

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

2 **vegetation: an empirical simulation**

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8

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

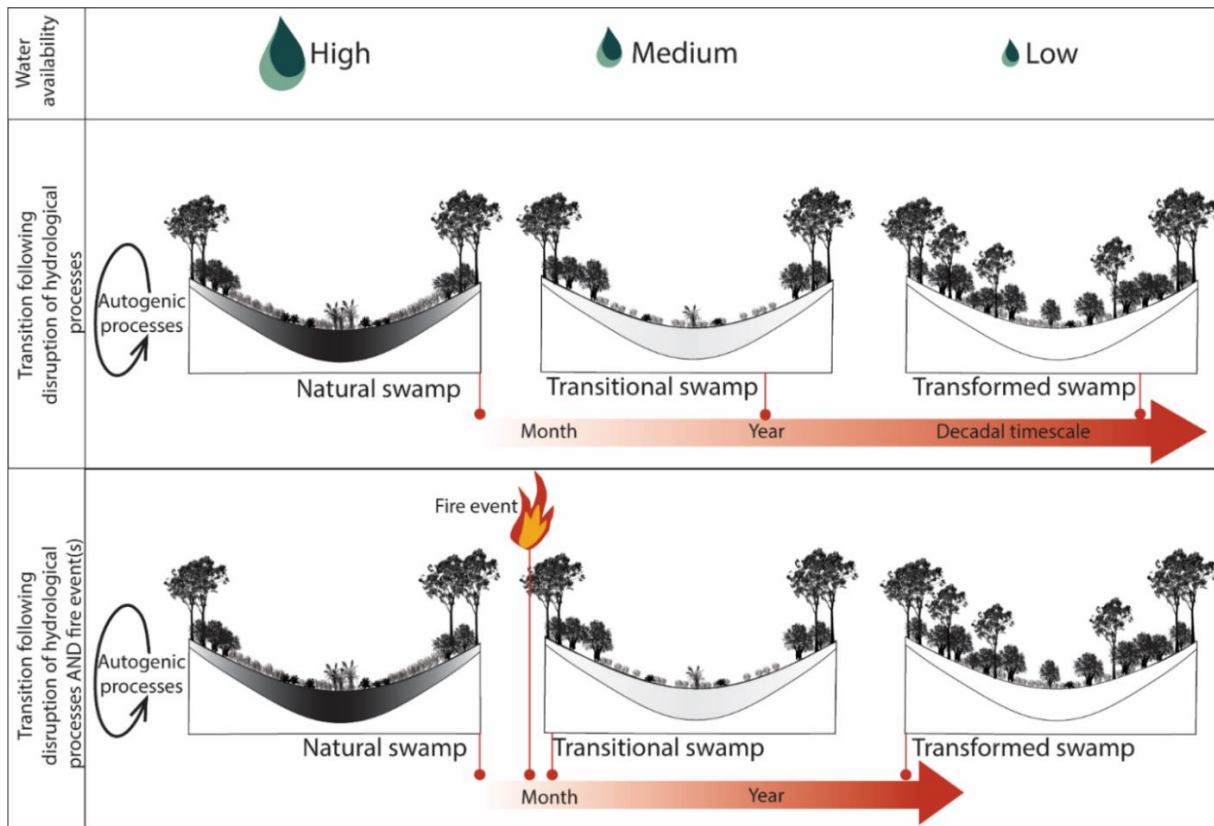
58 gradients (e.g. Zweig et al., 2020). However, if community reorganisation remains within thresholds
59 for wetland function, redistribution of species along a hydrological gradient could represent an
60 autonomous adaptation of an ecosystem while maintaining its function (Serrao-Neumann et al.,
61 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).



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

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

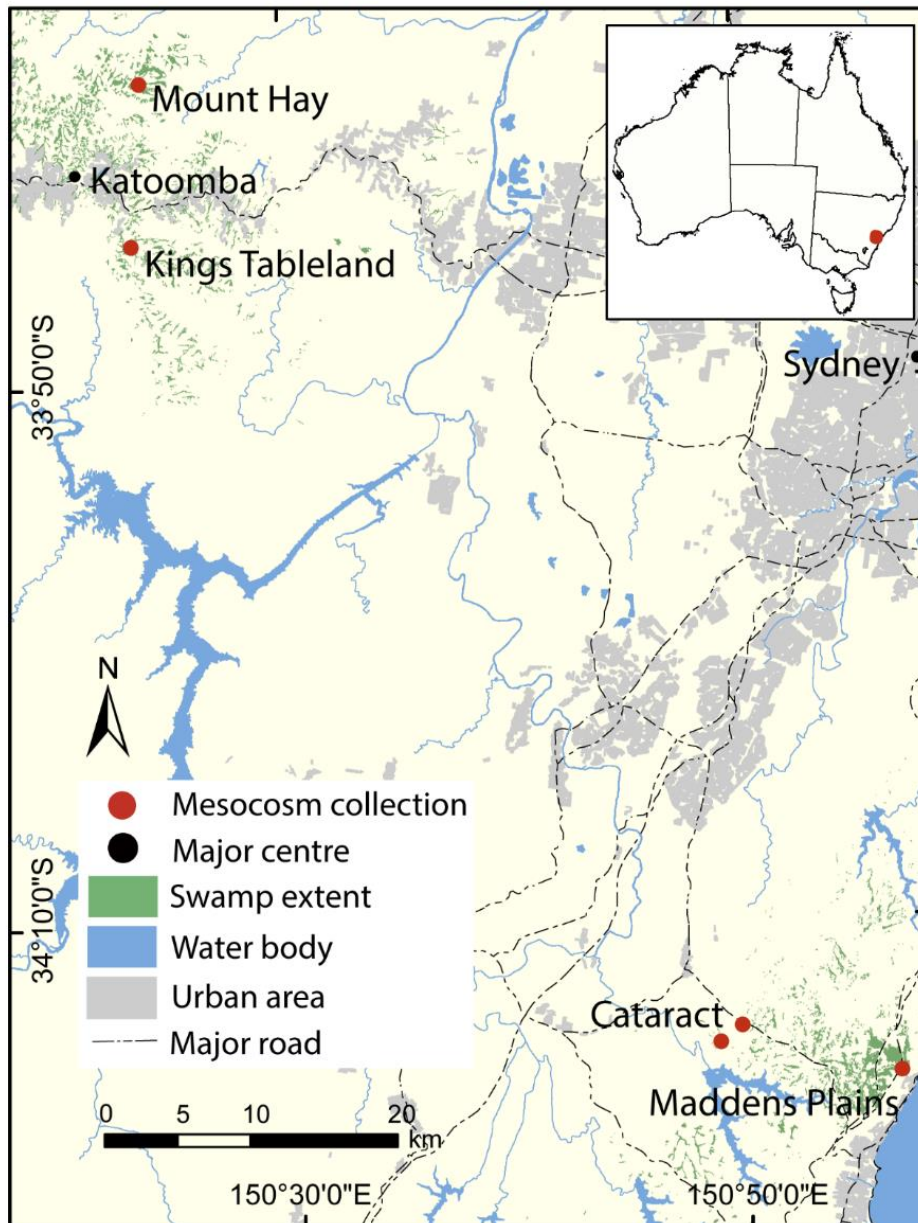
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Materials and Methods

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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).



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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 24th of March and completed on the 28th 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 $> 60^{\circ}\text{C}$ 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 ($^{\circ}\text{C}$) 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 (McGillcuddy 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.

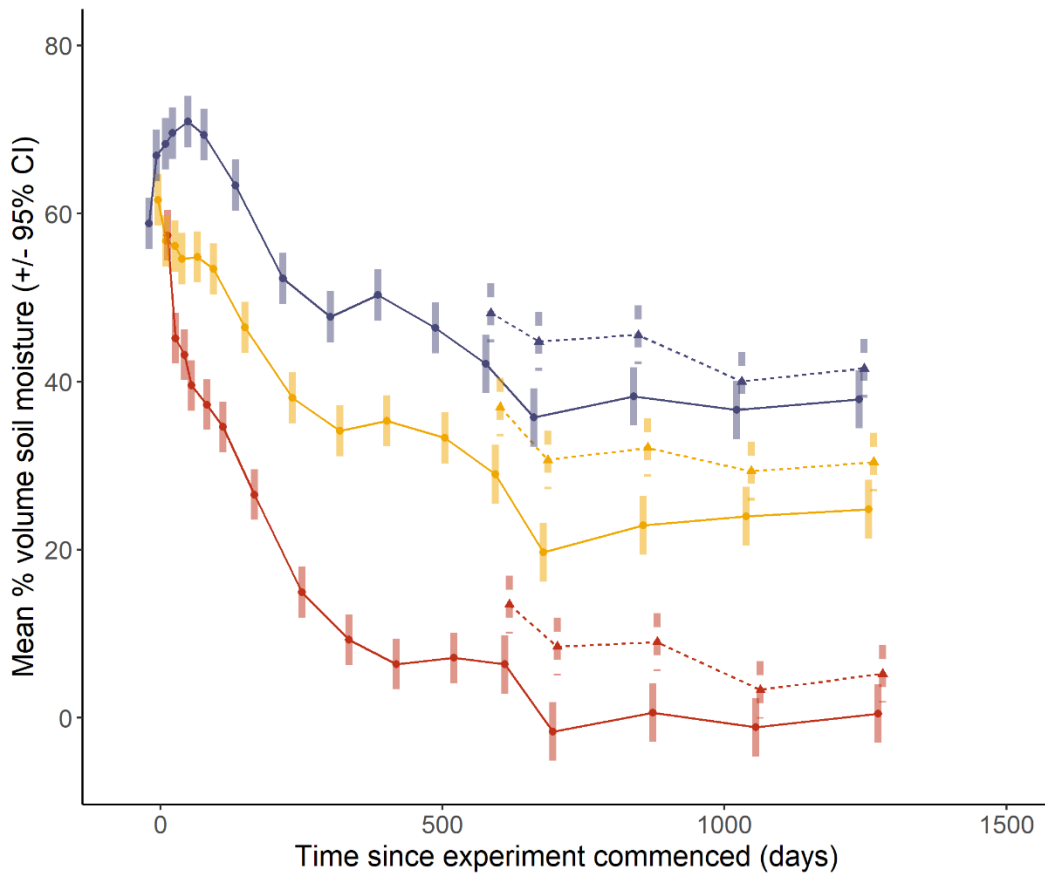
232 For all models, residuals were checked, and the response was transformed, or distribution changed,
233 as necessary to meet model assumptions. The final model for biomass used log (biomass +1) as the
234 response. For biomass and richness, we compared changes by treatment between two time points
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.



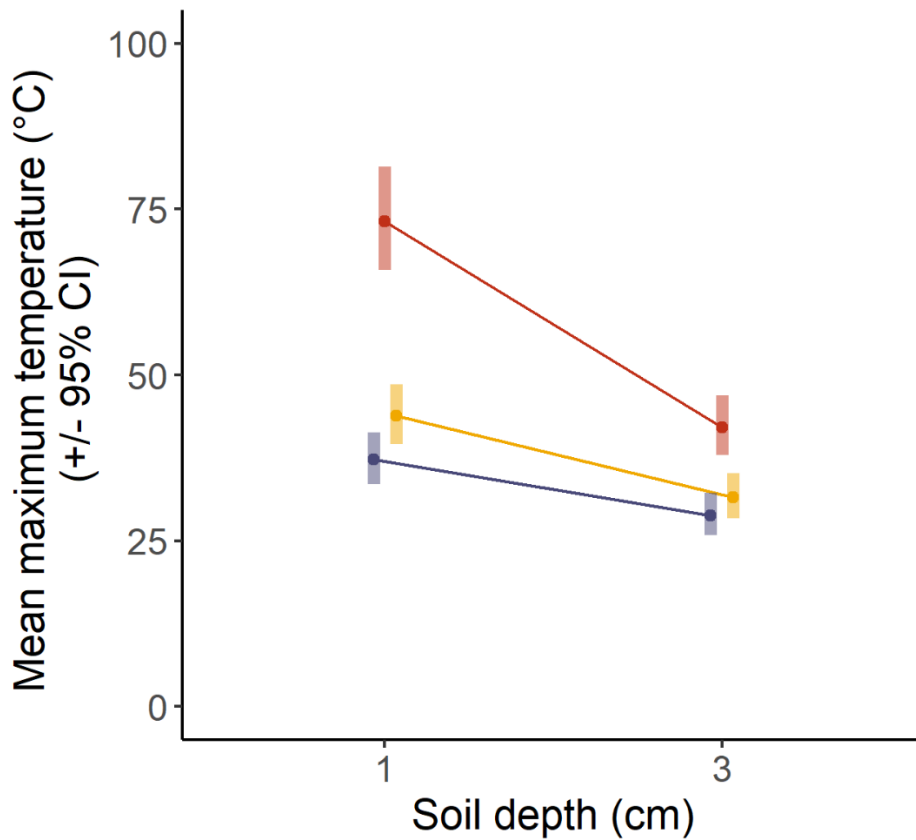
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253 *Figure 3: Estimated marginal means (\pm 95% confidence intervals) for mesocosm soil moisture (% volume)*
254 *since commencement). Treatment levels are high (—■—) medium (—▲—) and low (—●—) water availability and unburnt*
255 *(—■—) and burnt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

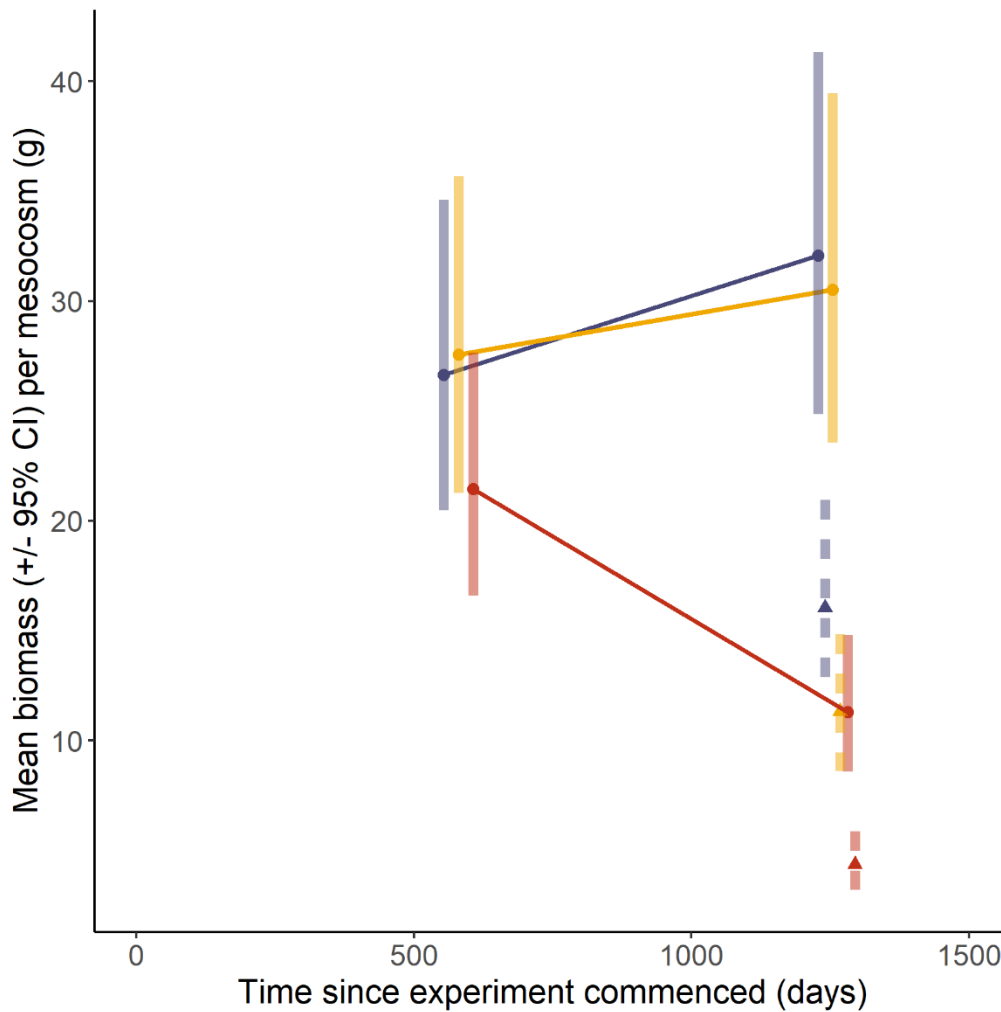


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269 *Figure 4: Estimated marginal means (\pm 95% confidence intervals) for maximum temperature ($^{\circ}$ C) at 1 cm and 3 cm soil*
270 *profile depth in burnt mesocosms during fire simulation (Day 587 of experiment). Treatment levels are high (■)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

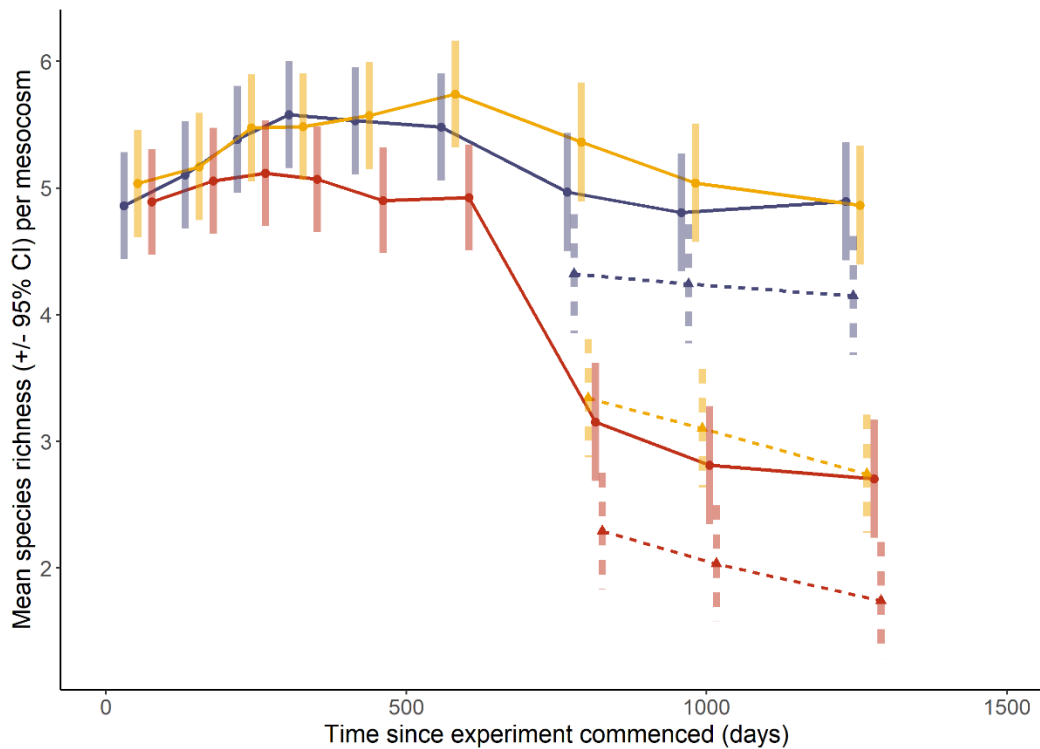
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292 *Hydrological and fire effects on species richness*

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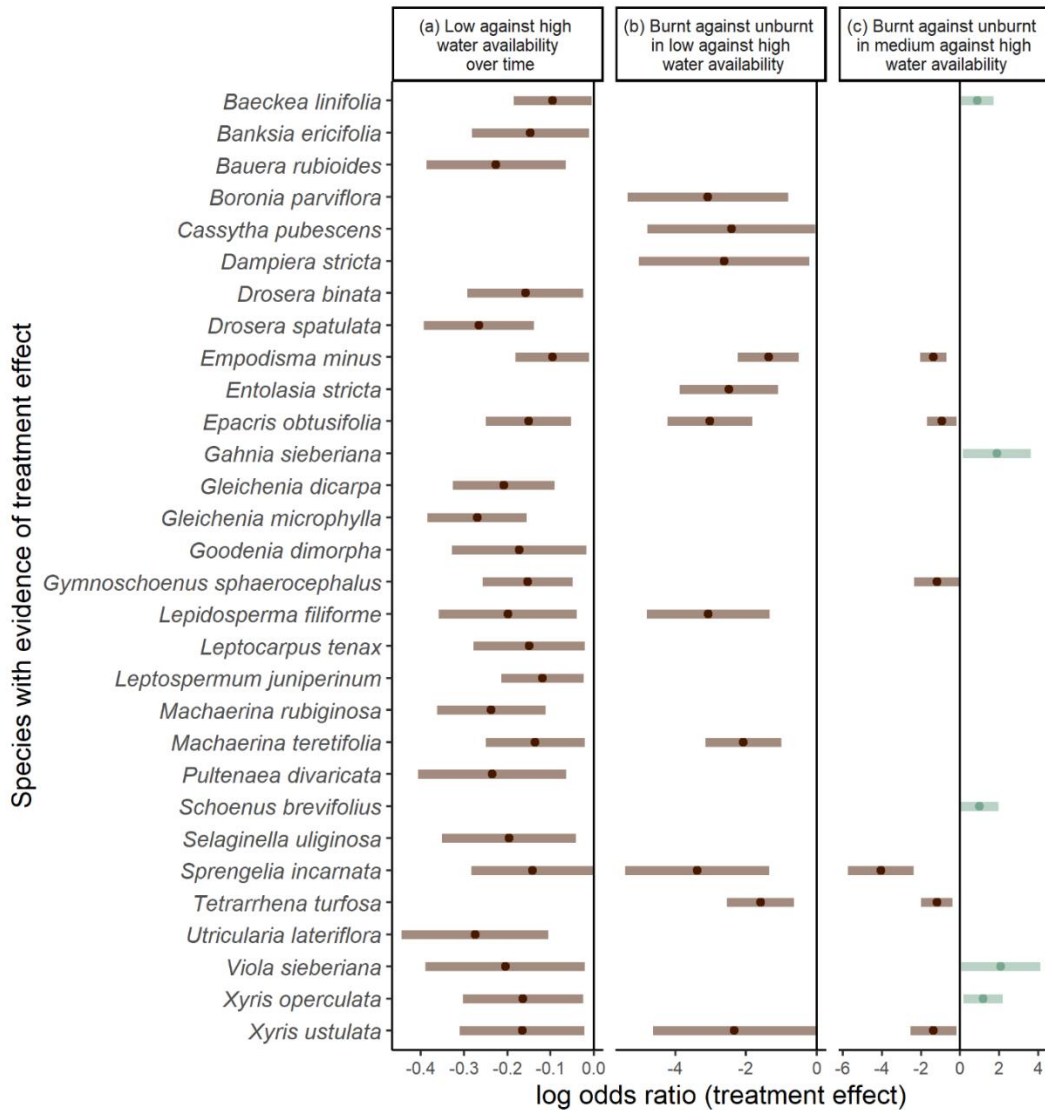
312 *Figure 6: Estimated marginal means (\pm 95% confidence intervals) for species richness over time (days since commencement)*
313 *in treatment mesocosms. Treatment levels are high (■) medium (●) and low (▲) water availability and unburnt*
314 *(—) and burnt (---▲---) fire treatment levels.*

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).



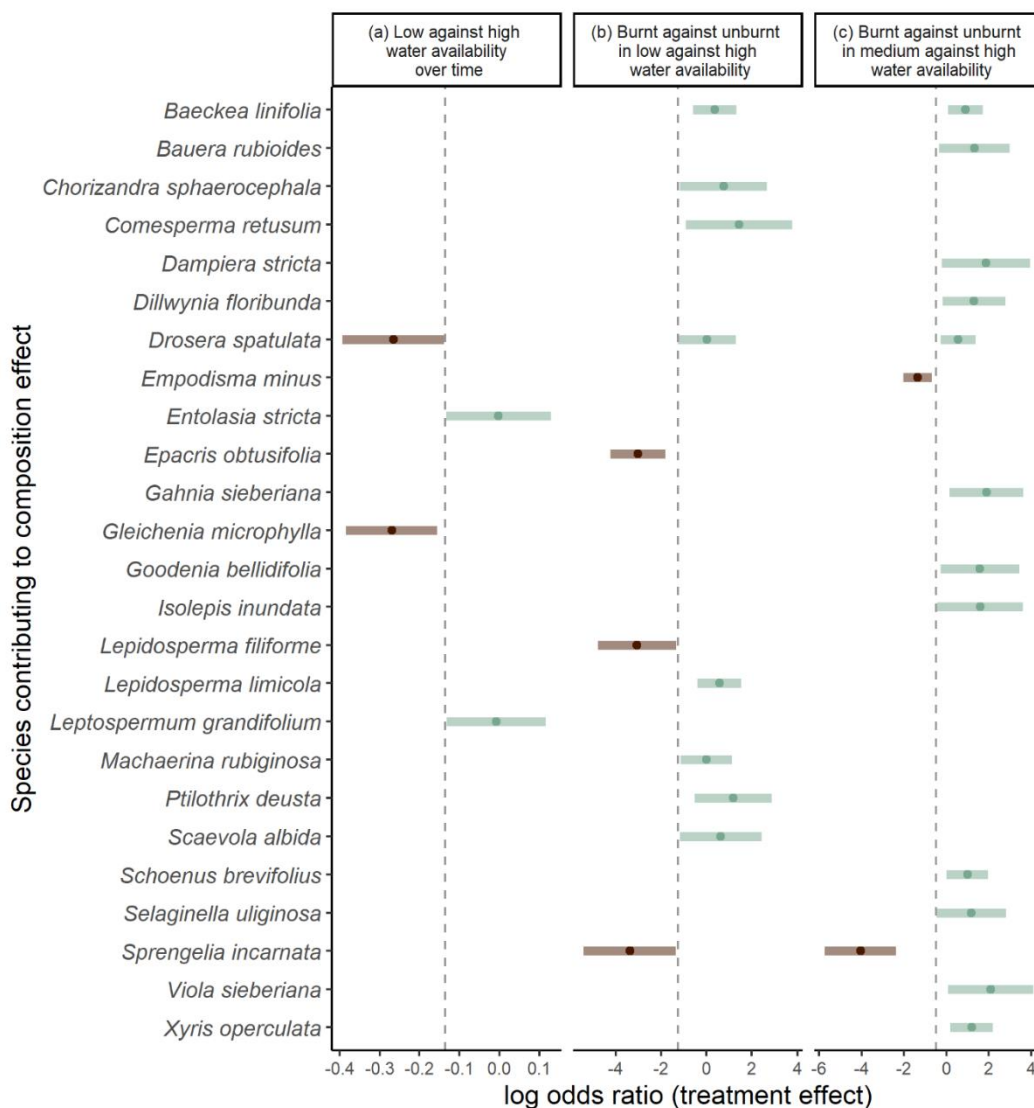
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331 Figure 7: Treatment effect (log odds ratio \pm 95% confidence interval) for species exhibiting (a) a change over time or (b-c)
 332 synergistic water and fire effect. Species shown in brown (■) had large reductions in representation. Species shown 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 terrestrialsation 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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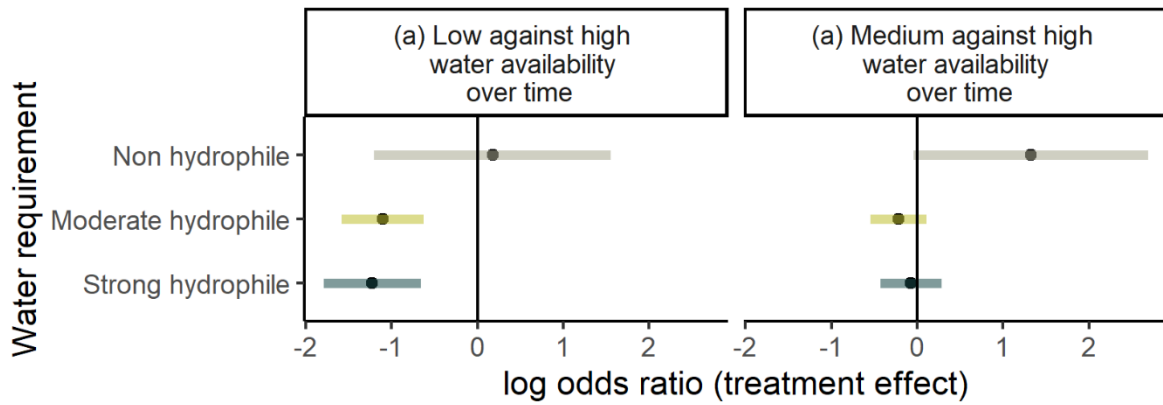
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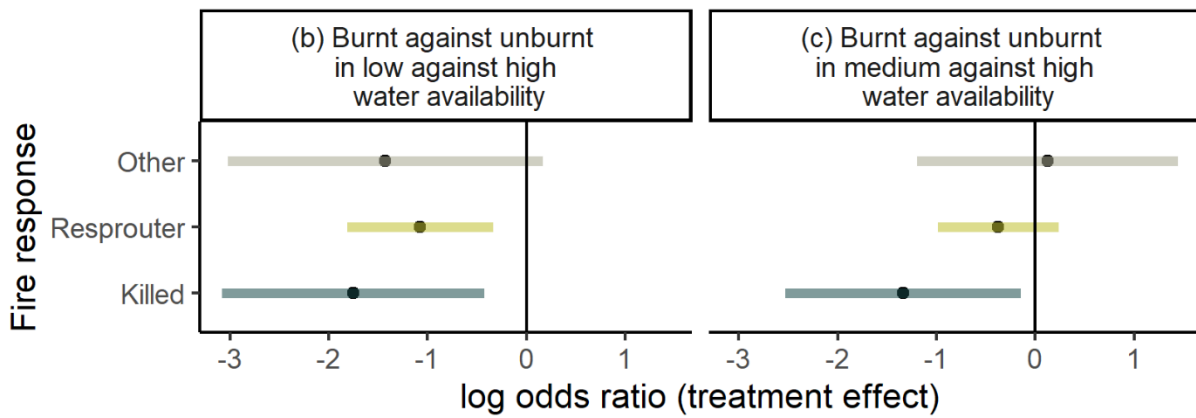
647 **Appendices**



648

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

651



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.*

655

656