

1 **Title:** Long-term drivers of vegetation turnover in Southern Hemisphere temperate  
2 ecosystems

3

#### 4 **Abstract**

##### 5 **Aim:**

6 Knowledge of the drivers of ecosystem changes in the past is key to understanding present  
7 ecosystem responses to changes in climate, fire regimes and anthropogenic impacts. Northern  
8 Hemisphere-focussed studies suggest that climate and human activities drove turnover during  
9 the Holocene in temperate ecosystems. Various drivers have been invoked to explain changes  
10 in Southern Hemisphere temperate vegetation, but the region lacks a quantitative assessment  
11 of these drivers. To better understand the regional drivers of past diversity, we present a  
12 quantitative meta-analysis study of turnover and richness during the lateglacial and Holocene  
13 in Australian temperate ecosystems.

14

##### 15 **Location:**

16 Southeast Australia (Tasmania, Bass Strait, SE Mainland)

17

##### 18 **Methods:**

19 We conducted a meta-analysis study of 24 fossil pollen records across southeast Australian  
20 temperate ecosystems, applying an empirical turnover threshold to fossil records to identify  
21 periods of major turnover for the first time in Australia. We tested pollen richness as a proxy  
22 for vegetation richness to estimate past richness and applied this to fossil pollen data. The  
23 resulting reconstructions were compared to independent records of climate, sea-level change  
24 and fire through generalised linear modelling.

25

##### 26 **Results and conclusion**

27 Our results show changes in available moisture and sea level drove turnover and richness in  
28 most parts of SE Australia in the past, explaining up to ~97% deviance. However, fire mainly  
29 drove turnover in Bass Strait. Our richness reconstructions also support the Intermediate  
30 Disturbance Hypothesis, suggesting that high biodiversity was partially maintained by  
31 anthropogenic-managed fire regimes. While temperature change is considered key to  
32 Northern Hemisphere palaeodiversity, past turnover and richness in Southern Hemisphere  
33 temperate ecosystems responded mainly to moisture availability and sea-level change  
34 (considering its role in modulating regional oceanic climate).

35

36

37 **Keywords:** Bass Strait, climate, diversity, fire, Holocene, Intermediate Disturbance  
38 Hypothesis, Squared Chord Distance, southeast Australia, turnover, Tasmania.

39

40

## 41 Introduction

42 Temperate ecosystems harbour many of the world's largest biodiversity hotspots and carbon  
43 sinks (Forseth, 2010; Dean & Wardell-Johnson, 2010), but are also the most disturbed by  
44 human activities (Heath et al., 1993). These ecosystems are dependent on cool winter  
45 temperatures and are sensitive to climatic shifts (Kreyling, 2010; Giesecke, Brewer,  
46 Finsinger, Leydet & Bradshaw, 2017). Numerous quantitative regional studies have shown  
47 that temperature change was the major regional driver of ecosystem turnover (magnitude of  
48 change through time) during the Holocene in the Northern Hemisphere temperate ecosystems  
49 (e.g., Seddon, Macias-Fauria & Willis, 2015; Overpeck, Webb & Prentice, 1985; Stivrins et  
50 al., 2016), but recent research from the Mediterranean region argues that humans were the  
51 major driver of Holocene turnover (Connor et al., 2019). Studies targeted at understanding  
52 the drivers of regional ecosystem turnover are hitherto lacking in Southern Hemisphere  
53 temperate ecosystems. Quantitatively assessing the rates of long-term regional vegetation  
54 turnover and richness, as well as their respective drivers in Australian ecosystems will  
55 provide insights into the regional dynamics, degree of resilience/stability and potential for  
56 future changes in these ecosystems.

57 Southern Hemisphere temperate ecosystems are different from the Northern Hemisphere  
58 counterparts. Species pools (composition) are vastly different due to the Gondwanan heritage  
59 of Southern Hemisphere ecosystems, as well as a climate marked by greater oceanic  
60 influence and the limited extent of glaciation during the Last Glacial Maximum compared to  
61 the Northern Hemisphere (Markgraf et al., 1995). This explains why the floristic  
62 physiognomy (especially of rainforests) in temperate Australia, New Zealand and southern  
63 South America is similar (McGlone, Lusk, & Armesto, 2016). Southern Australia is  
64 characterized by temperate forest ecosystems dominated by *Eucalyptus* and *Nothofagus s.l.*  
65 (Keith, 2017). These temperate ecosystems are resilient and resistant to fires to a large extent  
66 (Knox & Clarke, 2012). However, recurrent large fires and a rapidly changing climate are  
67 transforming sclerophyllous temperate forests to the point where these ecosystems risk  
68 tipping into a new state (Laurance et al., 2011; Fairman, Nitschke & Bennett, 2016).

69 Australian palaeoecological studies have mostly attributed Holocene vegetation changes in  
70 Australia's temperate ecosystems to fire and climate, while anthropogenic impact accelerated  
71 since British colonisation in the late 18<sup>th</sup> century (e.g., Black, Mooney & Martin, 2006;  
72 Black, Mooney & Haberle, 2007; McWethy, Haberle, Hopf & Bowman, 2017). On the  
73 'island continent', the sea also modulates regional temperature and moisture, especially in  
74 areas with an oceanic climate (Australian Bureau of Meteorology – ABM, 2018). Past sea-  
75 level changes are thought to have affected vegetation development in coastal areas, especially  
76 on the small islands in Bass Strait during the sea-level transgression around 8000 years ago  
77 (Thomas & Kirkpatrick, 1996; McWethy et al., 2017). However, no study has quantitatively  
78 assessed the above-mentioned patterns on a regional scale for Australia, even though pollen  
79 records elsewhere have proven to be useful in quantitatively estimating long-term vegetation  
80 turnover and richness, especially on a regional scale (e.g., Seddon et al., 2015; Connor et al.,  
81 2019; Jacobson, Webb, & Grimm, 1986; Shuman, Bartlein, & Webb, 2005).

82

83 The dynamics of ecosystem floristic richness is largely dependent on interactions between  
84 plant functional traits and disturbance regimes (e.g., Dornelas et al., 2014; Vellend et al.,  
85 2013). Disturbance can both promote or reduce richness, depending on the ecosystem type  
86 and magnitude and nature of disturbance (e.g., Biswas & Mallik, 2010; He, Lamont, &  
87 Pausas, 2019). For example, fire may promote richness in fire-adapted woodlands and  
88 heathlands through enhanced seed germination, while fire may drive extirpation in fire-

89 sensitive rainforests (Gill, 1996). The idea of disturbance promoting richness is encapsulated  
90 in the Intermediate Disturbance Hypothesis (IDH) which theorises that: (1) disturbance  
91 significantly affects species richness, (2) competitive exclusion is driven by interspecific  
92 competition, and (3) moderate disturbance suppresses interspecific competition (Wilkinson,  
93 1999; Kricher, 2011; Catford et al., 2012). While richness change has been mainly driven by  
94 human activity during the Holocene in the Northern Hemisphere's temperate and  
95 Mediterranean ecosystems (Giesecke et al., 2017), research into the past richness/diversity  
96 dynamics of Australia's temperate ecosystems is lacking. In Australia, diversity was thought  
97 to have been promoted by moderate burning by humans in the past (Bowman, 1998; Bird,  
98 Bird, Coddington & Taylor, 2016); however, few studies have directly and quantitatively  
99 addressed the role of fire in promoting ecosystem richness/diversity during the Holocene in  
100 Australia (Thomas, Enright & Kenyon, 2001; McWethy et al., 2013).

101 Here, we present a meta-analysis that assesses the drivers and timing of past turnover and  
102 richness change in temperate Southern Australia, using a quantitative approach. The SE  
103 Australian regions included in this study include the SE mainland (continent), Bass Strait  
104 islands (an archipelago, formerly a land bridge) and Tasmanian mainland (continental island,  
105 formerly connected to the mainland) (Fig. 1). We hypothesise that sea-level change may have  
106 driven vegetation turnover and changes in richness during the Holocene in addition to climate  
107 and anthropogenic land-use/fire. We also hypothesise that intermediate levels of fire (biomass  
108 burned) likely promoted floristic richness in the past. To test these hypotheses, we estimated  
109 palynological richness and rates of vegetation change using fossil pollen records across SE  
110 Australia. We developed objective measures of turnover and richness by adopting an  
111 empirical turnover threshold to identify the timing of major vegetation turnover and by  
112 verifying palynological richness as a proxy for plant species richness. We use generalised  
113 linear models to compare the reconstructions to independent records of fire, climate and sea-  
114 level changes to identify possible drivers of regional vegetation turnover and richness during  
115 the lateglacial (~13,000–11,700 years ago) and Holocene (the last 11,700 years) in SE  
116 Australia.

117

118 [Figure 1 here]

119

## 120 **Southeast Australian vegetation and climate**

121 Australia's vegetation follows a precipitation gradient, ranging from wet to dry landscapes  
122 characterized by forests and non-forest vegetation types (Keith, 2017). The vegetation of the  
123 SE Australian mainland is characterized by *Eucalyptus* open forests and woodlands, as well  
124 as mallee shrublands. The central to eastern part of Tasmania is dominated by *Eucalyptus*  
125 open forests and open woodlands, while the western to southern part is characterized by cool  
126 temperate rainforests, wet sclerophyll forests and moorland (Keith, 2017). The Bass Strait  
127 islands' vegetation is characterized primarily by myrtaceous heaths and related scrub, with  
128 very little rainforest (Kitchener & Harris, 2013). A large part of the Australian mainland has  
129 been transformed into grazing pasture and dryland cropping, as have widespread areas in the  
130 central eastern parts of Tasmania. In Bass Strait, however, only King and Flinders Islands  
131 have been largely modified into grazing pastures (Department of Agriculture, 2018).

132 The climate of the southern Australian mainland is controlled by strong Southern Westerly  
133 Winds (SWW) during winter, bringing high rainfall, while an anticyclonic influence comes  
134 into play during summer, causing dry summers (ABM, 2019). The El Niño Southern

135 Oscillation (ENSO) also drives interannual climatic variability on the SE mainland and in NE  
136 Tasmania (Mariani, Fletcher, Holz & Nyman, 2016; Risbey, Pook, McIntosh, Wheeler &  
137 Hendon, 2009). In contrast, high rainfall in southern to western Tasmania is generally driven  
138 by the Pacific–South American mode and SWW (Mariani & Fletcher, 2016; Hill, Santoso &  
139 England, 2009; ABM, 2019; Risbey et al., 2009).

140

## 141 **Methods**

### 142 Data selection

143 Pollen records from 117 sites across SE Australia were considered for this study. From these,  
144 we used strict criteria to select 24 sites ranging between 1 and 1955 m asl, which include the  
145 SE mainland (11 sites), Tasmania (9 sites) and the Bass Strait islands (4 sites; Fig. 1; see  
146 Table S1 in Appendix S1 for list of sites and site details; see Appendix S2 for references of  
147 data sources not cited in text). Site selection was made based on at least one pollen sample  
148 every 500 years and at least one radiocarbon date every 3000 years. Most pollen data were  
149 obtained from a SE Australian pollen database (Herbert & Harrison, 2016), some by  
150 contacting individual analysts, and five sites from the Neotoma Paleoecology Database  
151 (<http://www.neotomadb.org/>). Four unpublished records were also used with permission, due  
152 to the scarcity of high-resolution pollen records.

153 Overall, 14 sites were used spanning the last 13,000 years, while the remaining 10 sites span  
154 the last 9000 years. *Pinus*, introduced to Australia in the 19<sup>th</sup> century, was used as a dating  
155 marker for seven sites by assigning a date of 150 cal yr BP to the first appearance of *Pinus*  
156 pollen in the records. The age-depth model for one of the sites (Middle Patriarch Lagoon –  
157 MPL) from the Bass Strait islands was corrected by re-running a Bacon age-depth model  
158 (Blauuw & Christen, 2011), using *Pinus* as a marker for ~150 cal yr BP (see Table S2 in  
159 Appendix S1 for new age-depth model and age estimates).

160

### 161 Composite charcoal analysis

162 In order to compare turnover and richness results with an independent record of regional fire  
163 activity, 61 and 13 charcoal accumulation datasets from different sites in SE mainland and  
164 Tasmania were selected from the Global Paleofire Database, respectively  
165 (<https://paleofire.org/index.php>). Four charcoal records (not from the Global Paleofire  
166 Database) were added from the Bass Strait region (Adeleye et al., submitted.; Hopf et al., in  
167 prep.). Composite z-scores were then calculated for each region using the ‘paleofire’ package  
168 in R (Blarquez et al., 2014b; R Core Team, 2019).

169

### 170 Numerical analysis - turnover

171 To estimate the rate of vegetation turnover through time at each site, we conducted a rate-of-  
172 change analysis, using the Squared Chord Distance (SCD) dissimilarity metric (Overpeck et  
173 al., 1985; Seddon et al., 2015; Connor et al., 2019). There are many metrics that can be used  
174 to estimate rates-of-change, however the SCD metric has been proven to be the most suitable  
175 for palynological data due to its better handling of the signal-noise effect (Overpeck et al.,  
176 1985). ‘Rates-of-change’, ‘compositional change’ and ‘temporal turnover’ are often used  
177 interchangeably in the literature, as they can all be interpreted from the SCD of fossil pollen  
178 spectra; however, we will use the term ‘turnover’ in this study to refer to these. After

179 calculating fossil pollen percentages, a binning approach (Connor et al., 2019, after Seddon et  
180 al. 2015) was chosen over interpolation due to the risk of artefacts created by interpolation  
181 (Birks, 2012). The binning approach involves dividing pollen records from each site into time  
182 bins, selecting random samples from adjacent bins, calculating the inter-sample SCD, then  
183 repeating this random selection 50 times to obtain an average bin-to-bin SCD score. A bin  
184 width of 1000 years was used due to the low dating resolution of most available records.  
185 Spores and aquatic/wetland taxa were excluded from the pollen sum. We also tested an  
186 alternative dissimilarity metric known as Hellinger transformation with Euclidean distance  
187 (Plumpton, Whitney & Mayle, 2019) for comparison with SCD results.

188 In order to determine an empirical SCD threshold for significant change in SE Australian  
189 vegetation, surface pollen rain and modern vegetation survey data from different sites on the  
190 mainland and Tasmania were obtained (Fig. 1). For Tasmania, samples were collected from  
191 27 sites (see Mariani, Connor, Theuerkauf, Kuneš & Fletcher, 2016 for more information and  
192 sampling methods). Using the same approach, we included 25 sites from the SE Mainland,  
193 with 11 sites from the Alpine National Park, 4 sites from Wilson's Promontory National Park  
194 and 10 sites from Grampians National Park (Mariani et al., submitted).

195 SCDs were calculated between modern samples in the two regions and SCDs of vegetation  
196 and corresponding pollen data were then compared using a Mantel dissimilarity test  
197 (Legendre & Legendre, 2012) to determine whether dissimilarity in vegetation translated into  
198 dissimilarity in pollen assemblages. This step was repeated using distance-weighted plant  
199 abundance of target taxa, which is the product of each taxon's cover and respective weighting  
200 factor (weighted with Lagrangian Stochastic pollen-dispersal model) to verify relationships  
201 between modern pollen and vegetation (see Mariani, Connor, et al., 2016 for details on  
202 calculating distance-weighted plant abundance). We then set a numerical SCD threshold  
203 based on modern pollen and vegetation SCDs, using the analogue matching technique and a  
204 dissimilarity score greater than the 5<sup>th</sup> percentile was selected as the cut-off for significant  
205 dissimilar vegetation groups, i.e. an indicator of ecosystem turnover (Plumpton et al., 2019;  
206 Simpson, 2007). Mainland and Tasmanian vegetation were also grouped by SCD, using  
207 Ward's clustering method, with similar and dissimilar vegetation groups separated in line  
208 with the SCD threshold. Similar assessments of thresholds have been done in the Northern  
209 Hemisphere (e.g., Overpeck et al., 1985; Huntley, 1990b; Davis, Collins & Kaplan, 2015).

210

### 211 Numerical analysis - richness

212 To estimate palaeo-richness for each site, we conducted a rarefaction analysis by randomly  
213 resampling each pollen sample (1000 times) to the minimum pollen sum from each pollen  
214 record (excluding introduced species). Random resampling reduces the bias effect of pollen  
215 taxa with high counts over taxa with low counts (Felde, Peglar, Bjune, Grytnes & Birks,  
216 2016). For this study, pollen richness is taken to reflect floristic richness at a site, though  
217 there are complexities surrounding the use of pollen spectra in estimating vegetation richness.  
218 These complexities include differential pollen production, dispersal and preservation, as well  
219 as pollen taxonomic resolution (Birks et al., 2016). Despite these complexities, pollen records  
220 have proven useful in reconstructing past floristic richness (Giesecke et al., 2017). To verify  
221 palynological richness as a proxy of richness in Australian vegetation, we compared plant  
222 richness in modern vegetation to surface pollen richness from SE Australia.

223

224

## 225 Modelling

226 In order to identify major drivers of turnover and richness, we applied Generalized Linear  
227 Modelling (GLM), with Gaussian distribution and each potential driver (fire, ENSO,  
228 temperature, sea level and precipitation:evaporation) as a predictor of vegetation turnover and  
229 changes in richness. We removed the effect of temporal autocorrelation by resampling each  
230 variable at a lower resolution and re-running each model 1000 times (bootstrapping) (Mellin,  
231 Bradshaw, Meekan, & Caley, 2010). All variables were initially included as predictors of  
232 turnover and richness, and significant variables were selected for final GLMs using a  
233 stepwise variable selection procedure. Corrected Akaike's information criterion (AICc) and  
234 delta AICc (dAICc) were then used to rank final models, with additional consideration given  
235 to the amount of deviance explained by each variable. All data analyses in this study were  
236 done in R (R core team, 2019) using the 'vegan', 'analogue', 'TSA', 'stats', 'EnvStats',  
237 'mgcv' and 'MASS' packages (Oksanen et al. 2007; Simpson, 2007; Cryer & Chan, 2012;  
238 Millard, 2013; Ripley et al., 2020; Wood, 2020). We used composite charcoal results as a  
239 proxy for fire, sedimentation record of Laguna Pallcacocha lake as a proxy for ENSO events  
240 (Moy, Seltzer, Seltzer, & Anderson, 2002), EPICA Dome C Antarctic deuterium record as a  
241 proxy for temperature (Stenni et al., 2001), precipitation:evaporation reconstruction from  
242 southwestern Victoria as a proxy for SWW-driven moisture availability (Wilkins,  
243 Gouramanis, De Deckker, Fifield, & Olley, 2014) and biological indicator-based  
244 reconstructed sea levels for SE Australia as a proxy for sea-level change (Sloss, Murray-  
245 Wallace, & Jones, 2007).

246 We applied Generalized Additive Modelling (GAM), with non-linear effect to assess the  
247 Intermediate Disturbance Hypothesis in SE Australia, using charcoal composite (fire  
248 disturbance) and reconstructed palynological richness. Considering that pollen production  
249 may have differed under glacial climates (Mariani et al. 2016), we only used Holocene  
250 samples for this assessment.

251

## 252 **Results**

### 253 Squared Chord Distance (SCD) threshold assessment

254 Our SCD and Hellinger transformation results were similar ( $r = 0.9$ ), therefore we only  
255 present the former (see Fig. S4a–S4c in Appendix S1 for examples of SCD versus Hellinger  
256 transformation results). Results show a significant positive correlation (based on Mantel test)  
257 between Tasmania's ( $r = 0.4, p < 0.01$ ) and the mainland's ( $r = 0.6, p < 0.01$ ) modern vegetation  
258 survey SCD and surface pollen rain SCD, which means sites with similar vegetation tend to  
259 have similar pollen assemblages (Fig. 2a–b). Distance-weighted plant abundance results were  
260 similar to those of the unweighted vegetation data (Fig. 2c–d). After applying Ward's  
261 clustering method, the sites with the most similar vegetation had a pollen assemblage SCD  
262 value ranging from 0–0.4 in both regions, while SCD values for the most dissimilar sites  
263 mainly ranged from 0.1–1.0 (Fig. 3). Specifically, SCDs within *Eucalyptus* forests ranged  
264 from 0.15–0.3, however Tasmanian *Nothofagus* rainforest ranged between 0.3 and 0.8 (see  
265 Fig. S2 in Appendix S1).

266 Analogue analysis produced a dissimilarity threshold (5<sup>th</sup> percentile) of 0.143 for the  
267 mainland and 0.259 for Tasmania (Table 1). To obtain a single representative regional  
268 analogue threshold for SE Australia comparable to regional studies from the Northern  
269 Hemisphere, we averaged the analogue thresholds for the mainland and Tasmania, yielding a  
270 final threshold value of 0.2. Also, our results show a positive relationship between pollen and

271 plant richness ( $r = 0.33$ ,  $p < 0.05$ ). We found that excluding high elevation sites across the  
272 region, as suggested by Felde et al. (2016), further improved the relationship ( $r = 0.53$ ,  
273  $p < 0.05$ ) (Fig. 3).

274 [Figure 2 here]

275 [Figure 3 here]

276 [Table 1 here]

277

## 278 Generalized Linear Models (GLM)

279 For Bass Strait, only fire was significantly ( $p < 0.05$ ) related to turnover during variable  
280 selection. Only sea-level change was significant for richness. Hence, fire and sea-level  
281 change are taken as the major drivers of Holocene turnover and richness in the region,  
282 respectively (Table 2a).

283 For the mainland, precipitation:evaporation, sea-level change and ENSO were significantly  
284 ( $p < 0.05$ ) related to turnover. A combination of these variables best predicted turnover  
285 (AICc=186, dAICc=0, Rm=50, Deviance=71%). For richness, a combination of  
286 precipitation:evaporation, sea-level change, temperature, and fire most significantly ( $p < 0.05$ )  
287 predict richness (AICc=61, dAICc=0, Rm=91, Deviance=96%) on the mainland. Of these  
288 variables, fire appears to be less important, considering the similar deviance explained (95%)  
289 by models 2–4 (Table 2a & b).

290 For Tasmania, a combination of precipitation:evaporation, sea-level change, temperature, and  
291 ENSO best predicted turnover (AICc=141, dAICc=0, Rm=93, Deviance=96%). ENSO  
292 appears to be the least important variable, considering the similar deviance explained (97%)  
293 by model 2 (Table 2). Richness in Tasmania is best predicted by a combination of sea-level  
294 change, temperature and ENSO (AICc=95, dAICc=0, Rm=49, Deviance=63%).

295

296 [Table 2 here]

297 [Figure 4a here]

298

## 299 Rates of vegetation turnover, changes in richness and fire activity

300 For the SE mainland, significant vegetation turnover occurred in the late Holocene (~4000–  
301 present cal yr BP) with average SCDs reaching 0.25. Rarefaction analysis shows richness  
302 increased during the lateglacial–early Holocene, remained relatively stable until ~7000 cal yr  
303 BP and gradually increased from ~7000 cal yr BP–present (Fig. 4b). Results also show low  
304 fire activity on the mainland from the lateglacial to mid-Holocene (~13,000–7000 yr BP)  
305 with z-scores below 0, while fire activity increased over the last ~7000 years with z-scores  
306 consistently above 0 (Fig. 4b).

307

308 [Figure 4b here]

309

310 In Bass Strait, results show high rates of vegetation turnover from the lateglacial through the  
311 mid-Holocene with SCD values between 0.3 and 0.4 (~13,000–8000 cal yr BP), stabilizing  
312 during the mid- to late Holocene (~7000–1000 cal yr BP) with intermittent changes, as  
313 reflected in SCD values below 0.2. Turnover increased in the last ~1000 cal yr BP with a  
314 return to values >0.2. The highest richness is recorded during the lateglacial, after which it  
315 steadily decreased until ~5000 cal yr BP. Richness increased again from ~5000–2000 cal yr  
316 BP before finally decreasing during the last ~2000 years. Charcoal z-scores ranged between -  
317 1 and 0 from ~13,000 to 9000 cal yr BP, attained a maximum from ~8000 to 6000 cal yr BP  
318 with a maximum z-score of up to 0.5, then declined to below 0 for the last 2000 years (Fig.  
319 4b).

320 In Tasmania, rate of vegetation turnover was highest during the lateglacial–early Holocene  
321 (~13,000–11,000 cal yr BP) with average SCDs of up to 0.3, attaining stability by ~10,000  
322 cal yr BP and remaining stable (below threshold) throughout the rest of the Holocene.  
323 Richness was highest in the lateglacial–earliest Holocene and mid- to late Holocene (~7000  
324 cal yr BP–present) and lowest from ~11,000–7000 cal yr BP. Tasmanian fire records show  
325 the highest fire activity during the lateglacial–early Holocene (~13,000–10,000 cal yr BP)  
326 with z-scores above 0, decreasing through the mid-Holocene (~10,000–6000 cal yr BP) and  
327 then gradually increasing from ~6000 yr cal BP–present (Fig. 4b). In addition, overall results  
328 in all regions show that a high–intermediate level of charcoal corresponds with high richness  
329 (Fig. 5).

330

## 331 **Discussion**

### 332 Richness metrics and potential sources of error

333 This study presents the first attempt to confirm and apply richness measures to Holocene  
334 pollen data in Australia. We show that modern palynological richness has a positive  
335 relationship with floristic richness, especially in sites <800 m asl ( $r = 0.53$ ,  $p < 0.05$ ). Inclusion  
336 of sites >800 m asl weakened the relationship ( $r = 0.33$ ) but remained significant ( $p < 0.05$ ).  
337 This increased disparity between modern floristic richness and palynological richness in sites  
338 >800 m asl may be due to the openness of the sites (dominated by e.g., heathland, moorland)  
339 with increased extra-local pollen sources (Felde et al. 2016; Markgraf, 1980). Our results  
340 demonstrate a strong link between modern plant richness and pollen richness in SE Australia.  
341 This agrees with the findings of Meltsov, Poska, Reitalu, Sammuli, & Kull (2013) that,  
342 palynological richness better reflects floristic richness when a single climatic region is  
343 considered, with our study restricted to the SE Australian temperate zone. We are aware of  
344 the limitations that surround the use of rarefied pollen assemblages to estimate floristic  
345 richness, especially pollen taxonomic precision and differential pollen production (Birks et  
346 al., 2016). We limited these effects by ensuring consistency in taxonomic resolution of fossil  
347 and modern datasets as much as possible. Distance-weighted plant abundance was also used  
348 to verify the relationship between surface pollen and modern vegetation, which produced  
349 similar results to non-weighted plant abundance (Fig. 2c–d). However, the role of pollen  
350 productivity should be investigated in future studies. We used pollen counts for our modern  
351 and fossil pollen rarefaction analysis, which include potential effects of evenness (Odgaard,  
352 1999; van der Knaap, 2009). While fossil pollen accumulation rates can help to reduce this  
353 bias, they tend to incur large errors from sediment accumulation rate estimation (van der  
354 Knaap, 2009) and cannot be derived for the modern moss samples used here.

355 Other potential sources of error in this study include the nature of fossil pollen sites (e.g.,  
356 swamps, lagoon), the available high-resolution pollen records (e.g., Bass Strait has 4) and site



357 distribution in terms of location and elevation (in Tasmania, mostly mid- to high elevation in  
358 western and central parts). These are unavoidable biases due to the scarcity of high-resolution  
359 pollen records in SE Australia.

360

#### 361 Turnover metric (SCD) verification

362 The SCD threshold (0.2) verified in this study agrees with Northern Hemisphere studies  
363 (Overpeck et al., 1985; Davis et al., 2015). We show that turnover within *Eucalyptus* forests  
364 is low across space on the mainland and Tasmania, which is due to the relative homogeneity  
365 in *Eucalyptus* forest structure across SE Australia. Conversely, the relatively high turnover  
366 scores for *Nothofagus* rainforests are due to the floristic variety of rainforest communities  
367 (high beta diversity) in western Tasmania (Fig. S2 in Appendix S1). For example, several  
368 *Nothofagus*-dominated rainforest types were identified in the vegetation and surface pollen  
369 data, including *Nothofagus-Eucalyptus*, *Nothofagus-Phyllocladus*, *Nothofagus-Pomaderris*  
370 and *Nothofagus-Eucryphia* associations. *Nothofagus* pollen is strongly over-represented,  
371 comprising up to 50% of total pollen even in non-arboreal vegetation and surpassing non-  
372 arboreal pollen like *Gymnoschoenus*, which in fact dominates non-arboreal vegetation  
373 (Mariani, Fletcher, et al., 2016; Fletcher & Thomas, 2010; Macphail, 1979).

374

#### 375 Drivers of turnover and richness in SE Australian temperate ecosystems

376 Our GLM results suggest all predictors contributed to past changes in turnover and richness  
377 to some degree across SE Australia. (Table 2b). However, precipitation:evaporation (SWW-  
378 driven moisture availability), sea-level change (oceanic influence) and temperature appear to  
379 have affected turnover and richness in most regions, considering the lesser contributions of  
380 fire and ENSO (Fig. 4a). Human influence is not included as a driver in our GLMs due to the  
381 patchiness of the archaeological records but is included in our discussion to infer past  
382 anthropogenic land-use and its influence on past turnover and richness. While the proxy  
383 records we modelled are currently the best for the region, especially in terms of resolution,  
384 we acknowledge that the nature and quality of some of the proxies used as drivers of turnover  
385 and richness may have potentially influenced our results.

386

#### 387 *Turnover drivers: Moisture availability and sea-level change*

388 Moisture availability and sea-level change mainly explained Holocene turnover in most parts  
389 of SE Australia, while fire was the major driver of turnover in Bass Strait (Fig. 4a). These  
390 drivers are discussed in the following sections.

391 Changes in SWW flow pattern contribute to precipitation:evaporation changes in temperate  
392 Australia and determine available soil moisture, which is critical for plant growth, seed  
393 production and seedling recruitment (Keith, 2017; Wilkins et al., 2014). The interactions  
394 between precipitation (rainfall) and local factors such as slope and aspect also determine  
395 vegetation structure, composition and distribution on a landscape scale (Keith 2017; Enright,  
396 Miller, & Crawford, 1994). Biomass wetness/dryness influences fire regimes by modifying  
397 the quantity of fuel available to burn (Bradstock 2010), though anthropogenic activities also  
398 control fire regimes, particularly ignitions (Keith, 2017). The fire regime feeds back onto

399 vegetation structure and composition, with high fire activity promoting fire-adapted species  
400 (Keith, 2017; Bowman et al., 2016).

401 Oceanic circulation also modulates temperature and available moisture for plant  
402 growth/productivity in temperate Australia, especially in mid–higher latitudes such as  
403 Tasmania (Duran, England, & Spence, 2020; Keith 2017). Sea-level changes can also directly  
404 shape vegetation structure and composition, especially in coastal areas or small islands by  
405 filtering certain species and growth forms (Kirkpatrick & Harris, 1999; Keith, 2017).

406 Low SWW-driven moisture availability, an increase in ENSO events and higher sea levels  
407 are associated with turnover on the mainland (Table 2a; Fig. 4b). Significant turnover in the  
408 region after the mid-Holocene can be linked to decreasing moisture availability due, in part,  
409 to ENSO intensification, which overrode SWW-driven precipitation during this period  
410 (Fletcher & Moreno, 2012). Increasing drought and fire is thought to have promoted the  
411 expansion of sclerophyllous woodland on the mainland during this period. This may have  
412 also driven changes in understorey composition in woodlands, resulting in a major vegetation  
413 turnover (Kershaw et al., 1991). Furthermore, the increasingly oceanic climate (cool summer,  
414 mild winter) that gets established with sea-level rise would have also promoted longer  
415 growing seasons, a factor that has been linked to turnover in some Southern Hemisphere  
416 ecosystems (Lord, 2019).

417 Direct salt spray and wind damage driven by sea-level rise may have also driven vegetation  
418 changes by supressing trees to promote shrubby and herbaceous vegetation on the mainland,  
419 at least at sites exposed to direct oceanic influence (e.g., Hope, 1974; Martin, 1994). High  
420 soil salinity limits available soil moisture for tree growth and causes tree die-back, reducing  
421 competition in favour of shrub and herb communities (Cramer, Hobbs, Atkins, & Hodgson,  
422 2004; Briggs & Taws, 2003). Similarly, ocean-driven strong winds are capable of removing  
423 trees in woodlands/forests further inland, increasing understorey composition in  
424 woodland/forest gaps (Smart et al., 2014).

425 Conversely, lower sea levels, high moisture availability and low temperature are linked to  
426 high turnover in Tasmania (Table 2a; Fig. 4b). Major turnover before ~11,000 years ago may  
427 be mostly linked to increasing moisture during the lateglacial–Holocene climate transition,  
428 which featured increases in forest cover. The Tasmanian landscape was generally open prior  
429 to the Holocene under a cooler climate and lower sea level (Hopf et al., 2000). The overall  
430 decreasing turnover trend in the region may reflect vegetation stabilisation as climate  
431 transitioned from a continental, cool lateglacial climate, characterized by open vegetation, to  
432 an oceanic climate, characterized by increasing forest cover, as Tasmania became separated  
433 from the Australian mainland due to rising sea-level around 14,000 years ago (Lambeck &  
434 Chappell, 2001; Fig. 4b). High-resolution pollen records spanning beyond the ~13,000-year  
435 records considered in our study are required to better understand turnover in Tasmania during  
436 the glacial period.

437 In Bass Strait, low fire activity is associated with turnover, and the coherence between  
438 turnover and human occupation patterns suggests Aboriginal burning at least partly drove  
439 turnover in the region before the mid-Holocene (Table 2a; Fig. 4b). Aboriginal people may  
440 have used low-intensity fire to shape vegetation in Bass Strait for country keeping during this  
441 period. Low turnover after the mid-Holocene may be related to reduced Aboriginal fire usage  
442 in the region (McWethy et al., 2017; Sim, 1998), with occasional natural fires resulting in  
443 stable vegetation. Contrastingly, Romano & Fletcher (2018) concluded that intensive  
444 Aboriginal land usage stabilized vegetation in northwest Tasmania during in the late

445 Holocene. This disparity may reflect the heterogeneous nature of Aboriginal land use in  
446 southeast Australia in the past.

447

448 *Richness drivers: Sea-level change, temperature and moisture (SWW and ENSO)*

449 Sea-level change primarily explains richness variations across the three regions (Fig. 4a;  
450 Table 2a). As discussed for mainland turnover, higher sea levels are also associated with high  
451 richness on the mainland (Table 2a) and can be related directly to sea-level disturbance (salt  
452 spray and wind damage) and indirectly to the prevalence of an oceanic climate (extended  
453 growing seasons).

454 Conversely, low sea level is associated with high richness in Bass Strait. This can be  
455 explained by the increase in salt stress/damage to plants as Holocene sea levels rose in this  
456 low-lying coastal region. Increased salt stress/damage (e.g., leaf necrosis) can suppress  
457 growth of shrubby/short vegetation, selecting for salt-tolerant species, especially in coastal  
458 sites, reducing richness by promoting only salt-adapted species (Griffiths, 2006). This would  
459 have been pronounced on the Bass Strait islands (which are more exposed to direct salt-laden  
460 winds), as sea level rose through the lateglacial–mid- Holocene, contributing to the  
461 decreasing richness trend in the region during this period (Fig. 4b). As a more oceanic  
462 climate developed, temperate forest and woodland cover spread rapidly in Bass Strait and  
463 Tasmania (McWethy et al., 2017; Hopf et al., 2000). This expansion may have suppressed  
464 open vegetation communities (grasslands and heathlands), resulting in the overall trend in  
465 richness decline in the two regions during the early Holocene.

466 Holocene richness trends can also be interpreted in the light of ecosystem-level responses to  
467 drought. Ecological studies in Asia have shown that resource partitioning is more effective in  
468 saplings of drought-tolerant trees during periods of drought, which in turn promotes tree  
469 diversity (Sugden, 2020). High diversity also reduces the impact of drought in drought-prone  
470 environments such as SE Australia (Grossiord et al., 2014). High richness is associated with  
471 low moisture availability, which might relate to weakened SWW and/or ENSO intensification  
472 in this region (Table 2a). Increasing drought under a warmer climate, likely promoted  
473 species-rich drought-tolerant sclerophyllous woodland, especially on the mainland from the  
474 mid-Holocene (Hopf et al., 2000; Jones, Thomas & Fletcher, 2017; Kershaw et al., 1991;  
475 Yuan, Wang, Cui, Meng, Kurban, & De Maeyer, 2017; Pickett et al., 2004). Aboriginal  
476 managed burning is thought to have also promoted vegetation richness in Australia in the past  
477 (Bird, Bird, & Codding 2016; Bowman, 1998) and the overlap between richness trends and  
478 human occupation patterns across regions suggests Aboriginal land-use may have also  
479 promoted/maintained richness, especially on the mainland and Tasmania in the past (Fig. 4b).

480

481 Fire regime and Intermediate Disturbance Hypothesis (IDH) in SE Australia

482 Fire plays an important role in Australian ecosystems, providing opportunities for on-plant  
483 and in-soil seed bank germination for species continuity and colonization of new habitats  
484 (O’Bryan, Prober, Lunt & Eldridge, 2009; Williams et al., 2012). In line with the IDH, a lack  
485 of fire promotes competitive exclusion, decreasing richness (Keith, McCaw & Whelan,  
486 2002), whereas too much fire selects for pyrophytes, also decreasing richness (Wilkinson,  
487 1999; Kricher, 2011; Catford et al., 2012).

488 Our GAM-based IDH assessment for SE Australia is not statistically significant at the  $p < 0.05$   
489 level (Fig. 5). This is due to the low resolution of pollen records (few data points). Further

490 study to improve sampling resolution is recommended to investigate fire–richness  
491 relationships (IDH) in temperate Australia. Nonetheless, our IDH model shows a hump-  
492 shaped trend, especially in Bass Strait and Tasmania, suggesting moderate fire promoted  
493 richness in these regions during the Holocene, while decreases in richness are associated with  
494 low or high levels of biomass burning. This is in agreement with previous tests of the IDH in  
495 temperate and tropical forest ecosystems (e.g., Colombaroli et al., 2013; Molino & Sabatier,  
496 2001). It is important to note that charcoal records for Tasmania and Bass Strait are of high  
497 resolution (contiguously analysed), while few contiguous records are available for the  
498 mainland. Fire episodes (charcoal peaks) are likely to be missing in mainland records. For  
499 this reason, the IDH pattern for the mainland is considered less robust than that of the other  
500 regions. The overlap between periods of increased human occupation and increase in richness  
501 across regions also suggests Aboriginal-managed burning may have at least partly promoted  
502 richness in SE Australia during the Holocene (Bowman, 1998; Bird, Bird, & Coddling, 2016;  
503 Fig. 4b & 5).

504 [Figure 5 here]

505

## 506 **Conclusion**

507 This is the first comprehensive meta-analysis study of long-term vegetation turnover in  
508 Australia, which provides insight into drivers of change in temperate ecosystems using a  
509 quantitative approach.

510 This study has successfully established an empirical turnover threshold ( $SCD = 0.2$ ),  
511 comparable to pollen-based thresholds developed in other temperate ecosystems globally.  
512 Our study shows different interacting drivers were responsible for vegetation turnover and  
513 changes in richness in SE Australian temperate ecosystems during the lateglacial and  
514 Holocene. Overall, turnover and richness were driven by a combination of moisture  
515 availability, sea-level change, temperature, fire and ENSO. However, moisture  
516 availability/variability (related to SWW and ENSO) and sea-level change appears to be the  
517 primary drivers in most regions. This contrasts with the Northern Hemisphere, where  
518 temperature change was a major driver of turnover during the Holocene.

519 Our Holocene richness reconstructions support the Intermediate Disturbance Hypothesis,  
520 especially in Bass Strait and Tasmania, promoting the notion that high biodiversity was at  
521 least partially maintained by (managed) fire regimes. We propose that moisture availability  
522 (both in terms of amount and variability) and sea-level change (considering its role in  
523 modulating regional oceanic climate) be recognized as key drivers of ecosystem turnover and  
524 richness in Southern Hemisphere temperate ecosystems. These long-term drivers may prove  
525 critical in shaping future turnover and richness changes in SE Australian ecosystems.

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838 **Data accessibility**

839 More information on raw data graphical representation can be found in Appendix S1. Five of  
840 the pollen records used for this study (e.g., Paddy’s Lake—site ID:18866, Granta pool—site  
841 ID:10047, Lake Dove—site ID:19924, Lake St. Clair—site ID:10085) were downloaded  
842 from the Neotoma Paleoecology Database and other pollen records are currently being  
843 uploaded to the same database. Raw surface pollen and vegetation survey data can be  
844 accessed directly by contacting Michela Mariani (University of Nottingham, UK). The 61  
845 southeast Australian mainland charcoal records (and site ID) used in this study can be directly  
846 accessed through the Global Paleofire Database in ‘R’ using the following code after loading  
847 the ‘paleofire’ package: ID=pfSiteSel(lat>-39, lat<(-28), long>140,  
848 long<154,date\_int<=3000). Tasmanian charcoal records (13 sites) can be accessed using the  
849 following code: ID=pfSiteSel(lat>-42, lat<(-40.17), long>140, long<154,date\_int<=3000).

850

851 **Table 1:** Percentiles of the squared chord dissimilarities for the mainland and Tasmania  
852 training set after analogue matching. SCD score above 5% reflect dissimilar vegetation  
853 (Simpson, 2007). Averaged threshold (5%) represents SCD threshold for SE Australia.

	<b>1%</b>	<b>2%</b>	<b>5%</b>	<b>10%</b>	<b>20%</b>
<b>SE Mainland</b>	0.104	0.109	0.143	0.192	0.268
<b>Tasmania</b>	0.162	0.208	0.259	0.327	0.405
<b>Average threshold</b>			0.201		

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856 **Table 2a:** Summary GLMs for the selection of significant predictors of turnover (SCD) and  
 857 richness in Bass Strait (BS), southeast mainland (SEM) and Tasmania (Tas).

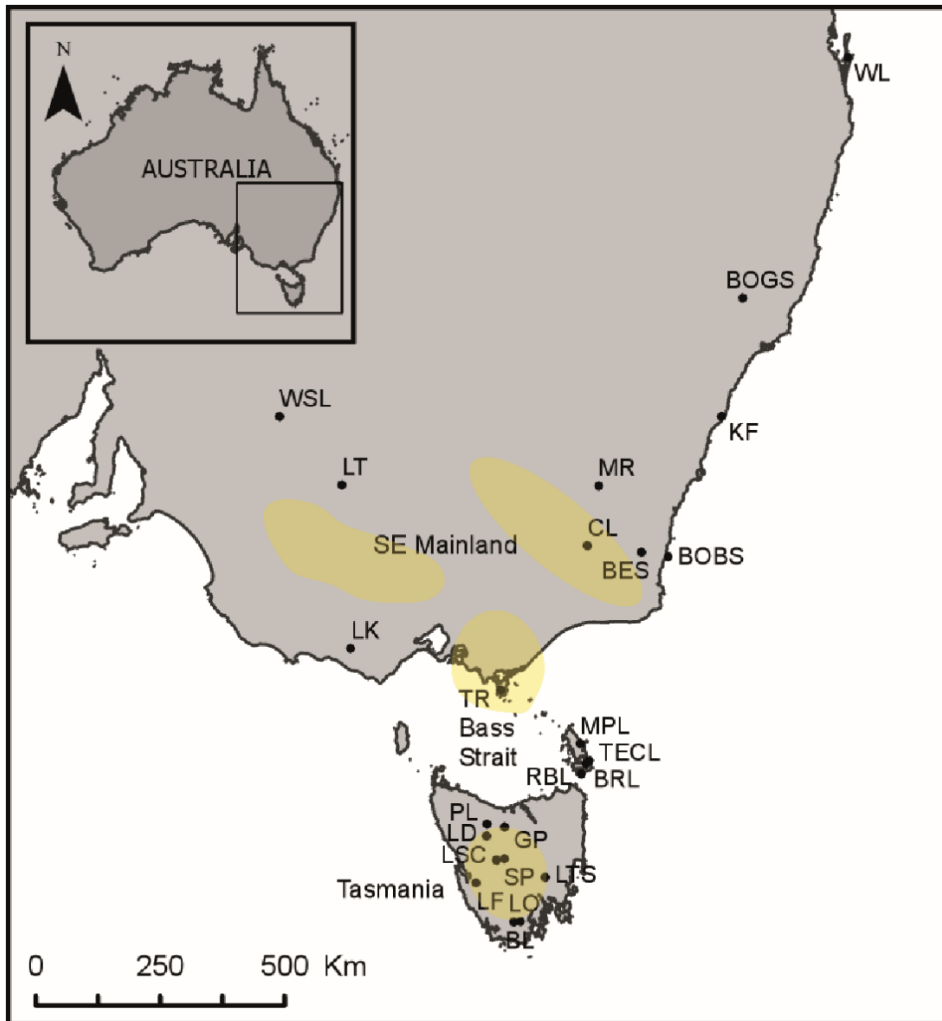
	<i>Turnover (SCD)</i>				<i>Richness</i>		
	<b>Variable</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>BS</b>	<i>Fire</i>	<b>2.33489</b>	<b>-4.331</b>	<b>5.74E-05*</b>	0.25521	-1.771	0.0816
	<i>P:E</i>	1.79148	0.103	0.918	0.19582	-1.563	0.1233
	<i>Sea</i>	0.09587	0.276	0.7839	<b>0.01048</b>	<b>-6.336</b>	<b>3.35E-08*</b>
	<i>Temp</i>	0.17516	-1.775	0.0809	0.01915	-1.744	0.0863
	<i>ENSO</i>	0.16319	0.22	0.8267	0.01784	-1.812	0.075
<b>SEM</b>	<i>Fire</i>	2.07872	1.516	0.134648	<b>0.340735</b>	<b>4.511</b>	<b>3.06E-05*</b>
	<i>P:E</i>	<b>0.76058</b>	<b>-3.204</b>	<b>0.002173*</b>	<b>0.124671</b>	<b>-4.768</b>	<b>1.22E-05*</b>
	<i>Sea</i>	<b>0.03703</b>	<b>3.545</b>	<b>0.000769*</b>	<b>0.00607</b>	<b>15.909</b>	<b>&lt; 2E-16*</b>
	<i>Temp</i>	0.07251	1.694	0.095512	<b>0.011885</b>	<b>4.455</b>	<b>3.72E-05*</b>
	<i>ENSO</i>	<b>0.06799</b>	<b>2.97</b>	<b>0.004276*</b>	0.011144	0.131	0.896
<b>Tas</b>	<i>Fire</i>	0.67282	0.608	0.545684	0.40109	-0.646	0.520714
	<i>P:E</i>	<b>0.41441</b>	<b>4.292</b>	<b>6.56E-05*</b>	0.24704	-0.967	0.337668
	<i>Sea</i>	<b>0.02777</b>	<b>-12.654</b>	<b>&lt; 2E-16*</b>	<b>0.01655</b>	<b>-2.517</b>	<b>0.014518*</b>
	<i>Temp</i>	<b>0.03488</b>	<b>-4.769</b>	<b>1.22E-05*</b>	<b>0.02079</b>	<b>-2.963</b>	<b>0.004361*</b>
	<i>ENSO</i>	<b>0.03497</b>	<b>2.145</b>	<b>0.035972*</b>	<b>0.02085</b>	<b>3.975</b>	<b>0.000192*</b>

858 \*Significant ( $p < 0.05$ ) variables selected for GLMs in Table 2b.

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875 **Table 2b:** GLMs relating vegetation turnover (SCD) and richness (Rich) as a function of  
876 significant predictors identified for southeast mainland (SEM) and Tasmania (Tas) in Table  
877 2a, which included temperature (temp), ENSO, fire, precipitation:evaporation (P:E) and sea-  
878 level change (sea). Models are ranked based on Akaike's information criterion corrected for  
879 small sample sizes (AICc) and delta AICc. Also shown are percentage of deviance explained  
880 and marginal R<sup>2</sup> (Rm). For Bass Strait, only fire (sea-level change) was significantly ( $p<0.05$ )  
881 related to turnover (richness) during variable selection in Table 2a. Therefore, fire and sea-  
882 level change are taken as the major driver of turnover and richness in the region, respectively.

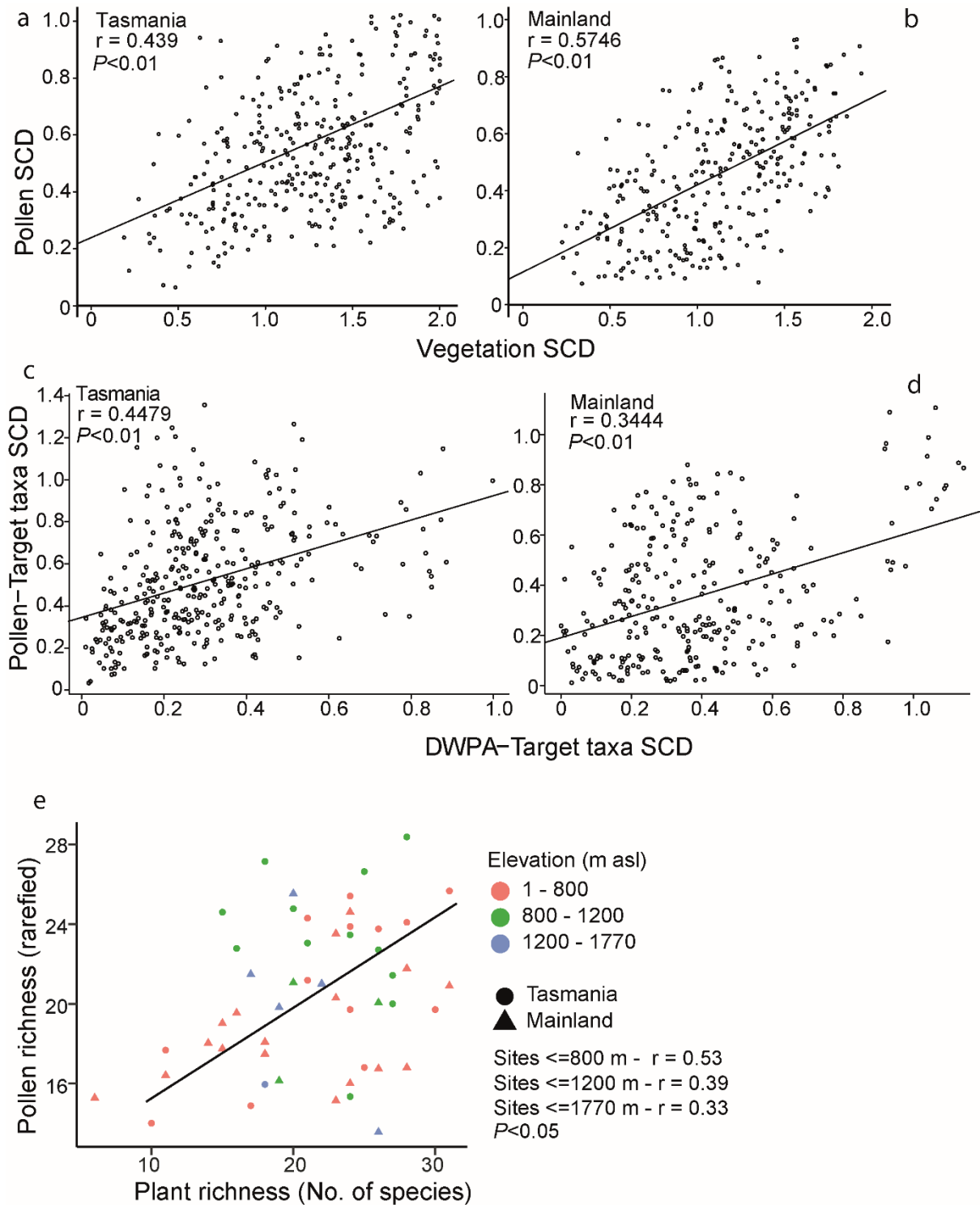
	<b>Model</b>	<b>AICc</b>	<b>dAICc</b>	<b>Rm</b>	<b>%Deviance</b>
<b>BS</b>	1 <i>SCD ~ Fire</i>	-	-	-	-
	1 <i>Rich ~ Sea</i>	-	-	-	-
<b>SEM</b>	1 <i>SCD ~ ENSO+P:E+Sea</i>	185.9702	0	49.6	70.6
	2 <i>SCD ~ ENSO+Sea</i>	186.6286	0.658	45.15	62.4
	3 <i>SCD ~ ENSO+P:E</i>	188.6671	2.697	42.2	52.5
	4 <i>SCD ~ Sea+P:E</i>	197.0497	11.079	28.34	63.1
	<i>Null</i>	205.2042	19.234	0	
	1 <i>Rich ~ Sea+Temp+P:E+Fire</i>	61.152	0	90.79	95.8
	2 <i>Rich ~ Sea+Temp+P:E</i>	69.40632	8.254	87.87	94.8
	3 <i>Rich ~ Sea+Temp</i>	69.78211	8.63	86.92	94.1
	4 <i>Rich ~ P:E+Sea</i>	75.81581	14.664	84.79	94.8
	5 <i>Rich ~ Fire+Sea</i>	81.52133	20.369	82.46	87
	6 <i>Rich ~ Fire+Temp</i>	121.4014	60.249	52.47	0
	7 <i>Rich ~ P:E+Temp</i>	129.9882	68.836	41.09	0
	8 <i>Rich ~ Fire+P:E</i>	137.1007	75.949	29.63	0
	<i>Null</i>	146.3388	85.187	0	
	<b>Tas</b>	1 <i>SCD ~ Sea+Temp+P:E+ENSO</i>	141.0679	0	93.25
2 <i>SCD ~ Sea+Temp+P:E</i>		145.0892	4.021	91.96	96.7
3 <i>SCD ~ Sea+P:E</i>		150.2798	9.212	90.17	84.2
4 <i>SCD ~ Sea+Temp</i>		153.851	12.783	89.23	92
5 <i>SCD ~ ENSO+Sea</i>		164.5718	23.504	85.82	0
6 <i>SCD ~ Temp+P:E</i>		219.5086	78.441	42.02	
7 <i>SCD ~ ENSO+Temp</i>		221.9746	80.907	38.23	
8 <i>SCD ~ ENSO+P:E</i>		235.4719	94.404	12.69	
<i>Null</i>		235.9219	94.854	0	
1 <i>Rich ~ Sea+Temp+ENSO</i>		94.76423	0	49.2	63.2
2 <i>Rich ~ ENSO+Sea</i>		96.20435	1.44	43.59	59.8
3 <i>Rich ~ Sea+Temp</i>		101.6355	6.871	35.16	0
4 <i>Rich ~ ENSO+Temp</i>		110.4195	15.655	18.78	57.3
<i>Null</i>		113.6897	18.925	0	



884

885 **Figure 1:** Map showing site location of temporal and spatial data used in this study. Black  
 886 dots represent sites of fossil pollen records on the mainland, Bass Strait islands and  
 887 Tasmania. Key to site codes is included in Table S1 in Appendix S1. Yellow shading  
 888 indicates area where modern vegetation survey and surface pollen were sampled on the  
 889 mainland and Tasmania (Mariani, Connor, et al., 2016).

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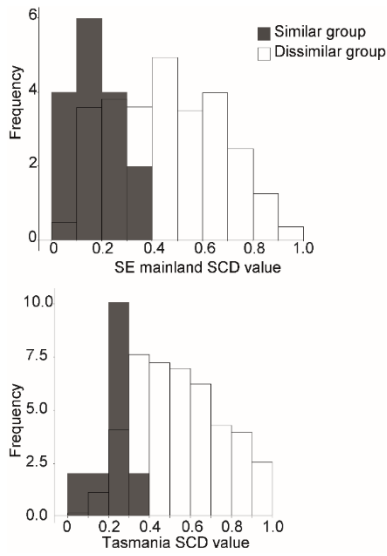
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892 **Figure 2:** Scatter plot showing positive relationship (based on Mantel test) between  
 893 dissimilarities of modern vegetation and surface pollen in SE mainland and Tasmania (a–b),  
 894 and similar pattern is observed using distance-weighted plant abundance (DWPA) of major  
 895 vegetation and pollen taxa (c–d). Richness comparison (e) between plants and pollen using all  
 896 samples from mainland and Tasmania, showing relationship distribution along elevation  
 897 gradients. Regression line shows best relationship ( $r=0.53$ ) with the removal of high-  
 898 elevation sites  $>800$  m asl (following Felde et al. 2016).

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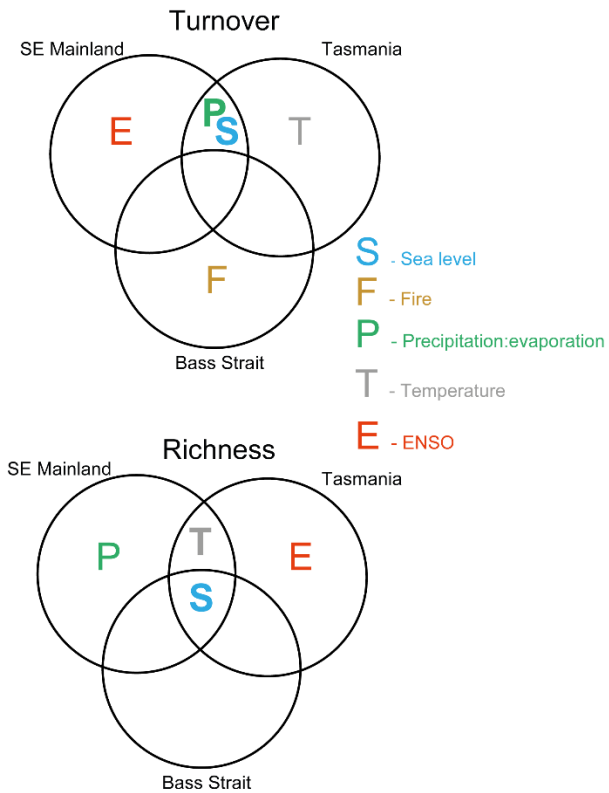
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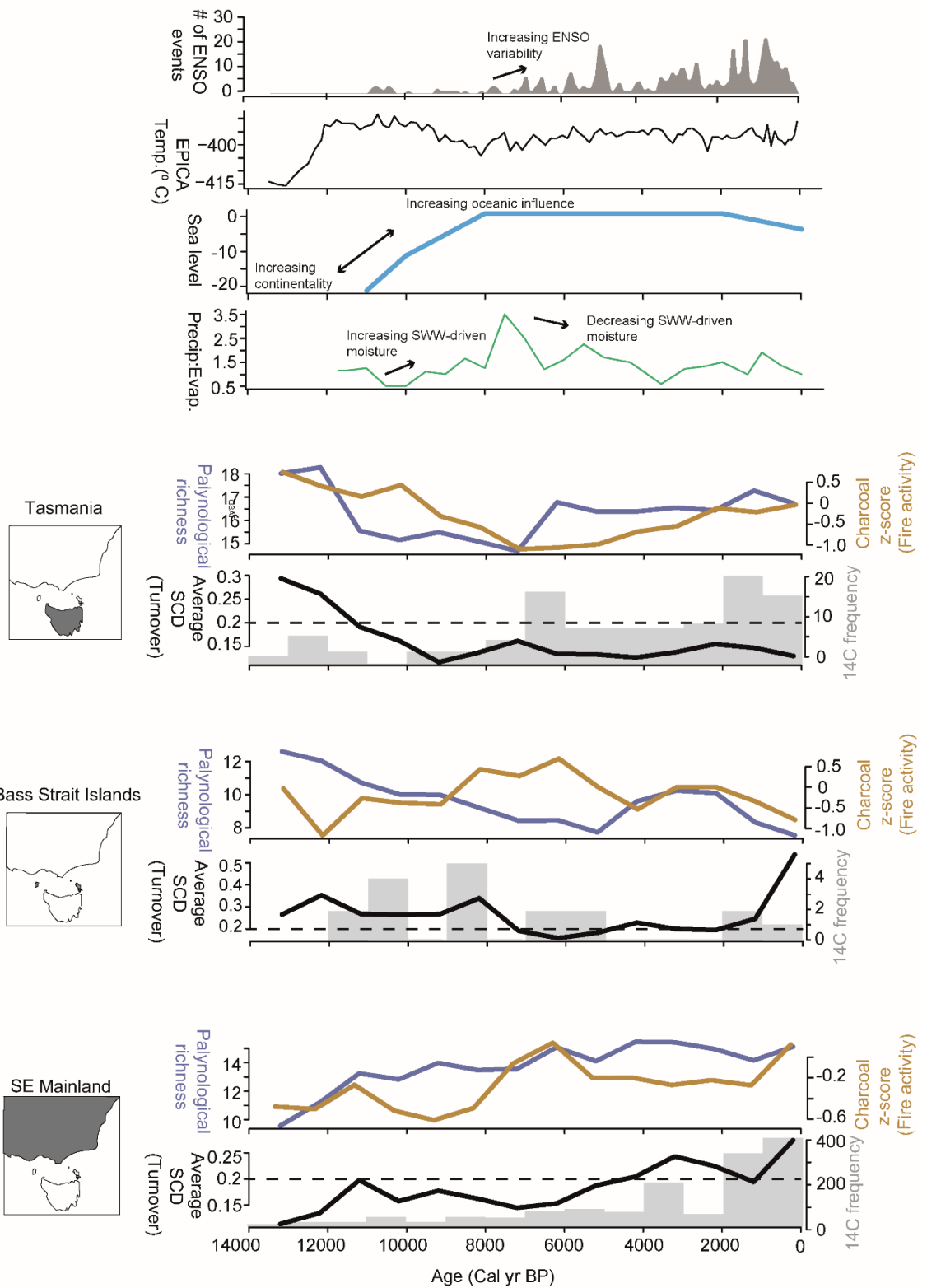
902 **Figure 3:** Histogram showing Squared Chord Distances (SCDs) of similar and dissimilar  
 903 vegetation groups/sites on the SE mainland and Tasmania, used in developing the empirical  
 904 turnover threshold. In general, similar vegetation types (grey) have an SCD < 0.3, while most  
 905 dissimilar vegetation groups/sites are above SCD > 0.3. The empirical threshold of 0.2 SCD  
 906 indicates significant vegetation turnover in pollen assemblages (Table 1).

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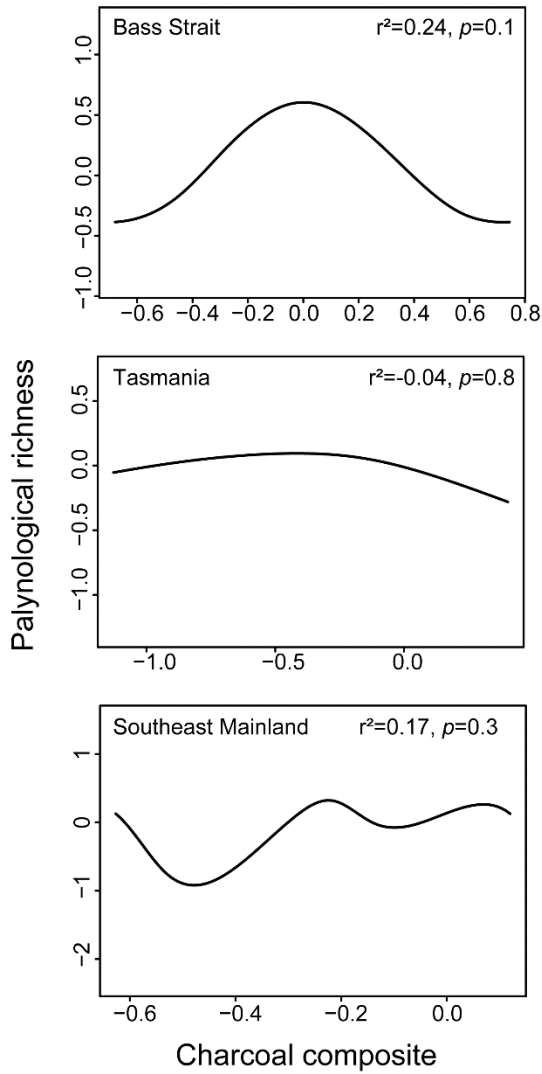
909 **Figure 4a:** Summary Venn diagrams showing major predictors of turnover and richness  
 910 based on GLM results in Table 2b. Predictors in bold explain turnover and/or richness in  
 911 more than one region.



914 **Figure 4b:** Lateglacial and Holocene rates of turnover (black) and richness (purple) in SE  
 915 Australia in relation to composite charcoal concentration z-score (yellow), number of El Niño  
 916 Southern Oscillation (ENSO) events (Moy et al., 2002), precipitation:evaporation (available  
 917 moisture)(Wilkins et al., 2013), relative Holocene sea levels of coastal SE Australia (Sloss et  
 918 al., 2007), and EPICA Dome C temperature (Stenni et al., 2001). Grey histograms represent

919 the number of radiocarbon dates from human occupation sites, drawn from the Australia  
920 Archaeology data base (Williams et al., 2014). Black dash line represents the empirical  
921 threshold ( $SCD > 0.2$ ) for significant vegetation turnover. Each average SCD point represents  
922 dissimilarity between adjacent time bins e.g., the average SCD point at ~1000 represents the  
923 dissimilarity between 500 and 1500 cal yr BP.

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925

926 **Figure 5:** Testing the Intermediate Disturbance Hypothesis: Generalized Additive Model,  
927 showing relationships between charcoal composite (fire) and reconstructed richness in Bass  
928 Strait, Tasmania and the southeast mainland.

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