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1 **Running Head: A fire driven switch between stable states**

2 **Title: A fire driven shift from forest to non-forest: evidence for alternative stable**

3 **states?**

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25 **Abstract**

26 We test the validity of applying the alternative stable state paradigm to account for the

27 landscape-scale forest/non-forest mosaic that prevails in temperate Tasmania, Australia.

28 This test is based on fine scale pollen, spore and charcoal analyses of sediments located

29 within a small patch of non-forest vegetation surrounded by temperate forest. Following

30 nearly 500 years of forest dominance at the site, a catastrophic fire drove an irreversible

31 shift from a forested Cyperaceae-*Sphagnum* wetland to a non-forested Restionaceae

32 wetland at ca.7000 cal yr BP. Persistence of the non-forest/Restionaceae vegetation state

33 over 7000 years despite long fire-free intervals implies that fire was not essential for the

34 maintenance of the non-forest state. We propose that reduced interception and

35 transpiration of the non-forest state resulted in local waterlogging, presenting an eco-

36 hydrological barrier to forest reestablishment over the succeeding 7000 years. We further

37 contend that the rhizotamous nature of the non-forest species presented a reinforcing eco-

38 physical barrier to forest development. Our results satisfy a number of criteria for

39 consideration as an example of a switch between alternative stable states, including

40 different origin and maintenance pathways, and provide insights into the role of threshold

41 dynamics and hysteresis in forest/non-forest transitions.

42

43 Keywords: Alternative stable states, Palaeoecology, Forest, Non-forest, Fire, regime

44 shift, Tasmania, Australia, Hysteresis.

45 **Introduction**

46 Large sudden shifts in ecosystem states, such as sudden shifts between forest and

47 grassland, occur when an ecological system crosses a threshold (Scheffer et al. 2001,

48 Scheffer and Carpenter 2003). Such shifts in ecosystem states can have serious

49 ramifications for ecosystem functioning, for example forests have a substantially higher

50 carbon storage potential relative to grasslands (Casini et al. 2009). Understanding of how

51 and why they occur is, thus, a critical endeavour. Triggers for shifts across ecological

52 thresholds include large external perturbations, small incremental environmental changes

53 and internal feedbacks (Scheffer and Carpenter 2003). Following a catastrophic regime

54 shift, a system may return to its original state or the system may settle around a new state

55 (Scheffer and Carpenter 2003). This latter situation may arise from the existence of

56 alternative stable ecosystem states.

57

58 The model of alternative stable states is often invoked to account for the persistence of

59 different species assemblages within the same environment (Petraitis and Latham 1999).

60 Shifts between stable ecosystem states occur when (i) a critical threshold is crossed that

61 results in the removal of species required for the self-maintenance of one state, (ii) the

62 arrival of species that initiate a switch to an alternative state and (iii) the new species

63 assemblage is capable of self-maintenance for more than one generation (Connell and

64 Sousa 1983, Petraitis and Latham 1999, Scheffer et al. 2001, Scheffer and Carpenter

65 2003). In terrestrial vegetation systems, alternative stable states often manifest spatially

66 as sharp transitions in either assemblage and/or physiognomic state (Wilson and Agnew

67 1992), while temporal shifts may manifest as historical discontinuities in vegetation

68   communities that may be represented as jumps in time-series data (Scheffer and

69   Carpenter 2003).   Despite the recent widespread application of the alternative stable state

70   model to a range of natural systems (e.g. Scheffer et al. 1993, Scheffer and Carpenter

71   2003, Petraitis and Dudgeon 2004, Warman and Moles 2009, Odion et al. 2010, Hirota et

72   al. 2011, Mayer and Khalyani 2011), demonstrating that the same site conditions can

73   support alternative states in terrestrial vegetation systems is far from easy (Petraitis and

74   Latham 1999, Schröder et al. 2005, Odion et al. 2010).   A complicating factor in

75   terrestrial vegetation systems is demonstrating *stability*: the ability of the vegetation state

76   to maintain itself through more than one generation (Connell and Sousa 1983, Peterson

77   1984).   This problem is most salient in long-lived vegetation systems, such as forests and

78   shrublands, where generational times are long. Such systems require novel approaches to

79   gathering the data needed to understand the underlying mechanisms governing their

80   apparent stability (e.g. Warman and Moles 2009, Odion et al. 2010, Hirota et al. 2011,

81   Jeffers et al. 2011). Here, we use palaeoecology to reconstruct a regime shift between

82   temperate forest and non-forest vegetation states in the southern hemisphere.

83

84   Mosaics of forest, savanna and grasslands have been used as a model system for

85   exploring the efficacy of the alternative stable states model for terrestrial landscapes

86   (Staver et al. 2011; Lehmann et al. 2011; Mayer et al. 2011; Hirota et al. 2011). In this

87   system, vegetation transitions between three states - forest, savannah, grassland -

88   according to feedback mechanisms related to rainfall and fire (Mayer and Khalyani

89   2011). Drawing on the state and transition concepts put forward for the forest-savannah-

90   grassland system and the early work of Jackson (1968) in Tasmania, Wood and Bowman

91   (2012; see also Wood et al. 2011a,b) framed the vegetation landscape of temperate

92   southwest Tasmania in the alternative stable states framework. This system has four

93   vegetation states: rainforest, eucalypt forest, sclerophyll shrubs and moorland. Rainforest

94   and eucalypt forest in southwest Tasmania are sensitive to frequent fires, but produce a

95   considerable amount of fuel that is flammable when dry (particularly eucalypt forest).

96   The forest state is maintained by an infrequent fire regime (70-400 year fire-return

97   interval for eucalypt forest and >400 year fire-return interval for rainforest) that has a

98   twofold effect: (1) the establishment of slower growing trees relative to non-forest

99   species; and (2) the accumulation of soil nutrients that are essential for forest

100 development in this extremely oligotrophic region (Jackson 1968, Pyrke and Marsden-

101 Smedley 2005, Bowman and Wood 2009, Wood and Bowman 2012). These positive

102 feedbacks between fire, vegetation and soil characteristics engender an inertia to change

103 in these vegetation states, but repeat fires or high severity fires can trigger transitions

104 between vegetation states.

105

106 While there is evidence for fire-vegetation-soil feedbacks that reflect the mechanisms of

107 self-maintenance in this system (Wood and Bowman 2012), the factors leading to the

108 establishment of these alternative vegetation states remain untested (i.e. the problem of

109 *'origin'*; Petraitis and Latham 1999). Only one study that unequivocally documents the

110 establishment of non-forest vegetation in place of forest in this region and the factors

111 leading to the establishment of non-forest at that site (the *origin*) are unknown (Ellis and

112 Thomas 1988). Moreover, while fire clearly plays a key role in this vegetation landscape,

113 relatively little attention has been given to the potential role of other factors, such as

114   hydrology, in maintaining alternate vegetation states in this system (Pemberton 1989).

115   Anecdotal information on the role of hydrology in temperate forest/non-forest dynamics

116   can be drawn from other high-rainfall temperate regions, where permanent

117   transformations from forest to non-forest are observed after forest removal and is

118   explained by reduced transpiration rates under forest canopies relative to non-forest (Díaz

119   and Armesto 2007). The altered transpiration regime results in soil waterlogging and

120   excludes tree seedling reestablishment (Díaz and Armesto 2007). While not explicating a

121   mechanistic pathway, Pemberton (1989) invoked hydrology as a possible factor in the

122   apparent inability of forest to encroach upon some non-forest patches in the humid

123   landscape of Tasmania. However, the influence of hydrology in this system has been

124   largely ignored.

125

126   Here, we interrogate the roles of fire and hydrology in the origin and maintenance of

127   forest and non-forest vegetation states by reconstructing vegetation and fire history over

128   the last 7500 years of a small (<18 ha) moorland (non-forest) patch surrounded by forest

129   on the Gog Range in Tasmania, Australia. The plateau of the Gog Range is characterised

130   by a series of discrete non-forest patches nested within a larger forest matrix (Fig. 1).

131   Palaeoecological research from within a patch of moorland on the Gog Range reveals that

132   at least parts of the plateau that now host moorland were occupied by forest during the

133   mid Holocene, with fire implicated in the permanent transition from forest to non-forest

134   (Webb et al. 1994). We focus on multi-decadal scale dynamics close to a forest/non-

135   forest boundary and specifically ask: (1) what are the extrinsic factors leading to the

136   establishment of non-forest in place of forest in this temperate system (i.e. the problem of

137   *origin*)? (2) do forest and non-forest represent alternative stable states in this system; and

138   (3) what are the mechanisms of self-maintenance of vegetation states in this system?

139

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140 **Methods**

141 To reconstruct vegetation and fire history over the last 7500 years on the Gog Range

142 (41°30'28"S, 146°23'5"E), we retrieved a 94 cm core from Granta Pools using a D-

143 section corer. The Gog Range is a low (~750 m) 13 km range that is crested by a flat

144 narrow plateau. The climate is humid, with an annual winter dominant rainfall of 1200

145 mm. The Granta Pools are surrounded by a <18 ha patch of non-forest moorland (one of

146 many that line the plateau), and tall *Eucalyptus* forest with an understorey of mesophyte

147 wet forest and rainforest species (temperate eucalypt/wet sclerophyll forest) cloak the

148 northern and southern slopes of the Gog Range, growing to within 120 m of Granta Pools

149 (Fig. 1). The site occupies a shallow depression in the Ordovician conglomerate bedrock

150 that has in-filled with organic sediments. Ordovician conglomerate, along with

151 Precambrian quartzite, are low nutrient yielding and highly resistant rock types that

152 dominate the geology of west and southwest Tasmania (Woodward et al. 1993), giving

153 rise to the extreme oligotrophy that characterises this landscape.

154

155 To enable the vegetation and fire reconstruction, we analysed contiguous 1 cm-thick

156 sediment samples from the Granta Pools core for pollen, spores and charcoal following

157 standard protocols (Faegri and Iversen 1989, Whitlock and Larsen 2001). Pollen

158 percentages were calculated with two sums: one including all taxa, and the other

159 including terrestrial taxa only. Pollen analysis is a powerful tool for vegetation

160 reconstruction that relies on an appreciation of the relationship between pollen deposition

161 and vegetation (Bunting 2003). Of particular relevance to the present study are the well

162 established depositional characteristics of wetland and arboreal pollen types: wetland

163   pollen types are rarely transported far from their source plants and are good indicators of

164   local wetland dynamics (e.g. Bunting 2003), while arboreal pollen types can be grossly

165   over-represented in pollen spectra relative to their presence in the vegetation. Critically,

166   all key tree pollen types in Tasmania are over-represented in the modern pollen rain

167   (Macphail 1979, Fletcher and Thomas 2007).

168

169   Fletcher and Thomas (2007) conducted a thorough numerical analysis of pollen-

170   vegetation relationships in western Tasmania that is vital for interpreting pollen data in

171   this region in terms of vegetation. The key relevant findings of that study for the present

172   paper are summarised here. The principal rain forest species in Tasmania, *Nothofagus*

173   *cunninghamii*, can comprise up to 50% of the terrestrial pollen sum of pollen spectra

174   from non-forest vegetation. *Eucalyptus*, the dominant tree type in the study area, can

175   contribute more than 30% of the terrestrial pollen sum at sites where *Eucalyptus* species

176   are *absent* from the local vegetation. Likewise, the other dominant arboreal taxon at

177   Granta Pools *Pomaderris apetala*, can register values higher than 20% of terrestrial

178   pollen sums at sites where it is *absent* from the local flora (Fletcher and Thomas 2007).

179   In contrast, non-forest taxa (*Gymnoschoenus sphaerocephalus*, *Melaleuca* and

180   *Leptospermum*/*Baeckea*) are uniformly under-represented in the modern pollen rain of

181   Tasmania and are rarely encountered in the pollen spectra of sites from which they are

182   absent (Fletcher and Thomas 2007). Indeed, the key moorland plant species,

183   *Gymnoschoenus sphaerocephalus*, registers pollen values as low as 5% at sites where it

184   comprises almost 60% of the local vegetation (Fletcher and Thomas 2007).

185

186   The accumulation rates of pollen and spores (PAR) and charcoal (CHAR), which reveal

187   changes in the actual influx of pollen or charcoal independent of variables other than

188   time, were calculated using ages interpolated to each sample level based on an age-depth

189   model derived from 4 radiocarbon ages. Radiocarbon ages were converted to calendar

190   years (cal yr BP) using the southern hemisphere calibration curve (McCormac et al.

191   2004) (see Fig. 5 and Table 1). Detrended Correspondence Analysis (DCA) was used to

192   identify compositional trends in the (relative) terrestrial pollen dataset using PCOrd 4.27

193   (McCune and Mefford 1999). To reconstruct the local fire history, we employed

194   CharAnalysis software (Higuera et al. 2009). The CHAR data was interpolated to the

195   median sample resolution (63 yr sample^{-1}) for the analysis of CHAR peak frequency.

196   Charcoal peaks, a proxy for local fire episodes (Higuera et al. 2010), were identified as

197   the positive residuals exceeding a locally fitted CHAR background model (400 year

198   window).

199 **Results**

200 In this section, we present a detailed analysis of the period between ca.7500-6500 cal yr

201 BP, highlighting the critical transition between forest and non-forest at the site.   The

202 dominant pollen and spores between ca.7400-7000 cal yr BP are Cyperaceae and

203 *Sphagnum* (aquatic/wetland component) and *Eucalyptus* and *Pomaderris* (terrestrial

204 component). Peak CHAR values at ca.7000 cal yr BP coincide with a spike in

205 *Botryococcus*, a replacement in the wetland flora of Cyperaceae by Restionaceae and in

206 the terrestrial flora by *Leptospermum*/*Beackea*, *G. Sphaerocephalus* and *Melaleuca*.

207 These latter taxa remain dominant for the remainder of the record.

208

209 Rapidly accumulating peat occurred under a *Sphagnum*-Cyperaceae wetland and a forest

210 dominated by *Pomaderris* and other forest elements between ca.7400-7000 cal yr BP

211 (Fig. 2). This 400 year phase documents a period when the temperate eucalypt forest that

212 presently cloaks the slopes of the Gog Range occupied the currently non-forested patch

213 of vegetation at the Granta Pools site. Our results mirror a lower resolution pollen record

214 from within moorland on the Gog Range plateau (Webb et al. 1994). Together these

215 results imply that significant portions of, if not the entire, summit plateau hosted

216 temperate eucalypt forest through this time. Peak CHAR values occur at ca.7000 cal yr

217 BP (Fig. 3c) coincident with a major, abrupt and transition in the terrestrial and wetland

218 systems (Fig. 2,3b). Cyperaceae replaced Restionaceae as the dominant wetland taxon

219 around 7000 cal yr BP, punctuated by a brief (33 year) *Botryococcus* (a colonial algae)

220 phase between ca.7060-7000 cal yr BP (Fig. 2). This brief algal phase is coincident with

221 peak CHAR values and a marked drop in *Sphagnum* (Fig. 2b), suggesting the destruction

222   of the *Sphagnum*-Cyperaceous wetland and the transitory development of areas of open

223   water prior to the colonisation of the site by Restionaceous species. A shift from high

224   arboreal pollen values (Fig. 2d) to high values of non-forest moorland/scrub taxa

225   (*Gymnoschoeunus sphaeocephalus*, *Melaleuca* and *Leptospermum*/*Beackea*) also begins

226   at ca.7000 cal yr BP (Fig. 2e), culminating in an arboreal minimum at ca.6800 cal yr BP

227   and a maximum of moorland/scrub taxa between ca.6650-6600 cal yr BP (Figs 2d,e).

228

229   The most salient feature of our data is the abrupt and unidirectional nature of the

230   transition between forest and non-forest at ca.7000 cal yr BP (Fig. 3b). The DCA of the

231   terrestrial pollen dataset reveals two statistically significant populations along the main

232   axis of variation (DCA axis 1) marking this transition (Figs 3c,4): a population of forest

233   taxa prior to the transition and a population of moorland/scrub taxa after (Fig. 4).

234   Following this transition, the non-forest state displays a remarkable degree of stability

235   throughout the record (Fig. 3). The stability of the non-forest state occurs despite more

236   than 700 years elapsing before another local fire episode at the site and despite prolonged

237   periods low fire episode frequency and between 4000-1000 cal yr BP (Fig. 3).

238

239 **Discussion**

240 FOREST/NON-FOREST TRANSITION

241 Various feedback mechanisms (Fig. 5) may have contributed to the changes changes

242 observed between ca. 7500-6500 cal yr BP at Granta Pools, and to the maintenance of the

243 stable vegetation states (*sensu* Wood and Bowman 2012). Each vegetation community

244 may modify the rate of fuel accumulation and fuel characteristics (and therefore fire

245 frequency), soil nutrient capital and light environment in a direction that enhances its own

246 growth and survival, and simultaneously hinders or constrains other vegetation types

247 (Fig. 5b). The results of the present analysis suggest an alternate self-maintenance

248 pathway in this system: eco-hydrology (Fig. 5c). High transpiration rates under forest

249 canopies in high rainfall regions facilitates the aeration of soils, which are susceptible to

250 waterlogging that can inhibit tree establishment (Díaz and Armesto 2007). *Eucalyptus*

251 species exhibit remarkably high evapo-transpiration rates (Sharma 1984) and the

252 persistence of temperate eucalypt forest at Granta Pools under a wet climate regime prior

253 to 7000 cal yr BP is consistent with high transpiration rates under forest vegetation.

254 Temperate eucalypt forest in Australia is sensitive to frequent fire, but produces a

255 considerable amount of flammable fuel and is maintained by an infrequent (70-400 year

256 fire return interval) fire regime. While able to persist as a distinct vegetation state for

257 millennia (Macphail 1984), under certain conditions (dry summer-autumn) temperate

258 eucalypt forest is a highly flammable vegetation type with a high fuel load (Bradstock

259 2010). The fire at ca.7000 cal yr BP at Granta Pools had a catastrophic local impact,

260 destroying the then extant forest system and resulting in an immediate transition to non-

261 forest vegetation at the site (Figs 3b,5c,d).

262

263   The destruction of the forest vegetation and *Sphagnum*-Cyperaceae wetland by fire

264   facilitated the invasion of the site by Restionaceae species and, subsequently, by the

265   rhizomatous sedge, *G. sphaerocephalus*. Restionaceae species commonly occupy the

266   most waterlogged areas in Tasmanian non-forest vegetation (moorland in this case) and

267   are the principal peat forming species in many ponds within moorland vegetation.

268   Elsewhere in the oligotrophic systems of Tasmania, the resilience of widespread tracts of

269   non-forest vegetation appears to be related to a complex suite of feedbacks related to a

270   high frequency of fire and interactions of fire with soil nutrients (Fig. 5b; reviewed by

271   Wood et al. 2011). However, the low levels of charcoal since the establishment of non-

272   forest vegetation at Granta Pools appear to discount frequent fire as a factor in the

273   maintenance of this system.

274

275   We suggest two additional feedback mechanisms that contribute to the inability of forest

276   species to invade into the non-forest system at Granta Pools and elsewhere in Tasmania

277   (Fig. 5c). The first is related to the effect of reduced interception and transpiration on the

278   hydrologic regime of the local non-forest vegetation system. Observations of increasingly

279   waterlogged soils across forest/non-forest boundaries are common in high-rainfall,

280   oligotrophic Tasmania, with most authors invoking topography (Di Folco and Kirkpatrick

281   2011) and a reduced interception and transpiration in non-forest systems (Brown et al.

282   1982, Aabay and Berglund 1986, Bowman et al. 1986, Rumpff 2002, Di Folco 2007,

283   Wood et al. 2011) as key factors in this disparity. At Granta Pools, reduced transpiration

284   rates due to the immediate replacement of trees by peat forming wetland plants,

285 rhizomatous sedges and non-forest species tolerant of waterlogged soils (such as

286 *Melaleuca*) may have amplified soil waterlogging in this local topographic depression,

287 effectively precluding seedling establishment (sensu Díaz and Armesto 2007). The

288 capacity for rhizomatous plants to endure, colonize and dominate waterlogged terrain

289 (Koncalov 1990) would act as a positive eco-hydrological feedback that effectively

290 excludes tree establishment and facilitates maintenance of waterlogging at the site.

291 Secondly, the dense sedge swards that dominate non-forest vegetation at Granta Pools (*G.*

292 *sphaerocephalus*) are likely to exclude trees through inter-specific competition (Fensham

293 and Kirkpatrick 1992). Field and pot experiments have demonstrated that the

294 development of grass swards in open environments in Tasmania inhibits the

295 establishment of trees by blanketing the ground, and if germination occurs, seedling

296 growth is likely to be inhibited because of the grass root mat imposes a physical barrier to

297 root development (Fensham and Kirkpatrick 1992, Kube 1993).

298

299 A CATASTROPHIC REGIME SHIFT BETWEEN ALTERNATIVE STABLE

300 STATES?

301 A call for an application of the alternative stable state theoretical framework to the

302 vegetation landscape of the humid regions of Tasmania draws support from conceptual

303 models (Jackson 1968, Bowman and Jackson 1981). It is also consistent with recent

304 studies that provide tentative (Wood and Bowman 2012) and more speculative (Fletcher

305 and Thomas 2010) evidence that forest and non-forest are alternative stable states in the

306 landscape of western and southern Tasmania. The fire-driven transition from forest to

307 non-forest vegetation at Granta Pools, Tasmania, represents a clear example of a

308 catastrophic regime shift. Catastrophic regime shifts occur when a regime threshold is

309 crossed in response to environmental forcing and a system reorganizes around a new

310 basin of attraction (Scheffer and Carpenter 2003). This type of response can be an

311 artefact of a non-linear reaction to a gradual environmental change or response to a

312 stochastic event, such as fire. Within the alternative stable state paradigm, if a system has

313 only one basin of attraction (stable state), it will follow a trajectory back toward that same

314 state after a perturbation. If there are multiple basins of attraction (alternative stable

315 states), a sufficiently severe event will force the system toward an alternative basin and

316 the system settles around an alternative stable state (Scheffer and Carpenter 2003). Such

317 critical transitions are manifest on either side of a breakpoint in time-series data (Willis et

318 al. 2010, Jeffers et al. 2011). Our time-series data of vegetation change at Granta Pools

319 display a clear breakpoint at ca.7000 cal yr BP (Fig. 5b), coincident with maximum

320 CHAR values that documents a regime shift from a forest (temperate eucalypt forest) to a

321 non-forest (moorland) basin of attraction in response to a stochastic fire episode (Figs

322 4,5).

323

324 ON THE PROBLEM OF "ORIGIN"

325 Broad-scale palaeoecological studies of the Tasmanian forest/non-forest system argue

326 that the application of fire after the arrival of people to a largely non-forested landscape

327 through the Last Glacial Stage essentially deflected post-glacial vegetation development

328 toward species that could tolerate the altered fire regime and increasing humidity through

329 the transition to the succeeding interglacial period (the Holocene): namely non-forest

330 moorland species (Fletcher and Thomas 2010). Fletcher and Thomas (2010) further

331   contend that the inherent flammability of non-forest vegetation in this region was

332   sufficient to maintain non-forest dominance throughout the climatic vicissitudes of the

333   Holocene to the present day. While this thesis may hold at the coarse spatio-temporal

334   scale (landscape and millennial) afforded by their regional palaeoecological synthesis, it

335   is very likely that transitions between forest and non-forest occurred at smaller scales of

336   space and time through the Holocene resulting from, for example, stochastic fire events

337   like we have documented here. Underpinning this notion, and indeed all attempts to

338   account for the contemporary vegetation landscape of southwest Tasmanian, is the

339   widespread and untested assumption that fire is the key factor in the *origin* of this

340   landscape mosaic. Importantly, our study is the *only* study to-date that reveals fire as the

341   causal factor leading to the establishment of non-forest vegetation in place of forest in

342   Tasmania. The implication from our data that, once established, the self-maintenance of

343   non-forest vegetation at Granta Pools is facilitated via eco-hydrological and eco-physical

344   feedbacks, whilst in need of empirical data for conclusive support, is consistent with

345   experimental and observational studies documenting the eco-hydrological effects of

346   forest removal (e.g. Tallis 1991, Díaz and Armesto 2007). Further, the implication that

347   hydrology, rather than fire, was sufficient for self-maintenance of the non-forest state

348   corroborates the notion that self-maintenance pathways can vary from those that lead to

349   the establishment of an alternative stable state (Drake 1991). Moreover, in potentially

350   identifying both the origin and maintenance mechanisms of this system, we satisfy those

351   who require independent treatment of these key processes in order to validate the

352   existence of alternative stable states (Petraitis and Latham, 1999).

353

354 **Conclusion**

355 We have documented an unequivocal transition between forest and non-forest in the

356 humid forest/non-forest landscape mosaic of Tasmania. Critically, we have identified

357 different origin and maintenance pathways in this regime shift between alternative stable

358 states. Initially, fire destroyed the then extant forest, opening the system to an invasion

359 by a suite of non-forest plant species that altered the local hydrological and physical

360 environment. The maintenance of the non-forest state for ca. 7000 years following the

361 forest/non-forest transition occurs despite widely varying fire-regimes and we postulate

362 that the maintenance of the non-forest state is via eco-hydrological and eco-physical

363 feedbacks that differ from the origin (fire).

364

Acknowledgements

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499

500

501

502   Table 1 Table showing the results of the radiocarbon dating. Upper and lower ranges are

503   based on 2-sigma error ranges. Calibrations are based on the southern hemisphere

504   calibration curve of McCormac *et al.* (2004).

Lab Code	Depth (cm)	Radiocarbon Age (^{14}C years)	Median probability (cal yr BP)	Lower range (cal yr BP)	Upper range (cal yr BP)
S-ANU4630	19	1590	1429	1332	1530
S-ANU4631	42	4675	5400	5089	5467
S-ANU4632	67	6185	6980	6907	7160
S-ANU4633	89	6470	7347	7254	7429

505

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506   Fig. 1 An image of the Gog Range plateau showing the coring site within Granta Pools

507   and highlighting (bordered in white) the non-forest vegetation on the plateau. The

508   location of the core site in Tasmania is shown in the inset. *Image source*: "Gog Range"

509   41°30'S, 146°23'E. Google Earth. March 22, 2010. March 22, 2013.

510

511   Fig. 2 Pollen and spore data from Granta Pools from 7500-6600 cal yr BP.

512

513   Fig. 3 A time series plot of environmental data over the last 7500 years pertinent to

514   Granta Pools. (a) The linear age-depth curve based on 5 radiocarbon ages. Error bars

515   indicate the 2-sigma error range of the calibrated radiocarbon ages; (b) Ordination axis

516   scores from a detrended correspondence analysis (DCA axis 1) of the terrestrial pollen

517   dataset from Granta Pools (the orange (green) horizontal bar indicates the mean axis

518   value for the non-forest (forest) vegetation states, while the shaded area indicates 2

519   standard deviations from the mean) ; (c) Charcoal accumulation (CHAR) and fire episode
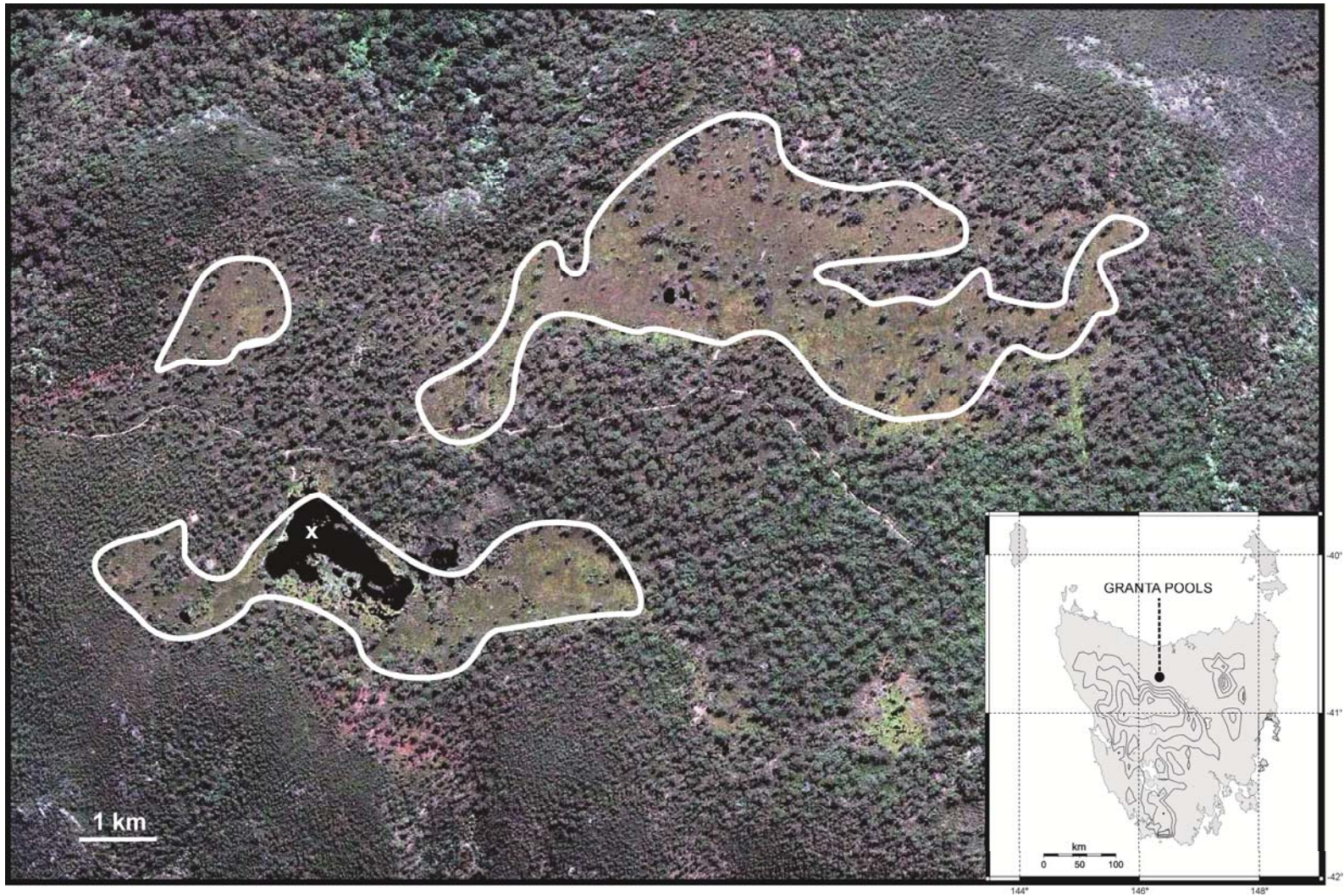
520   frequency at Granta Pools.

521

522   Fig. 4 Detrended correspondence analysis biplot of the terrestrial pollen dataset from

523   Granta Pools. The position of fossil samples is shown: Open circles denote samples with

524   a strong (negative) correlation to forest pollen taxa (green arrows pointing left); closed

525   circles denote samples with a strong (positive) correlation to non-forest pollen taxa

526   (orange arrows pointing right). The arrow length indicates the strength of the correlation

527   and the correlation statistics are listed. The ages indicate the timing of the transition from
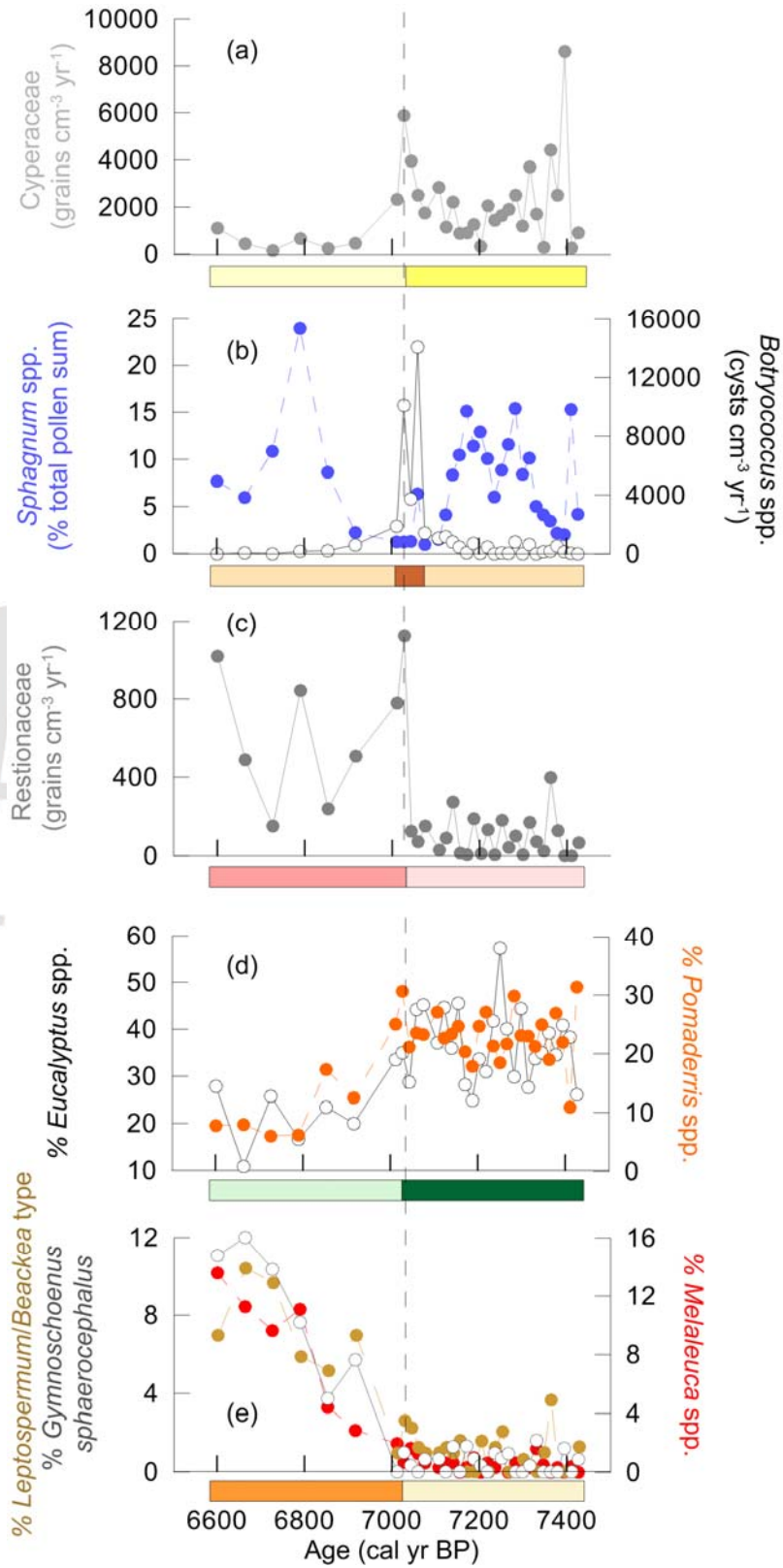
528   forest to non-forest.

529

530   Fig. 5 A hypothetical stability landscape (after Scheffer et al. 2001) and proposed

531   feedback mechanisms for the alternative stable states found in the humid landscape of

532   Tasmania based on our interpretation of the Granta Pools data (after Wood and Bowman,

533   2011). (a) a 3-dimensional stability landscape that depicts rainforest and non-forest

534   (moorland/scrub) as deep and resilient basins (with transitions into or out of these basins

535   requiring strong environmental forcing) and temperate eucalypt (wet sclerophyll) forest

536   as a shallower basin. The arrow follows the trajectory of the Granta Pools (this study)

537   vegetation system in response to a catastrophic fire. The position of the ball shows the

538   vegetation state after this stochastic disturbance event, with the vegetation state now

539   lying within the deep, stable and resilient non-forest basin. (b & c) The self-regulating

540   internal feedback mechanisms maintaining stability within the forest and non-forest

541   vegetation states: (b) those depicted by Wood and Bowman (2011) as operating in the

542   landscape of southwest Tasmania; and (c) those proposed as operating at Granta Pools.

543   (d) A summary of the temporal sequence between 7500-6500 cal yr BP that lead to the

544   critical transition between a forest and non-forest vegetation state at Granta Pools

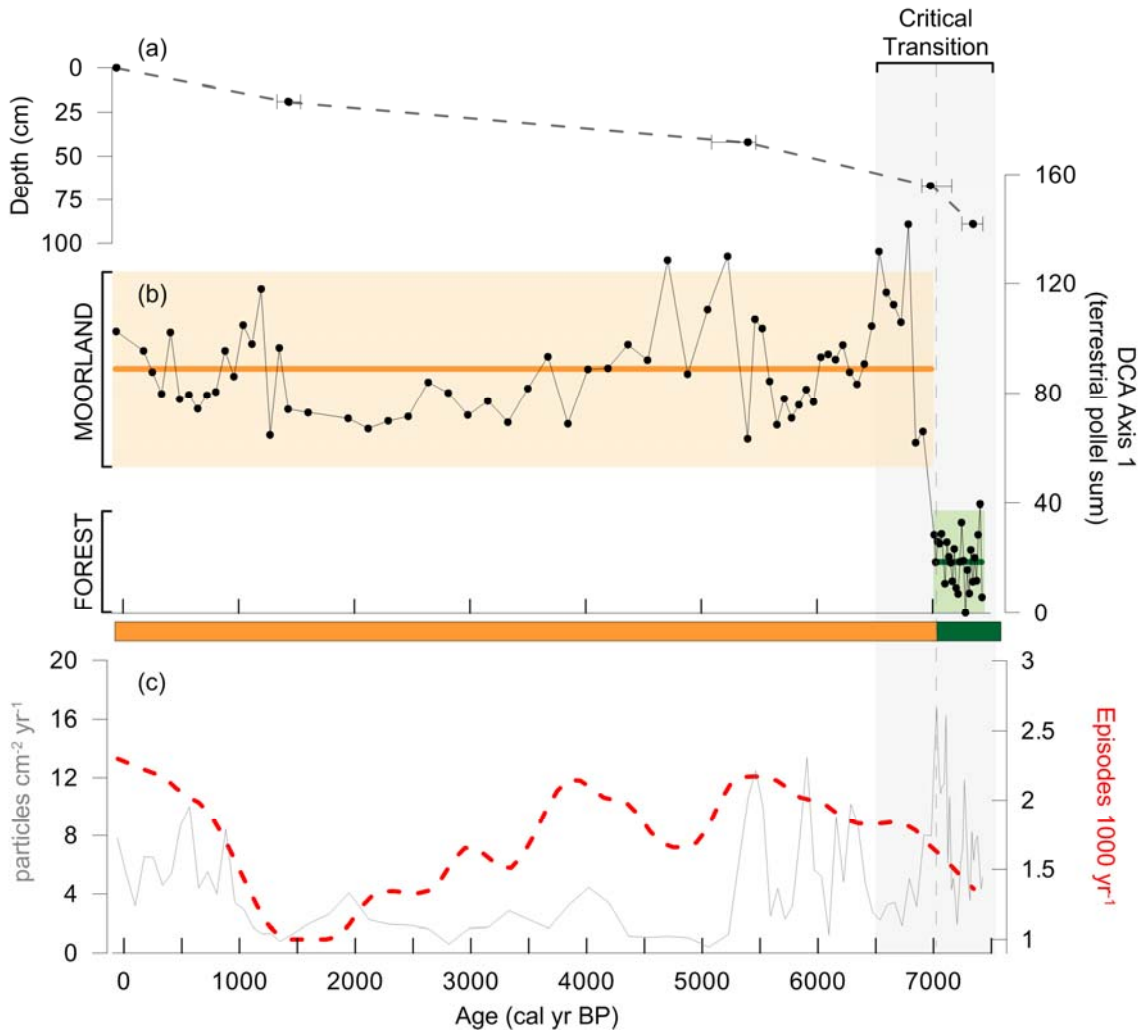545   following the stochastic fire event.

546   Fig. 1

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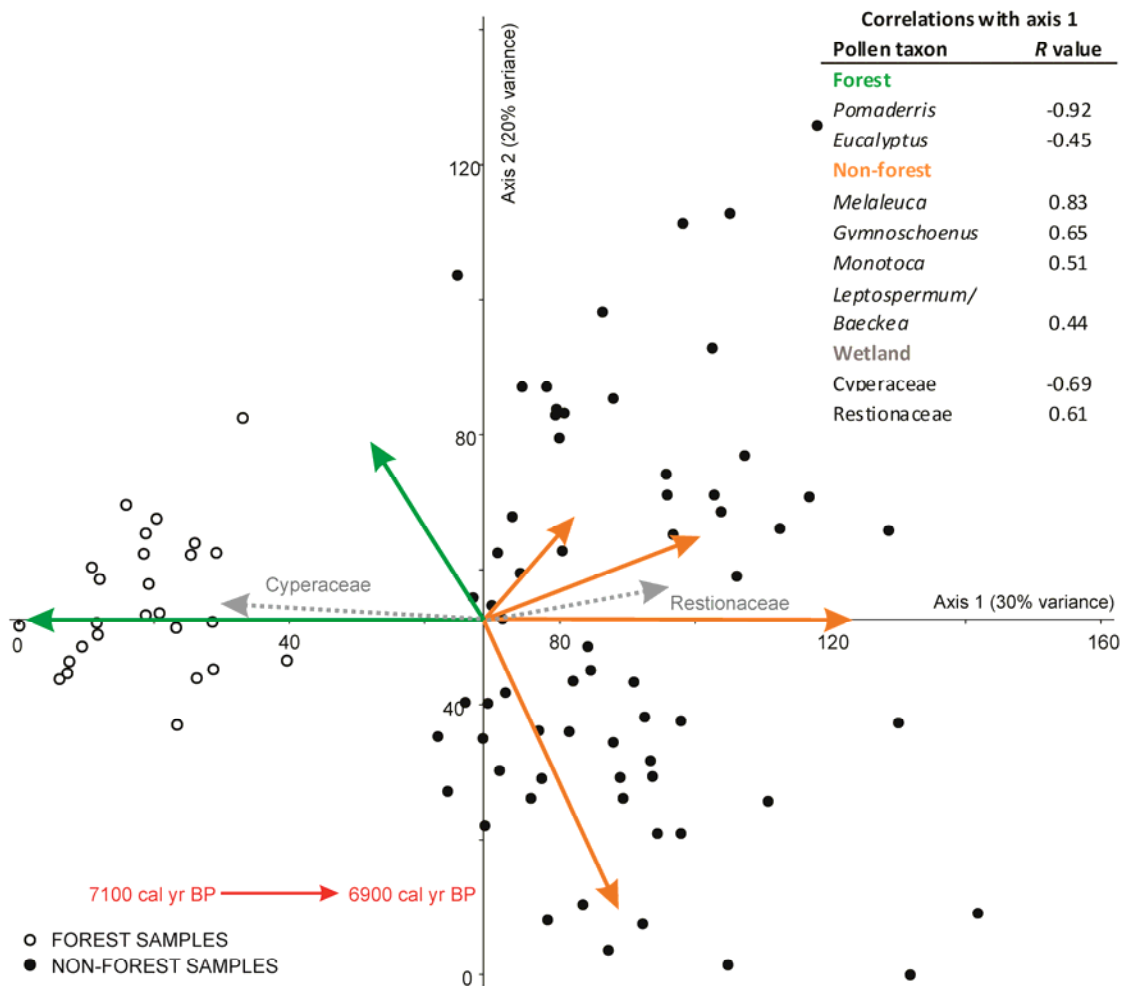Michael-Shawn Fletcher, Sam W. Wood and Simon G. Haberle

548   Fig. 2

549

550   Fig. 3

551

552

553

554   Fig. 4

555

(a)

Rainforest

Wet Sclerophyll

Non-forest

(b)

**Non-forest
stabilising feedbacks**

Higher flammabilty

Non-forest species dominate → More frequent fires

Establishing trees killed by fire

Reduced soil nutrients

Topography

**Wet Sclerophyll
stabilising feedbacks**

Lower flammability

Forest trees dominate → Less frequent fires

Trees shade out ← Trees can establish
non-forest species

Soil nutrients accumulate

Topography

(c)

Non-forest species dominate → *Low transpiration rates*
Dense sward/roots

Permanent waterlogging
Supression of seedlings

Forest trees dominate → *High transpiration rates*

Aerated soils

Time	6500	7000	7500

(d)

Broad Scale
Climate Signal

Significationly reduced precipitation Episodic drought	Catastrophic Fire	High precipitation Infrequent/Absent drought