1   **The role of species composition in the emergence of alternate vegetation states in a temperate**

2   **rainforest system**

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44   **Abstract**

45   **Context:** Forest systems are dynamic and can alternate between alternative stable states in response to

46   climate, disturbance and internal abiotic and biotic conditions. Switching between states depends on the

47   crossing of critical thresholds and the establishment of feedbacks that drive (and maintain) changes in

48   ecosystem functioning. The nature of these thresholds and the workings of these feedbacks have been

49   well-researched, however, the factors that instigate movement toward and across a threshold remain

50   poorly understood.

51   **Objectives**: In this paper, we explore the role of species composition in initiating ecosystem state change

52   in a temperate landscape mosaic of fire-prone and fire-sensitive vegetation systems.

53   **Methods**: We construct two 12-kyr palaeocecological records from two proximal (230 m apart) sites in

54   Tasmania, Australia, and apply the Alternative Stable States model as a framework to investigate

55   ecosystem feedbacks and resilience threshold dynamics.

56   **Results**: Our results indicate that, in this system, invasion by pyrogenic *Eucalyptus* species is a key factor

57   in breaking down negative (stabilising) feedbacks that maintain pyrophobic sub-alpine rainforest.

58   **Conclusions**: We conclude that the emergence of an alternative stable pyrogenic state in these relic

59   rainforest systems depends on the extent of pyrophytic species within the system. These findings are

60   critical for understanding resilience in forest ecosystems under future climate and land management

61   changes and are relevant to fire-adapted cool-temperate ecosystems globally.

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63   **Key words**

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68 **Introduction**

69 Critical transitions, or catastrophic regime shifts between ecosystem states are of profound importance,

70 given that they are often sudden, unpredicted and can substantially alter important ecosystem functions

71 and services (Folke et al. 2004). Critical transitions between alternative stable ecosystem states occur

72 when an ecosystem has multiple potential stable states that are separated by unstable equilibria (Scheffer

73 et al. 2001, Iglesias and Whitlock 2020). The emergence of alternative stable ecosystem states is induced

74 by feedbacks between the state of the system and limiting environmental factors, such as climate,

75 disturbance, soil moisture conditions or nutrient loading (Borgogno et al. 2007). A considerable body of

76 literature focusses on the feedback loops that hold an ecosystem in a stable state (Warman and Moles

77 2009, Wood and Bowman 2012), and on the various thresholds that must be crossed to tip an ecosystem

78 into a new state (Scheffer and Carpenter 2003, Scheffer et al. 2012). In contrast, comparatively little

79 attention has been paid to the factors required to initiate a switch between stable states. Once an

80 environmental and/or disturbance threshold has been crossed, factors such as the presence or absence of

81 species can initiate a positive feedback switch that modifies the local environment in such a way that

82 favours the new community/species (Wilson and Agnew 1992, Borgogno et al. 2007).

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84 Where multiple (alternative) stable states exist, a change in environmental conditions can influence

85 ecosystem dynamics and increase the response time of an ecosystem to repeated disturbance events

86 (Scheffer et al. 2009, Scheffer et al. 2012). Conceptually, this critical slowing down of recovery time is a

87 product of a shallowing basin of attraction that brings the system closer to a critical threshold (or

88 bifurcation point), which increases the potential of a switch between alternate stable states in response to

89 further environmental change, perturbation(s) and/or internal ecosystem dynamics (Scheffer et al. 2009,

90 Enright et al. 2015, Iglesias and Whitlock 2020). A shift between alternative states occurs when species

91 required for the self-maintenance of one state are removed and new species arrive that initiate a switch to

92 an alternative state. If the new species assemblage is capable of self-maintenance for more than one

93 generation, a switch to a new stable state has occurred (Connell and Sousa 1983, Petraitis and Latham

94 1999, Scheffer et al. 2001, Scheffer and Carpenter 2003). Thus, it can be postulated that in the absence of

95   species that initiate a feedback switch, that either crossing a critical environmental and/or disturbance

96   (e.g. fire, moisture, edaphic etc) threshold alone will be insufficient to drive a critical transition between

97   alternative stable states (Wilson and Agnew 1992, Borgogno et al. 2007), that no threshold is present or

98   that the alternate basin of attraction does not exist (i.e. has not yet emerged).

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100 Transitions between pyrophobic and pyrophytic vegetation states can be spatially and temporally abrupt

101 and are often viewed through the alternative stable states model (Warman and Moles 2009, Wood and

102 Bowman 2012, Odion et al. 2010). These antagonistic vegetation states are maintained by clear and

103 directly opposing feedback mechanisms: pyrophobic species tend to have low flammability and can

104 reproduce in the absence of fire, while pyrophytic species often promote fire and reproduction is often

105 stimulated by (or even dependent on) fire (Figure 1). Transitions between pyrophobic and pyrophytic

106 vegetation states mainly occur when moisture or fire thresholds are crossed that interrupt the internal

107 feedbacks in each state (e.g. burning of rainforest can facilitate the establishment of fire-promoting

108 species that increase the probability of subsequent burning) (Warman and Moles 2009). Importantly,

109 conceptual models of pyrophytic-pyrophobic vegetation systems principally focus on thresholds of

110 environmental change and/or disturbance frequency, and the presence or absence of species capable of

111 initiating a positive feedback switch is often overlooked (Warman and Moles 2009, Wood and Bowman

112 2012, Bowman et al. 2015). Here, we aim to identify what role species composition plays in the initiation

113 and maintenance of a switch from a pyrophobic to pyrophytic vegetation state.

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115 Understanding the factors involved in both the maintenance of alternative stables states and the initiation

116 of a switch between potential states is critical for sustainable, effective and efficient ecosystem

117 management. For example, attempts to mitigate against the potential loss of vulnerable ecosystems to

118 climate-driven wildfires comes at an enormous financial cost (Cochrane 2003, Gill et al. 2013) and the

119 relative lack of understanding of how post-fire changes in species composition either facilitate or mitigate

120 ecosystem state shifts exposes a critical knowledge gap in this endeavour (Bowman et al. 2015, Holz et al.

121   2015). Given the long generational times in many terrestrial ecosystems, gathering sufficient temporal

122   data to understand the cumulative impact of repeated disturbance, interrogate notions of stability, and

123   assess the factors involved in critical transitions is challenging (Petraitis and Dudgeon 2004, Fletcher et

124   al. 2014). It is here that palaeoecological data represents a powerful means of understanding long-term

125   ecosystem dynamics (Willis and Birks 2006). In this paper, we use high-resolution palaeoecological data

126   from two sediment sequences to investigate the roles of climatic change, disturbance, and species

127   composition in the transition between pyrophytic and pyrophobic vegetation states in a cool temperate

128   forest system.

129

130   We exploit a unique natural experiment by analysing archives of long-term vegetation and fire changes

131   stored in the sediments of two small and adjacent lakes (230 m apart) within a temperate forest landscape

132   in Tasmania, Australia. Tasmania's south and west are home to the largest remaining tracts of cool

133   temperate rainforest in Australia. While this perennially wet landscape is ideal for the development of

134   temperate rainforest (Jackson 1968), a landscape-scale decoupling of vegetation and climate has resulted

135   in the predominance of pyrogenic vegetation as a result of the long-term (>40,000-year) application of

136   fire by Indigenous people (Fletcher and Thomas 2010, Mariani et al. 2017). As a result, rainforest is

137   currently restricted to major low-altitude water courses and tiny topographic fire refugia, which, in this

138   topographically complex landscape, are steep south-facing mountain slopes (Wood et al. 2011).

139   Catastrophic wildfires have threatened these vegetation systems in recent years (particularly the 2016 and

140   2019 fire seasons) and an understanding the potential feedbacks between climate, vegetation composition

141   and fire in these rainforest systems is critical for their long-term survival. These forests house endangered

142   subalpine endemics such as *Nothofagus gunni* and *Athrotaxis* spp. – the latter of which has experienced

143   more than 30% range contraction driven by fire-regime changes since the removal of Indigenous fire

144   management by the British in the late 1700's (Holz et al. 2015).

145

146   The extreme flammability of *Eucalyptus* species and their ability to alter local fire regimes by initiating a

147   positive feedback switch is well known (Wilson and Agnew 1992, Williams and Woinarski 1997,

148   Bowman 2000). Many *Eucalyptus* species maintain physiological traits that facilitate recovery from fire,

149   such as reserve (lignotuber) and epicormic budding, heat-tolerant bark, post-fire seed germination and

150   rapid, light-tolerant seedling growth (Gill 1975). *Eucalyptus* communities can also actively encourage

151   higher fire frequencies by increasing fine-fuel loads, decreasing sub-canopy humidity, and supporting the

152   proliferation of flammable understorey species (Brooks et al. 2004, Bowman 2000). In Tasmania, a

153   synergistic relationship between climate and the extreme pyrophytic nature of *Eucalyptus* is implicated in

154   the conversion of rainforest communities to eucalypt forest (Jackson 1968, Gilbert 1959). Recurrent

155   infrequent fires and associated post-fire increases in *Eucalyptus* and other fire-promoting species are

156   thought to facilitate critical transitions between rainforest and *Eucalyptus* ecosystem states (Fletcher et al.

157   2014, Beck et al. 2017; Cadd et al. 2019), yet this relationship has not yet been tested. Following shifts

158   from rainforest to fire, positive feedbacks between *Eucalyptus* and fire are then able to maintain the new

159   ecosystem state by altering local fire regimes (Fletcher et al. 2014).

160

161   Our study lakes are located in the south of the cool temperate island of Tasmania, Australia, a

162   mountainous and topographically complex area that is bistable between pyrophobic rainforest and

163   pyrophytic *Eucalyptus* forest. We use sedimentary charcoal to reconstruct past fires and pollen for past

164   vegetation change over the last 12,000 years (12 ka). Tasmanian forest systems have a high biomass and

165   fires in these systems are climate-limited, with fires occurring during anomalously dry phases. Fires in the

166   study area are linked to El Niño-Southern Oscillation (ENSO), with an intensification of ENSO after

167   6,000 ka increasing both the likelihood and occurrence of fire in the region (Fletcher et al. 2014, Mariani

168   and Fletcher 2016, Mariani et al. 2016, Beck et al. 2017), while also decreasing the ability of some forest

169   types to recover post-fire (Mariani et al. 2019). Here, we use a proxy dataset for changes in the frequency

170   of El Niño events, binned to the number of events per year (Moy et al. 2002), to depict the long-term

171   hydroclimatic trajectory over the region. We predict that repeated burning of rainforest in response to the

172   onset of an increasingly variable climate through the last 6 kyrs will only result in a critical transition

173   between pyrophobic and pyrophytic vegetation states if species are present that can initiate a positive

174   feedback (such as *Eucalyptus*). Thus, in the absence of these species, rainforest will recover in the

175   prolonged absence of fire, irrespective of past wildfire history.

176

Methods

Core collection and chronology

179   This paper focusses on two previously published high-resolution pollen, spore and charcoal records from

180   the Southern Ranges in southern Tasmania, Australia: a 14,000 year (14 kyr) record from Lake Perry

181   (43°12'48"S, 146°45'16"E; 931 masl) (Cadd et al. 2019); and a 14 kyr record from Lake Osborne

182   (43°12'53"S, 146°45'30"E, 924 masl) (Fletcher et al. 2014, Fletcher et al. 2018). These neighbouring

183   lakes are 230 m apart and are situated on the Hartz Range, part of a series of ranges collectively known as

184   the Southern Ranges. The Southern Ranges were an early Holocene (ca. 10-8 ka) refugium for fire-

185   sensitive montane rainforest – an ecosystem dominated by *Athrotaxis selaginioides* (Cupressaceae) and

186   *Nothofagus gunnii* (Nothofagaceae), two long-lived (>500 years) and slow-growing species endemic to

187   Tasmania (Macphail 1979, Macphail and Colhoun 1985, Fletcher et al. 2018). Today, these ranges host

188   some of the most extensive areas of intact montane rainforest remaining in the region. Current rainfall

189   over the Hartz range is 971.2 mm p/a, while temperatures range from 17.6°C – 1.3°C. The current

190   vegetation of the Hartz Range is diverse and includes areas of alpine communities, sub-alpine woodlands,

191   scrub heath and wet *Eucalyptus* forest, with rainforest presently restricted to areas afforded protection

192   from fire by the complex topography.

193

Palynology and charcoal analysis

195   Full details of sample resolution and chronology of the Lake Osborne and Lake Perry are contained

196   within their respective publications (Fletcher et al. 2014, Fletcher et al. 2018, Cadd et al. 2019). Pollen,

197   spores and microscopic charcoal were isolated from a set volume of sediment using standard techniques

198   (Faegri and Iversen 1989). Macroscopic charcoal (>125 μm) was isolated from a set volume of sediment

199   in contiguous subsamples at both sites using standard techniques (Whitlock and Larsen 2001). Both

200   sediment sequences are anchored in time using radiometric dating techniques and statistical modelling. To

201   interpolate estimated ages (and associated errors) for each subsample analysed we used standard

202   analytical and modelling techniques in the software package *clam* v2.3.2 for R (Blaauw 2010, Blaauw and

203   Christen 2011).

204

Statistical analyses

206   Patterns of vegetation change at both sites were interrogated using detrended correspondence analysis

207   (DCA) in PC-ORD 6.08 (McCune & Mefford, 2011). A DCA was performed on a combined dataset of

208   terrestrial pollen types from both lakes, with the primary ordination axes from each site extracted for

209   further analysis. The time series plots of DCA axis 1 of each record were divided into three periods

210   corresponding to the geological subdivision of the Holocene epoch: early Holocene 12-8 ka; mid

211   Holocene 6-4 ka; and late Holocene 4 ka-present. We then created frequency distribution plots of the

212   DCA axis 1 scores for each time slice at each site to understand how the dominant compositional trend

213   compared at each site through time. We focussed on the Holocene epoch only (ca. <12 ka), as this

214   represents the time of establishment of essentially modern climate and vegetation composition at the sites

215   following the end of the Last Ice Age (Fletcher et al. 2018, Cadd et al. 2019).

216

217   To test for the relationship between fire-driven shifts in montane rainforest and *Eucalyptus* pollen, we

218   employed a two-step analytical procedure:

219   Step 1: Regime shift detection: the Sequential T-test Analysis of Regime Shifts algorithm (STARS)

220   (Rodionov 2004) was combined with classical multivariate techniques to identify statistically significant

221   changes in the mean of the palaeoecological time series employed in this study. The algorithm was

222   applied on a composite montane rainforest curve (comprised of Cupressaceae and *N. gunnii*), which was

223   sorted into 5-sample bins, standardized by the mean and passed through a red noise filter (subsample

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224   size=3). The significance value (*p*) was set to 0.001. Fire-driven regime shifts were identified as

225   significant negative shifts in montane rainforest that occurred synchronously with charcoal peaks (see

226   Online Resource Figure S1).

227   Step 2: Superposed Epoch Analysis (SEA) in R v.3.0.3 was used to identify a relationship between fire-

228   driven shifts in montane rainforest and *Eucalyptus* pollen. To satisfy the requirements of even age steps

229   and stationarity for the SEA, the eucalypt curves were first interpolated to 60-year age bins in both

230   records (the median combined age interval) and the interpolated datasets were differenced (Diggle, 1990)

231   prior to running the SEA. This analysis assesses the significance of the departure from the mean for a

232   given set of key event years and lagged years (Lough and Fritts, 1987). Using the STARS-identified fire-

233   driven montane rainforest shifts as event years (regime shifts), we tested for lagged correlation between

234   these pollen-inferred regime shifts and *Eucalyptus* pollen. Significance was set to $p<0.01$ in the SEA.

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236

237   **Results**

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239   **Palynology and charcoal analysis**

240   The full pollen and charcoal sequences can be seen in the respective publications for Lakes Osborne

241   (Fletcher et al. 2014, Fletcher et al. 2018) and Perry (Cadd et al. 2019). Here, we present combined

242   montane rainforest, *Eucalyptus*, macroscopic and microscopic charcoal curves for each site (Figure 2).

243

244   **Statistical analyses**

245   The DCA biplot shows correlations between pollen taxa and the ordination axis for both Lake Perry and

246   Lake Osborne (Online Resource Figure S2). The ordination space is organised into 4 time periods: Late

247   Glacial 14.5-12 ka; early Holocene 12-8 ka; mid Holocene 6-4 ka; and late Holocene 4 ka – present

248   (Online Resource S2). Axis 1 explains 59.4% of the variation in the dataset and is strongly correlated with

249   *N. gunnii* (negative), *Eucalyptus*, Restionaceae and *Allocasurina* (positive). Axis 3 explains 8.5% of the

250   variance and displays a strong negative correlation with Cupressaceae. Long-term vegetation

251   development at both sites follows the same trajectory in the ordination space between ca. 14.5-6 ka, with

252   a clear separation of the two sites commencing at ca. 6 ka and culminating in distinct populations within

253   the ordination space after ca. 2.6 ka, with Lake Osborne pollen spectra at this time notably higher in

254   *Eucalyptus* than Lake Perry. This is evident in the frequency distribution plots of the DCA axis 1 scores

255   over the Holocene (Figure 3, 5), which shows overlapping populations between 12-8 ka, separation of the

256   sites between 8-2.6 ka and discrete populations after 4 ka.

257

258   The STARS algorithm identified 4 negative montane rainforest shifts at Lake Perry and 4 at Lake

259   Osborne. Visual inspection identified that all shifts at both Lake Osborne and Lake Perry correspond to

260   charcoal peaks (Online Resource Figure S1). These shifts were interpreted as fire-driven montane

261   rainforest shifts and were used as event years in the SEA. The results of the SEA indicate a significant

262   positive departure of *Eucalyptus* with fire-driven montane rainforest shifts at 0-lag (i.e. 0-60 years

263   following charcoal peaks) at Lake Osborne, while no statistically significant relationship between fire-

264   driven montane rainforest shifts and *Eucalyptus* was observed at Lake Perry (Figure 4).

265

266   **Discussion**

267   *Temperate rainforest and* Eucalyptus *forest as alternative stable states*

268   The catchments of Lakes Perry and Osborne occupy the same biophysical environment and are

269   remarkably similar in elevation, size and overall topographic context. Establishment of montane rainforest

270   dominated by *Nothofagus gunnii* and Cupressaceae occurred at these adjacent sites between ca. 12-8 ka in

271   the absence of fire. Montane rainforest dominated across several nearby sites through this period

272   (Macphail 1979, Macphail and Colhoun 1985) and, collectively, indicates a stable cool and humid climate

273   regime and low fire activity across southern Tasmania at this time (Fletcher et al. 2018). The absence of

274   fire during this rainforest-dominated period at both Lake Osborne and Lake Perry is consistent with the

275   stabilising feedbacks proposed for rainforest vegetation in the alternative stable states model put forward

276   by Wood and Bowman (2012): low fuel flammability and high sub-canopy humidity of pyrophobic

277   rainforest inhibits the occurrence of fire and allows the establishment and dominance of pyrophobic

278   rainforest (Figure 1).

279

280   The series of fires at both lakes between ca. 8-2.5 ka (Figure 2) facilitated the establishment of discrete

281   vegetation states after 2.5 ka: pyrophytic eucalypt-dominant vegetation became established at Lake

282   Osborne, while pyrophobic (montane rainforest) vegetation persisted within the catchment of Lake Perry

283   (Figures 2,3). The juxtaposition of pyrophobic rainforest and pyrophytic eucalypt forest at these adjacent

284   sites for ca. 2.5 kyrs implies that these vegetation states are stable alternatives within this landscape. The

285   pyrophytic vegetation state is maintained by a positive feedback between fire and the establishment of

286   flammable fire-promoted species (Warman and Moles 2009, Wood and Bowman 2012).

287

288   The vegetation shift at Lake Osborne is accompanied by a clear shift in the charcoal signature deposited

289   within that lake (from macroscopic to microscopic dominance; Figure 2). While shifts in charcoal size

290   fractions are often interpreted as changes in local versus distant source area (Whitlock & Larsen, 2001),

291   this change in charcoal signature also reflects a change in fuel biomass (see also Mariani et al. 2019).

292   Rainforests have a high woody biomass and fires within rainforest vegetation are infrequent and high

293   intensity (Murphy et al. 2013), usually resulting in substantial tree mortality and consumption (Hill 1982).

294   In contrast, the eucalypt associations on the Hartz Mountains are comparatively sparse. Further,

295   *Eucalyptus* foliage is highly flammable, burns rapidly and, in the case of resprouting species such as *E.*

296   *coccifera* found in the study area today, usually only the leaf matter is consumed (Bowman 1998, 2000).

297   We contend that establishment of the pyrophytic vegetation state caused a shift from a low-frequency,

298   high-intensity rainforest fire regime to a higher–frequency, lower-intensity eucalypt fire regime that is

299   reflected by the higher microscopic charcoal content following this switch (Fletcher et al. 2014). Indeed, a

300   similar shift in charcoal particle size following the initial burning and deforestation of New Zealand

301   rainforest (which was replaced by lower-biomass grass- and scrublands) following the arrival of Maori

302   (McWethy et al. 2010) lends support to this inference.

303

304   *The role of climate in initiating vegetation state switches*

305   While the influence of the long-term shift in climatic variability through the Holocene over Tasmanian

306   climate and fire regimes is well described (Fletcher and Moreno 2012, Fletcher et al. 2015, Beck et al.

307   2017, Mariani and Fletcher 2017), comparatively little is known about how this shift influenced the

308   terrestrial ecology within this landscape. Montane rainforest appears to have dominated much of the

309   Southern Ranges of Tasmania through the early Holocene (ca. 12-8 ka). The overall lack of charcoal

310   peaks at our sites through this period is consistent with a stable cool and humid climate regime conducive

311   for rainforest development and prohibitive to fire (Macphail 1979, Macphail and Colhoun 1985, Fletcher

312   et al. 2018) (Figure 2). In contrast, there is a marked increase in fire activity in the Southern Ranges

313   through the last ca. 8 kyrs. Repeated fires during this period, several of which were synchronous at both

314   sites (Figure 2), occurred in response to an increasingly variable rainfall regime, driven principally by an

315   increase in the frequency and amplitude of ENSO variability in the tropical Pacific (Figure 3) (Fletcher et

316   al. 2014, Rees et al. 2015, Beck et al. 2017, Mariani and Fletcher 2017, Fletcher et al. 2018). Importantly,

317   we observe a divergence in the developmental trajectories of the vegetation within our adjacent study

318   catchments in response to this repeated disturbance. Repeated fires over the last ca. 8 kyrs led to the

319   emergence and subsequent establishment and spread of a pyrophytic vegetation state at Lake Osborne,

320   while montane rainforest persisted at Lake Perry (Figure 2,3,4,6).

321

322   *The role of species composition (i.e.* Eucalyptus*) in initiating vegetation state switches*

323   Theory predicts that the emergence of an alternative stable state can be induced by feedbacks between an

324   ecosystem state and limiting factors, such as precipitation and fire (Borgogno et al. 2007, Iglesias and

325   Whitlock 2020). The frequency distribution plots of the individual site ordination axis scores (DCA 1),

326 split in to ca. 12-8 ka; 8-4 ka; and <4 ka intervals (Figure 3, 5), allow a conceptualisation of the initial

327 emergence of an alternate basin of attraction after ca. 8 ka and the subsequent establishment of an

328 alternate basin of attraction after ca. 4 ka (Figure 3, 5). The transition from pyrophobic rainforest to

329 pyrophytic eucalypt forest at Lake Osborne, in contrast to the maintenance of pyrophobic rainforest at

330 Lake Perry, offers a critical insight into the factors leading to the emergence of an alternative stable

331 pyrophytic state within this system. We detect a significant difference in the relationship between

332 *Eucalyptus* pollen and fire-driven shifts in montane rainforest between our two study sites: Lake Osborne

333 (the pyrophytic site) displays a significant increase in *Eucalyptus* pollen synchronous with fire-driven

334 reductions in montane rainforest, while no relationship is evident between *Eucalyptus* and fire-driven

335 reductions in montane rainforest at Lake Perry (the pyrophobic site).

336

337 Our results indicate that a positive feedback between century-scale rainfall deficits, coupled with repeated

338 fire and pyrophytic species invasion and spread (here, *Eucalyptus*), led to the emergence and subsequent

339 establishment of an alternate pyrophytic vegetation state. Without a sufficient degree of pyrophytic

340 species invasion, the shifts in moisture and fire occurrence experienced at both sites appear to be

341 insufficient to have driven a switch between pyrophobic and pyrophytic vegetation states at Lake Perry. It

342 is probable that a threshold for the degree of species invasion must be breached before its presence can

343 drive a system toward an alternate stable state, however whether this threshold relates to the species'

344 relative proportions or patch size/s within the landscape (see also Van Nes et al. 2018) is impossible to

345 determine from our data. Nonetheless, our results indicate that a crucial component of a switch between

346 pyrophobic and pyrophytic vegetation states in this landscape is the post-fire establishment of *Eucalyptus*.

347 The implication of this result for all pyrophobic-pyrophytic vegetation transitions is that it is critically

348 important that post-fire species composition be considered when assessing the potential for recovery of

349 pyrophobic vegetation from fire. A case-in-point are assertions that the large-scale fire damage to

350 conifer-dominant rainforest across Tasmania in response to changes in fire use following British invasion

351 are irreversible (Holz et al. 2015). Previous research (Fletcher et al. 2014, Cadd et al. 2019) indicates that

352 Tasmanian montane rainforest systems require substantial (ca. 1 ka) fire-free periods to recover post-fire,

353 however our data indicates that recovery also hinges on the post-fire species composition (specifically the

354 proportion of eucalypts in the forest system). Thus, attempts to mitigate the effects of future fire and

355 conserve these ecosystems must bear these critical factors in mind.

356

357 **Conclusions**

358 Despite overall similar vegetation histories during the early Holocene, the vegetation trajectories of our

359 two study sites experience a marked divergence after 6 ka. The increased importance of *Eucalyptus*

360 species within the Lake Osborne catchment precipitated a positive feedback switch that resulted in the

361 emergence of an alternate stable pyrophytic state. The greater extent of *Eucalyptus* led to a shift in fire

362 regime from low-frequency/high-intensity to a higher-frequency/lower-intensity regime that precluded the

363 reestablishment of pyrophobic rainforest. We conclude that in this fire-prevalent landscape, the greater

364 incidence of *Eucalyptus* species initiates a feedback switch that drives transitions between pyrophobic and

365 pyrophytic vegetation states. Without sufficient cover of *Eucalyptus* species, crossing thresholds of

366 moisture deficit and fire disturbance alone are inadequate to cause a switch to an alternate stable state.

367

368 **References**

369

370 Beck KK, Fletcher M-S, Gadd PS, Heijnis H, and Jacobsen GE (2017) An early onset of ENSO influence

371   in the extra-tropics of the southwest Pacific inferred from a 14,600-year high resolution multi-

372   proxy record from Paddy's Lake, northwest Tasmania. Quat Sci Rev 157:164-175.

373 Blaauw M (2010) Methods and code for 'classical' age-modelling of radiocarbon sequences. Quat

374   Geochronol 5:512-518.

375 Blaauw M and Christen JA (2011) Flexible paleoclimate age-depth models using an autoregressive

376   gamma process. Bayesian Anal 6:457-474.

377 Borgogno F, D'Odorico P, Laio F and Ridolfi L (2007) Effect of rainfall interannual variability on the

378   stability and resilience of dryland plant ecosystems. Water Resour Res 43.

379 Bowman DM, Perry GL and Marston J (2015) Feedbacks and landscape-level vegetation dynamics.

380   Trends Ecol & Evol 30:255-260.

381 Bowman DMJS (1998) Tansley Review No. 101: The impact of Aboriginal landscape burning on the

382   Australian biota. New Phytol 140:385-410.

383 Bowman DMJS (2000) Australian rainforests: islands of green in a land of fire. First edition. Cambridge

384   University Press, Cambridge.

385 Brooks ML, Antonio CMD, Richardson DM et al (2004) Effects of invasive alien plants on fire regimes.

386   BioScience 54:677-689.

387 Cadd H, Fletcher M-S, Mariani M, Heijnis H and Gadd PS (2019) The influence of fine-scale topography

388   on the impacts of Holocene fire in a Tasmanian montane landscape. J Quat Sci 34:491-498.

389 Cochrane MA (2003) Fire science for rainforests. Nat 421:913.

390 Connell JH and Sousa WP (1983) On the evidence needed to judge ecological stability or persistence. Am

391   Nat 121:789-824.

392 Cullen P (1991) Regeneration of *Athrotaxis selaginoides* and other rainforest tree species on landslide

393   faces in Tasmania. Pap Proc R Soc Tasman 124:191-200.

394 Cullen PJ (1987) Regeneration patterns in populations on *Athrotaxis selaginoides* D. Don. from

395   Tasmania. J Biogeogr 14:39 - 51.

396 Diggle PJ (1990) Time series; a biostatistical introduction. Clarendon Press, New York.

397 Enright NJ Fontaine JB, Bowman DM, Bradstock RA and Williams RJ (2015) Interval squeeze: altered

398   fire regimes and demographic responses interact to threaten woody species persistence as climate

399   changes. Front Ecol Env 13:265-272.

400 Faegri K and Iversen J (1989) Textbook of pollen analysis. Wiley, New York.

401 Fletcher M-S, Benson A, Heijnis H, Gadd PS, Cwynar LC and Rees ABH (2015) Changes in biomass

402   burning mark the onset an ENSO-influenced climate regime at 42°S in southwest Tasmania,

403   Australia. Quat Sci Rev 122:222-232.

404 Fletcher M-S, Bowman D, Whitlock C, Mariani M and Stahle L (2018) The changing role of fire in

405   conifer-dominated temperate rainforest through the last 14,000 years. Quat Sci Rev 182:37-47.

406   Fletcher M-S and Moreno PI (2012) Have the Southern Westerlies changed in a zonally symmetric

407   manner over the last 14,000 years? A hemisphere-wide take on a controversial problem. Quat Int

408   253:32–46.

409   Fletcher M-S and Thomas I (2010) The origin and temporal development of an ancient cultural landscape.

410   J Biogeogr 37:2183–2196.

411   Fletcher M-S, Wolfe BB, Whitlock C, Pompeani DP, Heijnis H, Haberle SG, Gadd PS and DMJS

412   Bowman (2014) The legacy of mid-Holocene fire on a Tasmanian montane landscape. J Biogeogr

413   41:476-488.

414   Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L and Holling C (2004) Regime

415   shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol, Evol, Syst:557-

416   581.

417   Gilbert JM (1959) Forest succession in the Florentine Valley, Tasmania. Pap Proc R Soc Tasman 93:129–

418   151.

419   Gill AM (1975) Fire and the Australian flora: a review. Aust For 38:4-25.

420   Gill AM, Stephens SL and Cary GJ (2013) The worldwide "wildfire" problem. Ecol Appl 23:438-454.

421   Hill RS (1982) Rainforest Fire in Western Tasmania. Aust J Bot 30:583 - 589.

422   Holz A, Wood SW, Veblen TT and Bowman DM (2015) Effects of high severity fire drove the

423   population collapse of the subalpine Tasmanian endemic conifer *Athrotaxis cupressoides*. Glob

424   Chang Biol 21:445-458.

425   Iglesias V and Whitlock C (2020) If the trees burn, is the forest lost? Past dynamics in temperate forests

426   help inform management strategies. Philos Trans R Soc B 375:20190115.

427   Jackson WD (1968) Fire, air, water and earth – an elemental ecology of Tasmania. Proc Ecol Soc Aust

428   3:9-16.

429   Lough JM and Fritts H (1987) An assessment of the possible effects of volcanic eruptions on North

430   American climate using tree-ring data, 1602-1900 A.D. Clim Chang 10:219-239.

431   Macphail MK 1979 Vegetation and climates in southern Tasmania since the last glaciation. Quat Res

432   11:306-341.

433   Macphail MK and Colhoun EA 1985. Late last glacial vegetation, climates and fire activity in southwest

434   Tasmania. Search 16:43-45.

435   Mariani M, Conner SE, Fletcher M-S, Theuerkauf M, Kunes P, Jacobson G, Saunders KM and Zawadzki

436   A (2017) How old is the Tasmanian cultural landscape? A test of landscape openness using

437   quantitative land-cover reconstructions. J Biogeogr 44:2410-2420.

438   Mariani M and Fletcher M-S (2017) Long-term climate dynamics in the extra-tropics of the South Pacific

439   revealed from sedimentary charcoal analysis. Quat Sci Rev 173:181-192.

440   Mariani M and Fletcher M-S (2016) The Southern Annular Mode determines inter-annual and centennial-

441   scale fire activity in temperate southwest Tasmania, Australia. Geophys Res Lett 43:1702-1709.

442   Mariani M, Fletcher M-S, Haberle S, Chin H, Zawadzki A and Jacobsen G (2019) Climate change

443   reduces resilience to fire in subalpine rainforests. Glob Chang Biol 25:2030-2042.

444   Mariani M, Fletcher M-S, Holz A and Nyman P (2016) ENSO controls interannual fire activity in

445   southeast Australia. Geophys Res Lett 43:10891-10900.

446   Mariani M, Tibby J, Barr C, Moss P, Marshall JC and McGregor GB (2019) Reduced rainfall drives

447   biomass limitation of long-term fire activity in Australia's subtropical sclerophyll forests. J

448   Biogeogr 46:1974-1987.

449   McCune B and Mefford MJ (2011) PC-ORD. Multivariate analysis of Ecological Data, Version 6.0 for

450   Windows. MjM Software, Gleneden Beach, Oregon, U.S.A

451   McWethy DB, Whitlock C, Wilmshurst JM, McGlone MS, Fromont M, Li X, Dieffenbacher-Krall A,

452   Hobbs WO, Fritz SC and Cook ER (2010) Rapid landscape transformation in South Island, New

453   Zealand, following initial Polynesian settlement. Proc Natl Acad Sci 107:21343-21348.

454   Moy CM, Seltzer GO, Rodbell DT and Anderson DM (2002) Variability of El Nino/Southern Oscillation

455   activity at millennial timescales during the Holocene. Nature 420:162-165.

456   Murphy BP, Bradstock RA, Boer MM, Carter J, Cary GJ, Cochrane MA, Fensham RJ, Russell-Smith J,

457   Williamson GJ and Bowman DM (2013) Fire regimes of Australia: a pyrogeographic model

458   system. J Biogeogr 40:1048-1058.

459   Odion DC, Moritz MA and Dellasala DA (2010) Alternative community states maintained by fire in the

460   Klamath Mountains, USA. J Ecol 98:96-105.

461   Petraitis PS and Dudgeon SR (2004) Detection of alternative stable states in marine communities. J Exp

462   Mar Biol Ecol 300:343-371.

463   Petraitis PS and Latham RE (1999) The importance of scale in testing the origins of alternative

464   community states. Ecol 80:429-442.

465   Rees AB, Cwynar LC and Fletcher M-S (2015) Southern Westerly Winds submit to the ENSO regime: A

466   multiproxy paleohydrology record from Lake Dobson, Tasmania. Quat Sci Rev 126:254-263.

467   Rodionov SN (2004) A sequential algorithm for testing climate regime shifts. Geophys Res Lett

468   31:L09204.

469   Scheffer M. Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, Van Nes EH,

470   Rietkerk M and Sugihara G (2009) Early-warning signals for critical transitions. Nature 461:53-

471   59.

472   Scheffer M, Carpenter S, Foley JA, Folke C and Walker B (2001) Catastrophic shifts in ecosystems.

473   Nature 413:591-596.

474   Scheffer M and Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to

475   observation. Trends Ecol & Evol 18:648-656.

476   Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock W, Dakos V, Van De Koppel J, Van De

477   Leemput IA, Levin SA and Van Nes EH (2012). Anticipating critical transitions. Science

478   338:344-348.

479   Van Nes EH, Staal A, Hantson S, Holmgren M, Pueyo S, Bernadi RE, Flores BM, Xu C and Scheffer S

480   (2018). Fire forbids fifty-fifty forest. PLoS One 13:e0191027.

481   Warman L and Moles AT (2009) Alternative stable states in Australia's wet tropics: a theoretical

482   framework for the field data and a field-case for the theory. Landsc Ecol 24:1-13.

483   Whitlock C and Larsen C (2001) Charcoal as a fire proxy. Smol, JP, Birks, HJB and Last, WM (eds.)

484   Tracking environmental change using lake sediments Vol. 3, Terrestrial, algal, and Siliceous

485   Indicators: 75-97. Kluwer Academic Publishers.

486   Williams JE and Woinarski JCZ (1997) Eucalypt ecology: individuals to ecosystems. Cambridge

487   University Press, Cambridge.

488   Willis KJ and Birks HJB (2006) What is natural? The need for a long-term perspective in biodiversity

489   conservation. Science 314:1261.

490   Wilson JB and Agnew AD (1992) Positive-feedback switches in plant communities. Adv Ecol Res

491   23:263-336.

492   Wood SW and Bowman DMJS (2012) Alternative stable states and the role of fire–vegetation–soil

493   feedbacks in the temperate wilderness of southwest Tasmania. Landsc Ecol 27:13-28.

494   Wood SW, Murphy BP and Bowman DM (2011) Firescape ecology: how topography determines the

495   contrasting distribution of fire and rain forest in the south-west of the Tasmanian Wilderness

496   World Heritage Area. J Biogeogr 38:1807-1820.

497   Wood S and Wood MS (2007) The mgcv package. Retrieved from www.r-project.org.

Fig. 1 Conceptual model of the feedbacks within pyrophobic and pyrophytic vegetation states, based on Wood and Bowman (2012). Grey shading and dashed lines indicate the hypothesised role of species capable of initiating a positive feedback switch between vegetation states (sensu Wilson and Agnew, 1992). Thresholds of moisture and fire are drawn from Warman and Moles (2012)

Fig. 2 Pollen and charcoal stratigraphies from Lake Perry (LP - this study) and Lake Osborne (LO - Fletcher et al., 2018). Right panel shows the geographic location of each catchment and lake

Fig. 3 (top) Plot of frequency distribution histograms of DCA axis 1 scores for Lake Perry (green; this study) and Lake Osborne (orange; Fletcher et al., 2018) divided in to groups according to pollen stratigraphy; and (bottom) a 100-year binned plot of inferred El Nino frequency in the tropical east Pacific (Moy et al, 1992)

Fig. 4 Superposed epoch analysis (SEA) of departures of *Eucalyptus* pollen versus fire driven montane rainforest reductions at (a) Lake Osborne and (b) Lake Perry. Dark grey shaded bar indicates statistical significance ($P<0.01$). Lags are 60 years

Fig. 5 Conceptual model relating the potential stability landscapes to the stages of system transition that were realised at Lakes Perry and Osborne. Frequency histograms reveal the diverging dominance of *Eucalyptus* at each site through time – highlighting the invasion of *Eucalyptus* as a key factor in the emergence of the alternative stable state at Lake Osborne
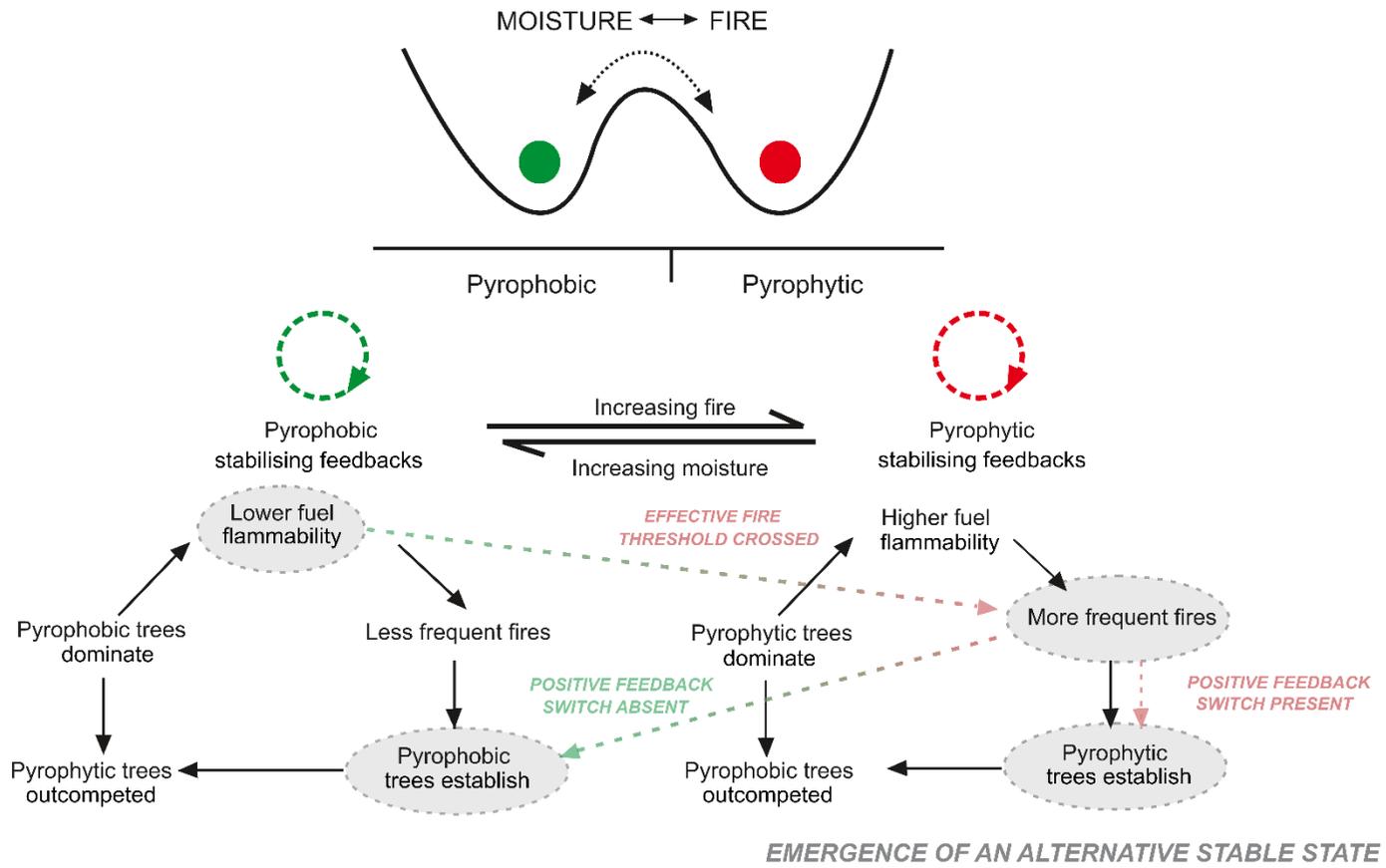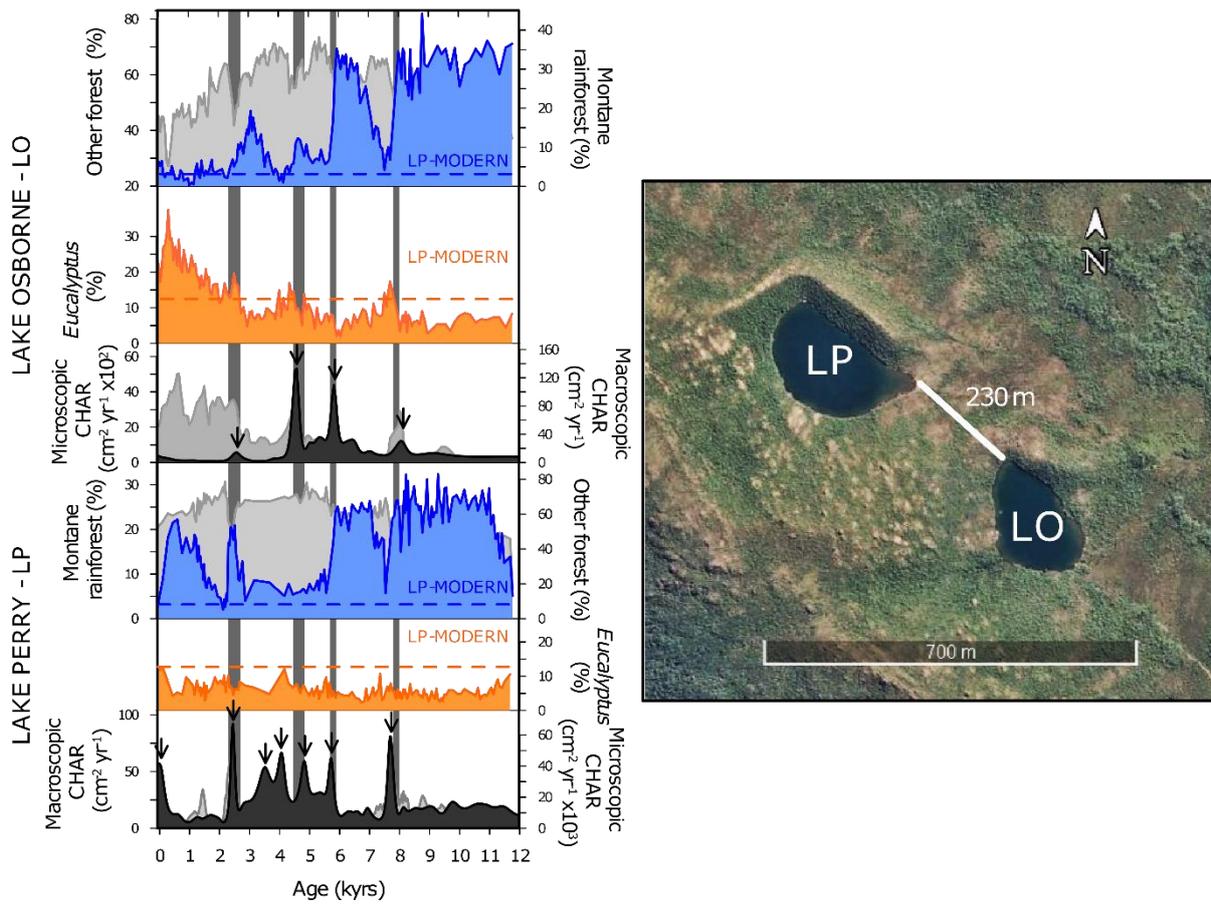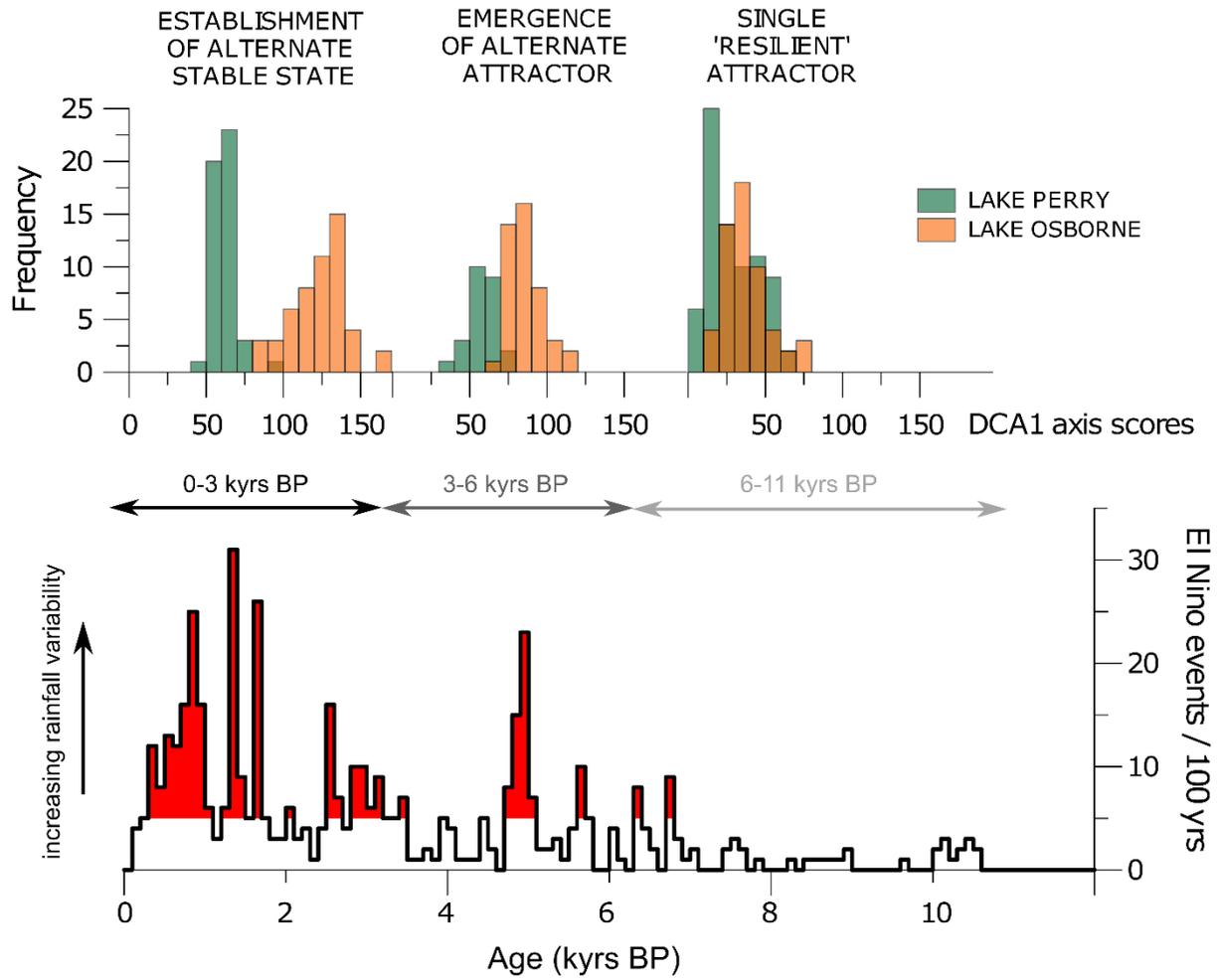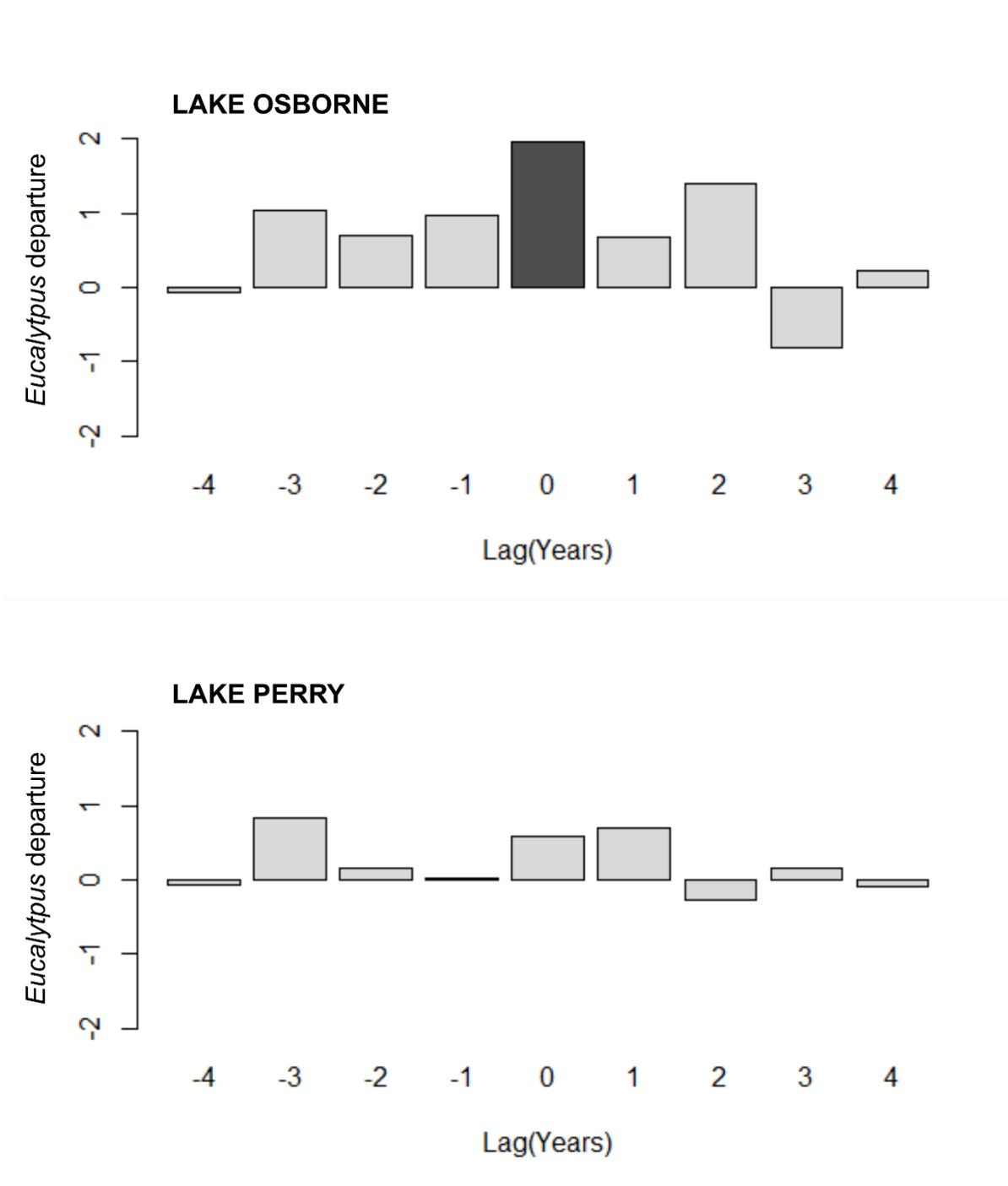
Figure 1

Figure 2

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