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Climate change reduces resilience to fire in subalpine rainforests

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TITLE: Climate change reduces resilience to fire in subalpine rainforests

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ABSTRACT

Climate change is affecting the distribution of species and the functioning of ecosystems. For species that are slow growing and poorly dispersed, climate change can force a lag between the distributions of species and the geographic distributions of their climatic envelopes, exposing species to the risk of extinction. Climate also governs the resilience of species and ecosystems to disturbance, such as wildfire. Here we use species distribution modelling and palaeoecology to assess and test the impact of vegetation-climate disequilibrium on the resilience of an endangered fire-sensitive rainforest community to fires. First, we modelled the probability of occurrence of *Athrotaxis* spp. and *Nothofagus gunnii* rainforest in Tasmania (hereon 'montane rainforest') as a function of climate. We then analysed three pollen and charcoal records spanning the last 7500 cal yr BP from within both high (n=1) and low (n=2) probability of occurrence areas. Our study indicates that climatic change between 3000 and 4000 cal yr BP induced a disequilibrium between montane rainforests and climate that drove a loss of resilience of these communities. Current and future climate change are likely to shift the geographic distribution of the climatic envelopes of this plant community further, suggesting that current high resilience locations will face a reduction in resilience. Coupled with the forecast of increasing fire activity in southern temperate regions, this heralds a significant threat to this and other slow growing, poorly dispersed and fire sensitive forest systems that are common in the southern mid- to high latitudes.

1. INTRODUCTION

Climate exerts a first order control over the functioning and distribution of species and ecosystems on Earth. Under current global climate projections, ecosystems are experiencing increased climatic pressures that alter their function and their provisioning of services to society (Milliennium Ecosystem Assessment, 2005). The rate of recent climatic change exceeds any period inferred from historic and geological records and the potential of organisms to adapt to these changes is poorly understood (Burrows *et al.*, 2014). Compounding the effects of climate change on ecosystem dynamics is the impact of disturbance events. Climatic change represents a 'press' perturbation on biological systems that can act synergistically with discrete extreme events ('pulse' disturbances), such as wildfires, bark beetles infestations or windstorms (Seidl *et al.*, 2014, Seidl *et al.*, 2016). Indeed, a number of recent ecosystem collapses have occurred in response to the loss of ecosystem resilience resulting from recent climate change and its impact on the ability of ecosystem to recover from extreme events (Harris *et al.*, 2018). Here, we use species distribution modelling and palaeoecology to assess and test the influence of long-term climate change on the ecological resilience to disturbance from fire of the UNESCO-listed and endangered temperate montane rainforests in Tasmania, Australia.

Climate change over the last century is already affecting resilience and distribution of species (Bateman *et al.*, 2016, Chen *et al.*, 2011, Hirota *et al.*, 2011, Lenoir & Svenning, 2015, Parmesan, 2006, Parmesan & Yohe, 2003). Amongst all ecosystems, mountains and their unique biota are the most exposed to climate and land-use change (Guo *et al.*, 2018), given the accentuation of climatic change by elevation and the diminishing area of land available upslope in most settings (Beniston, 2003, Nogués-Bravo *et al.*, 2007, Theurillat & Guisan, 2001). The montane rainforests located in the topographically complex landscape of Tasmania have a canopy dominated by long-lived (500-1500 years) tree species that are slow-growing, poorly dispersed and highly sensitive to disturbance from fire (Cullen, 1987). Longevity, poor dispersal and complex topography facilitate the persistence of ecosystems *in situ* following climate change, resulting in an increase in the potential for disequilibrium between ecosystems and climate (Lenoir *et al.*, 2013, Loehle, 2018). Resilience to disturbance events varies in response to climate (Beever & Belant, 2011, Crimmins *et al.*, 2011, Hirota *et al.*, 2011, VanDerWal *et al.*, 2013), with a shift toward less favourable climate conditions associated with a reduction in the rate of growth, recovery and reproduction of tree species following disturbance (Enright *et al.*, 2015). Thus, shifts in climate space following climatic changes may decrease the capacity of ecosystems to respond to disturbance, placing them at risk of loss and potential extinction.

Wildfires are one of the most important disturbance types within terrestrial vegetation (Bond *et al.*, 2005, Bowman *et al.*, 2009), and are particularly important in the Australian landscape (Hennessy *et al.*, 2005). Recent climate change has intensified fire weather severity worldwide (Aldersley *et al.*, 2011) which, coupled with a lengthening of fire seasons, has resulted in both an increase in 'mega-fires' (Stephens *et al.*, 2014, Westerling *et al.*, 2006) and an increase in the occurrence of lighting-ignited fires (Mariani *et al.*, 2018, Styger *et al.*, 2018). In this context of changing fire regimes, promoting the resilience of fire-sensitive species and reducing the risk of extinction is a crucial task for modern-day ecosystem managers (Seidl *et al.*, 2014, Seidl *et al.*, 2016). This objective is especially challenging in ecosystems featuring long-lived plant species, as historical records (spanning the last decades) are too short for us to understand the full range of variability of these organisms and how adaptable they are to climatic change (Birks *et al.*, 2016, Willis & Birks, 2006). Thus, to adequately manage ecosystems, the projection of magnitude and direction of environmental changes should be understood in the context of the long-term history of key species within the ecosystem of interest.

In this paper we take advantage of the well-studied long-term climatic history of Tasmania through the last 7500 years, which indicates a shift from a stable wet climate to a variable and overall drier climate between 3000 and 4000 cal yr BP, to assess and test how climatic change influences the resilience of montane rainforest in Tasmania to fire. We use species distribution modelling to estimate the probability of co-occurrence of two key montane rainforest tree taxa (*Athrotaxis* spp. and *Nothofagus gunnii)* as a function of climate. We then use palaeoecology to reconstruct montane rainforest and fire histories over the past 7500 years from sites of high probability of occurrence (Lake Wilks) and low probability of occurrence (Lake Osborne and Owen Tarn) in an attempt to understand the process of montane rainforest recovery from fire disturbance under varying climatic contexts (Fig. 1c, Fig. 2). We predict that a combination of the extreme longevity of key species in this system (>1000 years), landscape heterogeneity and long-term climatic change will have created a situation in which stands of this highly fragmented forest type are either at the limits of their climatic range or in disequilibrium with climate. Thus, we predict that the probability of occurrence produced by our climate-based species distribution model will provide a good approximation of the climate equilibrium state of existing montane rainforest stands in Tasmania, which, in turn, will provide an indication of the potential resilience of this forest type to disturbance from fire (*sensu* Hirota *et al.*, 2001). We hypothesize that sites with a low probability of occurrence will display a reduced resilience to disturbance from fire and sites with a high probability of occurrence will display a higher degree of resilience to disturbance from fire (i.e. high resilience).

2. MATERIAL AND METHODS

2.1 Study Area

Fire and montane rainforests in Tasmania

Today, *Athrotaxis* spp.-*N. gunnii* montane rainforests cover <5% of the Tasmanian landscape, mostly as small pockets of forest confined to the Central Plateau, the Tyndall Range and scattered mountain tops in the southwest (Fig. 1a). These species, and related rainforest taxa, were more widespread across Tasmania and continental Australia during the Cainozoic, a part of the so-called Gondwanan flora that dominated the southern latitudes (Hill, 1991). The modern-day restricted distribution of these species has resulted from a combination of increasing aridity, fire and the radiation of fire-adapted and fire-promoting plant taxa through the Cainozoic to present (Bowman, 2000). Humans colonised Tasmania during the Last Glacial Cycle (>40,000 years ago) (Cosgrove, 1999) imparting a substantial imprint on the vegetation landscape through the use of fine-scale fire management that further restricted the distribution of fire-sensitive plants (Fletcher & Thomas, 2010, Mariani *et al.*, 2017). Today, treeless pyrophytic vegetation dominates the landscape (including *Gymnoschoenus sphaerocephalus* and species of *Melaleuca* and *Leptospermum*), with fire-sensitive arboreal communities largely restricted to topographic fire refugia in Tasmania's west and south (Wood *et al.*, 2011). Key among the fire sensitive communities are the iconic and now endangered montane rainforests. Montane rainforest in Tasmania forms at high elevation (ca. 700-1000 m a.s.l.) and is dominated by endemic tree species, such as the UNESCO heritage-listed trees, *Athrotaxis cupressoides, A. selaginoides* and *Nothofagus gunnii* (syn. *Fuscospora gunnii*) (Harris & Kitchener, 2005). Here, we retain use of *Nothofagus* to maintain consistency with fossil records (*sensu* Hill *et al.*, 2015).

Athrotaxis spp. and *N. gunnii* display several life history attributes that suggest they are poorly adapted to disturbance by fire: (1) they are long lived (>1000 years for *Athrotaxis* spp.; >500 years for *N. gunnii*) and slow-growing (Allen *et al.*, 2011, Ogden, 1978); (2) they are obligate seeders that display almost complete stand-scale mortality following fire (Cullen, 1987, Cullen & Kirkpatrick, 1988, Kirkpatrick & Dickinson, 1984); (3) they display an apparent post-fire regeneration failure following moderate to severe fire events that indicates low post-fire soil seedbank survivorship (Holz *et al.*, 2014, Kirkpatrick & Dickinson, 1984); and (4) they have relatively large and poorly dispersed seeds, which are often produced at irregular, supra-annual intervals (Calais & Kirkpatrick, 1983, Cullen, 1987). Despite the apparent hyper-sensitivity and poor adaptation to fire, slow (>800 years) post-fire recovery of montane rainforest is evident in the palaeoecological record (Fletcher *et al.*, 2014, 2018; Cadd *et al.*, in review), with fire-driven elimination of this community considered a product of decreased resilience in response to repeated and more frequent burning and a shift to a climate less hospitable to the post-fire regeneration and growth of montane rainforest species through the Holocene (Fletcher *et al.*, 2014, 2018).

Importantly, it is unclear whether the loss of resilience to disturbance from fire in montane rainforest is solely the product of a synergistic interaction between the effects of repeated burning and climatic change, or whether climatic change alone is sufficient to reduce the capacity of this plant community to respond to fire. Both *Athrotaxis* spp. and *N. gunnii* have suffered major fire-driven landscape-scale losses across their entire range over the last 200 years (the post-colonial period) (Brown, 1988, Cullen, 1991, Holz *et al.*, 2014, Kirkpatrick & Dickinson, 1984), with an estimated fire-driven range reduction of >30% for *Athrotaxis* in this time (Brown, 1988; Figure 1a). To date, no post-fire recovery of these stands has been observed. It is unclear whether this is the result of 1) an insufficient recovery window following fires or 2) the underlying press of climate change now precludes the recovery of these species to fire (pulse) disturbance. This knowledge is critical for the long-term management of montane rainforest under current and predicted trends in climate and fire regimes. A case-in-point is the catastrophic landscape-scale 2016 wildfires that decimated the largest remaining patch of *A. cupressoides* vegetation in Tasmania (Harris et al., 2018). Future-proofing these systems from fire in the remote Tasmanian landscape requires enormous financial and logistical resourcing and there is an urgent need to understand the relative roles of the various factors that influence resilience to fire of these systems, such as fire history and climatic change, to guide effective and efficient environmental management.

Climate variability in Tasmania over the last 7500 years

Overall, the extensive palaeoclimate data from the region indicates an early high moisture period with a broadly stable temperature regime between ca. 7500-4000 cal yr BP, with a shift toward a more variable moisture and temperature regime after 4000 cal yr BP. There is a general agreement that the period between 7500 cal yr BP and 4000 cal yr BP (mid-Holocene) was relatively wet across the southeast sector of southern Australia as a consequence of an increase in precipitation delivered by a stronger zonal circulation (see Fletcher & Moreno, 2012, Mariani & Fletcher, 2017, and references therein) (Fig. 3d). Temperatures are thought to have been relatively stable through this period (Marcott et al., 2013), although sea-surface temperatures (SST) in the region suggest a decline in temperature from a Holocene optimum at ca. 7500 cal yr BP (Calvo *et al.*, 2007). In contrast, the late Holocene (ca. 4000 cal yr BP – present) was characterised by a shift toward a more variable and overall drier moisture regime over Tasmania and surrounding areas (Mariani & Fletcher, 2017, Rees *et al.*, 2015, Stahle *et al.*, 2017, Xia *et al.*, 2001), likely in response to the onset of ENSO-like climate variability in the Pacific region leading to more frequent El Niño (dry) phases (Donders *et al.*, 2008, Fletcher & Moreno, 2012), which drove an increase in wildfire across Tasmania (Fletcher *et al.*, 2015, Mariani & Fletcher, 2017)(Fig. 3d). Estimates of temperature change though this period indicate high variability (Marcott *et al.*, 2013)(Fig. 3e), while SSTs in the region suggest a continued decline toward the present (Calvo *et al.*, 2007).

Study sites

Owen Tarn (1-OT; 42.0998S, 145.6094E; 970 m a.s.l.) is a small subalpine lake, located on the eastern flank of Mount Owen (1,146 m a.s.l.) in central western Tasmania. Total annual rainfall is 2804 mm/yr and the annual mean temperature is 8.4°C. Today, the lake catchment is mostly characterised by exposed bedrock and small patches of western subalpine scrub (including *Leptospermum nitidum*, *Eucalyptus vernicosa*, *Monotoca submutica*, *Agastachys odorata* and *Cenarrhenes nitida*). The presence of tree stumps in the catchment indicate that the lake was formerly more densely vegetated (Hodgson *et al.*, 2000), but no individuals of montane rainforest trees occur today.

Lake Osborne (2-LO; 43.2159S, 146.7589E; 924 m a.s.l.) is a small moraine-bound subalpine lake, located in the Hartz Ranges in southwest Tasmania. Total annual rainfall at the closest meteorological station is 1443 mm/yr and the annual mean temperature is 9.7°C. Dominant species in the modern landscape are *Eucalyptus coccifera*, *Nothofagus cunninghamii* (syn. *Lophozonia cunninghamii*), *Eucryphia milliganii*, *Gahnia grandis* and a variety of Protaceae shrubs. Only a few fire-scarred individuals of *Athrotaxis selaginoides* are growing on the shore of the lake, although no living individuals are present around the catchment.

Lake Wilks (3-LW; 41.6729S, 145.9552E; 1060 m a.s.l.) is a small cirque lake located in UNESCO World Heritage Area in northwest Tasmania. Total annual rainfall is 2832 mm/yr and the annual mean temperature is 8.3°C. The present-day catchment of Lake Wilks is mostly occupied by *Athrotaxis-N. gunnii* rainforest.

A summary of the information on the three sites used for the analyses presented in this work is shown in Table 1.

Table 1 Summary information of the sites used for the long-term analyses in this work. Asterisks (*) indicates extrapolated values from BIOCLIM predictor layers (Fig. S1).

	Site code	**1**	**2**	**3**
	Site Name	Owen Tarn	Lake Osborne	Lake Wilks
	Latitude ^{o}S	-41.451196	-42.099683	-41.672829
	Longitude ^{o}E	145.961463	145.609434	145.956023
	Elevation	969	920	1058
	Temperature of the warmest quarter (^{o}C) - bio10	11.8	10.9	9.3
	Precipitation of the warmest quarter (mm) - bio18	593	234	388
	Temperature seasonality (^{o}C) - bio04	1.03	1.03	1.14
	Precipitation seasonality (%) - bio15	21	17	27
	Modern montane rainforest	NO	NO	YES
	MaxEnt value	**0.437**	**0.301**	**0.826**
Publications	**Charcoal data**	Mariani & Fletcher, 2017	Fletcher *et al*., 2014; 2018	Stahle *et al*., 2017
	Pollen data	This study (partial)	Fletcher *et al*., 2014; 2018	This study (partial)
	Chronology	Mariani & Fletcher, 2017 (updated in this study)	Fletcher *et al*., 2014; 2018	Stahle *et al*., 2017

2.2 Species distribution modelling

We used the MaxEnt v3.3.3k program (Phillips *et al.*, 2004) implemented into R (R Core Development Team, 2013) and the *dismo* package (Hijmans *et al.*, 2017) to model the probability of occurrence of montane rainforest across Tasmania as a function of climate. The

MaxEnt algorithm is designed for species distribution modelling using a set of environmental variables (Phillips *et al.*, 2004) and it was found to be more conservative than other models in predicting probability of species occurrence (Kumar *et al.*, 2009, Kumar & Stohlgren, 2009). This algorithm uses presence and pseudo-absence or background data of the variable of interest (i.e. species distribution) to compare the values of the environmental predictors associated with these presence points with those of a background (or pseudo-absence localities). This approach estimates the "maximum entropy" of sampling points compared to background locations, by taking into account the constraints derived from the predictor variables (Baldwin, 2009, Phillips *et al.*, 2004).

The probability of montane rainforest occurrence was modelled using the modern co-occurrence of *Athrotaxis* spp. and *Nothofagus gunnii* (757 data points) for 500 iterations. The two species were considered co-occurring if located within 1 km distance between each other. A total number of 10000 pseudo-absences (Barbet-Massin *et al.*, 2012) from the convex hull of the presence data were used for the MaxEnt runs to account for dispersal limitations of the chosen taxa (Fig. S1). Presence and pseudo-absence points were divided into two equal groups to create training and testing datasets. Spatial analyses were undertaken using ArcGIS 10.4 (ESRI). Four BIOCLIM predictor variables for temperature and precipitation (bio16, bio10, bio4 and bio15) at 0.01 degrees (ca. 1 km at the equator) resolution were used in this model (see Fig. S2 for climate variables maps). BIOCLIM climate predictors (Booth *et al.*, 2014, Nix, 1986) for Tasmania were derived using ANUCLIM v.6 on the Atlas of Living Australia (http://www.ala.org.au). The climatic variables were checked for collinearity (Fig. S2).

2.3 Fossil data: coring and chronology

Owen Tarn core was retrieved in 2015 using a Universal corer. The chronology of the OT sediment core is based on a combination of ^{210}Pb and ^{14}C dating techniques. Lead radioisotope activity was determined on six samples using alpha-spectrometry at the Australian Nuclear Science and Technology Organisation (ANSTO) after wet sieving the samples to remove sand particles. Eleven radiocarbon dates were obtained on the OT core at ANSTO and DirectAMS (Bothell, USA). Radiocarbon ages were calibrated to calendar years before present (cal yr BP; 1950 CE) using the Southern Hemisphere calibration curve (Hogg *et al.*, 2013). Age-depth modelling was performed using linear interpolation in OxCal 4.2 (Ramsey, 2009).

A combination of two sediment cores were retrieved from the deepest (10m) point of the Lake Osborne basin in 2011. A total of 11 radiocarbon dates and two ^{210}Pb dates were obtained on these cores and ages were modelled against depth using clam (Blaauw, 2010). Results were recently published in Fletcher *et al.*, 2018.

Lake Wilks core was obtained in 2000 with a modified Livingstone piston sampler. A total of 10 radiocarbon dates were obtained on the LW core and calibrated ages were modelled against depth using clam (Blaauw, 2010). Results from these analyses were previously published in Stahle *et al*., 2017.

2.4 Fossil data: pollen and charcoal analysis

Pollen, spores and microscopic charcoal sample preparation followed the standard procedures (Faegri & Iversen, 1989). Pollen analysis was undertaken on the OT core at 0.5 cm intervals for the top 40 cm and 1 cm intervals for the remaining bottom 30 cm. LO was sampled for pollen at 1 cm increments, while a variable resolution between 2 and 8 cm was used for LW. Relative pollen data were calculated from a basic pollen sum that included at least 300 terrestrial pollen grains per sample (excluding wetlands and ferns). Only the combined percentages of montane rainforest tree - *Athrotaxis* spp. and *Nothofagus gunnii* - were used in this study.

Macroscopic charcoal content was analysed to document the local fire history. A volume of 1.25 cm^3 was taken at continuous 0.5 cm intervals at OT and LO. Lake Wilks core was sampled at 1.0 cm intervals and 2 cm^3 were analysed for charcoal content. Charcoal analysis was performed following the method described by Whitlock & Larsen (2001), involving a sediment digestion in 10% hydrogen peroxide for a week (or 5% Sodium Hypochlorite for two weeks). After digestion, sediment was then sieved using 125-μm mesh diameter (Whitlock & Larsen, 2001) and the residues were counted under a stereomicroscope at 40x magnification. Charcoal concentrations and deposition times were calculated and converted to charcoal accumulation rates (CHAR; particles cm^2 yr^{-1}).

2.5 Numerical analyses

Box-and-whiskers plots were used to show the maximum, minimum, the first and third quartiles and median of the montane rainforest pollen data from the three study sites. Two time periods – pre and post 4000 cal yr BP - were chosen based on the reconstructed fire history from these sites and the regional climate changes from regional Tasmania (Mariani & Fletcher, 2017). Percentage pollen data were converted to z-scores prior to plotting to reduce skewness due to inter-site differences. Sites located on the 'edge' of the climate space (i.e. low resilience sites) - OT and LO - were combined to simplify the message.

3. RESULTS

3.1 Modelling species distribution

There was no detectable collinearity amongst the climate predictors used in the MaxEnt model (Fig. S3). The climate variables with the highest percent contribution to the model were the total precipitation and the mean temperature of the warmest quarter (summer season) with an explanatory power of 24% and 72% respectively (Fig. S4), the importance of these variables is as also highlighted in the response curves (Fig. S5, S6).The MaxEnt model was found to perform satisfactorily (AUC=0.877 (training dataset); AUC= 0.853 (testing dataset); random prediction AUC=0.5) when predicting the probability of montane rainforest occurrence based on the four climatic variables (Fig. S7). The MaxEnt model highlighted the areas with the probability of *Athrotaxis* spp. and *N. gunnii* co-occurrence being in the western portion of Tasmania with low annual temperatures of the warmest quarter (mostly <12°C) and relatively high precipitation amounts during this period (between 300 and 600 mm; Fig. S8). The highest probability of co-occurrence (>0.5) were found in the Central Plateau, in the Tyndall and in the Southern Ranges (Fig. 2).

3.2 Fossil data: chronology

The Owen Tarn record spans the last 7535 cal yr BP over 69 cm (Fig. S9). The list of radiocarbon and ^{210}Pb dates obtained on this core is presented in Table S1a,b. To better constrain the chronology at the bottom of the sequence, the sample at 67.75 cm was dated twice, but a large difference (>1,000 years) was found between the two runs. The older radiocarbon age of 7810 years was considered an outlier due to its impact on the performance of the age-depth model. The oldest radiocarbon age of 6537 years (7401 cal yr BP) was obtained at a depth of 67.75 cm. The age-depth model (Fig. S9) is showing a sigmoid curve, highlighting slower accumulation rates in the mid-section of the core (between 45 and 50 cm) and faster at the bottom and top sections. Accumulation rateswere relatively high in the uppermost 17 cm of this sequence (median = 0.14 cm/yr). However, throughout the rest of the sequence, sediment accumulation rates were slow with a median rate of 0.01 cm/yr.

The chronologies of LO and LW were previously presented and discussed in Fletcher *et al.*, 2018 (LO) and Stahle et al., 2017 (LW), respectively, and age-depth models were presented in Fig. S10. These records extend back to ca. 14000 cal yr BP (LO) and ca. 12000 cal yr BP (LW), however, in this study we only focused on the last 7500 cal yr BP to compare them with the OT record.

3.3 Fossil data: pollen and charcoal analysis

A total of 112 samples from OT were analysed for pollen and 138 samples for macroscopic charcoal. The median pollen and charcoal sample resolution is 50 and 49 years, respectively. In this core, montane rainforest pollen showed high abundances between 20-30% through the period from 7500 and 3500 cal yr BP (Fig. 2). A gradual decline in montane rainforest pollen was detected from 3500 cal yr BP up to the British settlement period (ca. 150 cal yr BP). This gradual decrease in the abundance of montane rainforest pollen was concomitant with a persistent increase in macroscopic charcoal (Fig. 2).

A sum of 118 samples from LO were processed for pollen analysis and a total of 208 samples were analysed for macroscopic charcoal. The median resolution for pollen samples was 64 years, whereas the median resolution for charcoal samples was 35 years. Montane rainforest pollen showed three alternating phases of high and low abundances through the period from 7500 and 2500 cal yr BP (Fig. 2). The oldest two declines in montane rainforest pollen percentages during this phase clearly coincided with two charcoal peaks (Fig. 2). The third (youngest) decline in montane rainforest percentage (ca. 3000 cal yr BP) occured slightly prior to the most recent charcoal peak (2700 cal yr BP). In the period between the present and 2500 cal yr BP, montane rainforest abundance was maintained below 10%. For more details about pollen and macroscopic charcoal records from LO see Fletcher *et al*., 2018.

Pollen was analysed on 58 samples from the LW core, while macroscopic charcoal was counted on 194 intervals. The median resolution for pollen samples was 83 years, whereas charcoal samples had a median resolution of 44 years. High abundance of montane rainforest pollen was detected throughout the entire sequence with values rarely below 30% (Fig. 2). Around 4000-4500 cal yr BP, a series of two charcoal peaks preceded a long-term decline in montane rainforest pollen percentages down to > 15% at 2700 and 2300 cal yr BP. Hereafter, we use the period between 3000 and 4000 cal yr BP as a boundary of significant change in the records. This reduction is followed by a relatively prompt (<400 years) increase back to the pre-charcoal peak values at ca. 2000 cal yr BP. For more information on the macroscopic charcoal record from Lake Wilks see Stahle *et al*., (2017).

3.4 Numerical analyses

Box-and-whiskers plots for the period between 7500 and 4000 cal yr BP showed similar montane rainforest data distributions between OT+LO and LW (Fig. 4a, left panel). In both cases, during this phase we observed positive deviations from the mean. Whiskers (representing minimum and maximum values) were substantially shorter in LW in comparison to OT+LO. During the period post-4000 cal yr BP, data distributions diverged, with LW maintaining a positive median value, while OT+LO show a tight range of values below zero (Fig. 4a, right panel). Whiskers in LW were broader than OT+LO during this phase.

4. DISCUSSION

4.1 Climate space and montane rainforest resilience

Climate exerts a first-order control over the growth, regeneration and reproduction of biota, with changes in climate associated with an impact on the ability of species to tolerate and respond to disturbance (Enright *et al*., 2015, Scheffer *et al*., 2015). The species modelling results indicate a good overall performance of our model based principally on climate input data, highlighting a relatively broad area of suitable climate conditions for the co-occurrence of *Nothofagus gunnii* and *Athrotaxis* spp. (i.e. montane rainforest) in Tasmania. This area is primarily restricted to the mountainous landscape of Tasmania's west and south (Fig. 1b), where a cool and wet climate is produced by the interaction between topography and orographic rainfall. The apparent failure of montane rainforest to fill all of the available climate space predicted by the model highlights the limitation of this approach for fine-scale mapping and predictive studies, and is attributable to the role of variables such as dispersal limitation, hydrology, geology, aspect, slope, biotic interactions and fire history in determining the local-scale vegetation distribution (Pradervand *et al*., 2014, Wisz *et al*., 2013). Nevertheless, our climate-based predictive model allows us to interrogate the role of climate change in determining the response of montane rainforest to disturbance from fire.

The probability of occurrence determined from climate-based species distribution models has often been interpreted as an indication of how resilient an ecosystem is (Deutsch *et al.*, 2008, Hirota *et al.*, 2011, Huey *et al.*, 2012). Most notably, Hirota *et al.*, (2011) modelled the probability of finding rainforest as a function of mean annual precipitation in the Amazon, concluding that the vast areas of this important forest type that display a low probability of occurrence were low resilience forests at risk of localised extinction following disturbance. Whilst the limitations of SDMs means our model reflects only part of the true niche space of our system, the model allows us to interrogate the role of climate in influencing the resilience of this system to fire in the modern landscape. Our model identified areas as having a high probability (>0.5) of occurrence as a function of climate that are spatially restricted to the cool and wet mountain tops in the west and far south (Fig. 2). These areas are likely to foster higher rates of growth and reproduction for montane rainforest trees, relative to areas identified as having low probability of occurrence (<0.5) – i.e. they are high resilience areas. Moreover, the cooler and wetter climate in these high resilience zones are also likely to impact the intensity and severity of fire via the control that climate exerts over fuel moisture content and fire intensity/severity in cool temperate landscapes (Mariani & Fletcher, 2016, McWethy *et al.*, 2013, Styger & Kirkpatrick, 2015). In contrast, areas of low probability of occurrence (<0.5) are those that are warmer and/or drier, factors that are likely to negatively impact the growth, recovery and reproduction of montane rainforest species, in turn reducing the ability of montane rainforest to recover from disturbance. Furthermore, these sites will also be more prone to fuel desiccation and fire occurrence.

4.2 Climatic change, fire and montane rainforest resilience

Montane rainforest was extant on several mountains across southern Tasmania where it is absent today during the early- to mid-Holocene (ca. 12000-6000 cal yr BP) (Fletcher *et al.*, 2018, Macphail, 1980, Macphail, 1979). Further, palaeoecological data indicates that this plant community was able to recover from fire during this time (Fletcher *et al.*, 2018, Fletcher *et al.*, 2014; Cadd et al., *in review*). Drawing on this data, Fletcher *et al*. (2018) argue that a broadly stable cool wet climate through early- to mid-Holocene facilitated the post-glacial establishment of montane rainforest across the region and provided conditions in which recovery from fire was possible. The fossil pollen and charcoal data analysed and compiled for our present study indicate that (1) montane rainforest was extant at each of our study sites at ca. 7500 cal yr BP, under the wettest and most stable climate regime of the past 7500 years and (2) that each site experienced some burning after ca. 4000 cal yr BP (Fig. 3). Critically, only the Lake Wilks catchment within the zone of high model-inferred resilience today (0.826) still supports montane rainforest (Table 1). Indeed, while clearly affected by fire, the local montane rainforest at this site displayed a remarkable resilience to burning (Fig. 2). In contrast, the catchments of Owen Tarn (0.437) and Lake Osborne (0.301) within zones of low model-inferred resilience today currently support fire-adapted vegetation. At Lake Osborne, the driest site today, repeated burning between ca. 7500-3000 is followed by recovery of montane rainforest, with an eventual collapse of the forest between ca. 2000-3000 cal yr BP (Fletcher *et al*., 2014). At the substantially wetter Owen Tarn site, montane rainforest also collapsed in response to repeated burning between ca. 2000-3000 cal yr BP, yet, unlike Lake Osborne, the preceding 4000 years were marked by low to absent fire activity and no evidence for an impact of fire on the vegetation. This difference in long-term fire histories between the sites suggests that fire-driven collapse of this forest system is not solely a product of a loss of resilience in response to repeated burning through multiple millennia (*sensu* Fletcher et al., 2014). Rather, it indicates that that fire events under the 'right' set of climatic conditions can be sufficient to cause the localised extinction of this community, irrespective of long-term disturbance history.

The agreement between the model-inferred resilience and the empirical response to fire of montane rainforest at our study sites is consistent with the role of climate in governing both the severity of fire and the ability of vegetation to recover from fire (*sensu* Enright *et a*l., 2015), and supports the use of the climate-based species distribution model as a proxy for resilience to fire in this system. Fires became more frequent in western Tasmania after ca. 4000 cal yr BP (Fig. 2d), a period characterised by a highly variable and overall drier climate over southern Australia (Mariani & Fletcher, 2017, Wilkins *et al.*, 2013). These regional long-term climatic changes likely created unfavourable conditions for post-fire regeneration and growth of *N. gunnii* and *Athrotaxis* spp., thus, limiting their ability to recover from fire. Very long-lived species, such as these, can persist *in situ* for extended periods following a shift in climate (Talluto *et al.*, 2017), resulting in a disequilibrium with climate following climatic change (Lenoir & Svenning, 2015, Loehle, 2018). This effect is exacerbated in topographically complex landscapes such as Tasmania where fine scale heterogeneity of microclimates can provide refuge for the persistence of species and communities outside of their broader climate niche (Lenoir *et al.*, 2013). We interpret the pattern of widespread establishment of montane rainforest through the early-mid Holocene (under a wetter climate regime), followed by the subsequent collapse of montane rainforest from OT and LO (low resilience sites) in response to burning, as a consequence of the onset of more variable and drier climatic conditions at the geographic locations in response to regional climatic change over the past ca. 4000 years (Fig. 4c). Further, we contend that the extreme longevity of key species in this ecosystem and the complex topography of the region have facilitated the persistence of montane rainforest stands in disequilibrium with climate and at risk of a shift to an alternate fire adapted vegetation state in response to fire (see Fig. 4b for a conceptual representation).

4.3 What is the fate of Tasmanian montane rainforests?

Our interpretation of the results of this study imply that large parts of montane rainforest in Tasmania today are either at the limits of their climatic range and/or are in disequilibrium with climate (Fig. 1 and 2). The slow demography of montane rainforest tree species disproportionally exposes them to a disequilibrium with climate following climatic change relative to faster growing trees (Talluto *et al.*, 2017). This situation results in the potential for both a high extinction debt (persistence under unsuitable conditions) and a high colonisation credit (failure to capture new locations) (*sensu* Talluto *et al.*, 2017). Indeed, the extinction risk (Loehle, 2018) for species such as *Athrotaxis* And *N. gunnii* is high, given the potential for climatic change to outpace the ability of species to capture new habitat (Loarie *et al.*, 2009, Loehle, 2018, Talluto *et al.*, 2017). This risk is further heightened in mountainous landscapes and on montane biota, given that steep environmental gradients force rapid response times and there is diminishing availability of habitat upslope in response to global warming (Beniston, 2003, Nogués-Bravo *et al.*, 2007, Theurillat & Guisan, 2001). Our contention that long-term climatic change and the slow demography of *Athrotaxis* and *N. gunnii* have fostered a disequilibrium between montane rainforest vegetation and climate, and that this conveys a reduction in resilience to disturbance from fire is significant. Fires are ubiquitous in the Australian landscape and the past ca. 200 years has seen an increase in fire activity in Tasmania that exceeds any point in the past 12000 years (Mariani and Fletcher, 2017). Increased efficacy of lightning as an ignition source, increased human activity and the continual invasion by fire-promoting plants (such as *Eucalyptus*) in to fire-sensitive vegetation all herald a significant threat to the long-term security of this endangered fire-sensitive plant community.

Fire prevention and mitigation are complex and expensive operations that require a clear strategy. The response to the 2016 wildfires in the Tasmanian highlands, which destroyed large areas of fire-sensitive *Athrotaxis cupressoides*, was largely reactionary due to both the logistical complexities involved in fire management in this remote and rugged region, and the unusual confluence of large-scale lightning storms and a very dry climate (Marris, 2016, Sharp, 2016). While our claimed high resilience locations currently act as an important refugium for montane rainforest, continued climatic change will see the gradual erosion of resilience in these areas. Given the difficulties of fire prevention, mitigation and remediation in this very remote and topographically complex landscape, we contend that resource allocation and strategic planning should be invested in fire mitigation strategies that further bolster high resilience sites from potential wildfire, rather than investing in low resilience sites for which the long-term probability of survival is low, even in a scenario of complete fire absence. We argue that similar approaches in other fire sensitive ecosystems that face increasing pressure from a rapidly changing climate and increasing risk of fire might enable a more realistic long-term strategy for survival.

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AUTHOR CONTRIBUTION

MM conceived ideas, elaborated data, performed pollen counts on OT and lead manuscript writing, MSF conceived ideas and edited manuscript text, SH contributed to manuscript editing, HC analysed pollen and charcoal data from Lake Wilks, AZ assisted with 210-Pb dating, GJ assisted with radiocarbon dating.

FIGURE CAPTIONS

Fig. 1 Map showing the location of modern co-occurrence of *Nothofagus gunnii* and *Athrotaxis* spp. (i.e. montane rainforest, green dots) and location of dead *Athrotaxis selaginoides* patches (orange triangles, data from TasVeg3.0 – Government of Tasmania, 2013). Black dots represent the study sites for the long-term charcoal and pollen analyses: 1-Owen Tarn (OT), 2-Lake Osborne (LO) and 3-Lake Wilks (LW).

Fig. 2 Summary plot showing macroscopic charcoal accumulation rates (black line) and montane rainforest pollen % (green filled curve) spanning the last 7500 cal yr BP from (a) Owen Tarn, (b) Lake Osborne and (c) Lake Wilks (location shown in Fig. 1). Black crosses in (a), (b) and (c) indicate fire events as detected in Figure S11 (OT), Fletcher *et al*., (2014; LO) and Stahle *et al*. (2017, LW). (d) Regional fire activity reconstruction from western Tasmania (Mariani and Fletcher, 2017). Orange-red fillings in (d) highlight inferred dry periods, whereas shades of blue represent inferred wet phases. (e) Southern Hemisphere temperature stack from Marcott *et al*., 2013 (black line), grey lines represent the 2σ range. (f) Number of El Niño events/100 years from Laguna Pallcacocha (Moy *et al*., 2002). Red fillings in (f) represent periods with a frequency of El Niño events higher that five/100 years. The shading from blue to orange indicates the gradual nature of climatic change after 4000 cal yr BP.

Fig. 3 Map showing the probability of co-occurrence of *N. gunnii* and *Athrotaxis* spp. (i.e. montane rainforest) derived using MaxEnt species modelling (see Material and Methods). Black dots represent the study sites for the long-term charcoal and pollen analyses: 1-Owen Tarn (OT), 2-Lake Osborne (LO) and 3-Lake Wilks (LW).

Fig. 4 a) Box-and-whiskers plots of the normalised montane rainforest pollen abundances (z-scores) from Owen Tarn (OT) + Lake Osborne (LO) and Lake Wilks (LW). Because of the respective position of these lakes in the climate space for montane rainforest, OT and LO are defined as 'low-resilience sites' (yellow boxes), while LW is defined as 'high-resilience site' (green boxes); b) conceptual model depicting a shift in climate space suitable for montane rainforest following the late-Holocene climatic transition in Tasmania (after 4000-3000 cal yr BP). Schematic edited from Ohlemüller et al. (2011); c) simplified timeline for the fire and vegetation changes occurred at the three study sites in this work. Red box in c) highlights the disequilibrium phase for OT and LO; MRF = montane rainforest.

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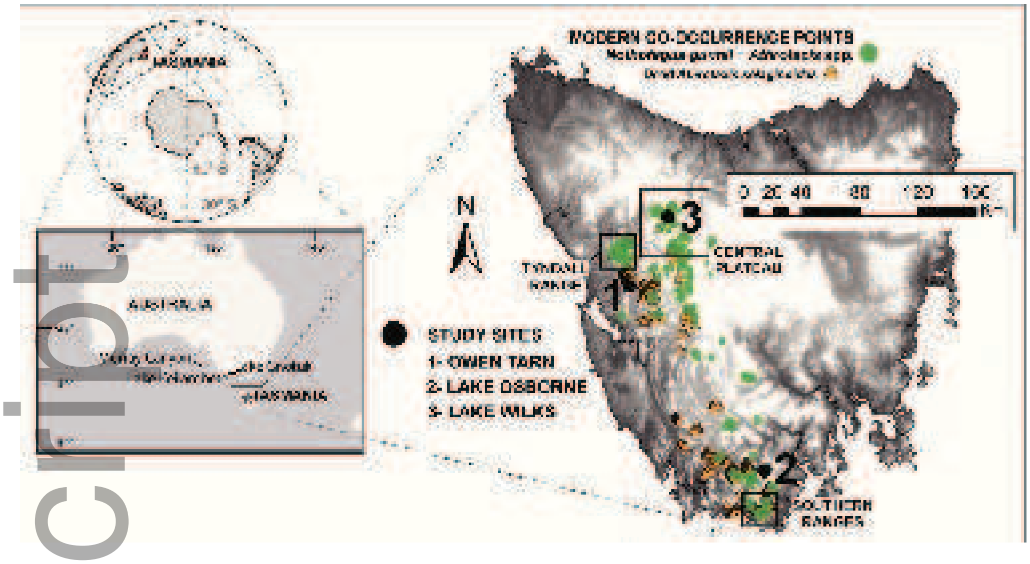

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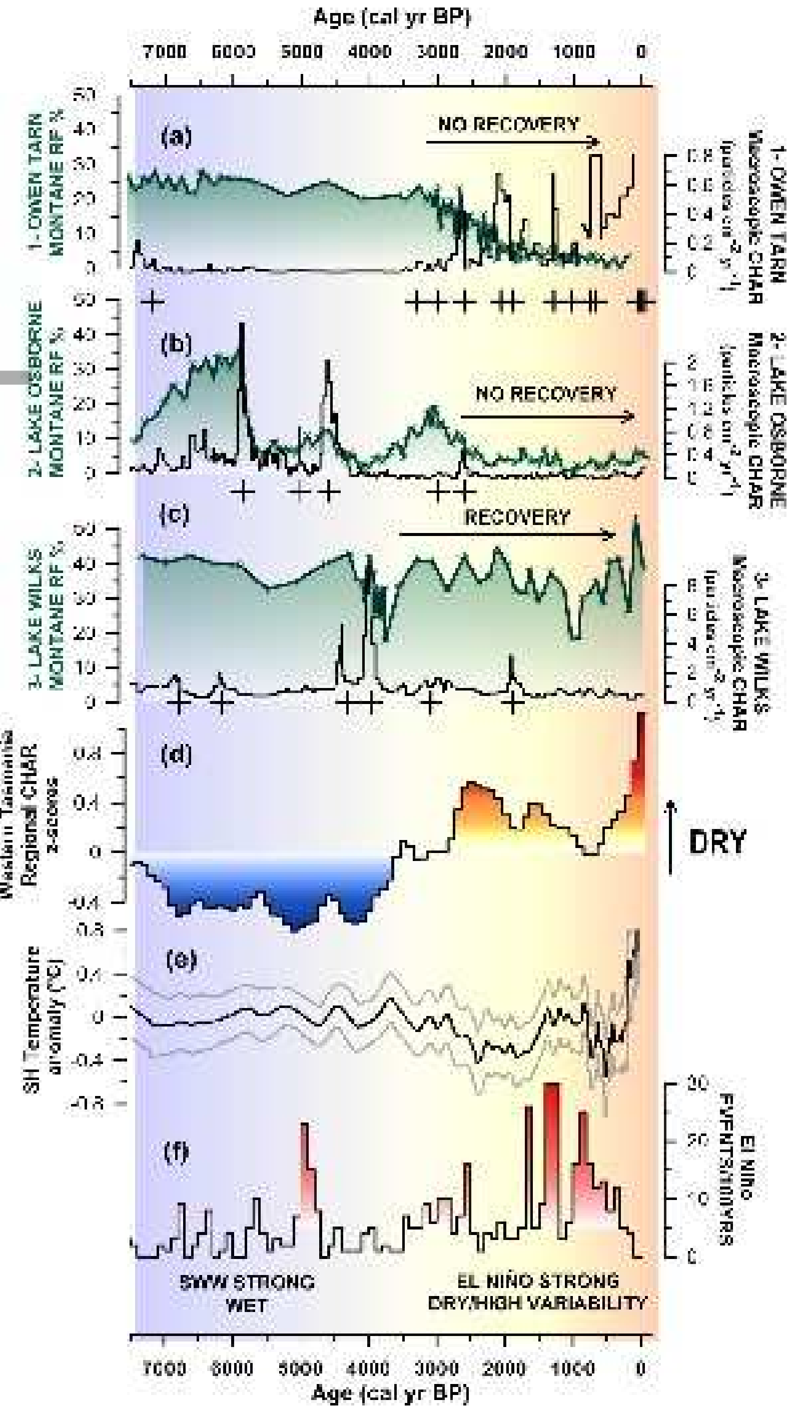

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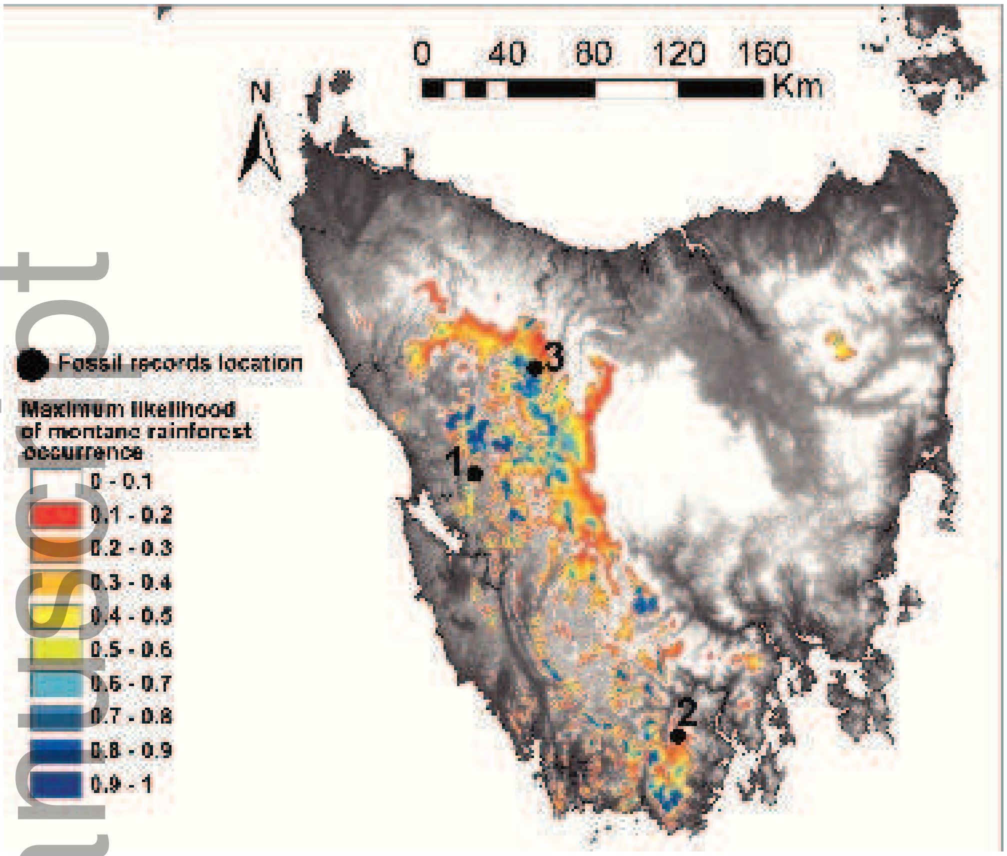

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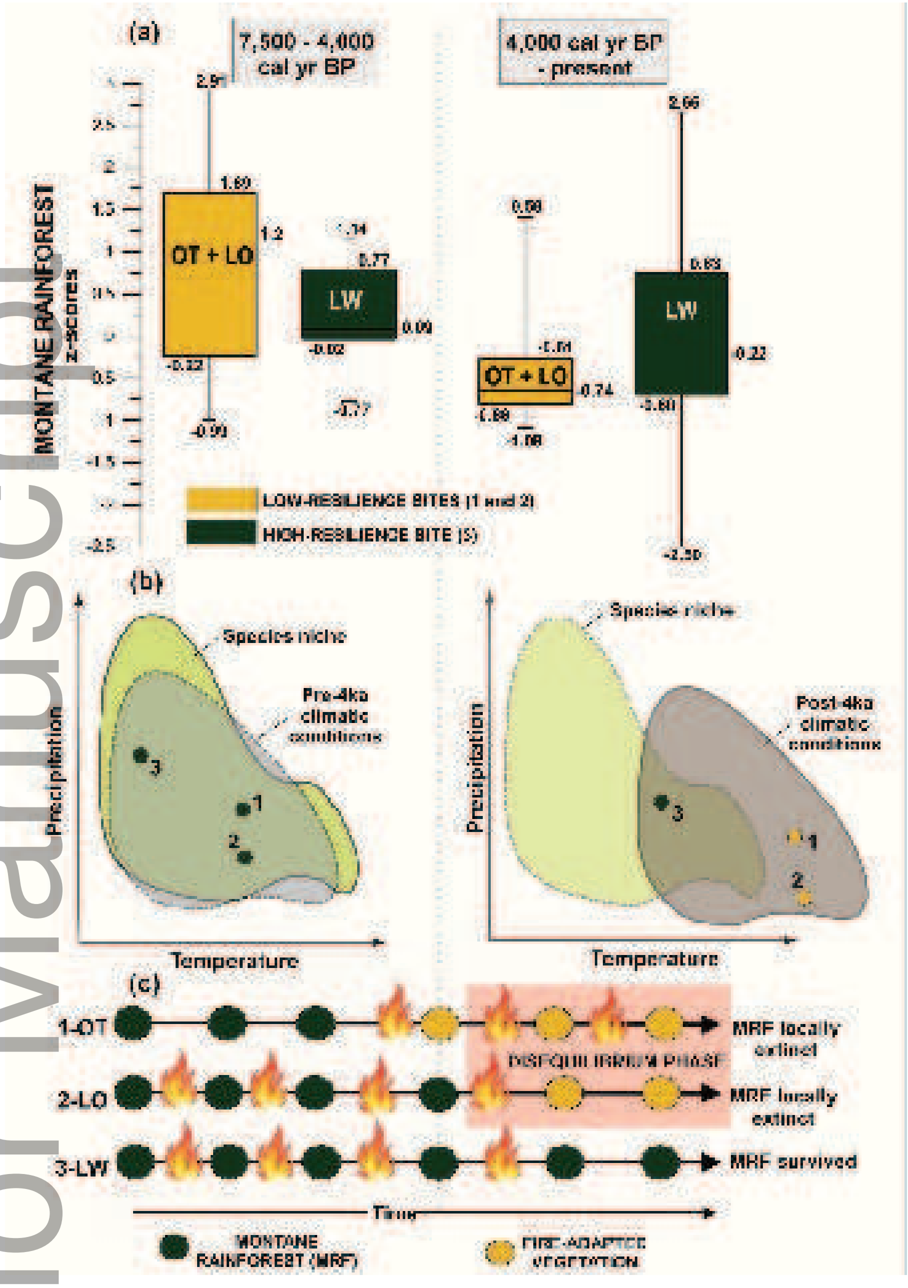

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