

# 1 **Effects of hydrological change in fire-prone wetland**

## 2 **vegetation: an empirical simulation**

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### 9 **Abstract**

10 Upland swamps are peat-accumulating, groundwater-dependent and fire-prone wetland  
11 ecosystems. Drying caused by anthropogenic processes such as underground mining, ditching and  
12 climate change may disrupt surface and groundwater flows effecting a bottom-up control on  
13 wetland expression. Fire is an endogenous, recurring disturbance that drives a top-down  
14 consumptive force in many of these systems. When compounded with anthropogenic drying, fire  
15 may facilitate permanent community transitions. A dearth of ecological data and temporal lags have  
16 hampered our ability to predict risks associated with multiple disturbances in wetland plant  
17 communities. We collected intact wetland mesocosms from valley floors and lower slopes of four  
18 undisturbed swamp sites. We transferred the mesocosms to a glasshouse and established three  
19 different soil moisture availability levels to simulate wetland drainage. After 20 months of the  
20 hydrological treatment, we simulated a fire event by sequentially applying biomass removal  
21 (clipping), heat and smoke to half of the mesocosms. We monitored species biomass, richness and  
22 composition over a 3.5-year time frame. We found evidence of a temporal lag in biomass response  
23 to low water availability and synergistic hydrological and fire effects on species richness. In unburnt

24 conditions, richness declined with low water availability but was maintained under high and medium  
25 water availability. After simulated fire in medium water availability, however, richness also declined  
26 and converged with depauperate low water mesocosm richness. Representation by many obligate  
27 swamp species declined in low compared with high water availability mesocosms over time, an  
28 effect that was amplified by the fire treatment.

29 **Synthesis:** Our evidence of lagged effects of hydrological change on wetland vegetation and  
30 compounding effects of fire should be considered in impact assessments, monitoring programs and  
31 ecosystem management to avoid irreversible wetland change in drying environments.

32

### 33 **Introduction**

34 The relative contribution of bottom-up (resource availability) or top-down (consumer pressure)  
35 processes to community assembly has long focused ecological enquiry (e.g. Hunter and Price, 1992,  
36 Hairston et al., 1960, Bond, 2021). Bottom-up forces may include abiotic resource availability such as  
37 nutrients or water (Matson and Hunter, 1992) while top-down forces may include predator or  
38 herbivore activity (Kriegisch et al., 2016, Spiller and Schoener, 1990) or even fire activity (Bond and  
39 Keeley, 2005) as consumptive controls. Bottom-up and top-down forces may act simultaneously or  
40 with alternating patterns of dominance (Litzow and Ciannelli, 2007). Analysis of vegetation change  
41 when these forces interact may assist in understanding the mechanism of freshwater wetland  
42 community transitions under environmental change.

43 Hydrology is a sensitive and fundamental driver of freshwater wetland function and ecosystem  
44 service provision. It is therefore unsurprising that bottom-up controls have been considered  
45 dominant in wetland systems (Moore and Schmitz, 2021 and references therein). Inundation  
46 duration, depth and frequency influence root hypoxia, plant zonation and ultimately species  
47 composition (Blom and Voeselek, 1996, Campbell et al., 2016). Hydrological regulating and  
48 provisioning services including water purification, flood mitigation and water supply, along with  
49 carbon sequestration and biodiversity (Ramsar Convention on Wetlands, 2018) are important  
50 ecosystem services offered by wetlands. However, delivery of these services is threatened by drying  
51 and associated change to bottom-up resource availability. At the local or regional scale,  
52 underground mining and fracking extractive processes (Mason et al., 2021) and ditching (Löhmus et  
53 al., 2015) or surface drainage (Woo and Young, 2005) affect water availability. At the global scale,  
54 climate change (particularly declining precipitation : evapotranspiration ratios), eutrophication and  
55 acid rain cause large-scale disruption of hydrological resources (Zedler and Kercher, 2005).

56 Alteration of water quantity through a change in flooding regimes may profoundly affect wetland  
57 expression by advantaging a new suite of species and driving community shifts along hydrological

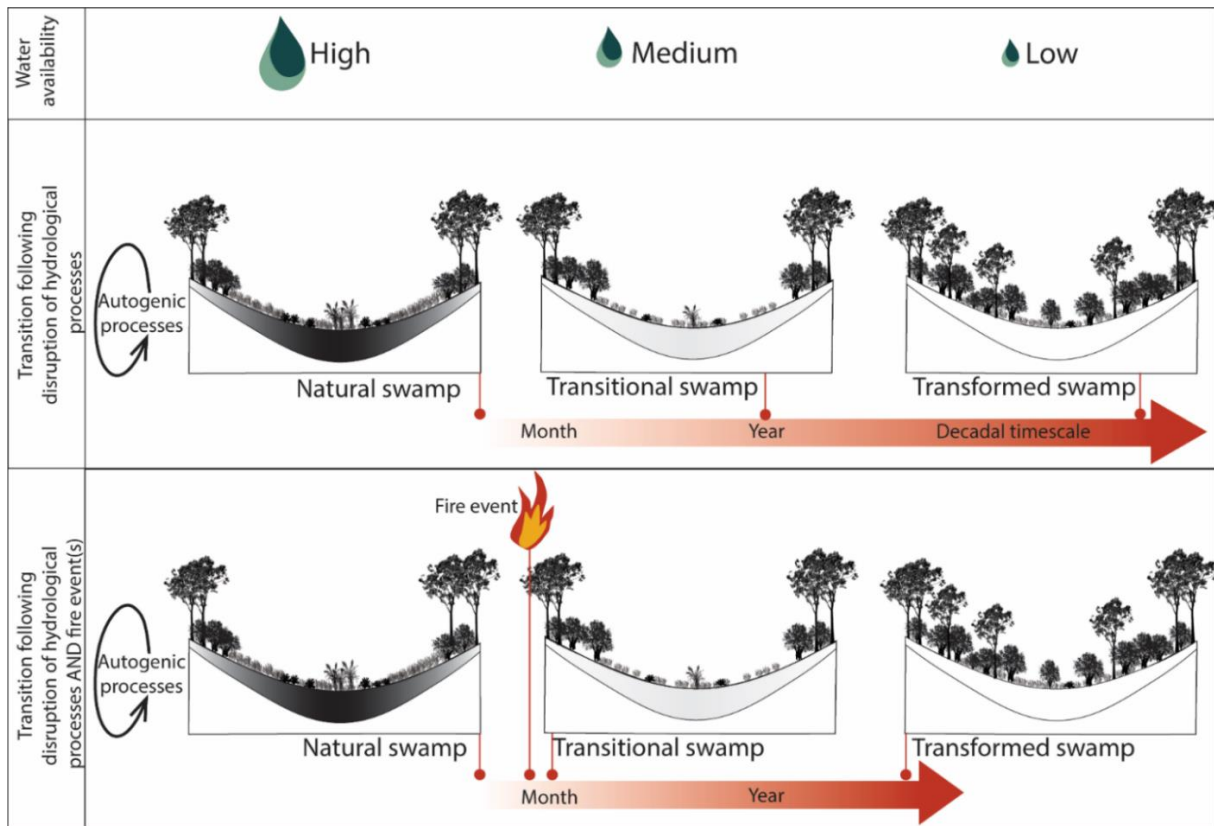
58 gradients (e.g. Zweig et al., 2020). However, if community reorganisation remains within thresholds  
59 for wetland function, redistribution of species along a hydrological gradient could represent an  
60 autonomous adaptation of an ecosystem while maintaining its function (Serrao-Neumann et al.,  
61 2016). Indeed, obligate wetland species have demonstrated considerable physiological tolerance to  
62 drying and may simply use flooded conditions as refugia from terrestrial competitors (Campbell et  
63 al., 2016, Blom and Voeselek, 1996).

64 Periodic imposition of top-down consumptive forces such as fire may “reset” wetland community  
65 status along divergent bidirectional succession trajectories towards either terrestrial or aquatic  
66 endpoints (Zweig and Kitchens, 2009). Fire consumes aboveground biomass and initiates  
67 recruitment through heat, smoke or light stimuli and enhanced resource availability (Whelan, 1995).  
68 The degree to which fire mediates a successional reset depends on hydrologic and vegetation  
69 legacies within the community (see Zweig and Kitchens, 2009 for a related discussion). If fire occurs  
70 when a wetland is within natural hydrological thresholds, the pre-fire community may re-establish  
71 (e.g. Clarkson, 1997, Flores et al., 2016). However, when fire occurs during novel hydrological  
72 conditions, it may initiate alternative successional pathways (e.g. Sulwiński et al., 2020).

73 Interactions between top-down and bottom-up processes may influence both the trajectory and the  
74 rate of successional change (Zweig et al., 2020 and references therein). Hydrological drivers alone  
75 may initiate gradual community change: Lõhmus et al. (2015) found that stand replacement  
76 occurred over multiple decades following forestry drainage (Lõhmus et al., 2015). Merritt and  
77 Cooper (2000) found that channel vegetation responded to river flow regulation over similar time  
78 frames. However, an interaction with fire may have synergistic effects that accelerate such  
79 transitions. For example, Turetsky et al. (2011) found elevated combustion losses of soil carbon  
80 when wildfire and water table drainage interacted in boreal peatland, while de Oliveira et al. (2014)  
81 found synergistic effects of fire on flood-prone riparian species composition and stem density. These  
82 interactions between top-down and bottom-up processes can strongly affect vegetation and

83 biodiversity outcomes (Hunter and Price, 1992, Naeem, 2008, Wilkinson and Sherratt, 2016).  
84 However, disentangling singular and synergistic effects and testing conceptual models require an  
85 empirical approach with realistic yet controlled conditions (Srivastava et al., 2004).

86 Upland swamps are climatically marginal ecosystems on uplands and plateaus of southeastern  
87 mainland Australia and Tasmania (Keith et al., 2014). These groundwater-dependent and peat-  
88 accumulating wetlands support mosaics of wet heath communities comprising sclerophyll shrubs  
89 and graminoids that range from Ti-tree thicket and Cyperoid heath in the wettest conditions to  
90 Restioid heath, Sedgeland and Banksia thicket in drier conditions (Keith and Myerscough, 1993).  
91 Within swamps, fire is a recurrent disturbance (Mooney et al., 2021) that shapes subcommunity  
92 distributions (Keith and Myerscough, 1993). Swamp-woodland mosaics are likely sensitive to climatic  
93 moisture and fire history (Keith et al., 2010) and recent longwall underground coal extraction has  
94 caused subsidence, diminishing water resources and homogenising of the hydrological gradient,  
95 effects that persist long after coal extraction (Mason et al., 2021). The recent 2019-20 major bushfire  
96 season in eastern Australia provided observational evidence that mined upland swamps experienced  
97 abiotic and biotic change relative to unmined swamps in the post-fire environment and exhibited  
98 symptoms of ecosystem collapse (Keith et al., 2022). While the results were consistent with top-  
99 down fire accelerating more gradual ecosystem responses to bottom-up hydrological change,  
100 controlled empirical manipulations are required. In the current study we postulated that: 1)  
101 hydrological change initiates a transition in which productivity and composition diverge from that in  
102 the groundwater-dependent community; and 2) that a subsequent fire event causes more rapid  
103 transformation to a novel state by resetting the community and enabling less hydrophilous species  
104 to gain dominance (Figure 1).



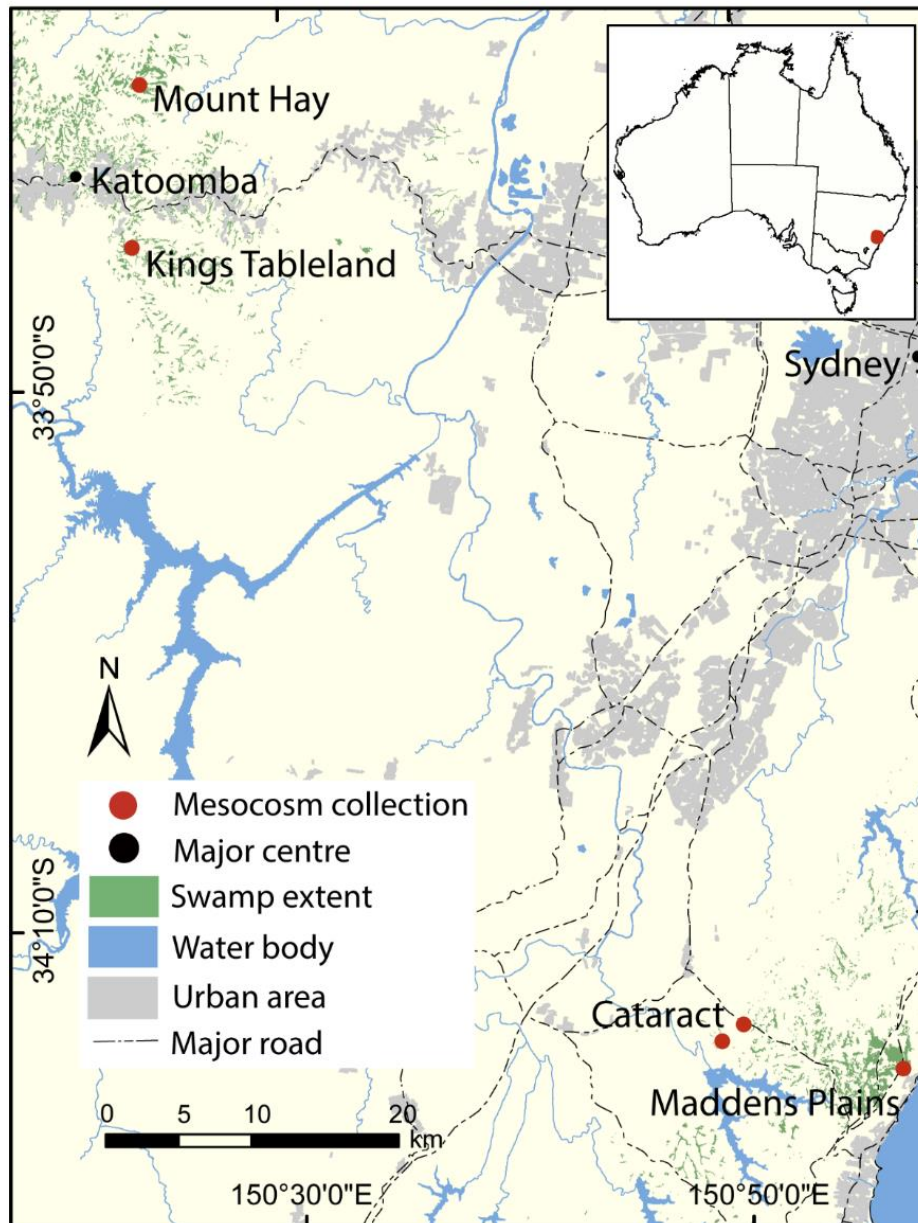
105  
 106 *Figure 1: Conceptual model of swamp transition after changes to bottom-up (underground longwall mining) and top-down*  
 107 *(periodic fire) processes over decadal time periods. Note that wet to dry soil conditions are illustrated with black (wet)*  
 108 *gradation to white (dry) for the idealised hydrological gradient in the Natural swamp. Vegetation properties may differ*  
 109 *among transformed swamps experiencing hydrological disruption alone vs. hydrological disruption and fire disturbance.*  
 110

111 Here we experimentally assessed the influence of bottom-up and top-down forcing on upland  
 112 swamp communities. We manipulated hydrological resource availability and fire occurrence in *ex*  
 113 *situ* swamp mesocosms. Specifically, we asked: (1) Does reduced water availability affect wetland  
 114 function and composition? (2) Is there evidence of a lagged response to bottom-up water resource  
 115 availability? (3) Does fire interact with hydrological change by accelerating the lagged response in  
 116 community function and composition? Comparing the importance of hydrological change and fire in  
 117 determining biomass allocation and species composition will help to understand whether fire  
 118 facilitates a transition of groundwater-dependent wetland communities to novel terrestrial  
 119 ecosystems.

120 **Materials and Methods**

121 **Field collection**

122 We collected intact mesocosms comprising above ground and root biomass along with soil material  
123 from four undisturbed upland swamp sites in the Sydney Basin during February and March 2017.  
124 Two sites were on the Woronora Plateau south of Sydney and two sites were in the Blue Mountains  
125 west of Sydney (Figure 2). Regional distinctions in species compositions have been recognised  
126 (Department of the Environment, 2014, Tozer et al., 2010).



127

128 *Figure 2: Location of mesocosm collection sites on the Woronora Plateau and Blue Mountains area. Inset top right shows*  
129 *location of study area (red) in Australia. Temperate Highland Peat Swamps on Sandstone layer obtained from Fryirs and*  
130 *Hose (2016). Note that transects at Cataract were at proximate swamps while transects at all other locations were at the*  
131 *same swamp.*



## 132 **Experimental procedure**

133 We used a stratified, random approach to collect mesocosms along transects within both drainage  
134 zone (Ti-tree thicket) and mid slope (Cyperoid heath) plant communities. Mesocosms were  
135 positioned at least 0.5 m distant from each other and all swamp sites had been recently burnt (<20  
136 months ago). In total, 248 mesocosms were collected (31 replicates x 2 plant communities x 4 sites)  
137 and their coordinates recorded. Mesocosms had a diameter of 150 mm and a depth of 250 mm and  
138 were housed in PVC sleeves which were hammered to ground level and extracted with trenching  
139 shovels. In order to minimise transplant shock, the above ground vegetation was clipped to  
140 approximately 10% of the original biomass and mesocosms were bagged, then transported to the  
141 glasshouse within 2 days of collection (Whalley and Brown, 1973). Mesocosms from each site were  
142 allowed to acclimatise for a month (28 days), with regular watering prior to treatment allocation.  
143 The experimental setup was therefore staggered according to dates of field collection, commencing  
144 on the 24<sup>th</sup> of March and completed on the 28<sup>th</sup> of April 2017. We found that some mesocosms  
145 subsided in the PVC casing after collection. This was problematic as the treatment effect relied on  
146 water depth in the tubs. We packed the lower section of the subsided mesocosms with a 50:50 mix  
147 of river sand and peat moss to facilitate capillary action up the casing. All mesocosms were capped  
148 at the bottom with a permeable polyester fabric and affixed with cable ties. Our approach balanced  
149 tractability (replication and precise treatment application) with realism (initial species composition  
150 and nutrient regimes) (refer to Srivastava et al., 2004 for a related discussion, Naeem, 2001).

151 Mesocosms were randomly allocated to three water treatment levels and dispersed in tubs  
152 throughout the glasshouse. They were randomly relocated periodically within their treatment tubs  
153 across the glasshouse to minimise location and neighbour competition bias. We manipulated tub  
154 water levels to simulate different groundwater availability within mesocosms. We maintained water  
155 levels of treatment tubs (without top watering the mesocosms) to 70 mm, 155 mm and 240 mm  
156 below the mesocosm surface for the high, medium and low water level respectively. Initially we



157 added water at weekly intervals (April 2017- December 2018). We increased the frequency of water  
158 addition (to biweekly) during summer (December to January) of 2018-19 to ensure emergence of  
159 seedlings immediately after fire simulation so their responses to water treatment could be tracked.  
160 We then added water at fortnightly (January 2019-November 2020) intervals to simulate ongoing  
161 drying of swamps above longwall mine paths (Mason et al., 2021). The same watering frequencies  
162 were applied across all water treatment levels. Volumetric soil water content (%) was monitored at  
163 interval using a Moisture Probe Meter (ICT International Pty Ltd MPM-160-B) with a 60 mm probe  
164 (average of three readings per mesocosm). Soil moisture values were initially within the range for  
165 the vadose zone of an undisturbed Cyperoid heath swamp (Mason et al., 2021). By the latter part of  
166 the experiment, the low water treatment yielded soil moisture values that overlapped the lower  
167 range for mined upland swamps (Keith et al., 2022).

168 After approximately 587 days (~20 months) of the water treatment, we simulated a single fire event  
169 by sequentially clipping, heating and applying smoked water to half (124) of the mesocosms. We  
170 randomly selected mesocosms for burning treatment from each combination of water level and site.  
171 During October and November 2018, we clipped all biomass at ground level and bagged each species  
172 separately. We applied heat to the clipped soil surface using a propane burner (refer to Vesk et al.,  
173 2004 for a similar method). The burner was held approximately 10cm from the soil surface and the  
174 flame was constantly played across the mesocosm surface for three minutes. A pilot study indicated  
175 that 3 minutes was sufficient duration to provide temperatures > 60°C at 1 cm depth, and this was  
176 sufficient to break dormancy of some buried seed (Auld and Bradstock, 1996). We monitored heat  
177 penetration during the fire simulation by deploying a temperature datalogger (Thermochron  
178 ibutton, Maxim Integrated Products, Inc. San Jose, USA) at approximately 1 cm and 3 cm depth in  
179 each mesocosm. We used the maximum temperature (°C) recorded at each depth.

180 We generated smoked water following the method of Dixon et al. (1995) and using locally sourced  
181 leaf and twig material. The smoked water was applied to the clipped and heated mesocosms at a

182 dilution of 1 part concentrate to 10 parts water (Read and Bellairs, 1999). Smoked water was applied  
183 to the soil surface 11 days after the heating component of the treatment. We used this approach to  
184 simulate a rain event after fire which would allow smoke particles to percolate through the soil and  
185 contact the seed bank. Unburnt mesocosms were top watered with tap water as a procedural  
186 control.

187 We monitored species composition at intervals throughout the experiment. We destructively  
188 harvested above ground biomass at two time points. Firstly, during the fire simulation and only for  
189 the fire-simulation mesocosms (~ Day 587), and secondly at the conclusion of the experiment (~ Day  
190 1261) where above ground biomass was harvested for all mesocosms. In both cases, individuals  
191 were clipped at ground level, bagged, oven dried at 60°C for at least three days and weighed (AND  
192 GR-202 Series Balance  $\pm$  1.0 mg).

### 193 **Data analysis**

194 To examine the responses of above ground live biomass (measured at two time points) and species  
195 richness (measured at nine time points), we fitted linear mixed models with main effects and two-  
196 way interactions of time (categorical with 2 levels), water treatment (3 levels) and fire treatment (2  
197 levels), controlling for fixed effects of swamp and vegetation type, and a random effect for  
198 mesocosm (to model dependence over time). To examine the responses of species composition, we  
199 used presence data and applied a multivariate linear mixed model, with a binomial distribution. The  
200 model used the same time points as the species richness linear model. We used a reduced rank  
201 correlation structure to model dependence between species (McGillycuddy et al. in prep). The  
202 model had fixed effects for time (linear), water treatment and fire treatment and their two-way  
203 interactions, and main effects of swamp and vegetation type. It also had (by species) random slopes  
204 corresponding to all the fixed effects, to allow species to respond differently to the treatment and  
205 environmental variables, as well as a mesocosm random effect to model dependence over time.  
206 Time was represented as a linear variable in the multivariate model as presence/absence data did

207 not have enough information to estimate effects for each of the nine time points. The multivariate  
208 model was an extension of a generalised linear latent variable model (Niku et al., 2019) to allow  
209 additional random effects. This model allowed us to distinguish between (a) overall (uniform across  
210 species) trends in presence/absence by looking at fixed effects and (b) compositional changes -  
211 where species with atypical presence probabilities contributed to the composition effect. A  
212 treatment effect confidence interval that did not bracket zero suggested evidence of a treatment  
213 effect for that species. In addition, if it did not bracket the fixed effect value, then this species  
214 differed from the average treatment effect for all species, and therefore contributed to a  
215 compositional effect.

216 In all models, we examined two effects of interest: (a) time x water treatment interaction, to  
217 compare trends over time between water treatments, and (b) the water treatment x fire treatment  
218 interaction, to examine synergistic effects of water and fire treatments. In addition, using the  
219 multivariate model above, we fitted fourth corner models (Brown et al., 2014) by adding an  
220 interaction with species traits to determine if compositional changes were explained by two species  
221 traits, hydrological niche and fire response. Hydrological niches were assigned to species as *non-*  
222 *hydrophile* (no specific water demand in the substrate), *moderate hydrophile* (intermittently moist  
223 substrate) or *strong hydrophile* (permanently moist substrate) requirements. Fire responses were  
224 assigned to species as resprouter, killed, variable or unknown. Hydrological niches and fire responses  
225 were assigned to species based on Benson and McDougall (1993 - 2002, 2005).

226 To verify the water treatment, we fitted a linear mixed model to soil moisture measured at 15 time  
227 points with water treatment (3 levels) and fire treatment (2 levels), as well as fixed effects of swamp  
228 and vegetation type, and a random effect for mesocosm (to model dependence over time). To verify  
229 the fire treatment, we fitted a model to mean maximum soil temperatures measured during the fire  
230 treatment. We included depth within soil profile (1cm or 3cm), water treatment and their  
231 interaction as fixed effects, and a random effect of mesocosm.

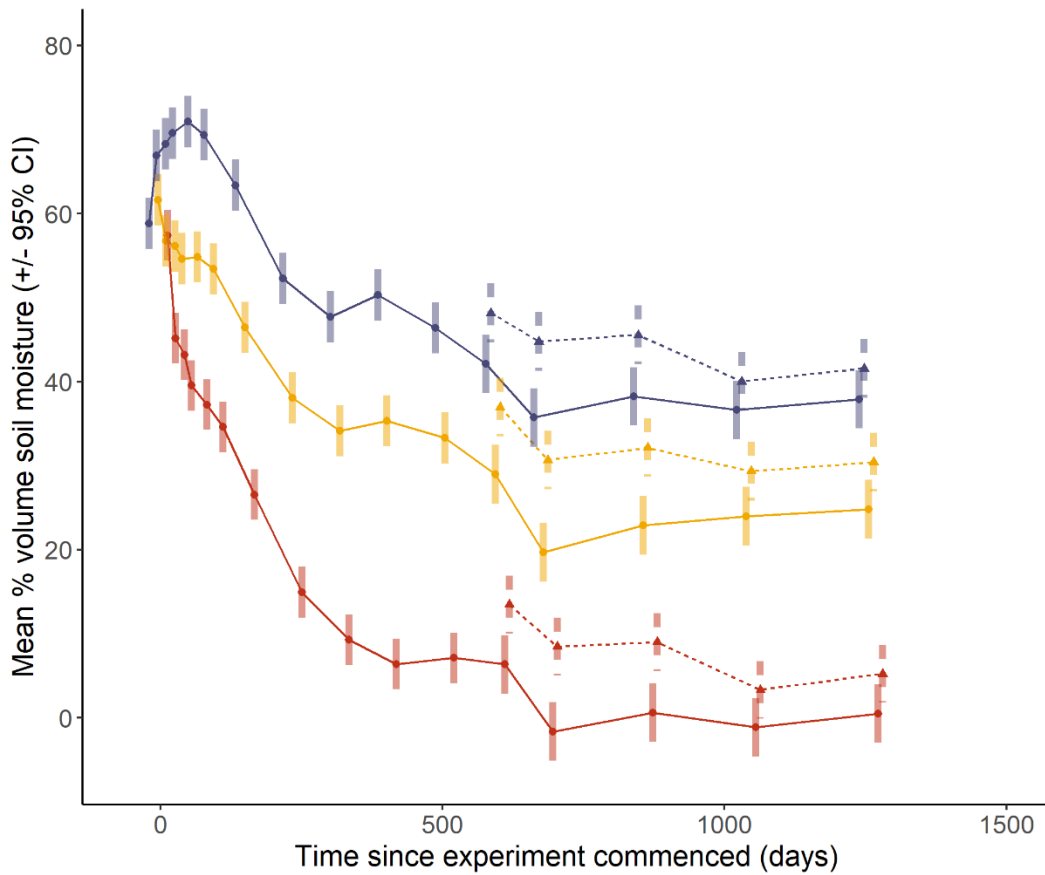
232 For all models, residuals were checked, and the response was transformed, or distribution changed,  
233 as necessary to meet model assumptions. The final model for biomass used  $\log(\text{biomass} + 1)$  as the  
234 response. For biomass and richness, we compared changes by treatment between two time points  
235 when data were mutually available: immediately prior to the fire treatment and at conclusion of the  
236 experiment. We adjusted for multiple pairwise tests using the multivariate t distribution. For  
237 multispecies models, we compared effects across species and traits, and did not control for multiple  
238 testing.

239 Most analyses used the glmmTMB package (Brooks et al., 2017) in R (R Core Team, 2021), with  
240 further analysis using the lme4 (Bates et al., 2015) and emmeans (Lenth, 2022) packages. We used  
241 lme4 when it interacted better with emmeans for rank deficient models (due to an unbalanced  
242 design for the fire treatment).

## 243 **Results**

### 244 *Hydrological and fire treatment effects on soil moisture and temperature*

245 We found very strong evidence that soil moisture levels differed as expected among the three water  
246 treatment levels (Figure 3). Low water mesocosms dried more quickly than either medium or high  
247 water mesocosms (water treatment : time interaction  $F_{30, 3674} = 19.070$ ;  $P < 0.001$ , Figure 3). High  
248 water mesocosms also experienced reduction in soil moisture across the experiment, presumably as  
249 shoot and root growth progressed after initial clipping. Burnt mesocosms had an average 6.89%  
250 (95% CI: 5.49 - 8.29) higher soil moisture per volume than unburnt mesocosms, suggesting greater  
251 transpiration in unburnt compared with burnt mesocosms.



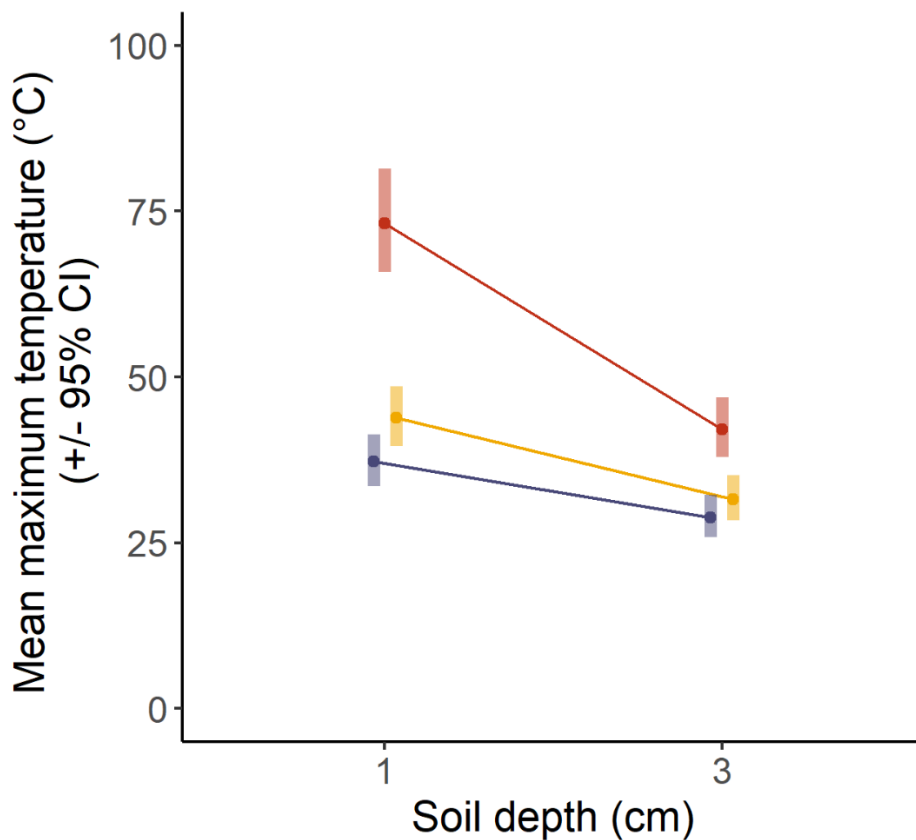
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253 *Figure 3: Estimated marginal means ( $\pm$  95% confidence intervals) for mesocosm soil moisture (% volume)*  
254 *since commencement). Treatment levels are high (—■—) medium (—▲—) and low (—●—) water availability and unburnt*  
255 *(—■—) and burnt (---▲---) fire treatment levels.*

256

257 Among burnt mesocosms, we found very strong evidence of differences in maximum soil  
258 temperature during the fire simulation. Temperatures depended on water availability and depth  
259 within the soil profile (water treatment : depth in soil profile interaction;  $\chi^2_2 = 20.858$ ;  $P < 0.001$ ,  
260 Figure 4). Contrast analyses revealed that at each soil profile depth, low water mesocosms  
261 experienced hotter maximum temperatures when compared with medium and high water  
262 mesocosms. There was no evidence of differences in maximum temperatures for medium and high  
263 water mesocosms (Figure 4). The mean maximum temperature was 1.966 (95% CI: 1.617 -- 2.389)  
264 times higher in low water mesocosms than high water mesocosms at 1cm, and 1.461 (95% CI: 1.195  
265 -- 1.786) times higher at 3cm depth. The mean maximum temperature was 1.670 (95% CI: 1.377 --

266 2.024) times higher in low water mesocosms than medium water mesocosms at 1cm, and 1.333  
267 (95% CI: 1.094 -- 1.625) times higher at 3cm depth.



268

269 *Figure 4: Estimated marginal means ( $\pm$  95% confidence intervals) for maximum temperature ( $^{\circ}$ C) at 1 cm and 3 cm soil*  
270 *profile depth in burnt mesocosms during fire simulation (Day 587 of experiment). Treatment levels are high (■) medium*  
271 *(■) and low (■) water availability.*

272

### 273 *Hydrological and fire effects on above ground biomass*

274 We found strong evidence that water treatment influenced changes in biomass over time ( $F_{2, 343} =$

275 5.804;  $P = 0.003$ ; Figure 5). Planned contrasts showed strong evidence ( $t_{341} = 3.093$ ,  $P = 0.006$ ) that

276 differences in biomass between unburnt low and high water mesocosms increased over time:

277 biomass differences between high and low water mesocosms more than doubled (2.183 (95% CI:

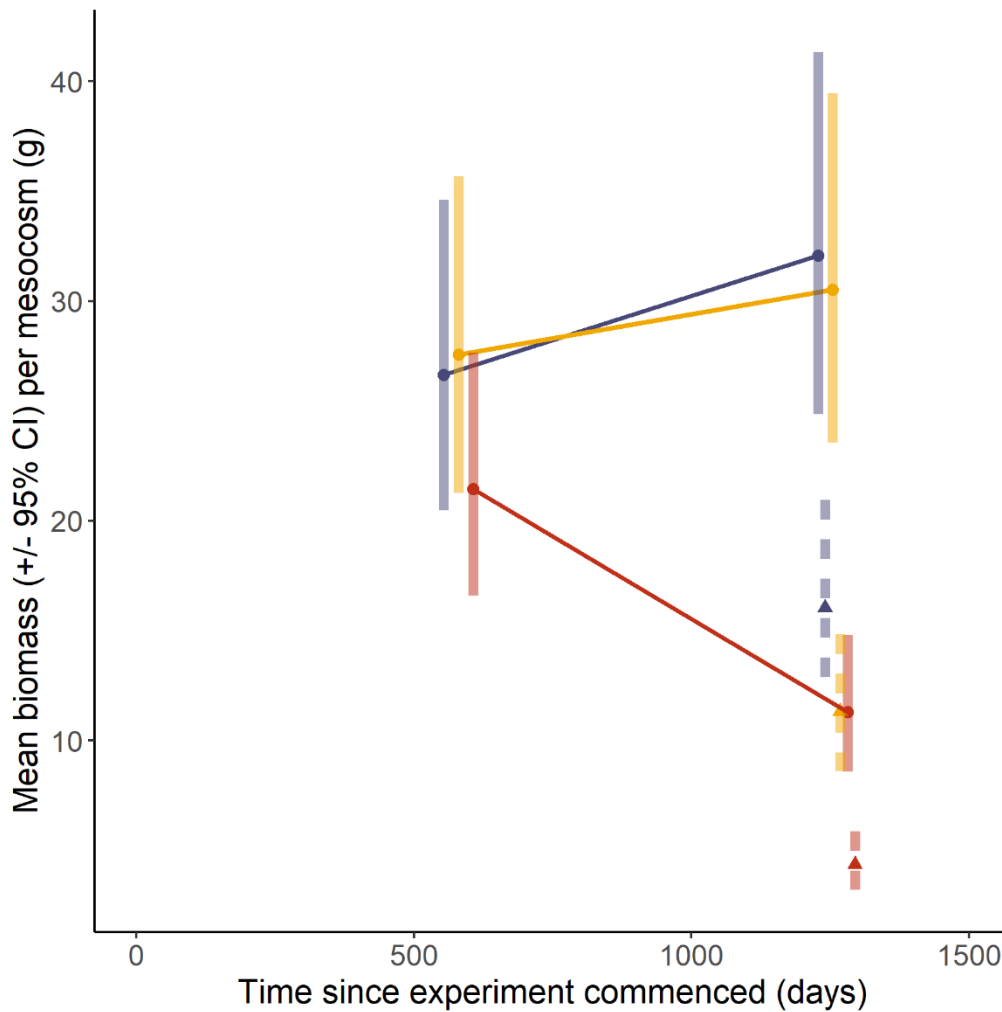
278 1.205 – 3.955)) between Day 587 and Day 1261 of the experiment. Similarly, differences in biomass

279 between unburnt low and medium water mesocosms more than doubled between Day 587 and Day

280 1261 ( $t_{341} = 2.771$ ,  $P = 0.016$ ; estimate = 2.013; 95% CI: 1.111–3.646), but there was no evidence of

281 differences in biomass changes between high and medium water mesocosms ( $t_{341} = 0.320$ ,  $P = 0.945$ ;

282 estimate = 1.085; 95% CI: 0.597 – 1.971). So above-ground biomass showed a lagged response to  
283 low water availability. We did not find any evidence of an interaction between fire and water  
284 treatments ( $F_{2, 344} = 0.600$ ;  $P = 0.549$ ), and therefore no evidence of a synergistic effect of fire and  
285 water on above ground biomass (Figure 5).



286

287 *Figure 5: Estimated marginal means ( $\pm$  95% confidence intervals) for above ground biomass (g) per mesocosm at Day 587*  
288 *and 1261 since commencement of the experiment. Treatment levels are high (■) medium (■) and low (■)*  
289 *water availability and unburnt (—■—) and burnt (···▲···) fire treatment levels. Note that biomass was collected*  
290 *immediately prior to the fire simulation and again at the end of the experiment.*

291

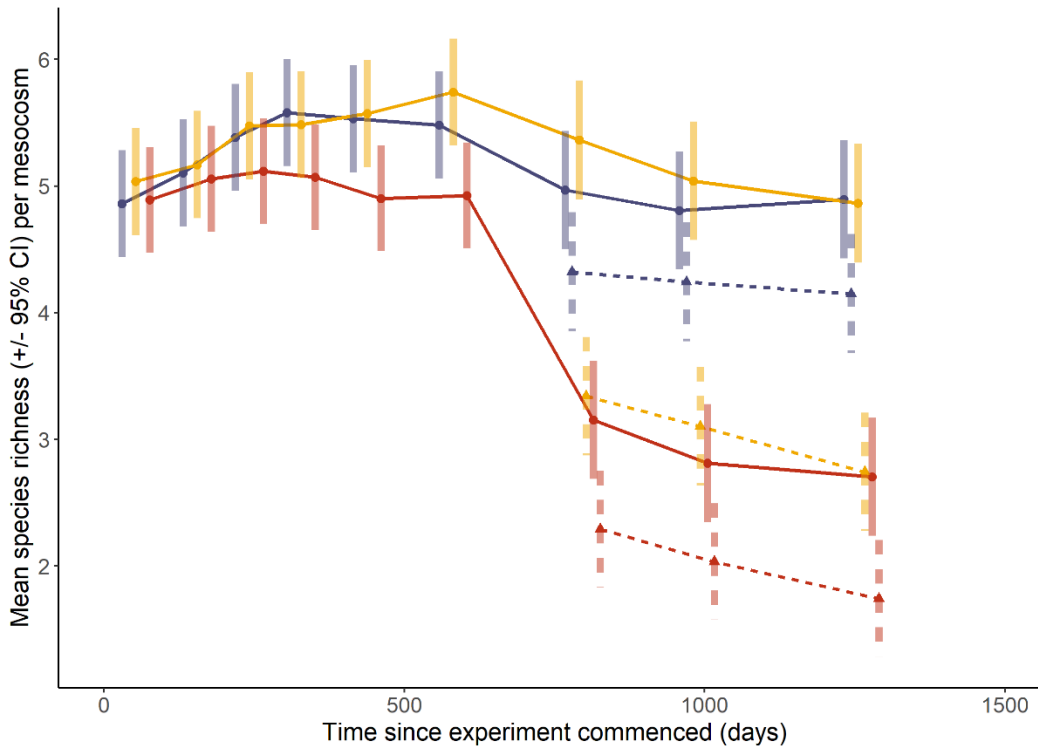
### 292 *Hydrological and fire effects on species richness*

293 We found very strong evidence that changes in richness over time differed by water treatment

294 ( $F_{16,1960} = 9.878$ ,  $P < 0.001$ ) for unburnt mesocosms. Species richness in low water mesocosms



295 diverged below richness in high water (H vs. L by time interaction  $t_{1974} = 6.027$ ,  $P < 0.001$ ; estimate =  
296 1.635; 95% CI: 0.933 – 2.337) and medium water (M vs. L by time interaction  $t_{1974} = 4.943$ ,  $P < 0.001$ ;  
297 estimate = 1.344; 95% CI: 0.640 – 2.047) mesocosms. However, there was no evidence of divergence  
298 between high and medium water mesocosms ( $t_{1973} = 1.068$ ;  $P = 0.759$ ; estimate = 0.291; 95% CI: -  
299 0.414 - 0.995, Figure 6). We found very strong evidence of an interaction between fire and water  
300 treatments - hence a synergistic effect of fire and water on richness ( $F_{2, 2044} = 18.801$ ;  $P < 0.001$ ;  
301 Figure 6). Contrasts showed very strong evidence of convergence between medium and low water  
302 availability after the fire treatment (burnt mesocosms) compared to the unburnt treatment level  
303 ( $t_{2044} = -4.829$ ,  $P < 0.001$ ; estimate = -1.160; 95% CI: -1.782 - -0.539), and divergence between high  
304 and medium water availability after fire ( $t_{2044} = 5.693$ ,  $P < 0.001$ ; estimate = 1.376; 95% CI: 0.751 –  
305 2.001) compared to the unburnt treatment level. There was no evidence of change in the difference  
306 between richness for high and low water availability with fire ( $t_{2044} = 0.898$ ,  $P < 0.854$ ; estimate =  
307 0.216; 95% CI: -0.406 – 0.838). In summary, the fire treatment accelerated species richness declines  
308 in medium water mesocosms, but not high water mesocosms. Richness declined in low water  
309 mesocosms independently of the fire treatment, but declines were not evident until nearly 2 years  
310 after the water treatment was implemented (Figure 6).



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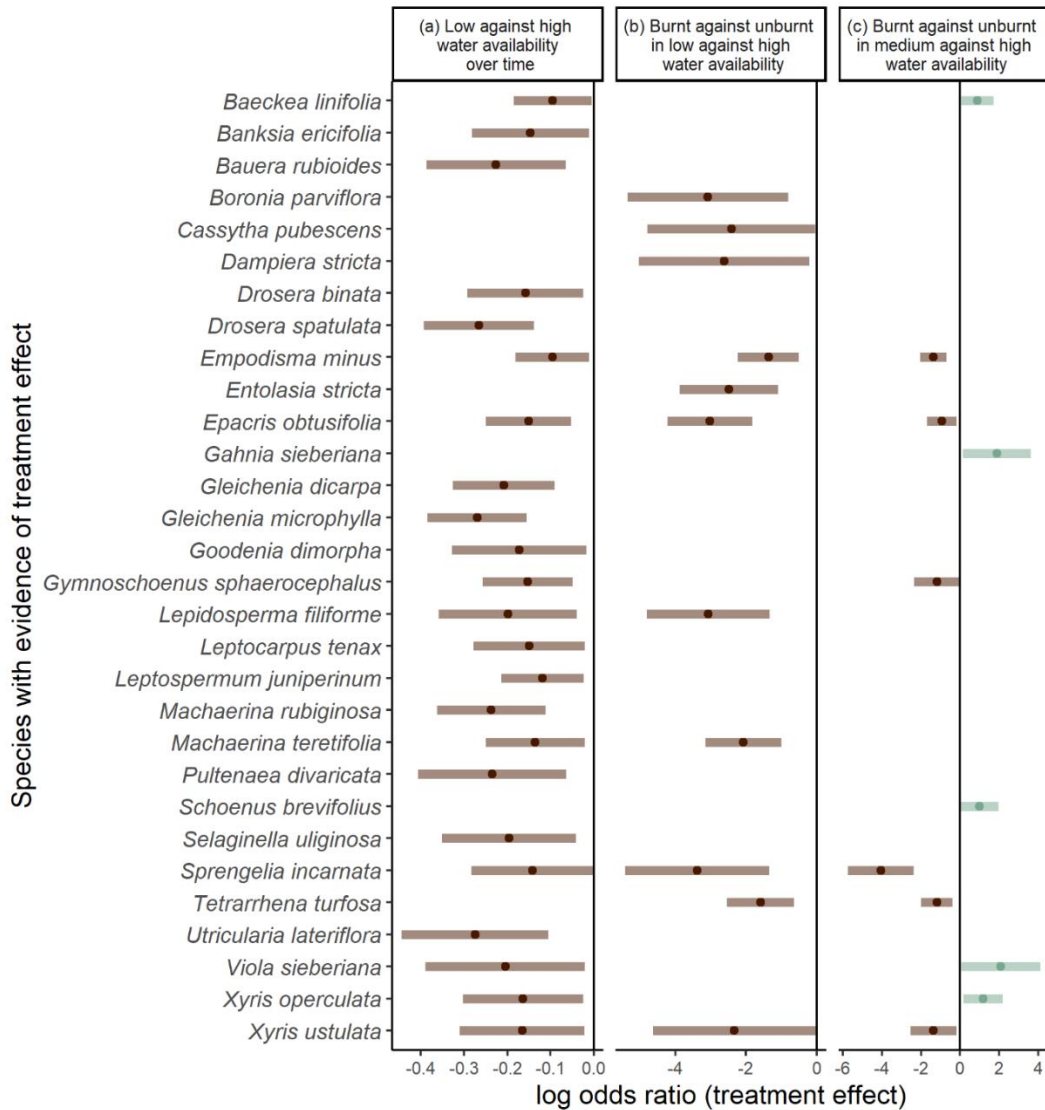
312 *Figure 6: Estimated marginal means (± 95% confidence intervals) for species richness over time (days since commencement)*  
 313 *in treatment mesocosms. Treatment levels are high (■) medium (●) and low (▲) water availability and unburnt*  
 314 *(—) and burnt (---▲---) fire treatment levels.*

315

### 316 *Hydrological effects on species composition and occurrence*

317 Consistent with a reduction in richness, the odds of representation (i.e. presence) across species  
 318 reduced 66% (95% CI: 49% - 78%) more in the low water than the high water mesocosms over the  
 319 experimental period. This effect was driven by twenty-three species (Figure 7 (a) species in brown).  
 320 The reduction of species representation in low water compared with high water availability  
 321 mesocosms was not uniform across species, with two species experiencing particularly large  
 322 reductions, and two species exhibiting smaller than average reductions (Figure 8 (a)). These variable  
 323 responses drove the compositional change ( $\chi^2_2 = 14.335$ ;  $P < 0.001$ ). We found evidence that some  
 324 of this compositional change was explained by reduced representation by hydrophile species ( $\chi^2_{12} =$   
 325  $24.638$ ;  $P = 0.017$ ), however we did not identify particular pairwise differences between species with  
 326 different hydrological niches: moderate and strong hydrophile species underwent similar reductions

327 when exposed to low water availability, and non-hydrophile species had large standard errors  
 328 (Appendix 1). There was no evidence of difference in average representation between medium and  
 329 high water availability (OR = 0.89; 95% CI: 0.68 - 1.17) (Appendix 1).



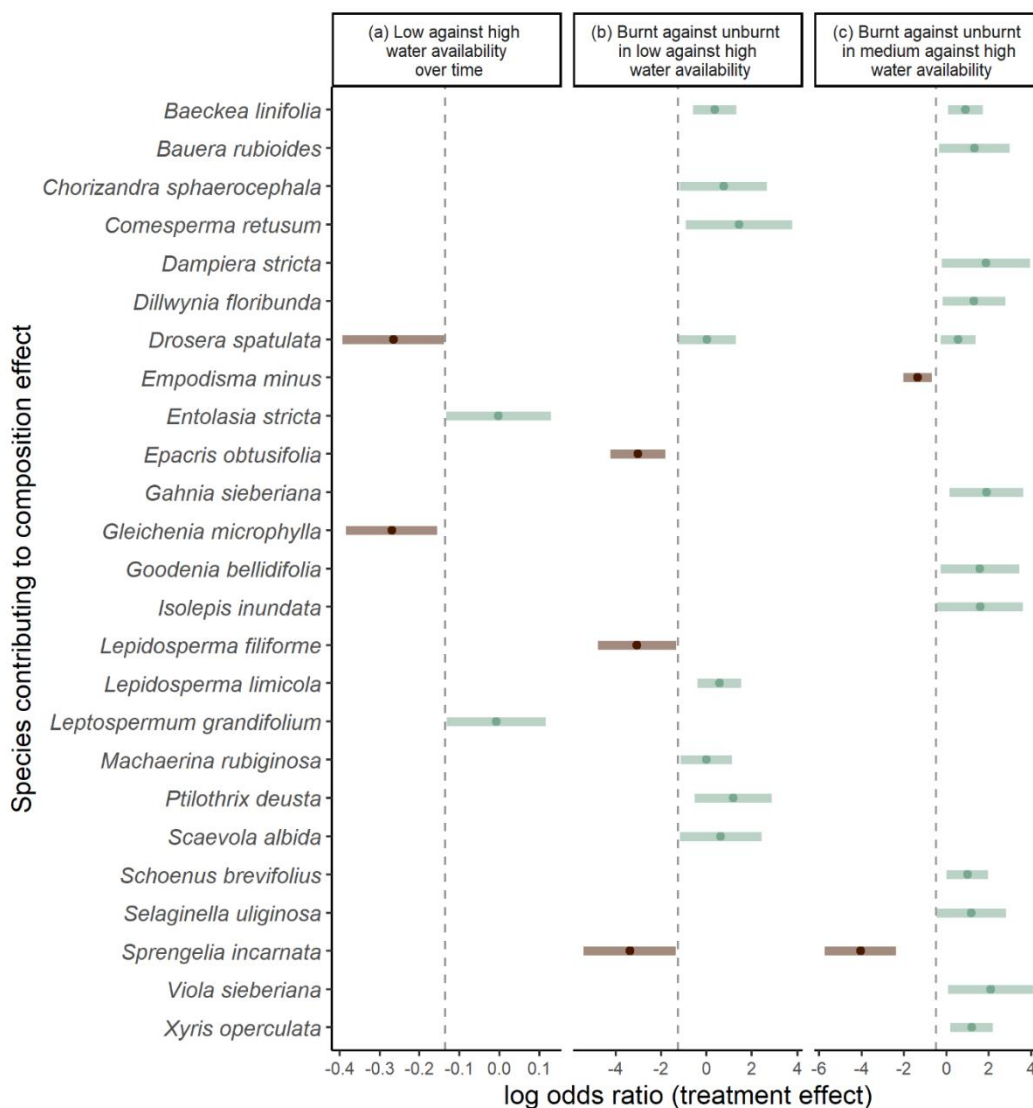
330

331 Figure 7: Treatment effect (log odds ratio  $\pm$  95% confidence interval) for species exhibiting (a) a change over time or (b-c)  
 332 synergistic water and fire effect. Species shown in brown (■) had large reductions in representation. Species shown in  
 333 teal (■) had smaller than average reductions or increases in representation.

334

335 Similarly to our species richness results, we found strong evidence of synergistic effects of water  
 336 availability and fire disturbance on species composition. Burnt mesocosms had a larger difference in  
 337 representation between high and low water availability than unburnt mesocosms (OR = 3.51, 95%

338 CI: 1.67 – 7.39), while we did not find evidence of a similar difference for burnt vs. unburnt  
 339 treatment levels in high and medium water availability mesocosms (OR = 1.62, 95% CI: 0.89 – 2.96).  
 340 The interaction was driven by 17 species (Figure 7 (b-c) species in brown). The reduction was not  
 341 uniform across all species ( $\chi^2_2 = 78.773$ ;  $P < 0.001$ ): five species experienced particularly large  
 342 reductions (Figure 8 (b-c) species in brown), and 20 had smaller than average reductions or increases  
 343 (Figure 8 (c) species in teal) relative to unburnt mesocosms. We found no evidence ( $\chi^2_{36} = 33.914$ ;  $P =$   
 344 0.568) that this compositional change could be explained by fire traits (Appendix 2).



345

346 Figure 8: Treatment effect (log odds ratio  $\pm$  95% confidence interval) for species whose compositional contribution changed  
 347 (a) over time or (b-c) with water and fire effects. Species shown in brown (■) had large reductions in representation.  
 348 Species shown in teal (■) had smaller than average reductions or increases in representation.

349

## 350 Discussion

351 Wetland function was detrimentally affected by disruption of water resource availability. The rate  
352 and magnitude of that effect was influenced by fire-mediated top-down regulation. These  
353 experimental results support our conceptual model of swamp transition (Figure 1). We found very  
354 strong evidence that water availability is a bottom-up driver of swamp vegetation structure. Above  
355 ground biomass, species richness and composition were all detrimentally affected by low water  
356 availability. Persistent reduction in water availability will drive a loss of species and primary  
357 productivity within swamp communities. Over the experimental timeframe of 3.5 years, we  
358 observed a lagged response of above-ground biomass and species richness to hydrological change.  
359 By the end of the experiment however, reduced water availability had caused declines in primary  
360 productivity (biomass) and biodiversity value (species richness and representation).

361 Strongly hydrophilic species appeared to have lower representation in the low than high water  
362 mesocosms. But non-hydrophile species did not show evidence of differentiation in the low vs. high  
363 water availability mesocosms. In addition, species disproportionately adversely affected by low  
364 water availability were often obligate wetland species (e.g. *Glechenia microphylla*) while many  
365 species less adversely affected than average were facultative wetland species (e.g. *Entolasia stricta*).  
366 These emerging compositional patterns may signal increased terrestriation of swamp vegetation  
367 as mining-induced wetland drying continues.

368 We found that fire disturbance compounded hydrological change and accelerated swamp transition,  
369 corroborating our conceptual model and field-based observations (Keith et al., 2022). By the end of  
370 the experiment, differences in species compositions were greater under water stress for burnt than  
371 unburnt mesocosms. Post-fire weather conditions are among the most important stochastic  
372 environmental factors affecting vegetation dynamics in Australian ecosystems (Keith et al., 2002)  
373 such as Cyperoid heath and Ti-tree thicket. Recruitment may fail when low rainfall follows a fire  
374 event (Keith et al., 2002). In our case, low water availability appeared to limit regeneration of both

375 resprouts and seedling recruits after the fire treatment. When combined, hydrological disruption  
376 and fire acted synergistically, with adverse effects on post-fire species richness and composition.  
377 While swamp communities may not immediately respond to changed water availability (evidenced  
378 by temporal lags in biomass and species richness in unburnt mesocosms), recurrent fire is likely to  
379 accentuate community change.

380 Our experiment simulated a low-intensity fire (Auld, 1986). Notably, low water mesocosms most  
381 effectively conducted heat down the soil profile. A study by Wright and Clarke (2008) on fire effects  
382 in central Australian spinifex communities also reported a strong effect of soil moisture on  
383 temperature profiles with high soil moisture strongly reducing soil heating during fire. Consumption  
384 of a large mass of ground fuels during fire is likely to generate hotter soil temperatures than those  
385 recorded during our fire simulation, and this may initiate smouldering substrate fires that cause  
386 elevated mortality of roots, seedbanks and rhizomes (Rein et al., 2008) in swamp sediments with low  
387 moisture content (Prior et al., 2020).

388 Fire stimulates plant emergence from seedbanks and underground organs (Keith, 2012). However,  
389 the interplay of fire and hydrology on biotic components of the soil profile may be complex. Tangney  
390 et al. (2018) identified a potentially countervailing phenomenon where elevated seed moisture  
391 content facilitated lower lethal temperature thresholds when compared with drier seed: when seeds  
392 and soil are moist, seed mortality increases. In our experiment, maximum soil temperatures for high  
393 and medium water mesocosms were mostly below temperature thresholds (50-180°C) used by  
394 Tangney et al. (2018). We therefore conclude that high and medium water levels in our experiment  
395 buffered against elevated soil temperatures and avoided risks of seed mortality (while probably also  
396 moderating the stimulative effect of fire on species richness).

397 After the fire simulation, we attributed higher soil moisture of burnt compared with unburnt  
398 mesocosms to lower above ground biomass and consequently lower transpiration rates in burnt  
399 mesocosms. Despite unconsumed water resources and potential stimulative fire effects, low water

400 mesocosms when burnt, did not support higher species richness or greater representation of swamp  
401 species compared with low water availability unburnt mesocosms. Our experimental design could  
402 not identify whether soil temperatures increased seed mortality or whether low soil moisture  
403 inhibited seed germination and seedling survival in low water mesocosms. However, we have shown  
404 that multiple disturbance selectively filtered swamp species and affected their long-term  
405 representation. These environmental changes and losses of diversity may ultimately lead to  
406 ecosystem collapse, where ecosystem function and identity are transformed (Keith et al., 2022).

407 By extracting mesocosms and exposing them to controlled conditions in the glasshouse, we closely  
408 simulated field conditions and compositions. However, the realism of our experiment was  
409 constrained by restricting groundwater variability and excluding any simulation of precipitation. In  
410 addition, our simulation of intensified swamp drying, with a decrease in water addition from weekly  
411 to fortnightly frequency, occurred soon after the fire simulation. However, differences across water  
412 treatment levels were already evident prior to this change in the frequency of water addition. The  
413 character of vegetation transformed by the drying treatment in our mesocosm experiment likely  
414 differed from *in situ* vegetation of drying swamps: glasshouse conditions essentially precluded  
415 colonisation from the regional species pool, including terrestrial species of the surrounding  
416 woodland matrix. In the absence of colonisation opportunities, and over our truncated timeline, we  
417 are unable to identify outcomes of the community transition. Natural experiments in mined and  
418 unmined swamps (e.g. Keith et al., 2022) provide some insights into the character of the derived  
419 communities that replace collapsed upland swamp ecosystems. Thus far, research indicates that  
420 swamps may either transition to terrestrial communities or remain as depauperate swamps  
421 comprising facultative rather than obligate swamp species (Keith et al., 2022).

#### 422 *Conservation and management implications*

423 Upland swamps of the Sydney Basin are substantively threatened by subsidence disturbance and  
424 disruption of groundwater following underground mining. While our empirical study was initially



425 aimed at simulating the effects of underground mining, global climate change (where increased  
426 evapotranspiration and reduced precipitation occur) or deforestation and landuse change may  
427 similarly affect water budgets. Wherever long-term hydrological disruption of wetland ecosystems  
428 occurs, policymakers should expect declines in ecosystem function and biodiversity. When combined  
429 with recurrent, endogenous disturbance such as fire, the impacts of hydrological change may be  
430 amplified and transition to alternative ecosystem states accelerated. Ultimately, the effects of  
431 hydrological disturbance cannot be comprehensively assessed by planning organisations without  
432 also considering recurrent disturbances - such as fire - in a landscape context.

433 Long-term field monitoring has indicated that, in the absence of exogenous hydrological change,  
434 plant communities in the wettest parts of swamps (Ti-tree thicket and Cyperoid heath) are more  
435 resistant to compositional change than those in drier parts of swamps (Restioid heath, Sedgeland  
436 and Banksia thicket) (Mason et al., 2017). Our current findings have shown that even plant  
437 communities in the wettest habitats are susceptible to transformation if hydrological thresholds are  
438 exceeded. Mining disturbance may entrain irreversible change in swamp vegetation and associated  
439 biota.

440 Upland swamps near the footprint of underground longwall mining (within a buffer zone ~600m)  
441 may experience drying due to increased permeability of sandstone aquifers in the surface cracking  
442 zone (Watershed HydroGeo, 2022). Within the buffer zone, swamps that source water from a  
443 regional water table rather than relying on rainfall alone, may also experience drying or partial  
444 drying (David et al., 2017). We found that even under partial dewatering, species richness was  
445 disproportionately diminished after fire. Consequently, swamps within and near the longwall mine  
446 footprint may be vulnerable to transition when fire follows hydrological disturbance and mine-  
447 related subsidence impacts should not be assumed to be confined to the direct underground mining  
448 footprint.

449 Upland swamp conservation requires an understanding of both bottom-up and top-down regulation  
450 processes. Substantial reductions in soil moisture initiates ecosystem-level change. Longwall mining  
451 generates almost immediate hydrological disruption (Mason et al., 2021) followed by longer-term,  
452 lagged biotic change as measured in our simulation experiment and in the field (Keith et al., 2022).  
453 The challenge for policymakers is to assess impacts of disturbance when plant community responses  
454 are lagged, cumulative or chaotic (Milchunas and Lauenroth, 1995). Climate change, while a less  
455 abrupt process, may have similar long term effects on swamp hydrology (Keith et al., 2014). Under  
456 both regional and global hydrological change, positive feedbacks may establish: dry conditions  
457 create more favourable fire weather and more frequent fire disturbance. Synergistic hydrological  
458 and fire disturbance accelerate vegetation and ecosystem change and imperil swamp conservation.  
459 Planners and policy makers must be cognizant that once hydrological disturbance occurs,  
460 compounding physical and biotic change are likely unavoidable.

#### 461 **Author contributions**

462 Tanya Mason, David Keith and Gordana Popovic conceived the ideas and designed methodology;  
463 Tanya Mason collected the data; Gordana Popovic, Maeve McGillicuddy and Tanya Mason analysed  
464 the data; Tanya Mason led the writing of the manuscript. All authors contributed critically to the  
465 drafts and gave final approval for publication.

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## 476 **References**

477 Auld, T. D. (1986) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Fire and the  
478 transition to seedlings. *Australian Journal of Ecology*, **11**, 373-385.

479 Auld, T. D. & Bradstock, R. A. (1996) Soil temperatures after the passage of a fire: do they influence  
480 the germination of buried seeds? *Australian Journal of Ecology*, **21**, 106-109.

481 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using  
482 lme4. *Journal of Statistical Software*, **67**, 1-48.

483 Benson, D. & McDougall, L. (1993) Ecology of Sydney plant species Part 1: Ferns, fern-allies, cycads,  
484 conifers and dicotyledon families Acanthaceae to Asclepiadaceae. *Cunninghamia*, **3**, 257-  
485 422.

486 Benson, D. & McDougall, L. (1994) Ecology of Sydney plant species Part 2: Dicotyledon families  
487 Asteraceae to Buddlejaceae. *Cunninghamia*, **3**, 789-1004.

488 Benson, D. & McDougall, L. (1995) Ecology of Sydney plant species Part 3: Dicotyledon families  
489 Cabombaceae to Eupomatiaceae. *Cunninghamia*, **4**, 217-431.

490 Benson, D. & McDougall, L. (1996) Ecology of Sydney plant species Part 4: Dicotyledon family  
491 Fabaceae. *Cunninghamia*, **4**, 552-752.

492 Benson, D. & McDougall, L. (1997) Ecology of Sydney plant species Part 5: Dicotyledon families  
493 Flacourtiaceae to Myrsinaceae. *Cunninghamia*, **5**, 330-544.

494 Benson, D. & McDougall, L. (1998) Ecology of Sydney plant species Part 6: Dicotyledon family  
495 Myrtaceae. *Cunninghamia*, **5**, 808-987.

496 Benson, D. & McDougall, L. (1999) Ecology of Sydney plant species Part 7a: Dicotyledon families  
497 Nyctaginaceae to Primulaceae. *Cunninghamia*, **6**, 402-506.

- 498 Benson, D. & McDougall, L. (2000) Ecology of Sydney plant species Part 7b: Dicotyledon families  
499 Proteaceae to Rubiaceae. *Cunninghamia*, **6**, 1016-1202.
- 500 Benson, D. & McDougall, L. (2001) Ecology of Sydney plant species Part 8: Dicotyledon families  
501 Rutaceae to Zygophyllaceae. *Cunninghamia*, **7**, 241-462.
- 502 Benson, D. & McDougall, L. (2002) Ecology of Sydney plant species Part 9: Monocotyledon families  
503 Agavaceae to Juncaginaceae. *Cunninghamia*, **7**, 695-930.
- 504 Benson, D. & McDougall, L. (2005) Ecology of Sydney plant species Part 10: Monocotyledon families  
505 Lemnaceae to Zosteraceae. *Cunninghamia*, **9**, 16-212.
- 506 Blom, C. W. P. M. & Voeselek, L. A. C. J. (1996) Flooding: the survival strategies of plants. *Trends in*  
507 *Ecology and Evolution*, **11**, 290-295.
- 508 Bond, W. J. (2021) Out of the shadows: ecology of open ecosystems. *Plant Ecology and Diversity*, **14**,  
509 205-222.
- 510 Bond, W. J. & Keeley, J. E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable  
511 ecosystems. *Trends in Ecology and Evolution*, **20**, 387-394.
- 512 Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J.,  
513 Maechler, M. & Bolker, B. M. (2017) glmmTMB balances speed and flexibility among  
514 packages for zero-inflated generalized linear mixed modeling. *The R Journal*, **9**, 378-400.
- 515 Brown, A. M., Warton, D. I., Andrew, N. R., Binns, M., Cassis, G. & Gibb, H. (2014) The fourth-corner  
516 solution - using predictive models to understand how species traits interact with the  
517 environment. *Methods in Ecology and Evolution*, **5**, 344-352.
- 518 Campbell, D., Keddy, P. A., Broussard, M. & McFalls-Smith, T. B. (2016) Small changes in flooding  
519 have large consequences: experimental data from ten wetland plants. *Wetlands*, **36**, 457-  
520 466.
- 521 Clarkson, B. R. (1997) Vegetation recovery following fire in two Waikato peatlands at Whangamarino  
522 and Moanatuatua, New Zealand. *New Zealand Journal of Botany*, **35**, 167-179.

- 523 David, K., Timms, W. A., Barbour, S. L. & Mitra, R. (2017) Tracking changes in the specific storage of  
524 overburden rock during longwall coal mining. *Journal of Hydrology*, **553**, 307-320.
- 525 de Oliveira, M. T., Damasceno-Junior, G. A., Pott, A., Filho, A. C. P., Suarez, Y. R. & Parolin, P. (2014)  
526 Regeneration of riparian forests of the Brazilian Pantanal under flood and fire influence.  
527 *Forest Ecology and Management*, **331**, 256-263.
- 528 Department of the Environment (2014) Conservation advice (including listing advice) for Coastal  
529 Upland Swamps in the Sydney Basin Bioregion. Department of the Environment, Canberra.
- 530 Dixon, K. W., Roche, S. & Pate, J. S. (1995) The promotive effect of smoke derived from burnt native  
531 vegetation on seed germination of Western Australian plants. *Oecologia*, **101**, 185-192.
- 532 Flores, B. M., Fagoaga, R., Nelson, B. W. & Holmgren, M. (2016) Repeated fires trap Amazonian  
533 blackwater floodplains in an open vegetation state. *Journal of Applied Ecology*, **53**, 1597-  
534 1603.
- 535 Fryirs, K. & Hose, G. (2016) THPSS mapping layer. 6 maps showing the spatial distribution of THPSS  
536 were produced for the following areas: Blue Mountains - VISID 4480 Budderoo - VISID 4481  
537 Gosford - VISID 4482 Newnes - VISID 4483 Woronora - VISID 4484 Penrose - VISID 4485.  
538 [https://portal.data.nsw.gov.au/arcgis/home/item.html?id=b18031ca90cd480dbc7ac8ccae82](https://portal.data.nsw.gov.au/arcgis/home/item.html?id=b18031ca90cd480dbc7ac8ccae82b92d)  
539 [b92d](https://portal.data.nsw.gov.au/arcgis/home/item.html?id=b18031ca90cd480dbc7ac8ccae82b92d).
- 540 Hairston, N. G., Smith, F. E. & Slobodkin, L. B. (1960) Community structure, population control, and  
541 competition. *The American Naturalist*, **94**, 421-425.
- 542 Hunter, M. D. & Price, P. W. (1992) Playing chutes and ladders: heterogeneity and the relative roles  
543 of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 724-732.
- 544 Keith, D. A. (2012) Functional traits: their roles in understanding and predicting biotic responses to  
545 fire regimes from individuals to landscapes. *Flammable Australia: Fire regimes, biodiversity*  
546 *and ecosystems in a changing world* (eds R. A. Bradstock, A. M. Gill & R. J. Williams), pp. 120-  
547 154. CSIRO Publishing, Collingwood.

- 548 Keith, D. A., Benson, D. H., Baird, I. R. C., Watts, L., Simpson, C. C., Krogh, M., Gorissen, S., Ferrer-  
549 Paris, J. R. & Mason, T. J. (2022) Interactions between anthropogenic stressors and recurring  
550 perturbations mediate ecosystem resilience or collapse. *Conservation Biology*, **preprint**.
- 551 Keith, D. A., Elith, J. & Simpson, C. C. (2014) Predicting distribution changes of a mire ecosystem  
552 under future climates. *Diversity & Distributions*, **20**, 440-454.
- 553 Keith, D. A., McCaw, W. L. & Whelan, R. J. (2002) Fire regimes in Australian heathlands and their  
554 effects on plants and animals. *Flammable Australia: the fire regimes and biodiversity of a*  
555 *continent* (eds R. A. Bradstock, J. E. Williams & M. A. Gill), pp. 199-237. Cambridge University  
556 Press, Cambridge.
- 557 Keith, D. A. & Myerscough, P. J. (1993) Floristics and soil relations of upland swamp vegetation near  
558 Sydney. *Australian Journal of Ecology*, **18**, 325-344.
- 559 Keith, D. A., Rodoreda, S. & Bedward, M. (2010) Decadal change in wetland-woodland boundaries  
560 during the late 20th century reflects climatic trends. *Global Change Biology*, **16**, 2300-2306.
- 561 Kriegisch, N., Reeves, S., Johnson, C. R. & Ling, S. D. (2016) Phase-shift dynamics of sea urchin  
562 overgrazing on nutrified reefs. *PLoS One*, **11**.
- 563 Lenth, R. V. (2022) emmeans: estimated marginal means, aka least-squares means.
- 564 Litzow, M. A. & Ciannelli, L. (2007) Oscillating trophic control induces community reorganization in a  
565 marine ecosystem. *Ecology Letters*, **10**, 1124-1134.
- 566 Löhmus, A., Remm, L. & Rannap, R. (2015) Just a ditch in forest? Reconsidering draining in the  
567 context of sustainable forest management. *BioScience*, **65**, 1066-1076.
- 568 Mason, T. J., Keith, D. A. & Letten, A. D. (2017) Detecting state changes for ecosystem conservation  
569 with long-term monitoring of species composition. *Ecological Applications*, **27**, 458-468.
- 570 Mason, T. J., Krogh, M., Popovic, G. C., Glamore, W. & Keith, D. A. (2021) Persistent effects of  
571 underground longwall coal mining on freshwater wetland hydrology. *Science of the Total*  
572 *Environment*, **772**, 144772.

- 573 Matson, P. A. & Hunter, M. D. (1992) Special Feature: The relative contributions to top-down and  
574 bottom-up forces in population and community ecology. *Ecology*, **73**, 723.
- 575 Merritt, D. M. & Cooper, D. J. (2000) Riparian vegetation and channel change in response to river  
576 regulation: a comparative study of regulated and unregulated streams in the Green River  
577 Basin, USA. *Regulated Rivers: Research and Management*, **16**, 543-564.
- 578 Milchunas, D. G. & Lauenroth, W. K. (1995) Inertia in plant community structure: state changes after  
579 cessation of nutrient-enrichment stress. *Ecological Applications*, **5**, 452-458.
- 580 Mooney, S., Martin, L., Goff, J. & Young, A. R. M. (2021) Sedimentation and organic content in the  
581 mires and other sites of sediment accumulation in the Sydney region, eastern Australia, in  
582 the period after the Last Glacial Maximum. *Quaternary Science Reviews*, **272**, 107216.
- 583 Moore, A. C. & Schmitz, O. J. (2021) Do predators have a role to play in wetland ecosystem  
584 functioning? An experimental study in New England salt marshes. *Ecology and Evolution*, **11**,  
585 10956-10967.
- 586 Naeem, S. (2001) Experimental validity and ecological scale as criteria for evaluating research  
587 programs. *Scaling relations in experimental ecology* (eds R. H. Gardner, M. Kemp, V. S.  
588 Kennedy & J. E. Petersen), pp. 223-250. Columbia University Press, New York.
- 589 Naeem, S. (2008) Green with complexity. *Science*, **319**, 913-914.
- 590 Niku, J., Hui, F. K. C., Taskinen, S. & Warton, D. I. (2019) gllvm: Fast analysis of multivariate  
591 abundance data with generalized linear latent variable models in r. *Methods in Ecology and*  
592 *Evolution*, **10**, 2173-2182.
- 593 Prior, L. D., French, B. J., Storey, K., Williamson, G. J. & Bowman, D. M. J. S. (2020) Soil moisture  
594 thresholds for combustion of organic soils in western Tasmania. *International Journal of*  
595 *Wildland Fire*.
- 596 R Core Team (2021) R: A language and environment for statistical computing. R Foundation for  
597 Statistical Computing, Vienna, Austria.

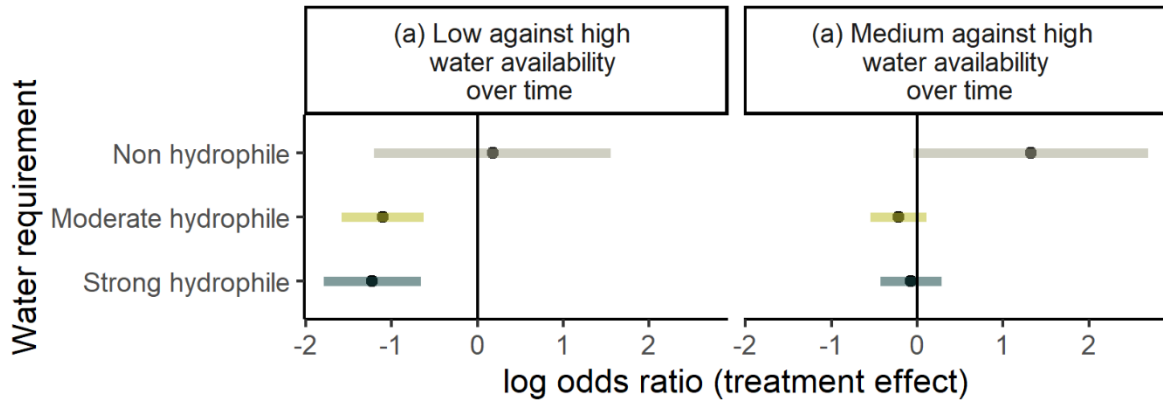


- 598 Ramsar Convention on Wetlands (2018) Global Wetland Outlook: State of the world's wetlands and  
599 their services to people. Ramsar Convention Secretariat, Gland, Switzerland.
- 600 Read, T. R. & Bellairs, S. M. (1999) Smoke affects the germination of native grasses of New South  
601 Wales. *Australian Journal of Botany*, **47**, 563-576.
- 602 Rein, G., Cleaver, N., Ashton, C., Pironi, P. & Torero, J. L. (2008) The severity of smouldering peat fires  
603 and damage to the forest soil. *Catena*, **74**, 304-309.
- 604 Serrao-Neumann, S., Davidson, J. L., Baldwin, C. L., Dedekorkut-Howes, A., Ellison, J. C., Holbrook, N.  
605 J., Howes, M., Jacobson, C. & Morgan, E. A. (2016) Marine governance to avoid tipping  
606 points: Can we adapt the adaptability envelope? *Marine Policy*, **65**, 56-67.
- 607 Spiller, D. A. & Schoener, T. W. (1990) A terrestrial field experiment showing the impact of  
608 eliminating top predators on foliage damage. *Nature*, **347**, 469-472.
- 609 Srivastava, D. S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S. P., Miller, T. E., Munguia, P.,  
610 Romanuk, T., Schneider, D. C. & Trzcinski, M. K. (2004) Are natural microcosms useful model  
611 systems for ecology? *Trends in Ecology and Evolution*, **19**, 379-384.
- 612 Sulwiński, M., Mętrak, M., Wilk, M. & Suska-Malawska, M. (2020) Smouldering fire in a nutrient-  
613 limited wetland ecosystem: long-lasting changes in water and soil chemistry facilitate shrub  
614 expansion into a drained burned fen. *Science of the Total Environment*, **746**.
- 615 Tangney, R., Merritt, D. J., Fontaine, J. B. & Miller, B. P. (2018) Seed moisture content as a primary  
616 trait regulating the lethal temperature thresholds of seeds. *Journal of Ecology*, **107**, 1093-  
617 1105.
- 618 Tozer, M. G., Turner, K., Keith, D. A., Tndall, D., Pennay, C., Simpson, C., MacKenzie, B., Beukers, P. &  
619 Cox, S. (2010) Native vegetation of southeast NSW: a revised classificaiton and map for the  
620 coast and eastern tablelands. *Cunninghamia*, **11**, 359-406.
- 621 Turetsky, M. R., Donahue, W. F. & Benscoter, B. W. (2011) Experimental drying intensifies burning  
622 and carbon losses in a northern peatland. *Nature Communications*, **2**, 514.

- 623 Vesk, P. A., Warton, D. I. & Westoby, M. (2004) Sprouting by semi-arid plants: testing a dichotomy  
624 and predictive traits. *Oikos*, **107**, 72-89.
- 625 Watershed HydroGeo (2022) Illawarra Metallurgical Coal Dendrobium mine extension project  
626 (DMEP) Groundwater assessment. pp. 439. Watershed HydroGeo Pty Ltd,  
627 [https://www.planningportal.nsw.gov.au/major-projects/projects/dendrobium-mine-](https://www.planningportal.nsw.gov.au/major-projects/projects/dendrobium-mine-extension-project-0)  
628 [extension-project-0](https://www.planningportal.nsw.gov.au/major-projects/projects/dendrobium-mine-extension-project-0).
- 629 Whalley, R. D. B. & Brown, R. W. (1973) A method for the collection and transport of native grasses  
630 from the field to the glasshouse. *Journal of Range Management*, **26**, 376-377.
- 631 Whelan, R. J. (1995) *The ecology of fire*. University of Cambridge, Cambridge.
- 632 Wilkinson, D. M. & Sherratt, T. N. (2016) Why is the world green? The interactions of top-down and  
633 bottom-up processes in terrestrial vegetation ecology. *Plant Ecology and Diversity*, **9**, 127-  
634 140.
- 635 Woo, M. & Young, K. L. (2005) High arctic wetlands: their occurrence, hydrological characteristics  
636 and sustainability. *Journal of Hydrology*, **320**, 432-450.
- 637 Wright, B. R. & Clarke, P. J. (2008) Relationships between soil temperatures and properties of fire in  
638 feathertop spinifex (*Triodia schinzii*(Henrard) Lazarides) sandridge desert in central Australia.  
639 *The Rangeland Journal*, **30**, 317-325.
- 640 Zedler, J. B. & Kercher, S. (2005) Wetland resources: status, trends, ecosystem services, and  
641 restorability. *Annual Review of Environment and Resources*, **30**, 39-74.
- 642 Zweig, C. L. & Kitchens, W. M. (2009) Multi-state succession in wetlands: a novel use of state and  
643 transition models. *Ecology*, **90**, 1900-1909.
- 644 Zweig, C. L., Newman, S. & Saunders, C. J. (2020) Applied use of alternate stable state modeling in  
645 restoration ecology. *Ecological Applications*, **30**.

646

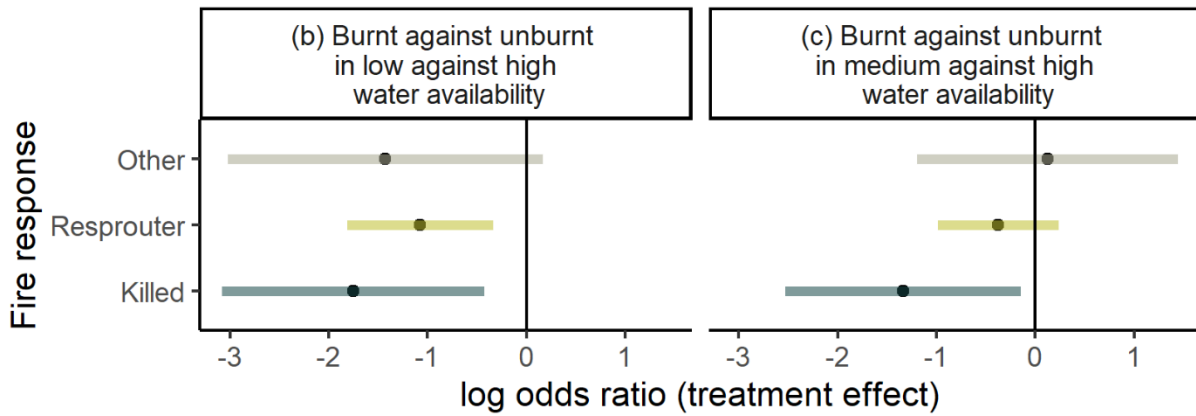
647 **Appendices**



648

649 *Appendix 1: Water availability treatment effect (log odds ratio  $\pm$  95% confidence interval) on water requirement traits over*  
650 *time.*

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652

653 *Appendix 2: Fire treatment effect (log odds ratio  $\pm$  95% confidence interval) on fire response traits. "Other" species have*  
654 *either variable or unknown responses.*

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