, vegetation in climates suitable for forest has been described as early successional stage caused by and maintained by disturbances, particularly repeated burning (Jackson 1968; Aleman et al. 2020; Pausas and Bond 2020). Vegetation biomass consumers, such as large herbivores and natural wildfires are also thought to maintain treeless vegetation patches in forested areas, and that the removal of these biotic and abiotic agents could possibly allow conversion to forests, the rate of transformation being controlled by the productivity of the sites (Van Langevelde et al. 2003; Murphy and Bowman 2012; Bowman and Perry 2017). An alternative explanation, known as the sharpening switch model (Wilson and Agnew 1992), explains biome partitioning under a common climate is due to variability in edaphic conditions and topography for example, where forest occurs on fertile, deep-soils with open vegetation growing on infertile, shallow soils (Mount 1979; Veenendaal et al. 2015). Effectively demonstrating the reality of ABS and discriminating the cause of the co-existence of forest and treeless ecosystems in the same environment is challenging given the need to conduct long-term field experimental studies. However, palaeoecological records provide the opportunity to investigate the stability and dynamics of ABS for centuries to millennia (Fletcher et al. 2014a, 2020). Recent frameworks (Bowman and Perry 2017; Pausas and Bond 2020) have stressed that palaeoecological and historical records are a key step to determining whether open and closed ecosystem are ABS.

In this study, we aim to test for ABS in Tasmanian temperate forest-moorland biome. Western and southern Tasmania receives the highest amount of rainfall in southeast Australia and is climatically suitable for temperate rainforest, however the vegetation patterns are characterised by coarse-scale mosaics of rainforest, fire adapted wet eucalypt forests, scrublands and treeless sedgelands. The cause of these vegetation patterns has been debated for decades with one school of thought positing that sedgeland and eucalypt forests are the products of past frequent burning of forests (Jackson 1968) and another school arguing that vegetation mosaic are primarily determined by topography and edaphic factors (Mount 1979). A review of available evidence was unable to conclusively differentiate between these alternative theories (Bowman and Perry 2017). A detailed analysis using historical aerial photography and post-fire ecological survey of recently burned sedgeland patch, known as Blakes Opening (Fig. 1), in wet eucalypt forest in southern Tasmania demonstrated stability of forest boundaries over 70 years (Bowman et al. 2023a, b). To extend the temporal perspective, we use palaeoecological analyses to investigate if forest and sedgeland mosaics are varied at Blakes Opening in the late-Holocene. Previous palaeoecological studies (Fletcher et al. 2014b, 2020) from the Hartz Mountains, southeast of Blakes Opening, has demonstrated the persistence of tree communities in the forested area for at least 12,000 years despite periods of severe fire episodes associated with the intensification of El Niño–Southern Oscillation (ENSO) in recent millennia. However, it remains unclear if this also the case for non-woody communities in moorland areas. Our main goal here is to use pollen and charcoal records to identify if present forest and moorland in the World Heritage Area have persisted irrespective of shifts in climate and fire occurrence in the late Holocene. Understanding these long-term vegetation dynamics will help identify the most appropriate and sustainable fire ecology model to base management in the Tasmanian Wilderness World Heritage Area. More broadly, results from this study will also contribute to understanding the applicability of ABS in explaining temperate forest vegetation distribution in the Southern Hemisphere, as well as highlight the role of palaeoecology in substantiating the reality of ABS in explaining forest-savanna mosaics in other world regions (Aleman et al. 2020; Pausas and Bond 2020).

Fig. 1 Location and geographic context of sediment cores (Hookeman Pond and Epic Pond) at Blakes opening in southern Tasmania, Australia. Hookeman Pond is the sedgeland site while Epic Pond is the forest site
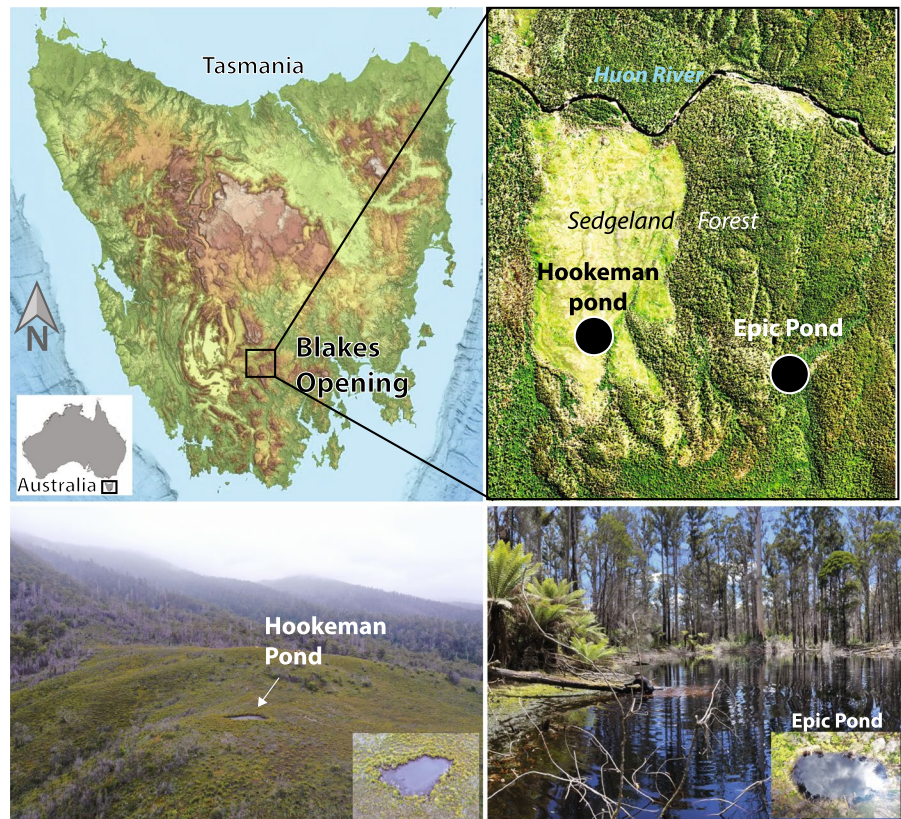
Methods

Study area, field survey and sampling

Blakes Opening (Fig. 1a) lies between the Huon River and the northern slopes of Mount Picton in southern Tasmania, with vegetation characterised by expanse of sedgeland fringed by scrub within a vast tract of wet eucalypt forest. Climate of the area and Tasmania in general is primarily modulated by the Southern Annular Mode and the El Niño–Southern Oscillation (Mariani et al. 2016b; Mariani and Fletcher 2016), with an average annual rainfall of about 971.2 mm and temperature range of 1.3–17.6 to °C. The entire area is part of the Tasmanian Wilderness World Heritage Area, one of the largest temperate nature reserve in the Southern Hemisphere that contains universally significant historic, cultural, natural heritage values (Bowman et al. 2021). A river sedimentary exposure in the area is recognised as being a key geo-heritage site due to its ancient glacial landforms, late-Pleistocene Gondwanan pollen assemblages, and charcoal

layers (Colhoun and Goede 1979). A full description of the site is provided by Bowman et al. (2023b).

Bowman et al. (2023b) undertook a comprehensive vegetation recovery survey following a fire in 2019, combined with lidar and historical aerial photography analysis demonstrating the fire-resilience and stability of the vegetation boundaries. We then targeted small sink-hole lake within wet eucalypt forest (Epic Pond (43° 7′1.13″S, 146°38′3.13″E) and a small pond in the sedgeland (Hookeman Pond 43° 7′5.57″S, 146°36′45.84″E) in the area at 1.8 km apart, and approximately at the same elevation (330 and 206 m asl) for sediment coring and palaeoecological evaluation of local vegetation dynamics (Fig. 1a).

Epic Pond is >5 m deep and likely formed on ancient lateral moraine ridgeline made up of quartz, dolomite and dolerite rocks and gravels: a 180 cm sediment core was retrieved from the edge of the lake that was free of tree logs. Hookeman Pond is a shallow small pond on a small terrace on a treeless moraine ridge, that seasonally dries out (in summer), around 10 m diameter surrounded by buttongrass

moorland: an 85 cm sediment core was obtained from the center of the catchment (Fig. 1a).

Sediment core analysis

A total of nine accelerator mass spectrometry radiocarbon dates were obtained for bulk subsamples from the sediment cores from DirectAMS, Washington, and resulting calibrated radiocarbon dates (based on SHCal20) (Hogg et al. 2020) were used to build age-depth models for the cores in R Bacon (Blaauw et al. 2022). Each sediment core was analyzed for pollen and spores at 4–8 cm intervals (Hookeman-4 cm, Epic-8 cm) to reconstruct forest and moorland history and sample preparation follows the standard protocol, which involves HCl, KOH and Acetolysis treatment (Faegri and Iversen 1975). A minimum of 300 terrestrial taxa were counted and identified in each pollen sample and results were presented as percentages calculated based on the sum of trees, shrubs, and herbs. Turnover analysis (dissimilarity in pollen spectrum through time) was further performed on pollen data using the Squared Chord Dissimilarity (SCD) in R 'analogue' package (Simpson et al. 2021). Turnover is the rates of compositional change in vegetation (pollen spectrum) through time. Adeleye et al. (2021b) have previously validated pollen turnover has as a proxy for vegetation turnover in western

Tasmania's vegetation communities and an empirical threshold for vegetation turnover was derived for the region (Fig. 2). Here, we applied the maximum turnover threshold (SCD = 0.4) for the region's vegetation to quantify temporal stability and instability in vegetation communities (Fig. 2). SCD > 0.4 indicates a complete shift in vegetation community composition. Turnover was computed for vegetation composition using all pollen taxa and for vegetation structure using the sums of life forms (trees, shrubs and herbs).

Sediment cores were contiguously sampled for macroscopic charcoal analysis at 1 cm interval to reconstruct fire history in each vegetation type. Sediment samples were bleached and sieved through a 125-μm sieve before counting macroscopic charcoal particles (Whitlock and Larsen 2001) and results were presented as influx (particles/cm^2/yr). CharAnalysis program was used to further calculate fire return interval (FRI) based on the frequency of charcoal peaks (Higuera et al. 2010). Charcoal peaks are the difference between total charcoal influx and background charcoal, and a percentile cut-off noise distribution with Gaussian mixed model was used to set peak detection threshold (minimum count cut-off probability = 0.05). Overall results were then discussed in the context of long-term changes in climate to identify relationships between vegetation, fire, and climate through time.
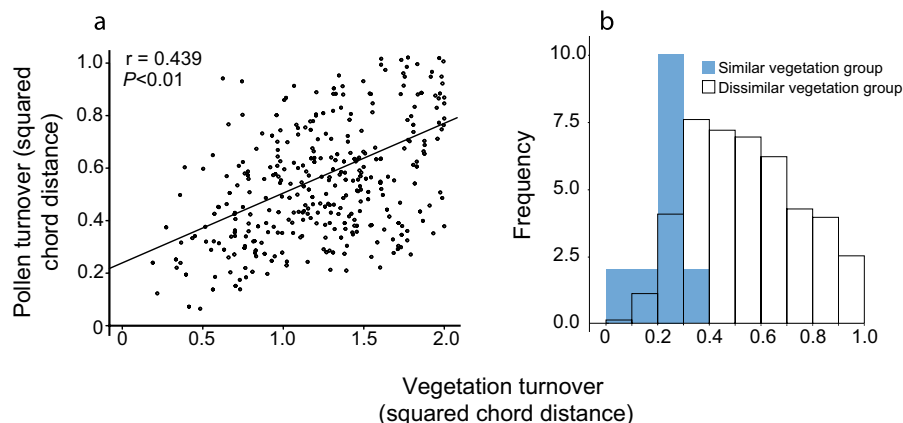

Fig. 2 Validation of pollen turnover as a proxy for vegetation turnover and turnover threshold for western Tasmania. **a** Comparison of modern pollen rain turnover and corresponding vegetation community turnover following Adeleye et al. (2021b). Pollen rain and vegetation community survey data were from 27 vegetation communities across western Tasmania (Mariani et al. 2016a). **b** Similar vegetation communities have a maximum turnover value of 0.4 while dissimilar ones have values greater than 0.4. Squared chord distance > 0.4 indicates a complete shift to a dissimilar vegetation community. See supplementary Table 1 for the 27 vegetation communities from which pollen rain and vegetation survey data were collected

Results and discussion

Both cores capture vegetation changes that occurred in the late-Holocene. Age-depth models produced an estimated basal age of ~1700 calendar years before present (cal yr BP) for Epic Pond and ~2600 cal yr BP for Hookeman Pond (Table 1; Fig. 3).

Epic Pond core is composed of rich organic mud from the base to 100 cm and the remainder of the core to the top is made up of peat. The entire Hookeman Pond core is uniformly composed of organic-rich mud (Fig. 3). *Phyllocladus asplenii-folius* and *Dicksonia antarctica* were dominant at the base of Epic Pond, followed by the expansion of *Eucalyptus* and *D. antartica* over the last 1400

years. Macroscopic charcoal influx (MCI) was greatest in the record from 1300 to 700 cal yr BP and the last 200 years; however, fire frequency was greatest in the last 1000 years with fire return intervals (FRI) mostly < 100 years (Fig. 4).

Hookeman Pond record shows a consistent presence of forest, shrubland and moorland taxa, with no major changes in abundance over the last 2600 years. Conversely MCI changed during this period, being highest between ~2600 and 1800 cal yr BP and low for the rest of the record (Fig. 3b). FRI mostly ranged from 100 to 200 years at the site. Of the turnover computed for both Epic Pond and Hookeman Pond, significantly high turnover (SCD > 0.4) was only observed for Epic Pond at the

Table 1 AMS radiocarbon dates for Epic and Hookeman Pond, southern Tasmania measured at Direct AMS, Washington

| Sites	LabID	^{14}C yr BP	Error (1σ)	Depth (cm)	Calendar age range
Epic	D-AMS 045832	123	18	20	5–252
Epic	D-AMS 045833	287	19	70	155–437
Epic	D-AMS 045834	954	21	120	742–906
Epic	D-AMS 045835	1714	21	170	1529–1692
Hookeman	D-AMS 045836	943	21	20	736–904
Hookeman	D-AMS 051800	1331	23	30	1126–1278
Hookeman	D-AMS 051366	1984	28	40	1827–1994
Hookeman	D-AMS 051801	2151	24	70	2008–2287
Hookeman	D-AMS 051367	2493	25	80	2361–2706
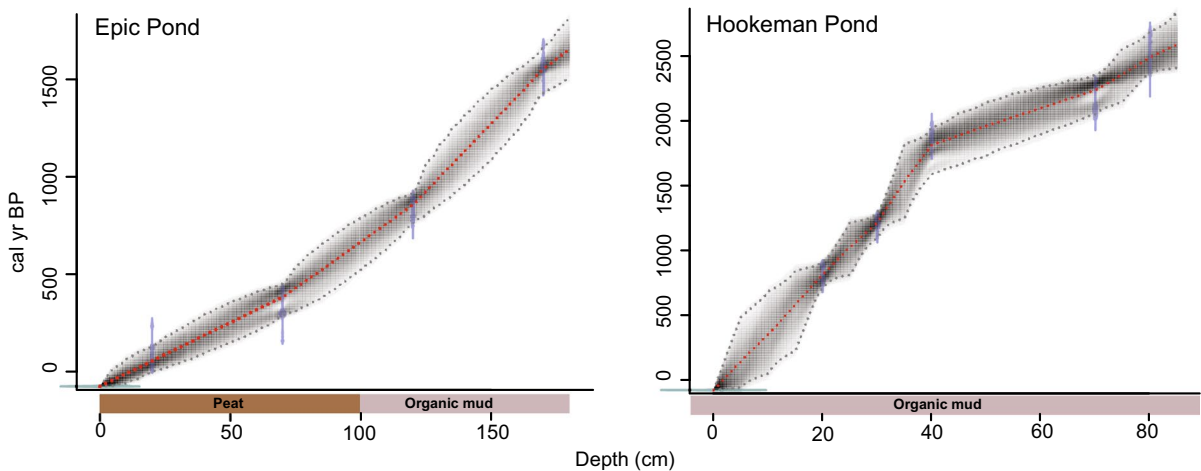
Fig. 3 Age-depth model for Epic and Hookeman Pond, Tasmania, showing calibrated radiocarbon dates (purple), age-depth model (dark grey), 95% confidence intervals of calibrated range (light grey), and single model based on the weighted mean age for each depth (red curve). 'cal yr BP'

is calendar years before present. See Appendix S1 for radiocarbon date results. Also shown is the core lithology for both sites, with Epic pond characterised by rich organic mud from 180–100 cm and peat in the top 100 cm, while Hookeman Pond is entirely composed of organic mud
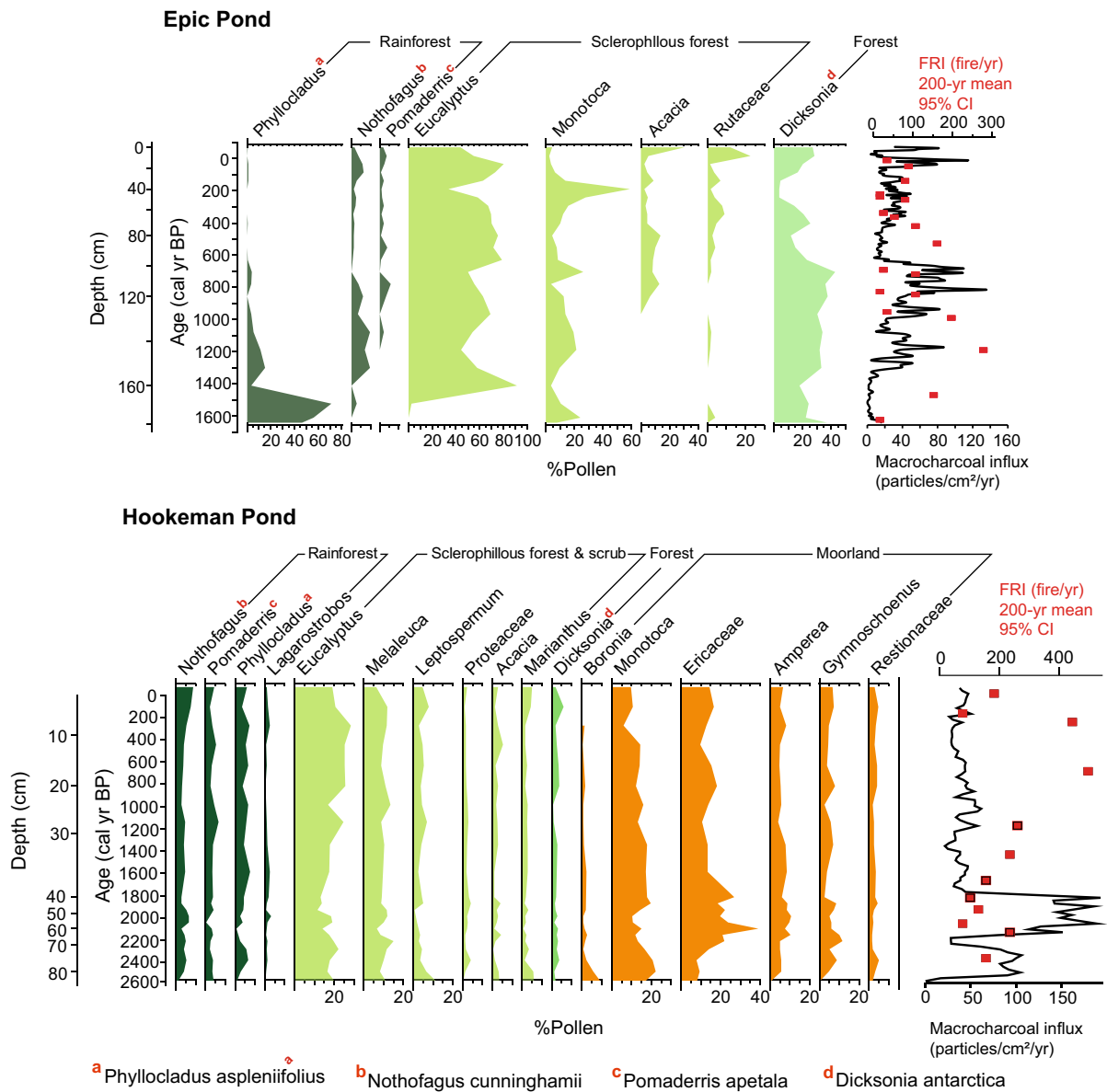
Epic Pond

Hookeman Pond

[a] Phyllocladus aspleniifolius   [b] Nothofagus cunninghamii   [c] Pomaderris apetala   [d] Dicksonia antarctica

Fig. 4 Vegetation and fire activity inferred for Blake Opening in southern Tasmanian based on percentages of major pollen taxa and charcoal record for Epic Pond and Hookeman Pond. Charcoal record include macrocharcoal influx (black curve) and fire return interval—FRI (red dots). See supplementary Figs. 1 and 2 for other pollen taxa diagrams

compositional scale between 200 cal yr BP and present (Fig. 5).

Our results show the dominance and stability of sclerophyllous forest vegetation at Epic Pond over the last two millennia, especially in terms of structure (SCD < 0.4), despite biomass burning and climatic changes, and major compositional changes (SCD > 0.4) have largely occurred in the last century

(Fig. 5). This is consistent with pollen and charcoal records from a nearby forest area (Fletcher et al. 2014b, 2020), which shows an expansion and persistence of fire-promoted eucalypt communities and decline of fire-sensitive rainforests due to drier and more fire prone conditions associated with more frequent and intense El Niño events in the last 3000 years. The occurrence of some Tasmanian endemic
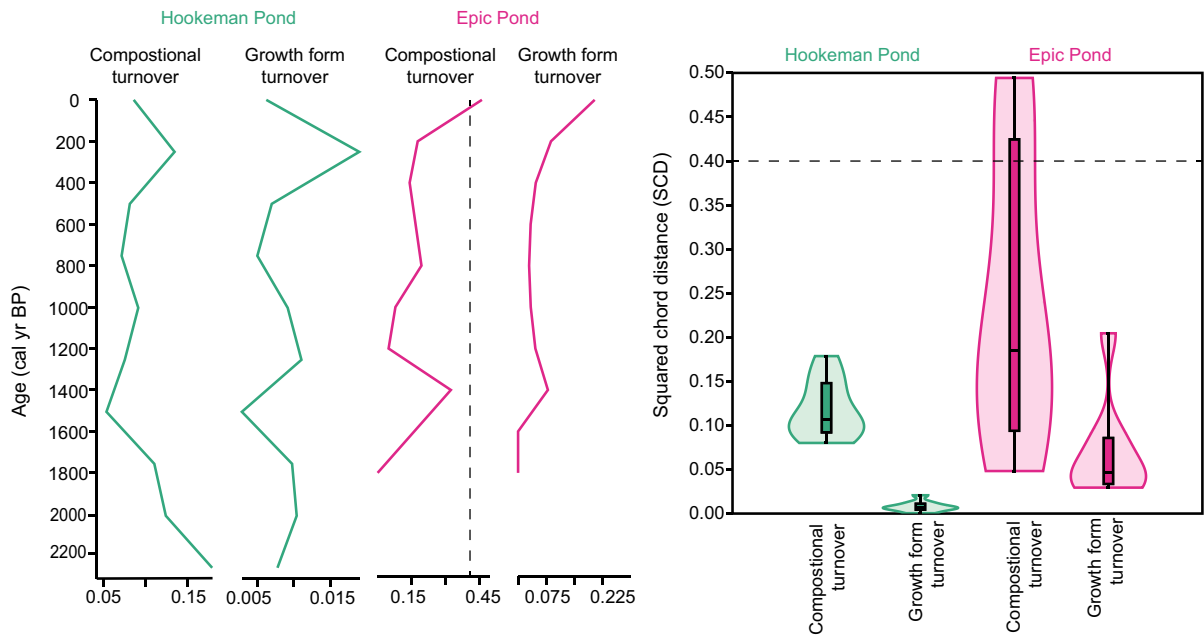
Fig. 5 Turnover record for Epic Pond and Hookeman Pond vegetation composition and life forms, with significantly turnover (SCD > 0.4—dashed line) only observed for Epic Pond vegetation composition. Note: SCD of 0.4 is the empirically-derived maximum threshold for western Tasmania's vegetation community turnover (Adeleye et al. 2021b). Each SCD point is the dissimilarity between adjacent time bins, for example, SCD point at 0 cal yr BP is the dissimilarity between −200 and 200 cal yr BP

conifers (e.g., *Athrotaxis*) have been found to be strongly controlled by variability in fire severity (Holz et al. 2015) whereas eucalypts in old-growth forest stands have been shown to persist over the last 500 years despite varying fire regimes and climatic condition (Wood et al. 2010). The expansion of eucalypts at Epic Pond from 1400 cal yr BP before increased burning at 1300 cal yr BP suggests the loss of *Phyllocladus* rainforest understorey from an old growth and senescent eucalypt forests at the site ~1500 years ago may be associated with a long-term drying trend associated with late Holocene increased ENSO intensity and niche changes given the absence of major fire peaks (severe fire episodes) (Baker 1993). Subsequent climate-driven recurrent severe fires in the established flammable eucalypt forest possibly further excluded more fire-sensitive taxa, including *Phyllocladus* (Furlaud et al. 2021) (Figs. 3b and 4). Biomass burning especially between 1000 and 600 cal yr BP at Epic Pond can also be linked to more variable annual rainfall and frequent dry years associated with increased ENSO intensity during this period (Barr et al. 2019). Accumulated fuel biomass during wet

episodes likely burn in following dry years. Sustained increased fires in the eucalypt forest likely resulted in changes in forest understorey composition, increasing the recruitment success of fire-promoted obligate seeders like species of *Acacia* and Rutaceae (Sabiiti and Wein 1987; Mackenzie et al. 2016). Nonetheless, despite many centuries of firing at Epic Pond, floristic composition in the forest remained largely stable until recent century. The greatest turnover in plant community composition in the Blake Opening during the last two millennia occurred in Epic Pond forest within the last 200 years, possibly relating to climate change and/or land-use change (Adeleye et al. 2021a). European burning, associated with harvesting of Huon pines (*Lagarostrobos franklinii*) may have accelerated forest changes during this period or perhaps extremely warmer and drier climatic trends over the last century markedly reduced biomass fuel moisture, making forests more prone to severe burns and high community turnover (Adeleye et al. 2021a; Mariani et al. 2022).

Vegetation at Hookeman Pond shows the greatest stability (SCD < 0.4) at both compositional and

structural levels (Fig. 5), with the persistence of sedgeland over the last ~2600 years matching the stability in surrounding woody vegetation apparent in Epic Pond record (Fig. 6). The abundance of forest, shrubland and moorland taxa in Hookeman Pond record is most due to the openness of the moorland site, with pollen supply from surrounding woody vegetation communities, including from nearby Epic Pond Forest. The small increase in moorland taxa abundance from 2600 to 1800 cal yr BP coincident with maximum fire activity suggests repeated burning caused minor changes in vegetation. The cause of fire during this period is unclear, as charcoal record from Hookeman Pond is not in phase with changes in climate over the last two and half millennia (Fig. 6). A plausible explanation for frequent fires at the site between 2600 and 1800 cal yr BP may be Aboriginal burning, which however, had no significant impact

on vegetation structure as opposed to previously suggested Aboriginal fire-promoted expansion of moorland in southwestern Tasmanian (Marsden-Smedley 1998). The analysis of charcoal found an average Fire Return Interval (FRI) of 215 years, with a maximum interval of 490 years, which is much longer than the previous estimate (50–70 years) required for the maintenance of sedgeland in south-western Tasmania (Jackson 1968). This finding harmonises with dendrochronological studies that have shown that the growth rate and longevity of eucalypts (Wood et al. 2010) and shrubs in sedgeland (French et al. 2016; Bowman et al. 2023a) is much slower than proposed by the Jackson model (Bowman and Perry 2017). The stability of the boundaries is also consistent with the study of Bowman et al. (2023b) that found the forest-sedgeland boundary at Blake Opening was very stable and that under the observed rate of expansion of
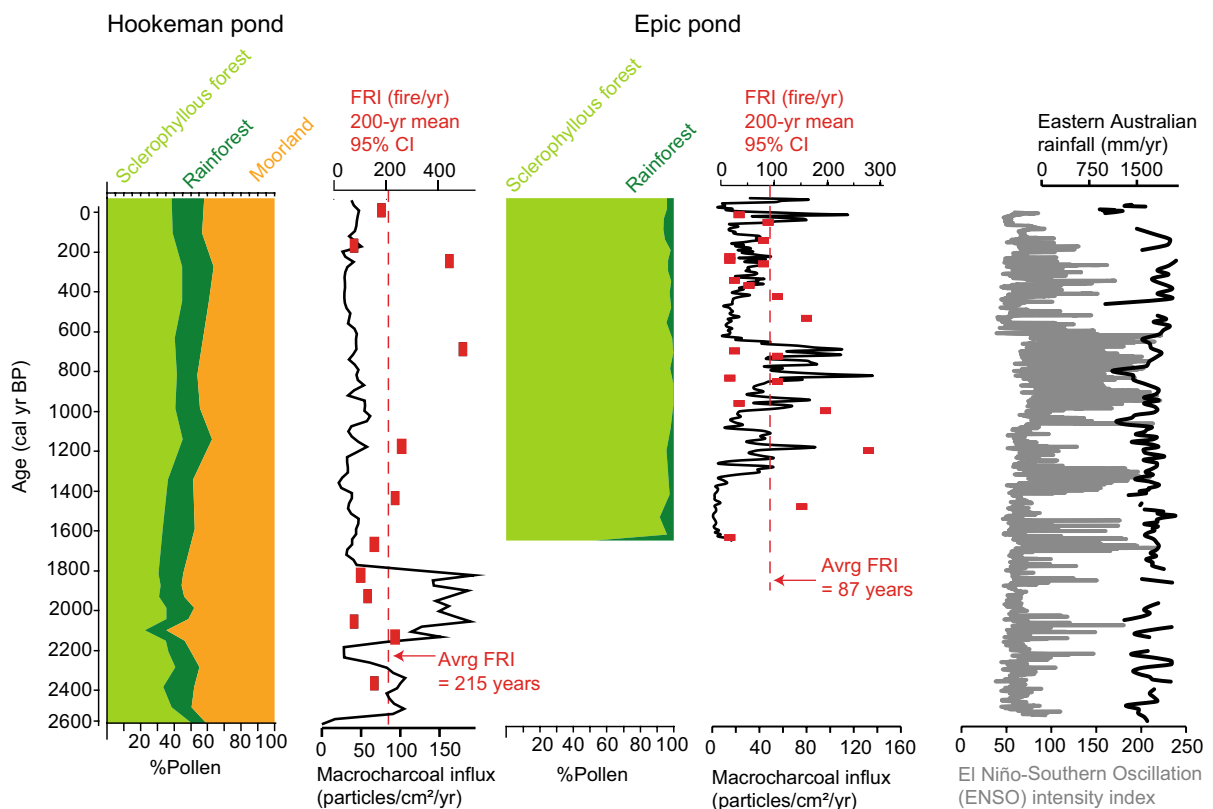

Fig. 6 Summary of fire and vegetation changes at Blakes Opening in southern Tasmania during the last two millennia. Both Hookeman and Epic cores show stable sedgeland and forest vegetation respectively regardless of changes in

fire regimes and changes in the intensity of El Niño-Southern Oscillation (Moy et al. 2002) and annual rainfall changes (Barr et al. 2019)

the forest it would take millennia for the sedgeland to be converted to forest if the area was unburned. Such stability concords with Mount's 'sharpening switch' model (Mount 1979; Wood and Bowman 2012; Bowman and Perry 2017; Bowman et al. 2023b).

Tree communities have likely persisted in forested areas of south and southwest Tasmania through the late Pleistocene and Holocene despite changes in climate, human land use and fire activity (Colhoun and Goede 1979; Fletcher et al. 2014b, 2020). Aside the major climatic shift that caused forests to shrink during the Last Glacial Maximum (LGM), previously published pollen record and new ^{14}C dates from the same sequence (see Supplementary Table 2 for new ^{14}C dates) from the area (Blake Opening) shows that forest persisted before and after human arrival in Tasmania ~ 40,000 years ago (Colhoun and Goede 1979). Climatic drying and wetting and corresponding changes in fire activity before the onset of the LGM ~ 29,000 years ago caused fluctuations from temperate rainforest to wet sclerophyllous forests (Colhoun and Goede 1979). Likewise, Holocene pollen records from the Hartz Mountain forested area (~ 14 km southeast of Blakes Opening) also show that climate and fire only drove shifts between fire-sensitive rainforest and fire-promoted eucalypt forest types in the area during the last 12,000 years and not shifts between forest and moorland communities (Fletcher et al. 2014b, 2020).

Overall palaeoecological records from southern Tasmania suggests the forest-moorland mosaic landscape of the area cannot be explained by ABS. The persistence of moorland in the climatically forest-suited area for millennia was likely primarily due to more localized factors such as topography, soil fertility, soil depth, physical properties and soil hydrology (Wood and Bowman 2012; Fletcher et al. 2014a; Bowman and Perry 2017). Climate in southern Tasmania may be wet enough for forest to cover the landscape, however, soils in moorland areas are often so infertile, shallow or poorly drained that this adversely affects tree growth, therefore resulting in the coexistence of forest and moorland in the environment for generations (Wood and Bowman 2012; Bowman and Perry 2017). Admittedly, occasional localised major environmental perturbations (e.g., extreme climatic event, catastrophic fire) could create an ABS (Pausas and Bond 2020) over much longer time frames. For example, in north-central Tasmania, palaeoecological

analyses of a swamp suggest a catastrophic fire caused forest to change to moorland about 7000 years ago by changing soil hydrological conditions (Fletcher et al. 2014a).

This analysis demonstrates the power of palaeoecological methods in testing the ABS model. A unique feature of the study was the pairing of sedimentary records that occur on either site a forest-treeless boundary. Such comparative analyses are also essential to progress understanding of tropical rainforest and savanna boundaries that have been explained as being due to top-down disturbance from fire and herbivores, that overwrite bottom-up controls of soils and climate (Zimov et al. 1995; Sankaran et al. 2005; Asner et al. 2009; Hoffmann et al. 2012; Dantas et al. 2013; Weigl and Knowles 2014; Pausas and Dantas 2017; Pausas and Bond 2020).

Conclusion

In this study, we set out to test for alternative biome states (ABS) in southern Tasmanian forest-moorland landscape and to identify the effect of changes in climate and fire on boundary dynamics. We have found that forest and moorland boundaries in the area have remained stable over the last two millennia regardless of slight changes in climate and associated alternations in fire regime. There is evidence that climatic changes and burning only caused minor successional changes, which is most evident in forest in the last century when European fire management replaced millennial of skilful Aboriginal fire use. Our findings harmonise with a detailed historical and ecological survey conducted at this site (Bowman et al. 2023b). We conclude that factors other than climate and fire regimes, such as topography and edaphic conditions have most likely maintained southern Tasmanian ABS, albeit this inference demands further research. Our findings are inconsistent with the ABS broadly, and specifically the ecological drift model of Jackson (1968) that often underpins fire management in the region. The long fire return intervals, slow pace of vegetation and floristic dynamics highlights the need for reconsideration of the ecological basis of fire management in the Tasmanian Wilderness World Heritage Area is warranted. Our unique study design shows how palaeoecological research that samples

proximate sites on either side of forest-treeless boundary can test and refine ABS models of tree-treeless vegetation mosaics elsewhere in the world.

Author contributions DB and SH conceived study and conducted field work. All analyses were performed by MA. The first draft of the manuscript was written by MA and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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