

1 **Knowing why Tasmanian *Eucalyptus obliqua* tall forests are so**
2 **sensitive to heatwaves informs management and policy for climate**
3 **change adaptation**

4 Timothy J. Wardlaw^{a*}

5 ^a *Climate Futures & School of Natural Sciences, University of Tasmania, Hobart,*
6 *Australia.*

7 *corresponding author (timothy.wardlaw@utas.edu.au)

8
9 **Abstract**

10 Tasmania's distinctive climate environment supports highly productive and carbon-
11 dense tall eucalypt forests, but also a vulnerability to climate change. Measurements in
12 *Eucalyptus obliqua* tall forest at the Warra SuperSite in southern Tasmania showed
13 them to be very sensitive to warmer temperatures. Gross primary productivity (GPP)
14 declines sharply when temperatures rise above the forest's relatively low temperature
15 optimum for GPP. Heatwaves (consecutive days of unusually high temperatures) cause
16 the forest to switch from being a net carbon sink to a net carbon source. As the climate
17 changes and heatwaves occur more often, the risk of severe adverse impacts to this
18 important ecosystem increases. Our current understanding of why the Tasmanian *E.*
19 *obliqua* tall forest is so sensitive to warmer temperatures, even if imperfect, can allow
20 appropriate management interventions to be identified and enabling policy settings to be
21 formulated.

22 Tasmania's climate environment was associated with several features of the unique
23 response by the tall eucalypt forests to heatwaves. The high sensitivity of GPP to
24 temperature in the forest was associated with a low temperature range – GPP sensitivity

25 to temperature increased as temperature range experienced by the forest decreased. The
26 decline of GPP during warm conditions was not associated with either moisture
27 limitation or atmospheric dryness (high vapour pressure deficits), a likely reflection of
28 the high rainfall environment in which tall eucalypt forests grow in Tasmania. Low
29 winter radiation associated with Tasmania’s high latitude, contributes to a lack of
30 seasonal temperature acclimation by the forest. Because the forest responses to
31 heatwaves were associated with the local climate environment, enhanced natural
32 selection of local genotypes is identified as the most prospective approach to help
33 Tasmania’s tall eucalypt forests adapt to a new, warmer climate. Enhanced natural
34 selection is only feasible to do in forests that are managed for wood production. Policy
35 settings that allow for the continuation of native forest harvesting will be needed if
36 enhanced natural selection is to supply future needs of climate-adapted seed for
37 regeneration and restoration of tall eucalypt forest areas in Tasmania.

38

39 Keywords: *Eucalyptus*, heatwave, climate change adaptation, carbon dynamics, forest
40 policy

41

42 **Introduction**

43 Tasmania has approximately 800,000 ha of tall eucalypt forests restricted to the high
44 rainfall areas of the state (Forest Practices Authority 2023). The largest concentration is
45 in a narrow band extending from the northwestern corner of the state to the south-east
46 coast (Harris and Kitchener 2013). The tall eucalypt forests are dominated by three
47 species – *Eucalyptus obliqua*, *E. regnans* and *E. delegatensis*. Forests dominated by *E.*

48 *obliqua* are the most widespread of the tall eucalypt forest type (Neyland et al. 2000).
49 Tall eucalypt forests are well represented in both conservation reserves and areas
50 available for timber harvesting (Forest Practices Authority 2018). These forests are very
51 productive in both an Australian context (Beringer Jason et al. 2016; Bennett et al.
52 2021) and globally (UNESCO et al. 2021). Their high productivity coupled with a
53 temperate climate, results in the forests accumulating very high biomass (Keith et al.
54 2009; Moroni et al. 2010; Wood et al. 2015). The value of Tasmania's tall eucalypt
55 forests for removing CO₂ from the atmosphere is reflected in UNESCO identifying the
56 Tasmanian Wilderness World Heritage Area (TWWHA) as their number one property,
57 globally, in terms of the amount of carbon sequestered annually by forests (UNESCO et
58 al. 2021).

59 A warming climate is jeopardising the high productivity and accumulated biomass of
60 Tasmania's tall eucalypt forests (Bowman et al. 2014, Prior and Bowman 2014).
61 Heatwaves are particularly impactful. During a record heatwave event in November
62 2017, the *E. obliqua* tall forest at the Warra SuperSite within the TWWHA switched
63 from being a net carbon sink to become a net carbon source (Wardlaw 2022). The
64 switch from a carbon sink to a source was due to significant reductions in gross primary
65 productivity (GPP) of the forest when compared with periods of closer-to-normal
66 temperatures. This heatwave response contrasts with those in other non-water-limited
67 temperate eucalypt forests on the Australian mainland. Griebel et al. (2020) found no
68 change in GPP of an *E. obliqua* / *E. radiata* forest in central Victoria during a heatwave
69 event, while (van Gorsel et al. (2016) found that GPP slightly increased during a
70 heatwave event in an *E. delegatensis* / *E. dalrympleana* in southern NSW.

71 The contrasting responses to heatwaves in these eucalypt forests reflects differences in

72 the relationship between GPP and temperature. A convex parabola (upside-down “u”)
73 represents the general relationship between GPP and temperature of vegetated
74 ecosystem (Bennett et al. 2021, Duffy et al. 2021). The apex of the parabola represents
75 the temperature when the GPP of the ecosystem reaches a maximum – the optimum
76 temperature for GPP. The steepness of the curves either side of the apex represents the
77 rate that GPP declines as temperatures depart from the optimum for the ecosystem - the
78 sensitivity of the ecosystem to changes in temperature. GPP of the Tasmanian tall
79 eucalypt forest was more sensitive to changes in temperature than was GPP for the
80 Victorian and NSW forests (Bennett et al. 2021). The high sensitivity of GPP to
81 temperature in the Tasmanian tall eucalypt forest was more like that of tropical
82 rainforest and tropical savanna forest in their wet season than it was for other temperate
83 eucalypt forests and woodlands.

84 Duffy et al. (2021) point out that the carbon balance of ecosystems represents the
85 combined effect of two components: GPP, which varies parabolically with temperature;
86 and ecosystem respiration, which increases exponentially (i.e. at an ever-increasing rate)
87 with temperature across the range of temperatures capable of supporting life. As
88 temperatures rise above the optimum for GPP, the carbon balance of the ecosystem
89 quickly declines. This is because the decline in GPP is reinforced by the increase in
90 respiration. A point is reached when temperature rises too much above the GPP
91 optimum that the carbon balance of the ecosystem becomes negative– the ecosystem
92 starts to lose carbon (i.e. it becomes a carbon source). As global warming progresses
93 ecosystems will have a negative carbon balance for an increasing proportion of the time.
94 Duffy et al. (2021) predict a warming-induced tipping point when the current generation
95 of plants in an ecosystem can no longer recover from a negative carbon balance. A
96 persistent negative carbon balance from crossing such a tipping point is expected to lift

97 the rate of tree mortality despite uncertainty about the mechanism(s) causing tree death
98 (Wang et al. 2021). Many ecosystems, mostly tropical, could reach a temperature
99 tipping point within three decades (Duffy et al. 2021). Tasmania's tall eucalypt forests
100 in being like tropical forests by having a high sensitivity of GPP to temperature, may
101 reach a temperature tipping point earlier than other temperate eucalypt forests.

102 Management intervention needs to be planned and developed to reduce or avert the
103 adverse consequences of warming temperatures to Tasmania's value-laden, tall eucalypt
104 forests. Developing effective interventions will require a diagnosis of why Tasmania's
105 tall eucalypt forests show such contrasting responses to temperature and heatwaves than
106 other temperate eucalypt forests.

107 Tasmania's distinctive environment (Thackway and Cresswell 1995) can make it
108 challenging to diagnose causality of syndromes affecting forest health. Spring needle
109 cast of *Pinus radiata* is a good example: a widespread needle-infecting fungus,
110 *Cyclaneusma minus*, is triggered into secondary pathogenic activity on high altitude
111 (>400 metres), wet (>1200 mm annual rainfall) sites (Podger and Wardlaw 1990). A
112 successful tree breeding program to identify *P. radiata* genotypes resistant to spring
113 needle cast focussed on the expression of disease on high altitude – wet sites, rather
114 than directly on resistance to the needle-infecting pathogen *C. minus* (Kube and
115 Wardlaw 2002a; Kube and Wardlaw 2002b). A confident diagnosis of causality is
116 needed to explain the unique response to heatwaves seen in Tasmania's tall eucalypt
117 forests as a first step towards developing climate adaptation actions.

118 The Terrestrial Ecosystem Research Network – TERN - (www.tern.org.au)
119 infrastructure provides extensive data that measures attributes of Australia's main
120 terrestrial ecosystems. Those data can be used for detecting and understanding change

121 in those ecosystems. TERN SuperSites (Beringer Jason et al. 2016; Karan et al. 2016)
122 provide detailed, local-scale measurements, both as continuous timeseries and from
123 hosting designed experiments. The continuous timeseries can detect change in
124 ecosystems that occur during extreme events like heatwaves (e.g. van Gorsel et al.
125 2016), droughts (e.g. Keith et al. 2012; Ma et al. 2016) and fire (e.g. Sun et al. 2020;
126 Wardlaw 2021). One of the 16 TERN SuperSites – the Warra Tall Eucalypt SuperSite –
127 is embedded in *E. obliqua* tall forests within the TWWHA. Measurements at that site
128 identified the threat that warming temperatures, and heatwaves pose to this ecosystem.

129 Here I review research findings from measurements made at Warra and other TERN
130 SuperSites, as well as other published studies, to characterise the unique response to
131 heatwaves shown by Tasmanian tall eucalypt forests. A putative diagnosis of causality
132 will be made through synthesis of those unique responses. The putative diagnosis will
133 then be evaluated against possible management options to determine the most suitable
134 option to use in helping tall eucalypt forests adapt to the new climate. Finally, I will
135 review policy settings for management of tall eucalypt forests in Tasmania to identify
136 how well settings align with management option that result in future forests that are
137 better suited to Tasmania’s new climate.

138

139 **Characterisation of unique responses in Tasmanian tall eucalypt forests**

140 *Association between changes in GPP and regulation of water loss*

141 In many eucalypt forests, stomatal regulation to limit water loss is a dominant driver of
142 declines in GPP during hot conditions (van Gorsel et al. 2016, Renchon et al. 2018,
143 Beringer et al. 2022), although leaf loss to limit transpiration has also been linked to

144 productivity declines (van Gorsel et al. 2013, Renchon et al. 2018).

145 In wetter environments where moisture limitation is rare, GPP of the eucalypt forests
146 show negligible change during hot conditions (van Gorsel et al. 2016, Griebel et al.
147 2020). The tall eucalypt forests of southern Tasmania behave differently. During a
148 record heatwave event in 2017 the GPP of *E. obliqua* tall forest at Warra in southern
149 Tasmania declined sharply, but that decline in GPP was not associated with stomatal
150 regulation to limit water loss (Wardlaw 2022).

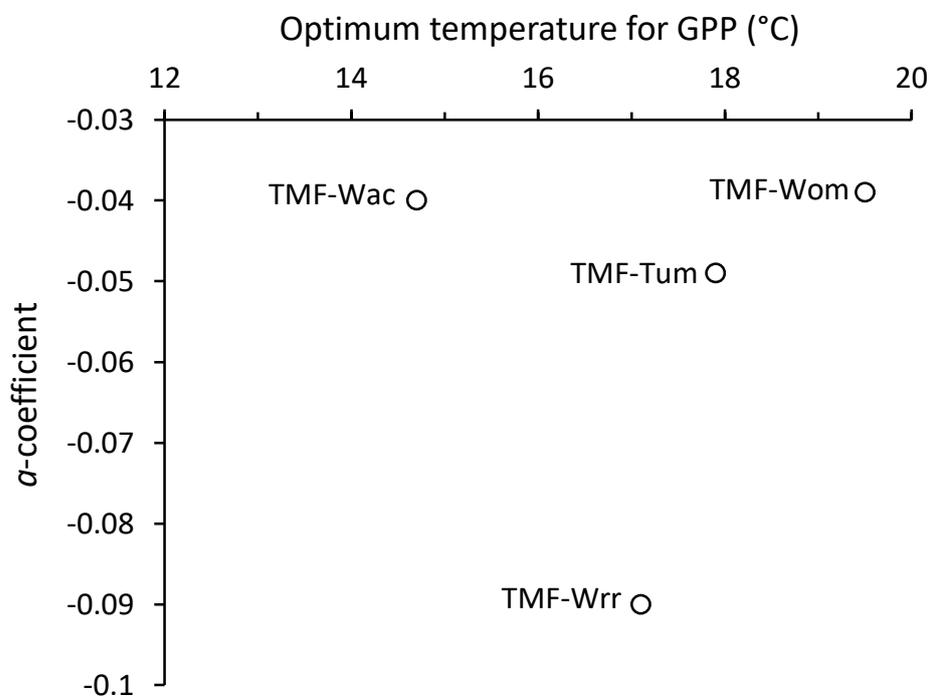
151 The heatwave response suggests the tall eucalypt forest ecosystem in southern Tasmania
152 exerts little control to limit water loss. Several independent lines of evidence support
153 limited regulation of water loss in these forests. Peters et al. (2021) found that canopy-
154 forming *E. obliqua* and understorey trees at Warra had low hydraulic safety margins,
155 like tropical rainforests. Salvi et al. (2021) found young *E. obliqua* saplings showed the
156 lowest degree of stomatal regulation to limit water loss among the ten eucalypt species
157 they examined: maintaining high rates of photosynthesis was a more important life
158 strategy than conserving water. Two other eucalypt species – *E. regnans* and *E. nitens* -
159 whose natural range are confined to mesic sites, behaved in a similar way. The
160 threshold response of stomata to increasing water stress in *E. obliqua* saplings found by
161 Salvi et al. (2021), matched a threshold response of stomata to increasing VPD (Figure
162 A1). This threshold response was measured in 70-years-old *E. obliqua* regrowth at
163 Hastings, southern Tasmania, during the hottest day on record in southern Tasmania on
164 15th February 1982. Measurements of changes in soil water content of the *E. obliqua*
165 forest at Hastings by Nicolls et al. (1982) found high rates of water loss via transpiration
166 were sustained over long periods of time. Such high rates of water loss only matched
167 model predictions of soil dryness if the soil dryness model was adjusted to maintain

168 maximum transpiration rates rather than declining rates of transpiration as the soil
169 became drier.

170 ***Role of optimum temperature for productivity***

171 Might a low optimum temperature for GPP explain the strong reduction in GPP at high
172 temperatures in southern Tasmania in contrast with other eucalypt forests during non-
173 water-limited conditions on the Australian mainland? Bennett et al. (2021) showed that
174 the temperature optimum for GPP was related to the historical temperature of the site.
175 But the temperature optimum for GPP at Warra was within the range of other tall
176 eucalypt forests on the Australian mainland (Figure 1). What does differentiate the tall
177 eucalypt forest at Warra from those on mainland Australia is the steepness of the
178 decline in GPP as temperatures depart away from the optimum (Figure 1).

179



180

181 **Figure 1.** Scatterplot of temperature optimum for GPP and the a -coefficient (defining
182 steepness of curve) of the binomial model describing the parabolic relationship between
183 GPP and temperature of four temperate eucalypt forests. Data extracted from Table 2 in
184 Bennett et al. (2021). Sites shown are: Wallaby Creek (TMF-Wac), Warra (TMF-Wrr),
185 Tumberumba (TMF-Tum) and Wombat Forest (TMF-Wom).

186

187 *Seasonal temperature acclimation*

188 The capacity of ecosystems to acclimate to changed temperature regimes can reduce the
189 sensitivity of their carbon dynamics to those temperature changes (Smith et al. 2015).

190 There is some evidence that forest and woodland ecosystems on the Australian
191 mainland can adjust the temperature dependence of their photosynthetic and respiratory
192 activity in response to the contrasting temperature regimes that occur in the winter and
193 summer (Zhu et al. 2018, Zhu et al. 2021). This is reflected in significantly higher tree
194 respiration rates at a common reference temperature of 25°C, but lower maximum rates
195 of respiration, for measurements done in winter compared with measurements done in
196 the summer (Table 1). Similarly, the critical temperature for photosynthesis increased
197 during the summer measurements compared with winter measurements (Table 1). In
198 contrast, forest species at Warra showed no evidence of adjustment in respiration rates
199 at 25°C or critical temperature for photosynthesis between winter and summer (Table
200 1). Zhu et al. (2021) attributed the lack of seasonal acclimation in respiration rates at
201 Warra to insufficient solar radiation in the winter. Tasmania's high latitude, coupled
202 with high cloudiness in the wetter parts of the state each contribute to the low winter
203 radiation (Grose et al. 2010).

204

Site	Warra	Cumberland Plains	Great Western Woodlands	Alice Mulga	Robson Creek	Cape Tribulation
Respiration rate @25°C	↓*	↑*	↑*	↑	↑*	↑*
Maximum respiration rate	↔	↓*	↓*	↓*	↓*	↓*
Critical temperature for photosynthesis	0.04 _a (0.02)	0.2 _{a,b} (0.06)	0.52 _b (0.09)	0.22 _{a,b} (0.08)	0.51 _b (0.13)	-

205 **Table 1.** Seasonal (Winter-Summer) differences in respiration rate at 25°C, maximum
206 respiration rate, and critical temperature for photosynthesis at six TERN SuperSites. For
207 respiration rate at 25°C, up arrows indicate higher rates in winter than summer, and for
208 maximum respiration rates, down arrows indicate lower rates in winter than summer
209 (asterisks indicated significant differences between the seasons). The values for critical
210 temperatures for photosynthesis indicate the increase in critical temperature for
211 photosynthesis in summer compared with winter, expressed as °C difference in critical
212 temperature per degree difference summer and winter ambient temperatures. Data for
213 respiration rates adapted from Figure 3a and Figure 3d in (Zhu et al. 2021). Data for
214 critical temperature for photosynthesis (with standard error shown in parentheses)
215 adapted from Table 2 in (Zhu et al. 2018).

216

217 *Temperature range*

218 The unusually high sensitivity of GPP to temperature in the tall eucalypt forest at Warra
219 is an outlier among temperate eucalypt forests (Figure 1). This high sensitivity is similar
220 to tropical rainforests and tropical savanna forests during their wet season (Bennett et al.
221 2021). No analysis has been done to try and explain these differences in the sensitivity

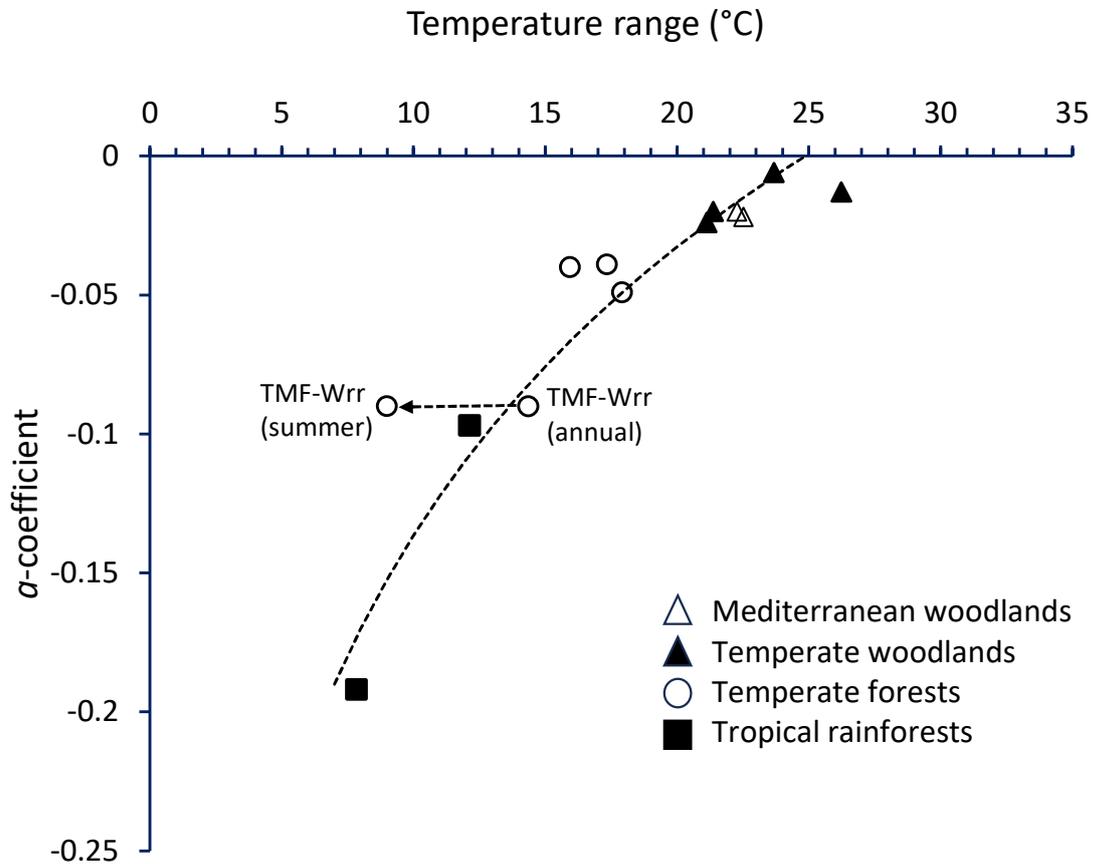
222 of GPP to changes in temperature.

223 In one of the very few studies done to examine variation in the sensitivity of GPP to
224 temperature, Wu et al. (2017) found the temperature sensitivity of GPP in northern
225 hemisphere vegetated ecosystems decreased as the variability in growing season
226 temperature increased. Can characteristics of the temperature regime of the site explain
227 the sensitivity of GPP to temperature?

228 Bennett et al. (2021) reported seasonal temperature ranges for the 17 forested sites in
229 Australia used to calculate their GPP - temperature response function. This provided an
230 opportunity to examine the relationship between seasonal temperature range and the
231 sensitivity of GPP to temperature for those sites. To do this the annual or seasonal
232 temperature range was extracted from Figures 2 and 4 in Bennett et al. (2021) and
233 plotted against the a-coefficient of the binomial model of $GPP \sim \text{temperature}$ (from
234 Table 2 in Bennett et al. (2021)) that was fitted to the 17 sites they were analysed. Data
235 from the five tropical savanna sites were excluded from the analysis because of the
236 confounding effect of C4 grasses that dominate productivity in their wet season (Moore
237 et al. 2018).

238 The plot of the a-coefficient of the binomial model and annual temperature range for
239 each of the 12 non-savanna sites shows the sensitivity of GPP to temperature (a-
240 coefficient) increases as the temperature range decreases (Figure 2). This result is
241 consistent with the findings of Wu et al. (2017). The temperature range for Warra may
242 be lower still if seasonal factors that limit GPP occur regularly. For example, a
243 latitudinally-driven limitation in radiation during winter that suppresses seasonal
244 temperature acclimation (Zhu et al. 2021) may also suppress GPP. Temperate forest
245 sites at lower latitudes on the Australian mainland do not have such a winter radiation

246 limitation. This provides those sites the flexibility to capitalise on more equable climatic
 247 conditions for carbon uptake in winter, e.g. Renchon et al. (2018).



248

249 **Figure 2.** Plot of the relationship between the a-coefficient of the GPP versus
 250 temperature binomial model and annual / growing-season temperature range of 12
 251 forested sites representing four Australian ecosystems. For the Tasmanian site (TMF –
 252 Wrr) two values are shown for temperature range: an annual range and a summer range
 253 that excludes winter data in accordance with a radiation limitation identified by Zhu et
 254 al. (2021). The dashed line shows the fitted model: $a\text{-coefficient} = -0.482 + 0.15$
 255 $\ln(\text{Temperature range})$.

256 A narrow temperature range is a plausible explanation for the higher sensitivity of GPP
 257 to temperature in the tall eucalypt forest at Warra. That explanation is consistent with

258 the findings from the limited studies done elsewhere. A more confident diagnosis of
259 causality will also need measurements be done in other tall eucalypt forests elsewhere in
260 Tasmania to confirm that the effect measured at Warra is general. Finally, the
261 mechanism through which a narrow temperature range increases the sensitivity of GPP
262 to changes in temperature needs to be discovered.

263 **Synthesis of responses and proposed diagnosis**

264 A strong decline of GPP during heatwave events during non-water-limited periods is the
265 effect that differentiates the tall eucalypt forest in Tasmania from those on the
266 Australian mainland. Stomatal regulation to limit water loss was not associated with the
267 strong decline of GPP in the Tasmanian tall eucalypt forest. Neither could the strong
268 decline of GPP in the Tasmanian forest be explained by a low optimum temperature (for
269 GPP), per se. Instead, the strong decline in GPP was the result of a high sensitivity of
270 GPP to temperatures that exceed the optimum for GPP. The high sensitivity of GPP to
271 temperature could be explained by the comparatively low temperature range of the
272 Tasmanian forest. The temperature range may be narrowed further if the growing
273 season is restricted by recurring seasonal limitations such as winter radiation.

274

275 **Alignment of adaptation options to the proposed diagnosis**

276 An effective adaptation response would seek to preserve the distinct traits of
277 Tasmania's tall eucalypt forests, notably their high growth rates, while lessening the
278 risks imposed by a warming climate. Two traits likely to be contributing to the
279 exceptional productivity of the tall eucalypt forests are: (i) maintaining high rates of
280 photosynthesis for as long as possible by sacrificing control of water loss via stomatal

281 adjustment (Nicolls et al. 1982, Salvi et al. 2021); (ii) peak rate of photosynthesis that is
282 high but confined to within a narrow temperature range bounding the optimum
283 temperature for photosynthesis (Bennett et al. 2021). The best way to maintain these
284 traits while lessening the risks imposed by a warming temperature would be for the
285 optimum temperature for GPP to increase as the climate warms, and for rainfall to
286 remain high.

287 Bennett et al. (2021) showed the optimum temperature for GPP was linearly related to
288 the historical temperature of the site. Temperature is rapidly increasing in Tasmania as
289 elsewhere (CSIRO and Bureau of Meteorology 2022). It is not known whether the
290 historical temperature reflects the temperature experienced over long periods of time
291 (e.g. Vizcaino-Palomar et al. 2020) or temperature experienced at critical stages of forest
292 development (de Araujo et al. 2019). Rainfall has decreased in Tasmania over the past
293 four decades Grose et al. (2010), but most of that decrease has been during autumn
294 months when soil moisture in tall eucalypt forests are at an annual nadir (Nicolls et al.
295 1982).

296 Three adaptation options are evaluated for their potential to lessen the climate risks to
297 the tall eucalypt forests while preserving their distinctive traits.

298 *Temperature acclimation*

299 Temperature acclimation of the existing tall eucalypt forests to reduce the impact of a
300 warming climate would be an ideal no regrets outcome. Smith et al. (2015) propose that
301 temperature acclimation of photosynthesis and respiration could provide considerable
302 benefit through reducing the sensitivity of carbon uptake to changes in temperature. The
303 evidence from measurements done in the forests at Warra is that, unlike sites on the
304 Australian mainland, they do not acclimate to the contrasting temperature environments

305 in summer and winter (Zhu et al. 2018, Zhu et al. 2021): a consequence of low winter
306 radiation (Zhu et al. 2021). Further, a capacity to acclimate to contrasting temperature
307 environments does not translate to acclimation at longer (decadal) time scales (Duffy et
308 al. 2021).

309 ***Climate adjusted provenancing (Assisted migration)***

310 Climate adjusted provenancing is one of the most common approaches for accelerating
311 forest adaptation to climate change (Prober et al. 2015, Prober et al. 2019, Booth and
312 Muir 2020). The approach involves introducing into a target area, climate-adapted
313 genotypes that evolved in those parts of the species range that are a climate analogue of
314 the predicted future climate of the target area. Rainfall and/or temperature are typically
315 used to determine climate analogues for the future climate of target areas (e.g. Drake et
316 al. 2017, Sáenz-Romero et al. 2020, Harrison 2021). Neither of those environmental
317 drivers contributed to the strong decline in GPP measured in the tall eucalypt forest at
318 Warra during a heatwave event.

319 A climate analogue that is determined by rainfall and/or temperature may have
320 difficulty in also meeting the distinctive traits associated with high forest productivity.
321 Genotypes from warmer and drier regions are more likely to have evolved in temperate
322 environments with wider temperature range and lower peak GPP, like those exhibited
323 by temperate forests on the Australian mainland (Bowman et al. 2014, Bennett et al.
324 2021). Another issue would be that genotypes from warmer and drier environments
325 would need to be sourced beyond the cool, moist band in the western half of Tasmania -
326 the stronghold of tall eucalypt forests in Tasmania (Harris and Kitchener 2013).
327 Populations of *E. obliqua*, *E. regnans* and *E. delegatensis* in that main western
328 Tasmanian band are distinctive from populations elsewhere in southeastern Australia as

329 shown by their chloroplast DNA (Nevill et al. 2009, Bloomfield et al. 2011, Nevill et al.
330 2014). Transfer of seed outside the western Tasmanian haplotype zone of those three
331 eucalypts would need to consider the implications of disrupting the historical patterns of
332 genetic diversity in these species (Bloomfield et al. 2011).

333

334 Maladaptation to local pests and pathogens can seriously impair the survival and growth
335 of non-local genotypes in the target area (Wardlaw and Palzer 1988, Camarretta et al.
336 2020, Sáenz-Romero et al. 2020). The western Tasmanian band of tall eucalypt forests
337 are concentrated in hotspots for epidemic *Teratosphaeria* (syn. *Mycosphaerella*) Leaf
338 Disease (Pinkard et al. 2010) and local populations have strong adaptations to this group
339 of leaf pathogens (Wilkinson 2008) . These co-incident threats to non-local genotypes
340 of these tall forest eucalypts are likely to be a severe constraint to successfully
341 introducing them into target areas as analogues for future climates.

342 In summary, climate adjusted provenancing would be an unsafe adaptation option for
343 use in Tasmania's tall eucalypt forests. Climate adjusted provenancing: would be
344 unlikely to preserve key traits associated with high productivity; would disrupt
345 historical genetic patterns in the main tall eucalypt species; and would increase the risk
346 of damage from maladaptation to local pest and pathogen populations.

347 ***Enhanced natural selection***

348 The proposed diagnosis of causality for the high sensitivity of GPP to temperature in
349 Tasmanian tall eucalypt forests aligns well with natural selection in local forest
350 populations. This is because natural selection in local populations would be expected to
351 preserve evolved traits linked to local environment of the western band of tall eucalypt
352 forests - small temperature range and high rainfall. In the western band of Tasmania's

353 tall eucalypt forests the predicted change in rainfall through the 21st Century due to
354 global warming is small (Grose et al. 2010). There is a rise of 0.5-1°C predicted in
355 summer temperature range (White et al. 2010) over the 21st Century. While a rise of that
356 magnitude would give Warra a similar annual temperature range as other temperate
357 forests, the growing season temperature range for Warra would still be well below other
358 temperate forests as winter radiation limitations in western Tasmania would remain
359 through the 21st Century (Grose et al. 2010). Natural selection in local populations
360 would also retain historical genetic patterns in the main tall eucalypt species and
361 adaptations to local pest and pathogen populations.

362 Evolution of adaptive traits as a response to climate change has been shown to confer
363 advantages in fitness to plant and animal species (Rauschkolb et al. 2022, Moiron et al.
364 2024). These examples show that evolution of adaptive traits can occur quickly (1-2
365 decades) in natural situations for short-lived species. Enhancing natural selection using
366 techniques such as managing for shorter generation times and screening to select
367 adapted / cull non-adapted genotypes (Prober et al. 2019) may be needed for forest
368 species that have longer generation times.

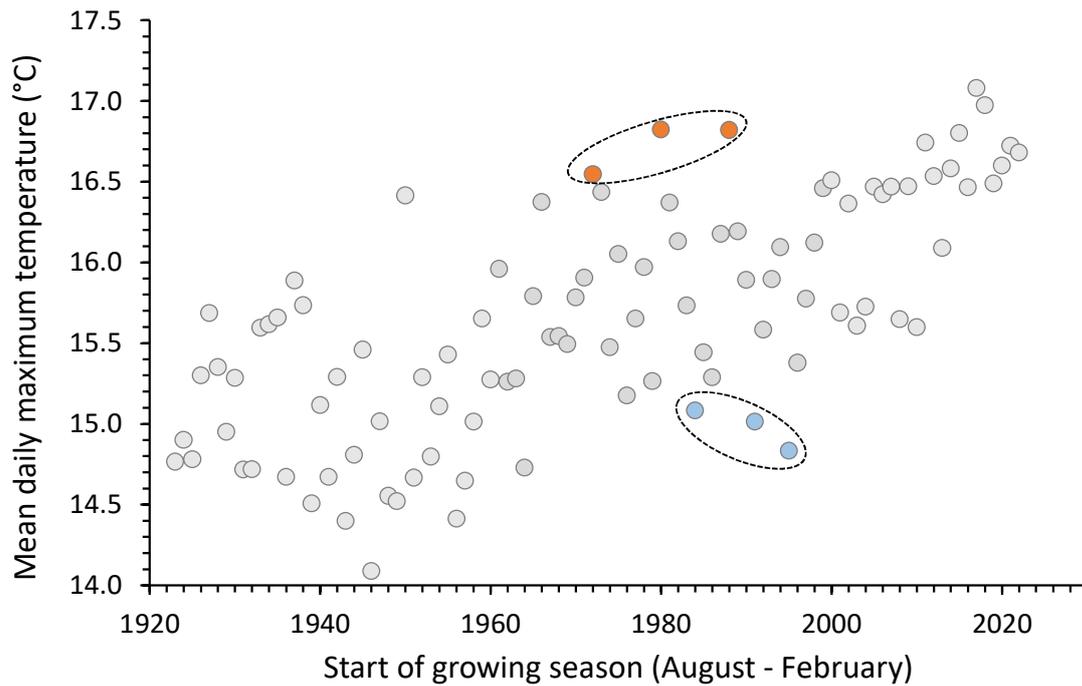
369 Evidence that evolution of adaptive traits is occurring in Tasmania's tall eucalypt
370 forests as a response to climate change is lacking. Temperature and rainfall conditions
371 during the first season of regeneration exert strong selection pressures in survivorship of
372 *E. regnans* and *E. delegatensis* (Singh et al. 2021). Bloomfield et al. (2011) postulated
373 that such selection pressure would establish adaptive patterns in each *E. obliqua*
374 generation. An increase in the optimum temperature for growth is an adaptive response
375 we might expect to see in response to a selection pressure imposed by unusually high
376 temperatures experienced during the first year of regeneration. Obtaining measurements

377 'to determine optimum growth temperatures would require sampling many sites to
378 detect a significant effect. This would be impractical using eddy covariance (as in
379 Bennett et al. 2021) but tractable using biometric methods such as dendrometry
380 (e.g.Zweifel et al. 2021).

381 Forest growth rates obtained biometrically can show good agreement with those
382 obtained by eddy covariance (Fenn et al. 2014, Dukat et al. 2021), although not always
383 (Griebel et al. 2017). There are good prospects that biometry and eddy covariance
384 would be in good agreement for Tasmania's tall eucalypt forests. This is because most
385 of the growth change measured by biometry is likely to be concentrated in the main
386 stem that is easy to measure using dendrometers. Tall eucalypt forests would be
387 expected to have low root:shoot ratios based on Mokany et al. (2005) who found
388 root:shoot ratios decreased with increasing stand height, total biomass and total rainfall
389 (all high in Tasmanian tall eucalypt forests). Furthermore, Ximenes et al. (2008) found a
390 high proportion of the aboveground biomass in *E. obliqua* in a tall forest at Warra was
391 concentrated in the main stem.

392 Because of the argument outlined in the previous paragraph, there is a strong prospect
393 that dendrometry would enable a determination of variation in optimum temperature for
394 growth be made from a sample of tall eucalypt forests throughout Tasmania. Many tall
395 eucalypt forest stands have been regenerated each year by sowing after harvesting and
396 burning of the logging slash since the mid-1960s in Tasmania. Screening these
397 regenerating stands according to the temperature environment they experienced during
398 their first year of growth would provide the basis of selecting stands with contrasting
399 temperature regimes. For example, in the southern Forests (tall eucalypt forests
400 southeast of the Huon River) stands regenerated in 1972, 1980 and 1989 experienced

401 unusually high temperatures in their first year of growth, while stands regenerated in
402 1984, 1991 and 1994 experienced unusually low temperatures in their first year of
403 growth. Installing a dendrometer network that sampled stands from the southern forests
404 regenerated in the three hot years and the three cold years should provide an opportunity
405 to measure the quantum of adaptation to warmer temperatures in one generation.



406

407 **Figure 3.** Plot of mean daily maximum temperature of the growing season (August-
408 February) measured at Cape Bruny Lighthouse (Bureau of Meteorology station 94010).
409 In the first three decades of clearfall, burn and sow silviculture (1970-1999) three
410 unusually hot years are shown with orange fill and three unusually cold years are shown
411 with blue fill.

412 Enhanced natural selection as described above requires a critical stage of regeneration
413 (seedling stage) to coincide with a selection event (hotter than normal temperatures).
414 Regeneration following natural disturbance by a high severity bushfire in tall eucalypt
415 forests is a rare event in Tasmania, even after factoring in climate change (Furlaud et al.

416 2021). Thus natural selection events driving adaptation to a warmer climate will be very
417 rare for natural disturbance. As a result, adaptation would be too slow to be of any
418 benefit in generating future tall eucalypt forests that are better suited to the new climate
419 we are rapidly moving towards. Tall eucalypt forest areas managed for wood
420 production, by contrast, generate disturbance events every year, so there will be some
421 regeneration at the critical stage of development every year a selection event occurs.
422 Significant flowering and seed production begins once tall eucalypt forests reach about
423 25 years of age (Ashton 1975). Areas managed for enhanced natural selection could
424 therefore enable several generations of natural selection to occur over, say, the next
425 century. This may be sufficiently fast to generate future forests can persist in the new
426 Tasmanian climate.

427 **Policy settings to enable management for adaptation**

428 Several Australian states have ceased logging of native forests and there is sustained
429 pressure to extend this to all states (Burnett 2023). The basis of the arguments for a
430 cessation of native forest logging in Tasmania is to protect biodiversity and carbon
431 sequestration to help lessen the risks from climate change. Most of the published
432 evidence presented in arguing for cessation of logging is based on carbon sequestration
433 benefits (Mackey et al. 2022, Wilderness Society 2022). Evidence supporting these
434 claims draws extensively on the Tasmanian and national greenhouse gas inventories
435 (Commonwealth of Australia 2021, Renewables Climate and Future Industries
436 Tasmania 2023).

437 The model used for greenhouse gas inventorying of the land use land use change and
438 forestry sector (LULUCF) – FullCAM – uses the 3-PG model to predict forest growth
439 (Landsberg and Waring 1997, Kesteven et al. 2004, Richards and Evans 2013). Forest

440 growth is a fundamental property in calculating the amount of carbon sequestered by a
441 forest (May et al. 2012). There are several climate variables used in the 3-PG model, but
442 temperature, vapor pressure deficit (VPD) and soil water content are most relevant in
443 the context of climate change. VPD and soil moisture content are much stronger
444 modifiers of forest growth than temperature in 3-PG (Kesteven et al. 2004). This is the
445 opposite of findings from eddy covariance measurements of productivity in the *E.*
446 *obliqua* tall forest at Warra (Bennett et al. 2021, Wardlaw 2022).

447 The small influence of the temperature modifier in the 3-PG model means, growth of
448 tall eucalypt forests in Tasmania predicted in FullCAM are likely to be over-estimated,
449 and the size of the over-estimation will increase as the climate warms. Carbon
450 sequestered by tall eucalypt forests in Tasmania will be less than the model predicts. If
451 the temperature rise crosses a tipping point for these forests causing death of the current
452 generation of eucalypts, the amount of carbon sequestered will drop sharply. This is
453 because the eucalypt component dominates aboveground biomass of these forests
454 (Moroni et al. 2017, Wardlaw 2021).

455 Analyses that conclude the protection of carbon-dense tall eucalypt forests is the safest
456 option for addressing climate change (Mackey et al. 2022) do not account for the impact
457 of the changed climate on future forest growth. Law et al. (2018) did conclude
458 protection as the safest climate mitigation option in the carbon dense coniferous forests
459 of the Pacific-Northwest USA. Their analysis was based on a prediction of higher
460 growth rates in a future warmer climate. Their conclusions may have been very
461 different if the analysis was based on lower forest growth rates in a warmer future
462 climate as is suggested by the evidence for tall eucalypt forests in Tasmania.

463 A policy to end native forest logging in Tasmania using the argument that it would be

464 the safest way to get climate change mitigation benefits from forests would be
465 dangerous if it relied on existing carbon inventory analyses. Good policy must first
466 require an analysis that takes account of the now known vulnerability of Tasmania's tall
467 eucalypt forests to a warmer climate. Because of the vulnerability to a warming climate,
468 good policy must also enable adaptation measures that will result in future tall eucalypt
469 forests that are better suited to the new, warmer climate. On the best available
470 knowledge, enhanced nature selection that relies on regeneration using locally sourced
471 seed is the most promising adaptation measure. As this adaptation option is only
472 feasible in production forests, a policy decision to end native forest logging would
473 preclude this adaptation measure.

474 **Conclusions**

475 Tasmania's unique climate environment is associated with the very different responses
476 to heatwaves measured in a Tasmanian tall eucalypt forest compared with similar
477 temperate eucalypt forests on mainland Australia. A narrow annual temperature range,
478 low moisture limitation, low winter radiation, but not low optimum temperature (for
479 GPP), all contribute to the distinctive responses to heatwaves measured in Tasmanian
480 tall eucalypt forest.

481 The distinctive responses to the climate environment determines enhanced natural
482 selection to be the most promising management option to assist future tall eucalypt
483 forests in Tasmania adapt to their new climate environment. Because enhanced natural
484 selection is only feasible to do in forests managed for wood production, careful
485 consideration needs to be given to ensure policy settings do not become an impediment
486 to climate change adaptation.

487

488 **Acknowledgements**

489 On oral presentation given at the ANZIF 2023 Conference by the author formed the
490 basis of this paper. Data generated by TERN infrastructure (a facility supported by the
491 National Collaborative Research Infrastructure Scheme) and independent studies using
492 TERN SuperSites produced the new knowledge that enable the putative diagnosis
493 detailed in this paper. Alison Phillips (Sustainable Timber Tasmania) provided technical
494 support for managing the Warra Supersite.

495

496 **References**

497

- 498 Ashton, D. H. 1975. Studies of flowering behaviour in *Eucalyptus regnans* F. Muell.
499 *Australian Journal of Botany* **23**:399-411.
- 500 Bennett, A. C., S. K. Arndt, L. T. Bennett, J. Knauer, J. Beringer, A. Griebel, N. Hinko-
501 Najera, M. J. Liddell, D. Metzen, E. Pendall, R. P. Silberstein, T. J. Wardlaw,
502 W. Woodgate, and V. Haverd. 2021. Thermal optima of gross primary
503 productivity are closely aligned with mean air temperatures across Australian
504 wooded ecosystems. *Global Change Biology* **27**:4727-4744.
- 505 Beringer, J., C. E. Moore, J. Cleverly, D. I. Campbell, H. Cleugh, M. G. De Kauwe, M.
506 U. F. Kirschbaum, A. Griebel, S. Grover, A. Huete, L. B. Hutley, J. Laubach, T.
507 Van Niel, S. K. Arndt, A. C. Bennett, L. A. Cernusak, D. Eamus, C. M. Ewenz,
508 J. P. Goodrich, M. Jiang, N. Hinko-Najera, P. Isaac, S. Hobeichi, J. Knauer, G.
509 R. Koerber, M. Liddell, X. Ma, C. Macfarlane, I. D. McHugh, B. E. Medlyn, W.
510 S. Meyer, A. J. Norton, J. Owens, A. Pitman, E. Pendall, S. M. Prober, R. L.
511 Ray, N. Restrepo-Coupe, S. W. Rifai, D. Rowlings, L. Schipper, R. P.
512 Silberstein, L. Teckentrup, S. E. Thompson, A. M. Ukkola, A. Wall, Y. P.
513 Wang, T. J. Wardlaw, and W. Woodgate. 2022. Bridge to the future: Important
514 lessons from 20 years of ecosystem observations made by the OzFlux network.
515 *Global Change Biology* **28**:3489-3514.

516 Bloomfield, J. A., P. Neville, B. M. Potts, R. E. Vaillancourt, and D. A. Steane. 2011.
517 Molecular genetic variation in a widespread forest tree species *Eucalyptus*
518 *obliqua* (Myrtaceae) on the island of Tasmania. *Australian Journal of Botany*
519 **59**:226-237.

520 Booth, T. H., and P. R. Muir. 2020. Climate change impacts on Australia's eucalypt and
521 coral species: Comparing and sharing knowledge across disciplines. *WIREs*
522 *Climate Change* **11**(5): e657.

523 Bowman, D. M. J. S., G. J. Williamson, R. J. Keenan, and L. D. Prior. 2014. A warmer
524 world will reduce tree growth in evergreen broadleaf forests: evidence from
525 Australian temperate and subtropical eucalypt forests. *Global Ecology and*
526 *Biogeography* **23**:925-934.

527 Burnett, P. 2023. Has time been called on the native forest logging deals of the 1990s?
528 Here's what the Albanese government can do. Pages
529 [https://theconversation.com/has-time-been-called-on-the-native-forest-logging-](https://theconversation.com/has-time-been-called-on-the-native-forest-logging-deals-of-the-1990s-heres-what-the-albanese-government-can-do-206860)
530 [deals-of-the-1990s-heres-what-the-albanese-government-can-do-206860](https://theconversation.com/has-time-been-called-on-the-native-forest-logging-deals-of-the-1990s-heres-what-the-albanese-government-can-do-206860) The
531 Conversation.

532 Camarretta, N., P. A. Harrison, T. Bailey, N. Davidson, A. Lucieer, M. Hunt, and B. M.
533 Potts. 2020. Stability of species and provenance performance when translocated
534 into different community assemblages. *Restoration Ecology* **28**:447-458.

535 Commonwealth of Australia. 2021. National Inventory Report 2019. Volume 1.
536 Department of Industry, Sciences, Energy and Resources, Canberra.

537 CSIRO, and Bureau of Meteorology. 2022. State of the Climate 2022. CSIRO and
538 Bureau of Meteorology, Australia.

539 de Araujo, M. J., R. C. de Paula, O. C. Campoe, and R. L. Carneiro. 2019. Adaptability
540 and stability of eucalypt clones at different ages across environmental gradients
541 in Brazil. *Forest Ecology and Management* **454**.

542 Drake, J. E., A. Varhammar, D. Kumarathunge, B. E. Medlyn, S. Pfautsch, P. B. Reich,
543 D. T. Tissue, O. Ghannoum, and M. G. Tjoelker. 2017. A common thermal
544 niche among geographically diverse populations of the widely distributed tree
545 species *Eucalyptus tereticornis*: No evidence for adaptation to climate-of-origin.
546 *Global Change Biology* **23**:5069-5082.

- 547 Duffy, K. A., C. R. Schwalm, V. L. Arcus, G. W. Koch, L. L. Liang, and L. A.
548 Schipper. 2021. How close are we to the temperature tipping point of the
549 terrestrial biosphere? *Science Advances* **7**:eaay1052.
- 550 Dukat, P., K. Ziemlińska, J. Olejnik, S. Małek, T. Vesala, and M. Urbaniak. 2021.
551 Estimation of biomass increase and CUE at a young temperate Scots pine stand
552 concerning drought occurrence by combining eddy covariance and biometric
553 methods. *Forests* **12**: 867.
- 554 Fenn, K., Y. Malhi, M. Morecroft, C. Lloyd, and M. Thomas. 2014. The carbon cycle of
555 a maritime ancient temperate broadleaved woodland at seasonal and annual
556 scales. *Ecosystems* **18**:1-15.
- 557 Forest Practices Authority. 2023. *State of the forests Tasmania 2022 booklet*. Forest
558 Practices Authority, Hobart, Tasmania.
- 559 Furlaud, J. M., L. D. Prior, G. J. Williamson, and D. M. J. S. Bowman. 2021.
560 Bioclimatic drivers of fire severity across the Australian geographical range of
561 giant *Eucalyptus* forests. *Journal of Ecology* **109**(6): 2514-2536.
- 562 Griebel, A., L. T. Bennett, and S. K. Arndt. 2017. Evergreen and ever growing – Stem
563 and canopy growth dynamics of a temperate eucalypt forest. *Forest Ecology and
564 Management* **389**:417-426.
- 565 Griebel, A., L. T. Bennett, D. Metzen, E. Pendall, P. N. J. Lane, and S. K. Arndt. 2020.
566 Trading water for carbon: Maintaining photosynthesis at the cost of increased
567 water loss during high temperatures in a temperate forest. *Journal of
568 Geophysical Research: Biogeosciences* **125**:e2019JG005239.
- 569 Grose, M., I. Barnes-Keoghan, S. Corney, C. White, G. Holz, J. Bennett, S. Gaynor, and
570 N. Bindoff. 2010. *Climate Futures for Tasmania: general climate impacts
571 technical report*. Antarctic Climate & Ecosystems Cooperative Research Centre,
572 Hobart, Tasmania.
- 573 Harris, S., and A. Kitchener. 2013. *From Forest to Fjaeldmark. Descriptions of
574 Tasmania's Vegetation*. (Edition 2). Department of Primary Industries, Water
575 and Environment, Hobart.
- 576 Harrison, P. A. 2021. Climate change and the suitability of local and non-local species
577 for ecosystem restoration. *Ecological Management & Restoration* **22**:75-91.

- 578 Kesteven, J., J. Landsberg, and URS Australia. 2004. Developing a national forest
579 productivity model. 23, Australian Greenhouse Office, Canberra, ACT.
- 580 Landsberg, J. J., and R. H. Waring. 1997. A generalised model of forest productivity
581 using simplified concepts of radiation-use efficiency, carbon balance and
582 partitioning. *Forest Ecology and Management* **95**:209-228.
- 583 Law, B. E., T. W. Hudiburg, L. T. Berner, J. J. Kent, P. C. Buotte, and M. E. Harmon.
584 2018. Land use strategies to mitigate climate change in carbon dense temperate
585 forests. *Proceedings of the National Academy of Sciences USA* **115**:3663-3668.
- 586 Mackey, B., W. Moomaw, D. Lindenmayer, and H. Keith. 2022. Net carbon accounting
587 and reporting are a barrier to understanding the mitigation value of forest
588 protection in developed countries. *Environmental Research Letters* **17**(5):
589 054028.
- 590 May, B., J. Bulinski, A. Goodwin, and S. Macleod. 2012. *Tasmanian Forest Carbon*
591 *Study*. CO2 Australia Limited.
- 592 Moiron, M., C. Teplitsky, B. Haest, A. Charmantier, and S. Bouwhuis. 2024. Micro-
593 evolutionary response of spring migration timing in a wild seabird. *Evolution*
594 *Letters* **8**:8-17.
- 595 Mokany, K., R. J. Raison, and A. S. Prokushkin. 2005. Critical analysis of root :
596 shoot ratios in terrestrial biomes. *Global Change Biology* **12**:84-96.
- 597 Moore, C. E., J. Beringer, R. J. Donohue, B. Evans, J. F. Exbrayat, L. B. Hutley, and N.
598 J. Tapper. 2018. Seasonal, interannual and decadal drivers of tree and grass
599 productivity in an Australian tropical savanna. *Global Change Biology* **24**:2530-
600 2544.
- 601 Moroni, M. T., R. Musk, and T. J. Wardlaw. 2017. Forest succession where trees
602 become smaller and wood carbon stocks reduce. *Forest Ecology and*
603 *Management* **393**:74-80.
- 604 Nevill, P. G., G. Bossinger, and P. K. Ades. 2009. Phylogeography of the world's tallest
605 angiosperm, *Eucalyptus regnans*: evidence for multiple isolated Quaternary
606 refugia. *Journal of Biogeography* **37**:179-192.
- 607 Nevill, P. G., T. Després, M. J. Bayly, G. Bossinger, and P. K. Ades. 2014. Shared
608 phylogeographic patterns and widespread chloroplast haplotype sharing in

609 *Eucalyptus* species with different ecological tolerances. *Tree Genetics &*
610 *Genomes* **10**:1079-1092.

611 Nicolls, K. D., A. M. Graley, and J. L. Honeysett. 1982. Soil storage of water under
612 eucalypt forest in S.E. Tasmania. *in* E. M. O'Loughlin and L. J. Bren, editors.
613 First National Symposium on Forest Hydrology. Institution of Engineers,
614 Australia, Melbourne.

615 Peters, J. M. R., R. Lopez, M. Nolf, L. B. Hutley, T. Wardlaw, L. A. Cernusak, and B.
616 Choat. 2021. Living on the edge: a continental scale assessment of forest
617 vulnerability to drought. *Global Change Biology* **27**:3620–3364.

618 Prior, L. D., and D. M. Bowman. 2014. Big eucalypts grow more slowly in a warm
619 climate: evidence of an interaction between tree size and temperature. *Global*
620 *Change Biology* **20**:2793-2799.

621 Prober, S. M., M. Byrne, E. H. McLean, D. A. Steane, B. M. Potts, R. E. Vaillancourt,
622 and W. D. Stock. 2015. Climate-adjusted provenancing: a strategy for climate-
623 resilient ecological restoration. *Frontiers in Ecology and Evolution* **3**. 65.

624 Prober, S. M., V. A. J. Doerr, L. M. Broadhurst, K. J. Williams, and F. Dickson. 2019.
625 Shifting the conservation paradigm: a synthesis of options for renovating nature
626 under climate change. *Ecological Monographs* **89**(1): e01333.

627 Rauschkolb, R., Z. Li, S. Godefroid, L. Dixon, W. Durka, M. Majekova, O. Bossdorf,
628 A. Ensslin, and J. F. Scheepens. 2022. Evolution of plant drought strategies and
629 herbivore tolerance after two decades of climate change. *New Phytologist*
630 **235**:773-785.

631 Renchon, A. A., A. Griebel, D. Metzen, C. A. Williams, B. Medlyn, R. A. Duursma, C.
632 V. M. Barton, C. Maier, M. M. Boer, P. Isaac, D. Tissue, V. Resco de Dios, and
633 E. Pendall. 2018. Upside-down fluxes Down Under: CO₂ net sink in winter and
634 net source in summer in a temperate evergreen broadleaf forest. *Biogeosciences*
635 **15**:3703-3716.

636 Renewables Climate and Future Industries Tasmania. 2023. *Tasmanian Greenhouse*
637 *Gas Emissions Report 2023*. Department of State Growth, Hobart, Tasmania.

- 638 Richards, G. P., and D. M. W. Evans. 2013. Development of a carbon accounting model
639 (FullCAM Vers. 1.0) for the Australian continent. *Australian Forestry* **67**:277-
640 283.
- 641 Sáenz-Romero, C., G. O'Neill, S. N. Aitken, and R. Lindig-Cisneros. 2020. Assisted
642 migration field tests in Canada and Mexico: Lessons, limitations, and
643 challenges. *Forests* **12**(1): 9.
- 644 Salvi, A. M., D. D. Smith, M. A. Adams, K. A. McCulloh, and T. J. Givnish. 2021.
645 Mesophyll photosynthetic sensitivity to leaf water potential in *Eucalyptus*: a new
646 dimension of plant adaptation to native moisture supply. *New Phytologist*
647 **230**:1844-1855.
- 648 Singh, A., P. J. Baker, S. Kasel, R. Trouvé, S. B. Stewart, and C. R. Nitschke. 2021.
649 The role of climatic variability on *Eucalyptus* regeneration in southeastern
650 Australia. *Global Ecology and Conservation* **32**: e01929.
- 651 Smith, N. G., S. L. Malyshev, E. Shevliakova, J. Kattge, and J. S. Dukes. 2015. Foliar
652 temperature acclimation reduces simulated carbon sensitivity to climate. *Nature*
653 *Climate Change* **6**:407-411.
- 654 van Gorsel, E., J. A. J. Berni, P. Briggs, A. Cabello-Leblic, L. Chasmer, H. A. Cleugh,
655 J. Hacker, S. Hantson, V. Haverd, D. Hughes, C. Hopkinson, H. Keith, N. Kljun,
656 R. Leuning, M. Yebra, and S. Zegelin. 2013. Primary and secondary effects of
657 climate variability on net ecosystem carbon exchange in an evergreen
658 *Eucalyptus* forest. *Agricultural and Forest Meteorology* **182-183**:248-256.
- 659 van Gorsel, E., S. Wolf, J. Cleverly, P. Isaac, V. Haverd, C. Ewenz, S. Arndt, J.
660 Beringer, V. Resco de Dios, B. J. Evans, A. Griebel, L. B. Hutley, T. Keenan, N.
661 Kljun, C. Macfarlane, W. S. Meyer, I. McHugh, E. Pendall, S. M. Prober, and R.
662 Silberstein. 2016. Carbon uptake and water use in woodlands and forests in
663 southern Australia during an extreme heat wave event in the “Angry Summer”
664 of 2012/2013. *Biogeosciences* **13**:5947-5964.
- 665 Vizcaino-Palomar, N., B. Fady, R. Alia, A. Raffin, S. Mutke, and M. Benito Garzon.
666 2020. The legacy of climate variability over the last century on populations'
667 phenotypic variation in tree height. *Science of Total Environment* **749**:141454.

- 668 Wang, W., N. B. English, C. Grossiord, A. Gessler, A. J. Das, N. L. Stephenson, C. H.
669 Baisan, C. D. Allen, and N. G. McDowell. 2021. Mortality predispositions of
670 conifers across western USA. *New Phytologist* **229**:831-844.
- 671 Wardlaw, T. 2021. Measuring a fire. The story of the January 2019 fire told from
672 measurements at the Warra Supersite, Tasmania. *Fire* **4**:1-19.
- 673 Wardlaw, T. J. 2022. *Eucalyptus obliqua* tall forest in cool, temperate Tasmania
674 becomes a carbon source during a protracted warm spell in November 2017.
675 *Scientific Reports* **12**:2661.
- 676 Wardlaw, T. J., and C. Palzer. 1988. Regeneration of *Eucalyptus* species in an Eastern
677 Tasmanian coastal forest in the presence of *Phytophthora cinnamomi*.
678 *Australian Journal of Botany* **36**:205-215.
- 679 White, C., M. Grose, S. Corney, J. Bennett, G. Holz, L. Sanabria, K. McInnes, R.
680 Cechet, S. Gaynor, and N. Bindoff. 2010. *Climate Futures for Tasmania:*
681 *extreme events technical report*. Antarctic Climate and Ecosystems Cooperative
682 Research Centre, Hobart, Tasmania.
- 683 Wilderness Society. 2022. *Tasmania's forest carbon. From emissions disaster to climate*
684 *solution*. Wilderness Society, Hobart.
- 685 Wilkinson, G. R. 2008. Population differentiation within *Eucalyptus obliqua*:
686 implications for regeneration success and genetic conservation in production
687 forests. *Australian Forestry* **71**:4-15.
- 688 Wu, X., H. Liu, X. Li, S. Piao, P. Ciais, W. Guo, Y. Yin, B. Poulter, C. Peng, N. Viovy,
689 N. Vuichard, P. Wang, and Y. Huang. 2017. Higher temperature variability
690 reduces temperature sensitivity of vegetation growth in Northern Hemisphere.
691 *Geophysical Research Letters* **44**:6173-6181.
- 692 Ximenes, F. A., W. D. Gardner, and A. Kathuria. 2008. Proportion of above-ground
693 biomass in commercial logs and residues following the harvest of five
694 commercial forest species in Australia. *Forest Ecology and Management*
695 **256**:335-346.
- 696 Zhu, L., K. J. Bloomfield, S. Asao, M. G. Tjoelker, J. J. G. Egerton, L. Hayes, L. K.
697 Weerasinghe, D. Creek, K. L. Griffin, V. Hurry, M. Liddell, P. Meir, M. H.

698 Turnbull, and O. K. Atkin. 2021. Acclimation of leaf respiration temperature
699 responses across thermally contrasting biomes. *New Phytologist* **229**:1312-1325.

700 Zhu, L., K. J. Bloomfield, C. H. Hocart, J. J. G. Egerton, O. S. O'Sullivan, A. Penillard,
701 L. K. Weerasinghe, and O. K. Atkin. 2018. Plasticity of photosynthetic heat
702 tolerance in plants adapted to thermally contrasting biomes. *Plant, Cell and*
703 *Environment* **41**:1251-1262.

704 Zweifel, R., S. Etzold, D. Basler, R. Bischoff, S. Braun, N. Buchmann, M. Conedera, P.
705 Fonti, A. Gessler, M. Haeni, G. Hoch, A. Kahmen, R. Köchli, M. Maeder, D.
706 Nievergelt, M. Peter, R. L. Peters, M. Schaub, V. Trotsiuk, L. Walthert, M.
707 Wilhelm, and W. Eugster. 2021. TreeNet–The Biological Drought and Growth
708 Indicator Network. *Frontiers in Forests and Global Change* **4**: 776905.

709

710

711 **Appendix 1. Stomatal diffusive resistance - vapor pressure deficit**
712 **relationship in regrowth *Eucalypts obliqua* forest at Hastings, southern**
713 **Tasmania.**

714 ***Methods***

715 The study was done in a tall open forest of *Eucalyptus obliqua* near Hastings Caves
716 State Reserve southern Tasmania (43°25'S. 146°53'E), which had regenerated naturally
717 from a bushfire in 1908. The site is at the base of the southern slopes of Coal Hill on the
718 edge of a wide floodplain of Lune River, which flows about 500m to the south. The soil
719 at the site is described as a yellow podzol (Nicolls et al. 1982).

720 Sectional aluminium tree climbing ladders were fixed to the stem of one co-dominant *E.*
721 *obliqua* with a healthy crown. The ladders provided access to the base of that tree's
722 crown at a height of approximately 25m. A lightweight aluminium pruning pole fitted
723 with a butterfly net was used to obtain samples of shoots for measurement. The pruning
724 pole allowed access to the crown of the ladder tree and eight adjacent *E. obliqua* trees.
725 Shoot samples captured in the butterfly net were put into a weighted plastic bag and
726 dropped to the ground for measurement. Measurements typically occurred within 5-10
727 minutes of sampling.

728 Measurement of stomatal diffusive resistance was done on a single, fully expanded leaf
729 on the excised shoot. A LI-65 autoporometer fitted with a LI-20S diffusive resistance
730 sensor (Licor, Lincoln, Nebraska, USA) were used to measure stomatal diffusive
731 resistance. Measurements were corrected for leaf temperature according to
732 manufacturer's instructions. A Sholander pressure bomb (Model 3000 Plant Water
733 Status Consul, Soil Moisture Equipment Corporation, Santa Barbara California) was
734 used to measure shoot water potential. An aspirated psychrometer enclosed in a
735 radiation shield was used to obtain wet and dry bulb temperatures at ground-level in the

736 forest. A psychrometric chart was used to obtain relative humidity and saturation vapor
737 pressure from the dry and wet bulb temperatures. Vapor pressure deficit (VPD) was
738 calculated as the difference between saturation vapor pressure and the partial pressure
739 of water vapour in the air as calculated from relative humidity.

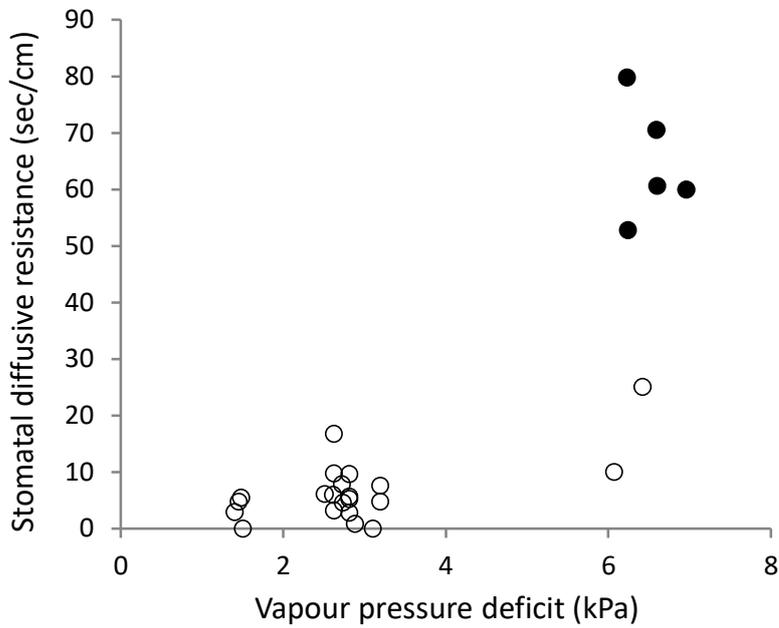
740 Shoot sampling and measurement campaigns were done on four occasions: 14-15 Jan
741 1981, 15-16 Feb 1982, 19-20 Mar 1982, 25-26 Jan 1983. Each campaign consisted of an
742 afternoon and a pre-dawn sampling of 5-8 of the sample trees. Measurements of
743 stomatal diffusive resistance and VPD and shoot water potential from afternoon
744 sampling visits were plotted to explore their relationship. Bureau of Meteorology
745 records of temperature and rainfall from the Cape Bruny Lighthouse, 23km southeast of
746 the study site, were extracted from the online data portal for four campaign days and
747 compared with long-term averages to detect any significant anomalies.

748 ***Results***

749 Rainfall during the four measurement campaigns was close to average for the two
750 campaigns in 1982 and within one standard deviation of average for the January 1981
751 campaign (below average) and January 1983 campaign (above average). Mean daily
752 temperature was close to average for the January 1981 and January 1983 campaigns, 1.5
753 standard below average for the March 1982 campaign and more than 3 standard
754 deviations above average for the February 1982 campaign. The afternoon of the 15th
755 February 1982 reached 39°C and is the hottest day on record for southern Tasmania.
756 The very hot conditions on 15th February 1982 resulted in very high VPDs, >6 kPa,
757 developing in the afternoon. Stomatal closure as evidenced by high diffusive resistance
758 values, appears to be a threshold response when VPD exceeds 6 kPa (Figure A1). By
759 contrast, stomatal closure occurred across a wide range of shoot water potentials: there

760 was no evidence of stomatal closure showing a threshold response to shoot water
761 potential (Figure A2).

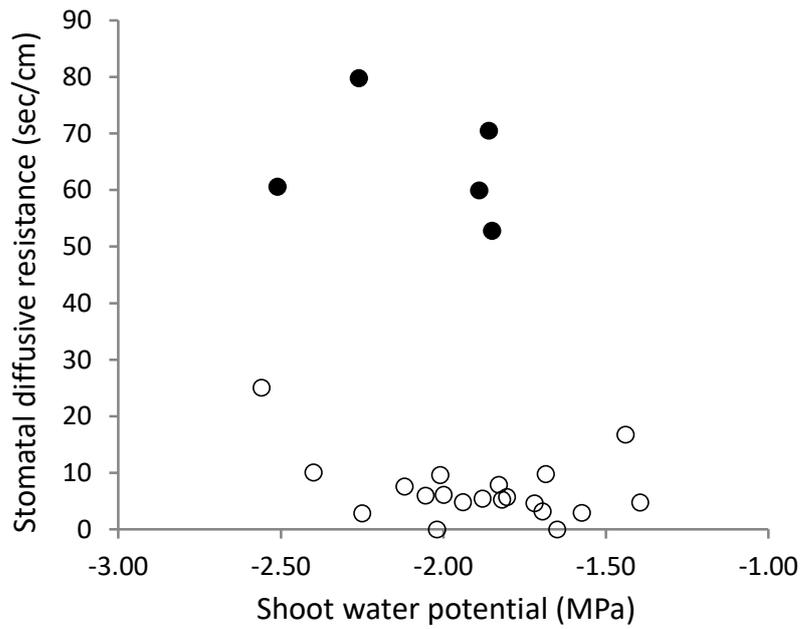
762



763

764 **Figure A1.** Plot of stomatal diffusive resistance and VPD of excised shoots from ca. 70
765 y.o. *Eucalyptus obliqua* at Hastings. All measurements were done during the afternoon
766 period of four campaigns. Filled symbols indicate inferred stomatal closure.

767



768

769 **Figure A2.** Plot of stomatal diffusive resistance and shoot water potential of excised
 770 shoots from ca. 70 y.o. *Eucalyptus obliqua* at Hastings. All measurements were done
 771 during the afternoon period of four campaigns. Filled symbols indicate inferred stomatal
 772 closure.