



**Wildfire Impact on Coastal Groundwater-Dependent  
Heathland: Structural and Floristic Responses and  
Management**

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1 **Title: Wildfire Impact on Coastal Groundwater-Dependent Heathland: Structural and Floristic**  
2 **Responses and Management**

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24

25 **Data availability**

26 Data on which the study is based is not publicly available.

27

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For Review Only

35 **Structural and floristic response of coastal groundwater-dependent heathland to**  
36 **wildfire and implications for its management**

37 **Abstract**

38 Fire is critical for developing and maintaining many Australian ecosystems, including groundwater-  
39 dependent heathlands on the east coast. In 2019, an intense wildfire impacted a long-term heathland  
40 monitoring site on Bribie Island, Queensland, unburnt for 20 years. A before-after control-impact  
41 study was conducted using a generalised linear model to assess the impact on vegetation structure and  
42 composition. This study tested accepted paradigms in heathland fire ecology, such as the idea that  
43 long fire intervals favour obligate seeder species, resprouter species are resilient to fire, and fire  
44 promotes species richness. The role of environmental factors like rainfall, soil moisture, and  
45 groundwater levels in post-fire outcomes was also evaluated. Three years post-fire, total shrub  
46 numbers recovered and exceeded pre-fire counts, and species richness returned to pre-fire levels after  
47 two years, though not to the peak levels observed during high moisture availability three years before  
48 the fire. Contrary to expectations, the post-fire response included a slow species richness rebound and  
49 incomplete recovery. Obligate seeders showed a variable response, with some dominant populations  
50 disappearing, and resprouter populations, expected to be resilient, saw a significant reduction. These  
51 outcomes are linked to the varying capacity of heathland flora to cope with intense fire during rainfall  
52 deficits, depleted soil moisture, and groundwater. Sustained rainfall trends, rather than individual  
53 events, were found to significantly influence species richness and shrub density, with wildfires  
54 imprinting these broader climatic controls. This study confirmed that intense wildfires during dry  
55 conditions negatively affect obligate seeder and resprouter populations, even after long fire intervals.  
56 It concludes that fire intensity, timing, groundwater levels, and soil moisture are essential regulators  
57 of vegetation structure and fire response. Effective fire management should focus on periods of high  
58 soil moisture to reduce fire severity and enhance post-fire regeneration.

59 **Key words:** Coastal heathland, wildfire, climate, soil moisture, groundwater

60

## 61 **Introduction**

62 Fire has played an evolutionary role in shaping many Australian ecosystems, influencing ecological  
63 functions through variations in fire intensity, extent, season, and frequency (Bradstock et al., 2012).  
64 One such fire-adapted ecosystem is the 'Wallum,' a floristic variant of coastal heathland characterised  
65 by Wallum banksia (*Banksia aemula*). Wallum extends over a coastal strip of more than 1000 km  
66 between Newcastle (33°S) and Rockhampton (23°S) (Griffith et al., 2003; Griffith & Wilson, 2007;  
67 Rutherford et al., 2013). It provides scenic amenities and habitats for a range of threatened fauna and  
68 flora species (Meiklejohn et al., 2021) and contributes significantly to the conservation estate of  
69 eastern Australia. The most extensive Wallum development occurs in drier, more elevated Pleistocene  
70 dune systems (Thom et al., 1981). However, it can form both wet and dry variants, with topographic  
71 variation predominantly controlling groundwater depth (Griffith et al., 2015; Griffith et al., 2008;  
72 Rutherford et al., 2013). Wallum banksia retreats from habitats with permanent soil saturation, but the  
73 transition from wet to dry is often gradual rather than sharp, with cycles of wetting and drying  
74 controlled by fluctuations in the shallow perched groundwater table (DES 2010; Griffith et al., 2008;  
75 Griffith et al., 2003; Griffith & Wilson, 2007; Zencich et al., 2002). Groundwater migration into the  
76 root zone defines many Wallum habitats as groundwater-dependent ecosystems (GDEs) (Eamus et al.,  
77 2006), which concentrate root material and belowground biomass in the upper 15 cm of the soil  
78 profile (Schmidt & Stewart, 1997). When groundwater retreats below the root zone, competition for  
79 soil moisture occurs, rendering many species susceptible to stochastic disturbances such as drought  
80 and wildfire.

81 Fire is a major factor in the composition and structure of heathlands (Benwell, 1988; Keith et al.,  
82 2002). Both wet and dry heathlands are resilient to the impacts of wildfires (Meiklejohn et al., 2021).  
83 However, this assumption is primarily based on observations of structural recovery without  
84 quantitative evidence from long-term monitoring that allows comparisons between burnt and unburnt  
85 habitats under varying fire regimes.

86 Heathland species employ one of two overarching recruitment strategies: 'obligate seeders' or  
87 'resprouters.' Obligate seeders are killed by fires that fully scorch their crowns and rely on seed  
88 germination and unburnt plants to maintain populations. They benefit from ecosystems with fire  
89 intervals that include unburnt patches, allowing time for seedling maturity, adequate seed production,  
90 and a reliable post-fire environment (Pausas & Keeley, 2014). Resprouters survive fire by vegetative  
91 growth from belowground buds or lignotubers in healthy plants (Pausas et al., 2004), and resprouting  
92 provides rapid regrowth due to stored reserves (Keeley, 2006). Some generally accepted paradigms  
93 associated with the response of heathlands to fire include:

- 94 1. Fire is necessary for maintaining species richness and diversity; species richness peaks shortly  
95 after a fire and then declines (Enright et al., 2015; Enright et al., 1994; Freestone et al., 2015;  
96 Russell & Parsons, 1978).
- 97 2. Obligate seeder species are sensitive to repeated short-interval fire regimes with few  
98 unburned patches, which do not allow multiple years for seed production, possibly resulting  
99 in species extinction (Benwell, 1998; Bradstock et al., 1996; Russell-Smith et al., 2002).
- 100 3. Resprouting strategies are stress-coping mechanisms (Benwell, 1998; Gill & Groves, 1981).  
101 Resprouting from subsoil buds (i.e., basal resprouting) provides greater resilience to high-  
102 intensity fires than aerial buds (i.e., epicormic resprouting), with soil acting as an excellent  
103 heat insulator, protecting subterranean lignotubers with soil depth and associated moisture  
104 content (Clarke et al., 2013; Clarke et al., 2014; Aula & Pausas, 2010; Pausas & Keeley,  
105 2014; Pausas et al., 2004).
- 106 4. Combining high-intensity fire and drought conditions may disadvantage resprouters (Pausas  
107 & Keeley, 2014).

108 Management prescriptions for heathlands focus on the fire interval and its capacity to maintain habitat  
109 diversity (Watson, 2001). These aim to preserve flora species richness by ensuring that vegetation  
110 reaches maximum reproductive maturity before burning, allowing obligate seeders—comprising 24–  
111 40% of coastal heathland species (Sandercoe, 1989)—time to fruit and replenish the soil seed bank

112 between fires. Coastal heathlands reach their maximum reproductive productivity eight years post-  
113 fire, after which productivity and biomass decline (McFarland, 1988). Harrold (1979) suggested that a  
114 minimum fire interval of six years is required to maintain the reproductive processes of most obligate  
115 seeder species.

116 The effects of fire intensity and timing on heathlands are less well understood than those of fire  
117 intervals (Dooley et al., 2023; Griffith et al., 2007; Griffith et al., 2004). General recommendations  
118 support burning when soil conditions are wet to saturated (i.e., groundwater is at or near the surface)  
119 (Watson, 2001) with moderate intensity and late summer to winter fires (DES, 2023). However,  
120 extreme fire severity exists because heath vegetation burns as a wind-driven crown fire or not at all  
121 (Clarke et al., 2013; Hammill & Bradstock, 2006; Keeley et al., 2008). Quantitative data are necessary  
122 to support recommendations regarding the timing and intensity of healthy fires.

123 This study evaluated a type of Wallum heath dominated by various Banksia, Fabaceae, and Myrtaceae  
124 species, designated as Regional Ecosystem 12.2.12 (DES 2023). It is a common coastal heath  
125 ecosystem in southeast Queensland (Pearl et al., 2024). Current fire interval guidelines for this heath  
126 recommend moderate-intensity fires at intervals of preferably 4–8 years, implemented from late  
127 summer to winter, following summer rains (DES, 2023).

128 An opportunity to assess the floristic impacts of intense wildfire in heathland arose when a wildfire  
129 impacted Bribie Island, burning one of two permanent floristic monitoring sites (the 'North' or 'Impact'  
130 site, each assessed with three transects) subject to extended monitoring. A maintained fire break  
131 protected the alternative site (the 'South' or 'Control' site), which did not burn.

132 This study aimed to test accepted theories about fire ecology in coastal heathlands using a quantified  
133 before-after control-impact (BACI) study and statistical models. The specific questions to be  
134 addressed are as follows:

- 135 1. Do environmental conditions such as soil moisture and groundwater level at the time of a wet  
136 heathland fire affect ecological outcomes in terms of species richness?

- 137 2. Is there evidence that long fire intervals always favour obligate seeder populations and that  
138 resprouter species are more resilient to the impacts of intense fires?
- 139 3. How do climatic and environmental variables regulate the ecological outcomes of fires in wet  
140 heathlands?

141 Answering these questions will facilitate the development of robust and informed fire management  
142 directives.

### 143 *Physical setting and climate*

144 The study site was Bribie Island, a sand-barrier island 65 km north of Brisbane, Queensland,  
145 Australia, part of the Moreton Bay Ramsar Site, a Wetland of International Importance (DoEE, 2018)  
146 (**Figure 1**). The island's topography is dominated by two Pleistocene-age accretionary beach ridges  
147 running parallel to the coastline and separated by a central swale. The island's maximum elevation is  
148 17m Australian Height Datum (AHD), with an average elevation of 5m (Armstrong & Cox, 2002).  
149 Shallow swales within the beach ridge system express surface water when groundwater levels rise.  
150 Groundwater occurs in a shallow, unconfined aquifer and a deeper, partially confined aquifer beneath  
151 coffee rock (Armstrong & Cox, 2002). The shallow aquifer supports heathland vegetation, which  
152 relies on groundwater migrating into the root zone and discharging at the surface when rainfall  
153 recharges the groundwater fully. Groundwater was not abstracted from the shallow aquifer near the  
154 monitoring area, although exotic *Pinus* plantations established nearby in the 1970s influenced aquifer  
155 discharge through increased transpiration rates (Fan et al., 2014).

156 Bribie Island has a subtropical climate with hot, humid summers and cool, dry winters. The mean  
157 annual rainfall over the past 33 years (1990-2023) is 1212.3 mm, while average annual pan  
158 evaporation for the same period is 1645.3 mm (DES, 2023), indicating that vegetation is rainfall-  
159 limited without the supporting aquifer. Evaporation exceeds mean monthly rainfall during winter  
160 (June to August) due to dry westerly winds and from spring to early summer (September to  
161 December) when soil moisture and groundwater reserves diminish. Groundwater recharge is most



162 active between January and May, receiving up to 70% of the annual rainfall, reducing the gap  
163 between rainfall and evaporation.

#### 164 *Fire History and Timing*

165 The Fire Management System for Bribie Island National Park (QNPWS 2004) indicates that the North  
166 and South monitoring areas burned between 1992 and 1994, with a potential additional burn in 2000.  
167 Post-2000 fire history from the North Australia and Rangelands Fire Information (NAFI 2023) shows  
168 a series of fires on the island between 2010 and 2015, but the monitoring areas did not burn.  
169 Therefore, before the 2019 wildfire, the study area had been unburned for at least 19 years, possibly  
170 up to 25 years. On 21 August 2019, a wildfire burned approximately 2400 ha of native vegetation in  
171 the wet heathland of Bribie Island National Park. Data from the Bribie Island National Park Alert  
172 Weather Station showed relative humidity at 16% at 25.9°C with a maximum wind velocity of 55.2  
173 km/hr from the southeast during the wildfire. The Bribie fire was part of a broader series of wildfires  
174 affecting the region between August 2019 and January 2020, including severe combustion of over  
175 2000 ha of wet coastal heathland in the Cooloola Recreation Area of Noosa National Park (DES,  
176 2021). The Bribie fire fully consumed vegetation at the North site but did not reach the South site due  
177 to established containment breaks and favourable wind direction. Spot 6 Normalised Difference  
178 Vegetation Index (NDVI) data, captured three weeks post-fire (9th September 2019), indicated a  
179 complete loss of living vegetation at the North site (**Figure 2**). Six weeks post-fire inspection showed  
180 intense heat had fully combusted all living vegetation and ground fuel. However, grass trees  
181 (*Xanthorrhoea* spp.), sedges, and some shrubs began to resprout. These burn characteristics align with  
182 Brewer's (2005) 'extreme' fire category, encompassing full canopy, sub-canopy, and understory  
183 consumption. The fire exceeded the recommended burn regime for this regional ecosystem (DES  
184 2023), being a high-intensity fire under drought conditions following a fire interval longer than the  
185 recommended four to eight years.

## 186 **Materials and Methods**

### 187 *Climate, Cumulative Rainfall Departure and Groundwater*

188 The SILO weather database (DES, 2024) provides comprehensive rainfall and climate data for the  
189 Bongaree Bowls Club, about 10 km south of the monitoring area. Supplementary temperature, relative  
190 humidity, wind speed, and direction data were obtained from the Bribie Island National Park Alert  
191 weather station, though this dataset is limited and contains significant gaps.

192 Precipitation is the primary source of recharge for unconfined aquifers and the main control of  
193 groundwater levels (Smail et al., 2019). Cumulative rainfall departure (CRD) is used to predict  
194 groundwater fluctuations in unconfined aquifers by assessing short-term rainfall recharge  
195 (Emelyanova et al., 2013; Mondal & Ajaykumar, 2022; Sen, 2019; Xu & Van Tonder, 2001; Kong et  
196 al., 2022; Yesertener, 2007; Weber & Stewart, 2004). CRD is calculated by taking the mean rainfall  
197 over a period, determining each data point's departure from the mean, and summing these values to  
198 assess cumulative effects. CRD was applied to monthly rainfall data at the Bongaree Bowls Club  
199 (DES, 2024) over 33 years (January 1990 to September 2023) to capture decadal rainfall cycles,  
200 following Giambastiani et al. (2018). The slope of the CRD curve indicates rainfall trends: a rising  
201 trend shows above-average rainfall and groundwater recharge, while a falling trend indicates moisture  
202 deficit (McCallum et al., 2009; Weber & Stewart, 2004).

203 Groundwater levels can be inferred from onsite soil moisture data. Bore 14100159a, located 6.5 km  
204 south of the South Site, provides real-time groundwater data for the island, with reliable data available  
205 from 2012. Although this bore is on an elevated sand ridge, possibly spanning two aquifers and not  
206 fully replicating the hydro-ecological setting at the monitoring transects, its continuous data were  
207 useful for visually calibrating the CRD curve.

## 208 *Soil Moisture*

209 Two installed soil moisture stations (SMSs) at the northern and southern sites provided continuous  
210 moisture data with sensors at 150, 350, 650, 950, and 1250 mm below ground level. The sensors  
211 measured soil moisture content (SMC) as a percentage of the soil volume, capturing automated  
212 readings every six hours between June 2014 and March 2017, shifting to four hours in 2017. Sensor  
213 malfunction created data gaps, although the temporal extent of the monitoring period and combined  
214 data from the two SMSs meant that the dataset helped inform broader trends in the SMC. The wildfire  
215 destroyed the northern SMS in August 2019, although sensor malfunction continued after replacement  
216 in February 2021, indicating that monitoring soil moisture trends after August 2019 relied on the  
217 southern SMS.

## 218 *Vegetation Monitoring Method*

219 **Floristic Assessment:** The northern and southern sites are located in Wallum Heathland within Bribie  
220 Island National Park, featuring similar floristics and geomorphic positions (Regional Ecosystem  
221 12.2.12). Both sites consist of three 50m monitoring transects, separated by about 25m, totalling six  
222 transects. Vegetation was monitored biannually from April 2016 to September 2023, with surveys in  
223 the post-wet season (March-May) and the dry season (September-November).

224 Three key floristic indicators were monitored: species richness, shrub stem count, and groundcover  
225 composition. Species were categorised into life forms: shrubs (woody stems), grasses (Poaceae  
226 family), graminoids (sedges, rushes, strap-leaf forms), and forbs (non-woody forms).

227 Data collection methods included:

- 228 1. **Species Richness:** The total number of species was recorded within a 50m x 10m (500m<sup>2</sup>)  
229 subplot, including quadrat data and a thorough search of the subplot.

230 2. **Shrub Stem Count:** The total number of woody stems  $>0.5\text{m}$  in height was counted within a  
231  $50\text{m} \times 4\text{m}$  ( $200\text{m}^2$ ) subplot using a narrow belt transect (2m on each side of a central tape) to  
232 enhance accuracy. Multi-stemmed shrubs were counted as single stems.

233 3. **Groundcover Composition:** The percentage cover of shrubs ( $<0.5\text{m}$ ), grass trees, forbs,  
234 grasses, and graminoids was estimated within ten evenly spaced  $1\text{m}^2$  quadrats. Leaf litter  
235 (dead vegetation, including blackened vegetative matter and ash after the fire), bare ground  
236 (fine quartz sand with humic matter), and cryptogams constituted a minor balance of cover  
237 values.

238 Stems  $<0.5\text{m}$  included mature forms of prostrate shrubs and immature seedlings/saplings of larger  
239 shrub species, both included in ground cover estimates. Shrub heights were systematically measured  
240 by staff, while data from the three transects/subplots were combined to measure species richness  
241 (species/ $1500\text{m}^2$ ), total stems (stems/ $600\text{m}^2$ ), and ground cover composition ( $30\text{m}^2$ ) at both northern  
242 and southern sites.

243 **Classification of floristics and regeneration strategies:** Plant species were identified and classified  
244 into one of the five life forms and then into one of the seven recruitment strategies defined by Gill and  
245 Bradstock (1992), consistent with Myerscough et al. (1995) and Benwell (1998), with the  
246 classification also considering field-based observations. The classification of species into broader  
247 groupings of 'resprouter' and 'obligate seeder' was applied to assist characterisation of fire response.

#### 248 ***Statistical analysis***

249 The transect-level stem and species counts were combined due to lack of spatial independence.  
250 Transect observations were merged by summing stem counts, combining species lists, and averaging  
251 ground vegetation cover, resulting in 32 values for each variable (two sites  $\times$  16 surveys). The fire  
252 impact at the North site enabled a before-after control-impact (BACI) study, using the North (impact)  
253 and South (control) sites for assessing shrub growth/recruitment, species richness, and fire response  
254 (resprouters versus obligate seeders). This method compared stem counts and species richness before  
255 and after the fire, accounting for natural variability by monitoring both sites. Sampling at only two

256 sites limited spatial analysis, so regression analysis modelled species richness and stem counts over  
257 time. A predetermined BACI model structure controlled spatial and temporal variance while testing  
258 the fire's destructive and temporal effects. Various models were explored to investigate the responses'  
259 linkages to environmental covariates.

260 **BACI model framework:** A generalised linear model (GLM) was used to test the initial (destruction  
261 of vegetation) and temporal (recovery) effects of fire on site-level stem counts and species richness.  
262 The fixed effects of the model were set to be 'Site-type' (control or impact), 'Period' (before or after  
263 fire impact), and 'Site-type:Period' (interaction term), allowing predicted differences in the mean  
264 counts between site type or period to be accounted for by the individual factors and any immediate  
265 destruction effect attributable to the fire impact would be accounted for by the interaction term (i.e., a  
266 significant interaction term would indicate that the fire impact affected observed counts). Modelling  
267 the temporal effect applied two additional fixed effects: time since impact in years (years) and an  
268 interaction term (tyears: site-type). Hence, the interaction term accounted for any temporal effect  
269 attributable to the fire, indicating that the impact had a significant temporal effect on the response  
270 variable. Neither stem counts nor species richness will likely recover as a linear factor of  $\log(\text{tyears})$   
271 (because the link function for the count GLM is a log function). The square and cubic root  
272 transformations of  $\text{tyears}$  (i.e.  $\text{tyears}^{(1/2)}$  and  $\text{tyears}^{(1/3)}$ ) were also tested, as the temporal effect in the model  
273 structure will only be valid during the period of recovery. For example, as stem counts approach the  
274 site-carrying capacity, the recovery effect diminishes.

275 **Regression models based on environmental variables:** Whereas the BACI model controlled (i.e.  
276 the structure of the model was predetermined) for variability in the response over both time  
277 (period/years since impact) and space (site), modelling the response as a function of environmental  
278 covariates, including rainfall and CRD, were also completed. Akiake's Information Criteria (AIC)  
279 corrected for small samples (AICc) were used to select between competing count models, whereby the  
280 model with the lowest AICc value was considered the 'best' of all the models fitted. Models with an

281 AICc less than or equal to two from the AICc of the best model were considered equivalent (Burnham  
282 & Anderson, 2003).

283 **Model evaluation:** The initial fitting of the count GLMs. However, stem counts were overdispersed  
284 (i.e. variance > mean), requiring fitting a negative binomial regression model. These models  
285 incorporate a dispersion parameter that accounts for additional variance in the count data. The 'glm'  
286 function in the 'stats' package (R Core Team, 2023) and 'glm.nb' in the 'MASS' package (Venables  
287 & Ripley, 2002) were used in the statistical software program R (R Core Team, 2023) to fit and  
288 evaluate the models.

## 289 **Results**

### 290 *Climate, Cumulative Rainfall Departure and Groundwater*

291 The calculation of the CRD over three decades of rainfall data revealed periods of reduced rainfall  
292 interspersed with shorter, wetter periods (**Figure 3A**). From 1997 to 2009, the deepest trough  
293 represented the 'millennium drought,' one of Australia's most severe droughts (Australian  
294 Government, 2023). The eight-year monitoring period covered an entire climatic cycle, with high  
295 rainfall recorded before monitoring began in 2015, declining until December 2019, then increasing to  
296 September 2022 before drying in 2023. January to September 2022 saw 1798.3 mm of rainfall,  
297 causing a sharp spike in CRD values, ranging from -233.2 mm in December 2019 to 1197.1 mm in  
298 July 2022 (DES 2024). Groundwater and CRD trends were consistent from 2012 to mid-2019 (**Figure**  
299 **3B**), but diverged from mid-2019 to early 2022, with increased groundwater recharge relative to CRD.  
300 Wildfires likely contributed by reducing canopy interception and transpiration, increasing infiltration,  
301 and thus raising the groundwater table until recovering vegetation began consuming the infiltrated  
302 water (Giambastiani et al., 2018; Silberstein et al., 2013).

### 303 *Soil Moisture and Wildfire*

304 A CRD curve trough coincided with soil drying to 65 cm depth at the north site and 95 cm at the south  
305 from January to March 2019 (**Figure 4**). Moisture recharge occurred at the southern site in February  
306 2020 following heavy rainfall. However, variability in soil moisture content persisted in the upper 65  
307 cm until February 2022, when intense rainfall led to sustained surface waterlogging until October  
308 2022. Subsequently, moisture content fluctuated as the climate dried until September 2023. Sandy  
309 profiles were saturated (>34% SMC), indicating groundwater levels consistently above 650 mm and  
310 never dropping below 1250 mm throughout monitoring.

311 SMC fluctuations were most pronounced in the top 35 cm at both sites. Wildfires occurred just before  
312 the lowest CRD value (**Figure 4**). At the north site during the fire, SMC was 12.9%, 23.58%, and  
313 34.3% at depths of 15, 35, and 65 cm respectively, after SMC dropped to 4.92% at 35 cm and 10.3%  
314 at 65 cm from January to April 2019. Pre-fire, saturation occurred briefly at 15 and 35 cm due to  
315 moderate rainfall in late March and June, followed by rapid drying.

316 The unburnt south site was drier than the north, with SMC rarely exceeding 10% at 15 cm and 20% at  
317 35 cm in 2019. At 95 cm, SMC dropped below 10% for two weeks in March 2019, indicating falling  
318 groundwater levels (**Figure 4**). The first significant post-fire rainfall, 19 mm on October 1-2  
319 (surveyed on October 2), and 37 mm on October 12, initiated recovery.

### 320 *Vegetation Indices*

321 Sixty-seven native flora species were recorded across 16 monitoring events, including 30 shrubs, 12  
322 graminoids, two grasstrees, two grasses, and 21 forbs. Obligate seedlings comprised 34% of the flora  
323 species, including eight forbs and 15 shrubs. The resprouter species included 13 forbs, 15 shrubs, 12  
324 sedges and rushes, and four grass and grasstree species. *Leptospermum liversidgei*, *Phyllota*  
325 *phyllicoides*, and *Banksia oblongifolia* were restricted to the northern site, whereas the  
326 orchids *Cryptostylis erecta* and *Microtus parviflora* occurred only in the south. **Table 1** presents the  
327 life forms and species classified according to fire regeneration responses from Gill and Bradstock

328 (1992) and Benwell (1998). This classification accounts for serotinous species that release their  
329 canopy-held seed bank in response to fire, including *Banksia oblongifolia* (V/FR5), which resprouts  
330 from the basal buds, and *Banksia aemula* (VI/FR5), which resprouts from the stem.

331 **Species richness:** The highest species richness occurred in September 2016, with 49 and 50 species  
332 recorded at the southern and northern sites, respectively. Species richness at the southern site  
333 decreased to 30 in April 2019, followed by a steady increase to 45 in October 2022. Floristic data  
334 from the north exhibited similar trends. Species richness at the northern site was slightly higher than  
335 that at the southern site up to the wildfire impact in August 2019, prior to the wildfire, and in October,  
336 six weeks post-fire, only 12 species were recorded (**Figure 5**). Forbs and shrubs had the greatest  
337 impact on species richness. Resprouter species dominated the post-fire recovery period, and obligate  
338 seeders were not recorded post-fire in October 2019. The first observed obligate seeder recovery at  
339 the northern site occurred in April 2020 (**Figure 6**), accompanied by a substantial increase in forb and  
340 shrub species richness. The 39 species reported at the northern site in the October 2022 survey were  
341 well below the peak of 50 species reported in October 2016 and were also lower than the species  
342 richness reported at the southern site (45 species). Both the North and South sites were affected by  
343 species richness declines at the end of monitoring, with 40 species recorded at the South site and 36 at  
344 the North site in September 2023, despite the baseline species richness being significantly higher in  
345 the north in the initial monitoring events (2016).

346 **Woody stem counts:** The highest number of stems (210) at the southern site was recorded in April  
347 2016. Subsequently, counts declined steadily to their lowest levels in October 2021 (46 stems), before  
348 increasing to 146 stems in April 2023, and then declining to 105 stems in September 2023. The  
349 northern site had a much greater shrub density (> 0.5 m) than the southern site in April 2016 (567  
350 stems). Similar to the southern site, stem counts declined in the north from the initial 2016 survey  
351 (567 stems) to May 2019 (286 stems), until the destruction of the shrub layer by the wildfire. A strong  
352 post-fire rebound in stem counts occurred at the North site, with stem counts exceeding pre-impact  
353 levels within three years and a maximum count of 910 stems in September 2023 (**Figure 7**).



354 In April 2016, the obligate seeder *Persoonia virgata* was the South Site's most abundant  
355 shrub. However, the *Persoonia* stem counts successively declined throughout the monitoring period,  
356 with a collapse after September 2018. *Persoonia* was almost absent from the southern site at the end  
357 of the monitoring period. Resprouter stems increased at the southern site after April 2022, with a  
358 substantial increase in *Leptospermum semibaccatum* and more subdued increases in *Baeckea*  
359 *frutescens* and *Leptospermum polygaliifolium* (**Figure 8**).

360 Counts of total obligate seeder plants (not separate species) at the northern site increased after the fire  
361 event, although they decreased in September 2023 as the number of resprouters increased. Robust  
362 germination of *Phyllota phyllicoides* accounted for most of the post-fire increase, and *Phyllota* was the  
363 only obligate seeder shrub with a post-fire stem count greater than the pre-impact levels. Most  
364 obligate seeders were recruited poorly after the fire, with no seedling germination for four out of ten  
365 species, including *Persoonia virgata*, the dominant obligate seeder shrub at the northern site when  
366 monitoring commenced in April 2016.

367 Several resprouter shrubs increased after the fire, including *Banksia oblongifolia* and *Baeckea*  
368 *frutescens*, and there was a delayed increase in *Boronia falcifolia* in April 2023. *Leptospermum*  
369 *liversidgei*, the dominant resprouter shrub in April 2016, suffered substantial fire-related stem  
370 reduction, with only minor species recovery evident by September 2023.

371 **Groundcovers:** Native perennial grass/sedge/rush, shrubs (<0.5m height), forbs, and grasstree are the  
372 four lifeform categories analysed in the groundcover assessment. An 'exotics' category relates to  
373 cover of *Pinus* seedlings. Bare ground and leaf litter comprised the residual cover values. Post-fire  
374 leaf litter values at the North site increased dramatically after the wildfire (**Figure 9**) because of the  
375 blackened vegetative matter and ash spread across scorched/bare areas by soaking rainfall on the days  
376 before the October 2019 assessment. Groundcover shrubs fluctuated within a consistent range of  
377 12.3% to 18.3% for the South and 15.7% to 26.8% for the North. However, at the northern site post-  
378 fire (October 2019), ground cover shrubs were destroyed. Post-fire shrub cover regenerated rapidly

379 due to the initial rapid nodal resprouting of *Baeckea frutescens* and *Banksia oblongifolia*, followed by  
380 the dense germination of *Phyllota phyllicoides* after the October rainfall.

381 Grass/sedge/rush and grasstree covers reestablished rapidly after combustion without any detectable  
382 structural or floristic composition changes. Grasstree cover had returned to pre-fire cover levels by  
383 May 2021, demonstrating abundant post-fire resprouting from subterranean rhizomes (Lamont et al.,  
384 2004; Taylor et al., 1998).

385 Forbs are a minor component of the total ground cover, with the highest values at the South site  
386 (3.02%) reported in April 2022, following five months of soil surface saturation (**Figure 9**). The  
387 highest forb cover value at the northern site occurred in October 2021 (4.2%), remained stable  
388 through 22 April (4.1%), and then decreased in September 2023 (2.38%). For both the northern and  
389 southern sites, the forb cover values were generally higher in the post-wet season assessments than in  
390 the dry season. Notably, bare soil increased at both sites post-fire (when the CRD increased).

### 391 **Model Analysis**

#### 392 **Stem Counts**

393 **BACI model:** The BACI-type model, which best supports the total stem count data, includes the  
394 cubic root of years since impact ( $t_{\text{years}}^{(1/3)}$ ) as an explanatory variable. The 'Site-type: Period' interaction  
395 term was found to be significant ( $\beta = -4.45$ ,  $se = 0.62$ ,  $p\text{-value} < 0.0001$ ), indicating that at  $t_{\text{years}}=0$ , the  
396 fire had a significant negative effect on mean total stem counts, consistent with destruction of the  
397 shrub layer. The  $t_{\text{years}}^{(1/3)}$  interaction was also significant ( $\beta = 4.02$ ,  $se = 0.47$ ,  $p\text{-value} < 0.0001$ ),  
398 indicating that the fire had a significant positive temporal effect on mean stem counts (see **Figure**  
399 **10A & B**).

400 Similarly, the BACI-type model best supporting both the measured resprouter and obligate seeder  
401 stem counts, included the cubic root of years since impact ( $t_{\text{years}}^{(1/3)}$ ) as an explanatory variable. The  
402 'Site-type: Period' interaction term is significant for both resprouters ( $\beta = -3.81$ ,  $se = 0.63$ ,  $p\text{-value} <$

403 0.0001) and obligate seeders ( $\beta = -6.31$ ,  $se = 1.01$ ,  $p\text{-value} < 0.0001$ ), demonstrating that at  $t_{\text{years}}=0$ ,  
404 the fire had a significant negative effect on mean stem counts for shrubs in both categories.

405 The ' $t_{\text{years}}^{(1/3)} \cdot \text{Site-type}$ ' interaction was significant in the BACI-model for both resprouter ( $\beta = 2.21$ ,  $se$   
406  $= 0.48$ ,  $p\text{-value} < 0.0001$ ) and obligate seeder species ( $\beta = 7.13$ ,  $se = 0.77$ ,  $p\text{-value} < 0.0001$ ). The  
407 model mean stem count prediction for September 2023 at the North site for resprouters (395.93, CIs =  
408 289.75, 541.03) was significantly larger than the pre-impact levels at the South site (impact: 248.14,  
409 95% CIs = 198.5, 310.25; control: 45.7, 95% CIs = 35.8, 58.4) (see **Figure 10C & D**). Similarly,  
410 mean stem count prediction in September 2023 for obligate seeders (1588.3, CIs = 999.96, 2522.7)  
411 was significantly larger than the pre-impact levels at both sites (impact: 118.14, 95% CIs = 85.7,  
412 162.78; control: 120.86, 95% CIs = 87.7, 166.5) (see **Figure 10E & F**), indicating that the fire had a  
413 significant positive temporal effect on mean stem counts for the resprouter and obligate seeder  
414 categories, although it was more pronounced for obligate seeders. The uncertainty in mean stem count  
415 predictions for resprouter and obligate seeder stems increases with time because the recovery effect  
416 diminishes and stem counts stabilise, with structural recovery limited by the site carrying capacity and  
417 exhaustion of the soil seed bank following mass germination for obligate seeders.

418 **Environmental covariates model:** The best-supported model using environmental covariates for  
419 total woody stem counts included CRD, site type, and period as explanatory variables. CRD was  
420 found to significantly increase mean stem counts ( $\beta = 0.0011$ ,  $se = 0.00026$ ,  $p\text{-value} < 0.0001$ ).  
421 Predicted mean stem counts for September 2023 at the North (Impact) site (1611.6, 95% CIs =  
422 1184.1, 2193.5) were significantly higher than pre-impact levels at both sites (Impact: 366.3, 95% CIs  
423 = 293.80, 456.67; Control: 166.6, 95% CIs = 133.1, 208.5).

424 CRD, site type, and period were also key explanatory variables in models for resprouter and obligate  
425 seeder stem counts. CRD showed a significant positive effect on resprouter mean stem counts ( $\beta =$   
426  $0.0010$ ,  $se = 0.00021$ ,  $p\text{-value} < 0.0001$ ) and obligate seeder mean stem counts ( $\beta = 0.00088$ ,  $se =$   
427  $0.00038$ ,  $p\text{-value} = 0.022$ ). Despite their correlation, CRD exerted a stronger influence on stem counts  
428 compared to rainfall.

429 **Species Richness**

430 **BACI model:** The best-supported BACI-type model for species richness included the cubic root of  
431 years since impact ( $t_{\text{years}}^{(1/3)}$ ) as the explanatory variable. However, the data supported two other models  
432 ( $AICc < 2$ ), suggesting a large uncertainty in the BACI model structure, and the results should be  
433 treated cautiously. The additionally supported models included 'Site-Type; Period + ( $t_{\text{years}}^{(1/3)}$ ) and  
434 CRD,' as explanatory variables, suggesting CRD may influence post-fire recovery in species richness  
435 after controlling for temporal effects. The 'Site-type: Period' interaction term was not significant in  
436 the model ( $\beta = -0.65$ ,  $se = 0.34$ ,  $p\text{-value} = 0.0539$ ), indicating that at  $t_{\text{years}}=0$ , the fire did not have a  
437 significant effect on species richness. However, the 'p' value was close to the significance level used  
438 in this study ( $\alpha=0.5$ ), and some floristic recovery occurred in the six weeks between the fire impact  
439 and the post-fire field survey (October 2019).

440 The '( $t_{\text{years}}^{(1/3)}$ ): Site-type' interaction was found to be not significant in the model ( $\beta = 0.37$ ,  $se = 0.25$ ,  
441  $p\text{-value} = 0.15$ ), indicating that the fire did not have a significant temporal effect on species richness.  
442 The prediction of mean species richness for September 2023 at the impact site (40.88, CIs = 34.56,  
443 50.03) was not significantly different from the pre-impact levels at either site (impact: 41.43, 95% CIs  
444 = 36.92, 46.48; control: 40.29, 95% CIs = 35.85, 45.27) (see **Figure 11A & B**).

445  
446 The 'null model' provided the best fit for resprouter species richness, which was not significantly  
447 different between the northern and southern sites ( $t = 1.91$ ,  $df = 19$ ,  $p = 0.071$ ), indicating that fire did  
448 not significantly influence resprouter richness.

449  
450 For obligate seeder species richness, the best BACI-type model included the cubic root of years (  
451  $t_{\text{years}}^{(1/3)}$ ) as the explanatory variable. However, similar to the overall stem counts, the data supported  
452 two other models ( $AICc < 2$ ), suggesting uncertainty in the model structure and that CRD may  
453 influence obligate seeder species richness. The 'Site-type: Period' interaction term was significant in  
454 the BACI-model ( $\beta = -1.73$ ,  $se = 0.73$ ,  $p\text{-value} = 0.017$ ), indicating that at  $t_{\text{years}}=0$ , the fire had a

455 significant adverse effect on obligate seeder species richness. The '(t<sub>years</sub><sup>(1/3)</sup>): Site-type' interaction is  
456 also significant in the BACI-model ( $\beta = 1.11$ ,  $se = 0.53$ ,  $p\text{-value} = 0.034$ ), indicating that the fire had a  
457 significant positive temporal effect on obligate seeder species richness (**Figure 11C & D**). While the  
458 fire event positively influenced the richness of obligate seeder species, it did not affect resprouter  
459 species richness.

460 **Environmental covariates model:** The best model based on environmental covariates included CRD  
461 and Period as explanatory variables (**Figure 12**). While CRD demonstrated a significant positive  
462 effect on species richness ( $\beta = 0.0003$ ,  $se = 0.000076$ ,  $p\text{-value} < 0.0001$ ), the influence of rainfall was  
463 not significant, agreeing with the supported environmental covariates model for stem counts. The best  
464 environmental covariate model for obligate seeder species richness included the CRD, site type, and  
465 period as explanatory variables. Whilst CRD was found to have a significant positive effect on overall  
466 species richness ( $\beta = 0.00058$ ,  $se = 0.00013$ ,  $p\text{-value} < 0.0001$ ), it was found not to have a significant  
467 effect on resprouter species richness.

## 468 Discussion

469 This study provides insight into the complex nature of fire dynamics in a coastal heathland ecosystem  
470 and presents several fire-response outcomes that are contrary to expectations. Even with extended fire  
471 intervals, an inappropriate fire regime may damage obligate seeders and some resprouter species, and  
472 a post-fire rebound in species richness is not guaranteed. This discussion addresses novel aspects of  
473 fire responses and elucidates critical regulators of post-fire ecological outcomes.

474 **Variability in fire response for obligate seeders:** Fire impacts, encompassing combustion and  
475 recovery effects, significantly influenced stem counts across all models, but the response differed  
476 between obligate seeders and resprouters. While resprouter stem counts were relatively static, obligate  
477 seeder stems rapidly surpassed pre-impact levels, driven primarily by mass recruitment of *Phyllota*  
478 *phylicoides*. Before the intense wildfire, *Persoonia virgata* dominated the shrub layer but failed to  
479 regenerate afterward. This loss may stem from differences in seed resilience; *Phyllota*'s hard-coated

480 seeds likely resisted topsoil scorching and were possibly buried deeper than *Persoonia*'s. *Phyllota*  
481 responded robustly to fire and subsequent rainfall triggers for germination, whereas *Persoonia* seeds  
482 likely perished due to high topsoil temperatures during the wildfire.

483 Over eight years of monitoring, *Persoonia virgata* populations declined at the southern site, possibly  
484 due to aging following an earlier fire event and a subsequent long fire interval. While long fire  
485 intervals (>8 years) may benefit fire-sensitive obligate seeders like *Persoonia virgata* by maximising  
486 seed bank storage (McFarland, 1998; DES, 2023), this study highlights that recovery can be hindered  
487 by intense fires amid dry pre-fire conditions, and that interval is only one aspect of the fire regime  
488 influencing post-fire ecological response of obligate seeder species.

489 **The influence of fire on species richness:** The BACI model revealed that fire did not affect overall  
490 species richness at the North site, although a modest increase in obligate seeder species richness was  
491 observed post-fire, consistent with the expected response (Freestone et al., 2015; Russell & Parsons,  
492 1978). However, by September 2023 (four years post-fire), only 13 obligate seeder species were  
493 recorded compared to 17 in September 2016. Species absent in 2023 included *Aotus lanigera*,  
494 *Drosera binata*, *Laxmannia compacta*, and *Pseudanthus orientalis*— the latter three delicate  
495 groundcover forbs unlikely to benefit from topsoil scorching. While fire positively impacted obligate  
496 seeders, species richness did not exceed the highest pre-fire levels recorded in 2016, and resprouter  
497 species richness was unchanged.

498 Contrary to predictions, the wildfire did not stimulate overall species richness, reaching its maximum  
499 three years post-fire instead of the anticipated rapid peak (Enright et al., 1994; Freestone et al., 2015;  
500 Russell & Parsons, 1978). The expected robust increase in obligate seeder species richness post-fire  
501 also failed to materialise (Benwell, 1998; Bradstock et al., 1996; Russell-Smith et al., 2002), despite a  
502 sufficient fire-free interval to develop a substantial soil seed bank. Following the fire, *Phyllota*  
503 *phylicoides* proliferated at the expense of other species, such as *Persoonia virgata*, which were  
504 eliminated. This unexpected ecological response is attributed to adverse burning conditions—intense

505 fire coinciding with a period of moisture deficit characterised by low SMC and depressed  
506 groundwater levels.

507 **The regulatory effect of soil moisture and groundwater:** Griffith and Bale (2004) suggest that  
508 short-term rainfall changes minimally affect plant species distribution in heathlands, a conclusion  
509 supported by this study. Both BACI and Environmental Covariate models found no significant  
510 influence of rainfall on woody stem count or species richness. However, longer-term trends in  
511 moisture availability, indicated by CRD, significantly impacted these indices. Positive CRD trends  
512 correlated with abundant soil moisture and high groundwater tables, while negative trends signaled  
513 moisture deficits, affecting heathland resilience.

514 The northern site consistently maintained higher moisture levels than the southern site, likely  
515 contributing to higher species richness observed in early assessments (2016-2017). Pearl et al. (2024)  
516 suggested that moist conditions in southeast Queensland heathlands act as refuges, buffering extreme  
517 fire and drought impacts (Reside et al., 2019). As climate dries, groundwater levels drop, soil  
518 moisture decreases, and heathland species become vulnerable to stress and wildfire (Myerscough &  
519 Clarke, 2007; Dudgeon, 2013). Modeling at the southern site, with long-term fire exclusion, predicts  
520 species richness regulated by CRD-driven wetting and drying cycles affecting soil moisture and  
521 groundwater. Forb species, less morphologically plastic or competitive than graminoids, significantly  
522 influence species richness due to their mesic nature (Casillo et al., 2012; Stampfli et al., 2018). Post-  
523 fire, increased bare ground supports forb colonisation, further influenced leaf litter / ash dispersion  
524 from intense rainfall events.

525 Modeling demonstrated CRD's positive influence on woody stem counts, consistent with findings in  
526 various habitats where soil moisture similarly influences woody biomass (Maguas et al., 2011;  
527 Kulmatisk & Beard, 2013; Ciruzzi & Loheide, 2021). At the unburnt southern site, resprouter species  
528 in the Myrtaceae family, like *Leptospermum semibaccatum*, showed positive responses to wetting  
529 trends. *Leptospermum polygalifolium* and *Baeckea frutescens* also responded positively to CRD, with  
530 post-fire groundwater table rises potentially aiding heathland recovery. Structural thickening towards

531 heath woodlands or tall shrub thickets without fire during drying cycles seems unlikely (Pierce &  
532 Cowling, 1991; Bennett, 1994; Bargmann & Kirkpatrick, 2014). Griffith and Bale (2004) noted  
533 Wallum species like *Banksia aemula* can tap into the water table, but most concentrate roots at the  
534 capillary fringe (Griffith et al., 2008). Species like *Leptospermum liversidgei*, rooted in damp sand  
535 above the water table, suffer moisture stress and severe wildfire impacts when groundwater drops  
536 rapidly. Root bud damage from extended dry periods before wildfires likely contributed to pre-fire  
537 stem declines, compounded by high mortality and limited post-fire recovery.

538 *Banksia oblongifolia* also concentrates roots at the capillary fringe (Griffith et al., 1994), showing  
539 increased stem counts post-fire due to effective resprouting strategies and greater drought tolerance.  
540 Coexisting with *Banksia aemula* in dry heaths, *Banksia oblongifolia* demonstrates resilience to drying  
541 soil conditions. *Banksia aemula*'s ability to extend roots rapidly during declining groundwater levels  
542 enhances wildfire resilience, although rapid groundwater decline can trigger drought responses,  
543 rendering plants vulnerable to intense fires if coinciding. In summary, this study underscores the  
544 influence of CRD trends in heathland dynamics, influencing soil moisture, groundwater levels, and  
545 species responses to fire and drought. Understanding these interactions informs effective fire  
546 management strategies, aligning prescribed burns with periods of high groundwater or wetting trends  
547 to protect heathland resilience and biodiversity.

## 548 **Conclusions**

549 The response of heathlands to fire is complex and challenging to predict, influenced by fire intensity,  
550 frequency, climate, and soil moisture conditions. This study addresses a critical knowledge gap  
551 regarding fire impacts on groundwater-dependent heathlands through a BACI study using field data.  
552 Contrary to conventional wisdom in heathland fire ecology, our findings reveal that post-fire recovery  
553 of species richness may not be swift, especially if intense fires coincide with dry climatic conditions  
554 suppressing soil moisture content (SMC) and groundwater levels. Even with a 20-year fire-free  
555 interval, obligate seeder regeneration varied significantly after fire events, with species like *Phyllota*  
556 *phylicioides* benefiting while others like *Persoonia virgata* were adversely affected. This variability is



557 linked to differences in seed coat resilience and burial depth in the soil, impacting protection against  
558 intense heat. Long-term rainfall patterns, affecting soil moisture and groundwater, positively influence  
559 heathland species richness and woody shrubs. However, severe wildfires, especially when poorly  
560 timed, can override these climatic influences, leading to destructive outcomes.

561 These findings underscore the critical role of fire timing and intensity in managing wet heathlands.  
562 Effective prescribed fire practices should align with periods when groundwater levels are high or near  
563 the surface, ideally during long-term wetting trends. This approach minimises damage to soil seed  
564 banks and protects underground roots and rhizomes from excessive heat exposure. In summary, this  
565 study highlights the nuanced interactions between fire, climate, and soil moisture in heathland  
566 ecosystems. It emphasises the need for adaptive fire management strategies that consider both  
567 immediate fire impacts and broader climatic influences on ecosystem resilience and biodiversity.

568

#### 569 **Author Contributions**

570 DS planned and designed the study, which was fundamental to the development and design of the  
571 manuscript. MD contributed to the field data collection, data analysis, and manuscript content and  
572 structure. RP designed and completed the statistical analyses. Paul Williams provided a critical review  
573 and commentary throughout all the stages of field data collection through the development of the  
574 manuscript. All the authors have read and approved the final version of the manuscript.

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864 aquifer. *Oecologia*, 131(1), 8–19.

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For Review Only

866 **Tables**

867 **Table 1.** Flora species in the various lifeforms recorded throughout the vegetation monitoring period classified by their fire recruitment  
 868 strategy by Gill and Bradstock (1992)<sup>†</sup> (cited in Myerscough, 1995) and Benwell (1998)<sup>‡</sup>. Taxonomic nomenclature is consistent with the  
 869 Bean (2024).

Lifeform	Fire Response -Gill and Bradstock (1992) cited in Myerscough (1995)/ Fire response – Benwell (1998); Species
<b>Obligate seeder</b>	
<b>Forbs</b>	<b>II/OSR-1:</b> <i>Cassutha glabella</i> , <i>Gonocarpus micranthus</i> , <i>Laxmannia compacta</i> , <i>Mirbellia rubiifolia</i> , <b>IV/OSR-1;</b> <i>Drosera binata</i> , <b>V/OSR-1;</b> <i>Hibbertia acicularis</i> , <i>Hibbertia salicifolia</i> , <i>Pseudanthus orientalis</i> ,
<b>Shrubs</b>	<b>II/FR-7:</b> <i>Phyllota phyllicoides</i> <sup>§</sup> <b>II/OSR-1;</b> <i>Acacia baueri</i> , <i>Acacia flavescens</i> , <i>Aotus lanigera</i> , <i>Dillwynia floribunda</i> , <i>Epacris obtusifolia</i> , <i>Epacris pulchella</i> , <i>Homoranthus virgatus</i> , <i>Persoonia virgata</i> , <i>Sprengelia sprengelioides</i> , <i>Pultenaea paleacea</i> , <i>Pultenaea robusta</i> <b>IV/OR-1;</b> <i>Melaleuca pachyphyllus</i> <sup>††</sup> <b>V/OSR-1;</b> <i>Ochrosperma lineare</i> , <b>V/OSR-2;</b> <i>Strangea linearis</i>
<b>Resprouter</b>	
<b>Forbs</b>	<b>IV/FR-4;</b> <i>Sowerbaea juncea</i> , <i>Stylidium trichopodom</i> , <i>Selaginella uliginosa</i> , <i>Stackhousia nuda</i> <b>V/FR-4;</b> <i>Mitrasacme</i> <i>alsinoides</i> , <i>Patersonia sericea</i> ; <i>Pimelea linifolia</i> <b>V/FR-6;</b> <i>Cryptostylis erecta</i> <sup>††</sup> , <i>Microtus parviflora</i> <sup>††</sup> , <b>V/FR;</b> <i>Blechnum cartilagineum</i> <sup>††</sup> , <i>Burchardia umbellata</i> , <i>Commosperma sphaericum</i> <sup>§</sup> , <i>Xyris complanata</i> ,
<b>Grasses</b>	<b>V/FR-4;</b> <i>Eriachne pallescens</i> var. <i>gracillis</i> , <i>Themeda triandra</i> <sup>§</sup>
<b>Grasstree</b>	<b>V2/FR-6;</b> <i>Xanthorrhoea fulva</i> ; <i>Xanthorrhoea johnsonii</i>
<b>Sedges and rushes</b>	<b>IV/FR-4;</b> <i>Baloskion heterophylla</i> , <i>Baloskion tenuiculme</i> , <i>Cyperus gracilis</i> , <i>Schoenus calostachys</i> , <i>Schoenus</i> <i>scabripes</i> , <i>Sporodanthus interruptus</i> , <i>Caustis recurvata</i> <b>IV/FR-7;</b> <i>Hypolaena fastigiata</i> , <i>Leptocarpus tenax</i> <b>V/FR-</b> <b>4;</b> <i>Gahnia seiberiana</i> , <i>Lomandra elongate</i> <b>V/OR-11;</b> <i>Lomandra longifolia</i>
<b>Shrubs</b>	<b>II/FR-5;</b> <i>Austromyrtus dulcis</i> <sup>††</sup> <b>IV/FR-4;</b> <i>Baeckea frutescens</i> , <i>Baeckea imbricata</i> , <i>Boronia falcifolia</i> , <i>Leptospermum</i> <i>semibaccatum</i> , <i>Olax retusa</i> <b>V/FR-5;</b> <i>Banksia oblongifolia</i> <sup>§</sup> , <i>Leptospermum liversidgei</i> <sup>§</sup> , <i>Leptospermum</i> <i>polygalifolium</i> , <i>Melaleuca quinquenervia</i> <b>VI/FR-4;</b> <i>Agiortia pedicellata</i> , <i>Conospermum taxifolium</i> , <i>Leucopogon</i> <i>leptospermoides</i> <b>VI/FR-5;</b> <i>Banksia aemula</i> <b>II/FR-4;</b> <i>Elaeocarpus reticulatus</i> <sup>§</sup>

870 <sup>†</sup>From Gill and Bradstock (1992); **I** -Killed- Canopy Stored Seed Bank; **II**: Killed-Soil Stored Seed Bank; **III**-Killed-No Local Seed Bank;

871 **IV**-Resprouts from Root Buds; **V**-Resprouts from Basal Buds; **VI**-Resprouts from Stem; **VII**-Resprouts from Unharmed Terminal Buds.

872 <sup>‡</sup>From Benwell (1998); **OSR-1**-Vegetative Regeneration-Absent Soil Seed Bank; **OSR-2**-Vegetative Regeneration Absent-Canopy Seed

873 Bank; **FR-4**-Vegetation Regeneration Present-Soil Seed Bank; **FR-5**-Vegetation Regeneration Present-Canopy Seed Bank; **FR-6**-Vegetation

874 Regeneration Present-Post Fire Flowering; **FR-7**-Vegetation Regeneration Present-Clonal Increaser soil seed Bank; **OR-11**-Vegetation

875 Regeneration Present Clonal Increaser -seeding absent.

876 <sup>§</sup>Species recorded only at the North site; <sup>††</sup>Species recorded only at the South site.

877

878 **Figure Legends**

879 **Figure 1.** Bribie Island study site within the Moreton Bay Ramsar Wetland, showing the North site  
880 (northern transects) and South site (southern transects).

881  
882 **Figure 2.** Spot 6 NDVI imagery shows the extent and severity of the burn scar relative to monitoring  
883 sites. Red wash indicates healthy green vegetation, while black scalding indicates complete  
884 combustion of living vegetation. The straight clearings are maintained firebreaks, typically over 20  
885 meters wide (A). Photograph (B) shows vegetation monitoring transect 6b at the North site before  
886 burning in April 2019, compared to six weeks after the severe wildfire on 21st August 2019 (C). The  
887 post-burning photograph (C) demonstrates complete scorching of the shrub layer and ground cover,  
888 with areas of bare sand and black ash, among newly resprouting grass trees.

889  
890 **Figure 3.** Cumulative Rainfall Deficit (CRD) for 33 years at Bongaree, located at the southern end of  
891 Bribie Island, shows a trough in rainfall volumes coinciding with the Millennium Drought (1997 to  
892 2009) and the monitoring period between 2016 and 2023 (A). The relationship between groundwater  
893 levels and CRD is shown in (B), with an offset between groundwater and CRD in mid-2019 attributed  
894 to the wildfire. M-REF indicates meters below the reference point.

895  
896 **Figure 4.** Monthly mean Soil Moisture Content (SMC, volume %) at the survey sites (North and  
897 South) compared to monthly rainfall and CRD during the vegetation monitoring period. A red vertical  
898 dashed line indicates the timing of the fire event, coinciding with a plunge in both CRD and SMC.  
899 Red-colored bars indicate periods when CRD was below 0 for both rainfall and CRD plots.

900  
901 **Figure 5.** Species richness assessed by survey, site, and habit. The red dashed line indicates the  
902 timing of the fire event.

903  
904 **Figure 6.** Species richness by survey, site, and fire response. The fire event is indicated by the red  
905 dashed line.

906

907 **Figure 7.** Woody (shrub) stem counts by survey, site, and fire response, showing an increase in total  
908 stem counts at the North site following fire impact. The counts of obligate seeder species dramatically  
909 increased at the North site following the August 2019 wildfire.

910

911 **Figure 8.** Trends in shrub stem counts for obligate seeders at the South and North sites (top left and  
912 top right, respectively) and resprouter species at the South and North sites (bottom left and bottom  
913 right). A large increase in *Phyllota phyllicioides* stem counts is evident at the North site following the  
914 August 2019 wildfire, while a collapse in *Persoonia virgata* stem counts is evident at the South site  
915 after the April 2018 assessment.

916

917 **Figure 9.** Groundcover at the North and South monitoring sites for individual survey events. The red  
918 dashed line indicates the fire event.

919

920 **Figure 10.** Impact of fire on predicted stem counts using the best Before-After-Control-Impact  
921 (BACI) model ( $t_{years}^{(1/3)}$ ) for total mean stem counts (panels A and B), resprouter stem counts (panels C  
922 and D), and obligate seeder stem counts (panels E and F). The data illustrates a significant temporal  
923 increase in stem counts following fire impact, particularly evident at the South site. Shading  
924 represents 95% confidence intervals across all models

925

926 **Figure 11.** Impact of fire on predicted mean species richness using the best Before-After-Control-  
927 Impact (BACI) model ( $t_{years}^{(1/3)}$ ) for total species richness (panels A and B) and obligate seeder species  
928 richness (panels C and D). The data shows no significant temporal effect of fire on total species  
929 richness, whereas it demonstrates a significant positive impact on obligate seeder species richness.  
930 Shading indicates 95% confidence intervals in all models.

931

932 **Figure 12.** Impact of CRD (Cumulative Rainfall Departure) on predicted mean species richness using

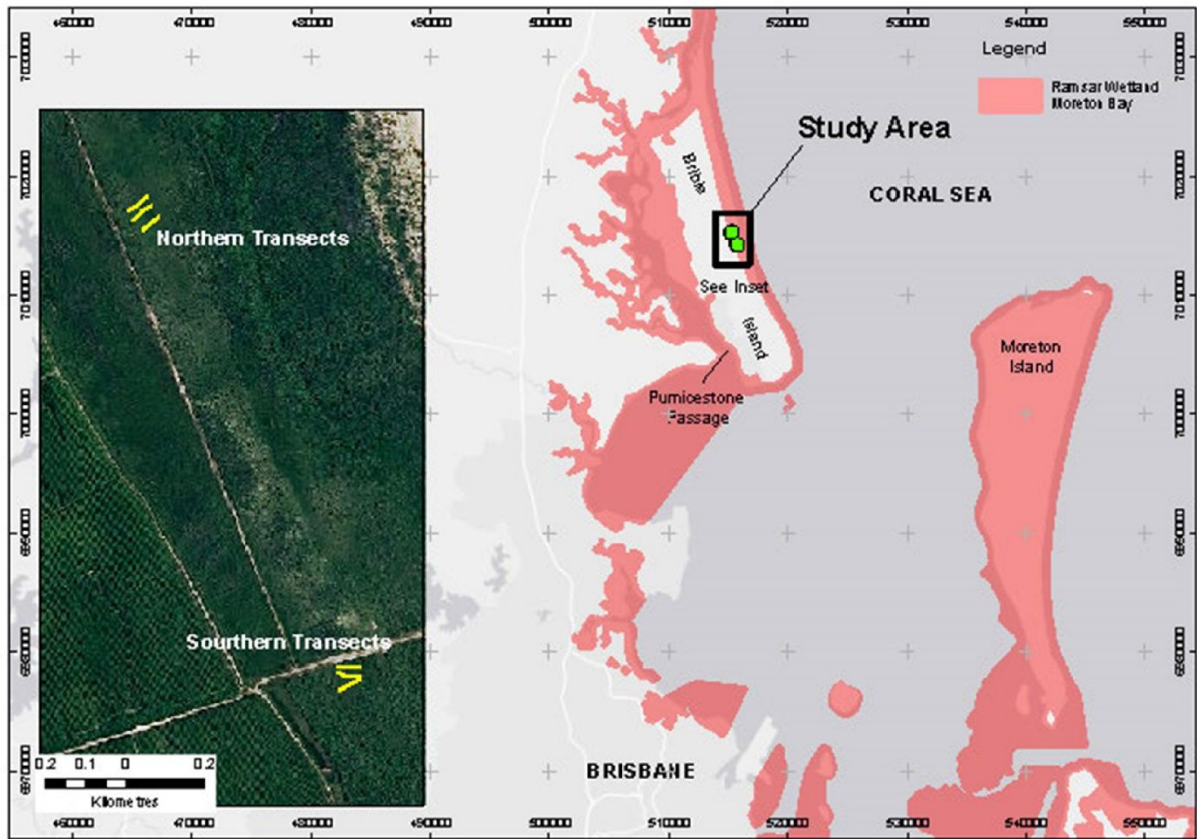
933 the best model incorporating environmental covariates (CRD and Period). Bars represent 95%

934 confidence intervals. CRD values reflect the range between April 2016 and September 2023.

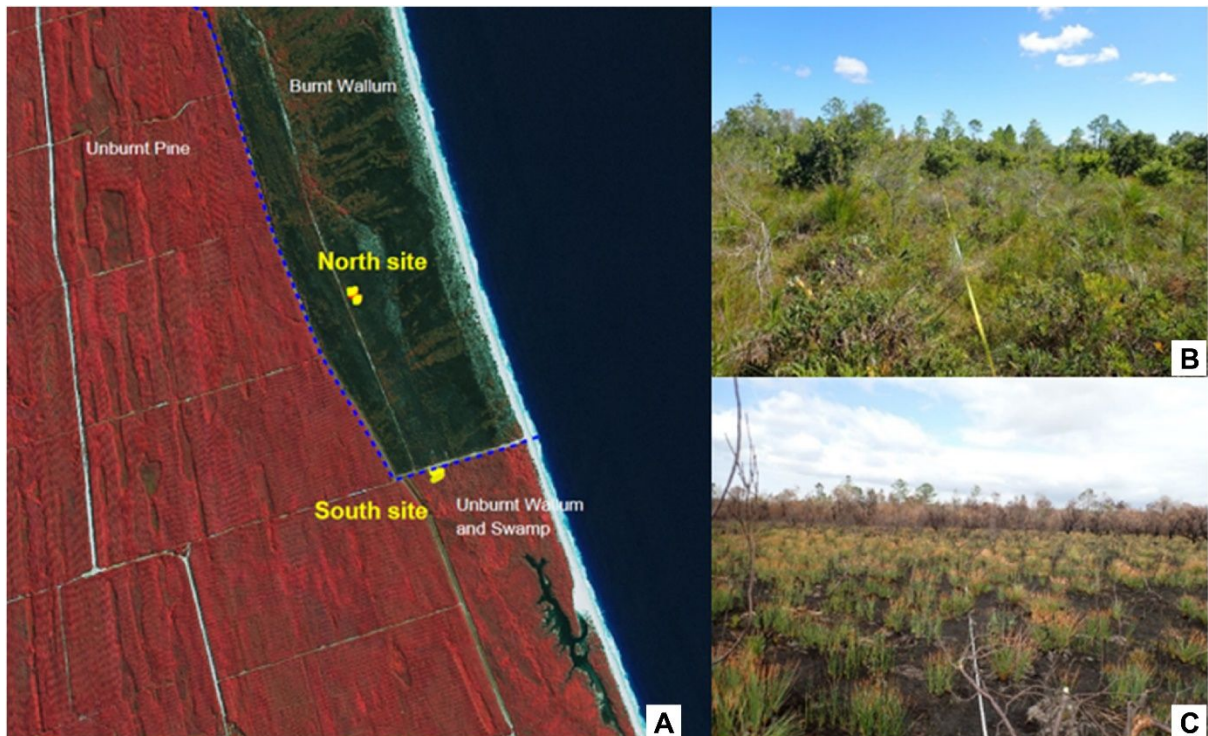
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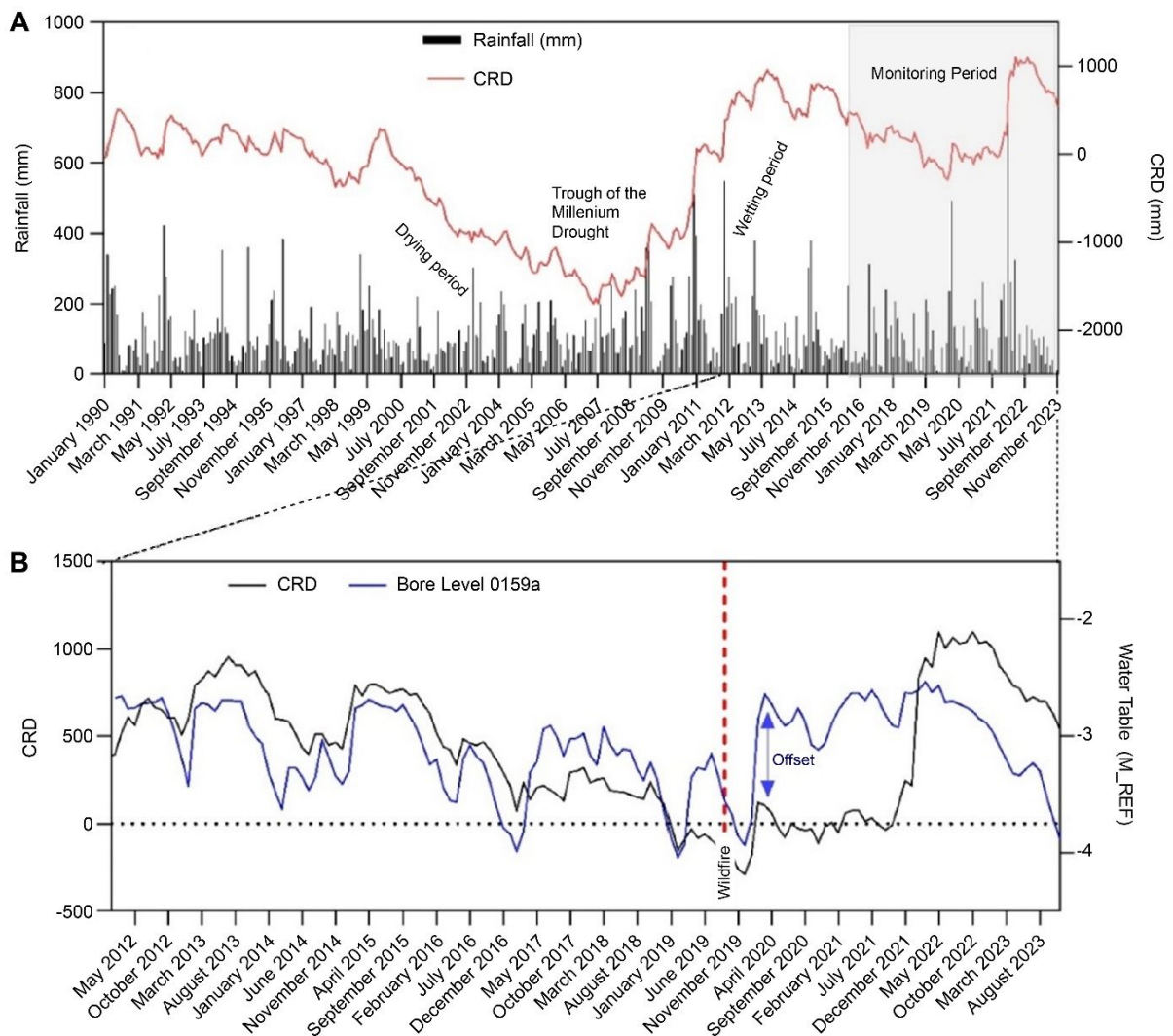




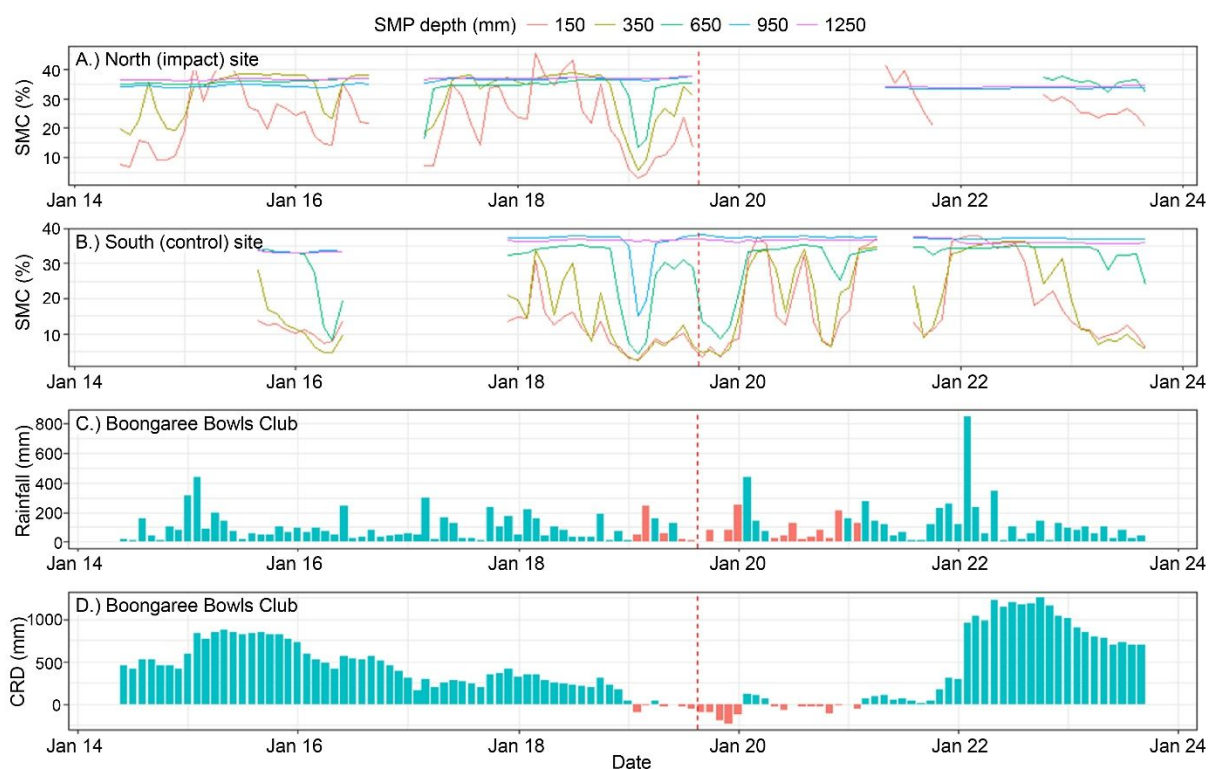
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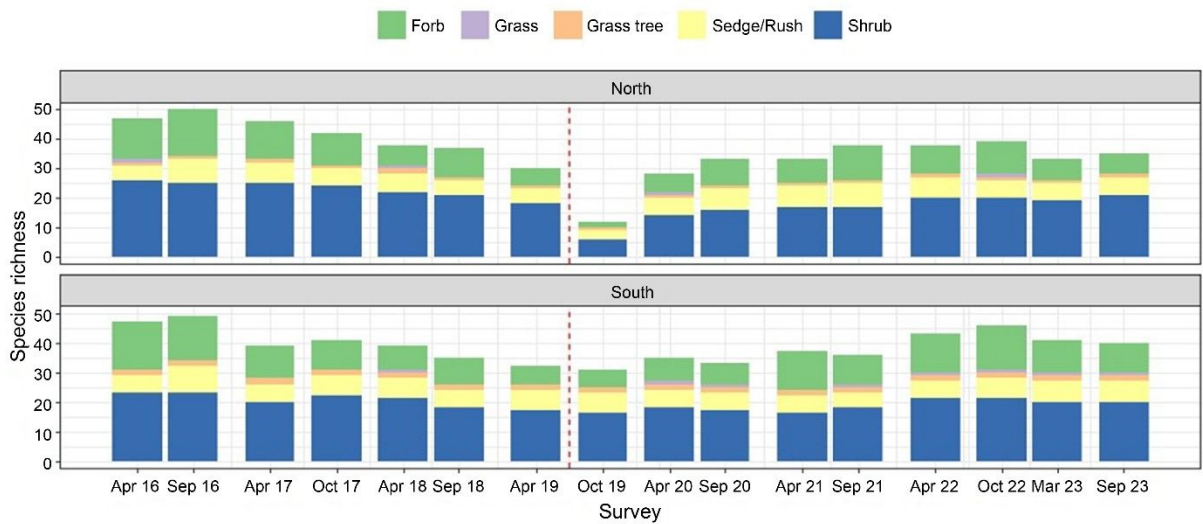
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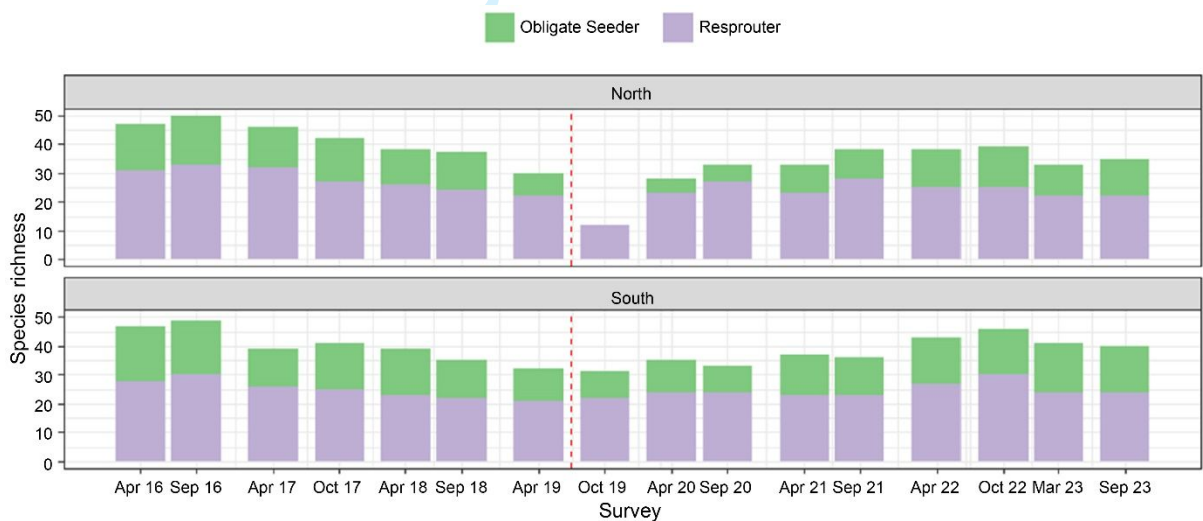
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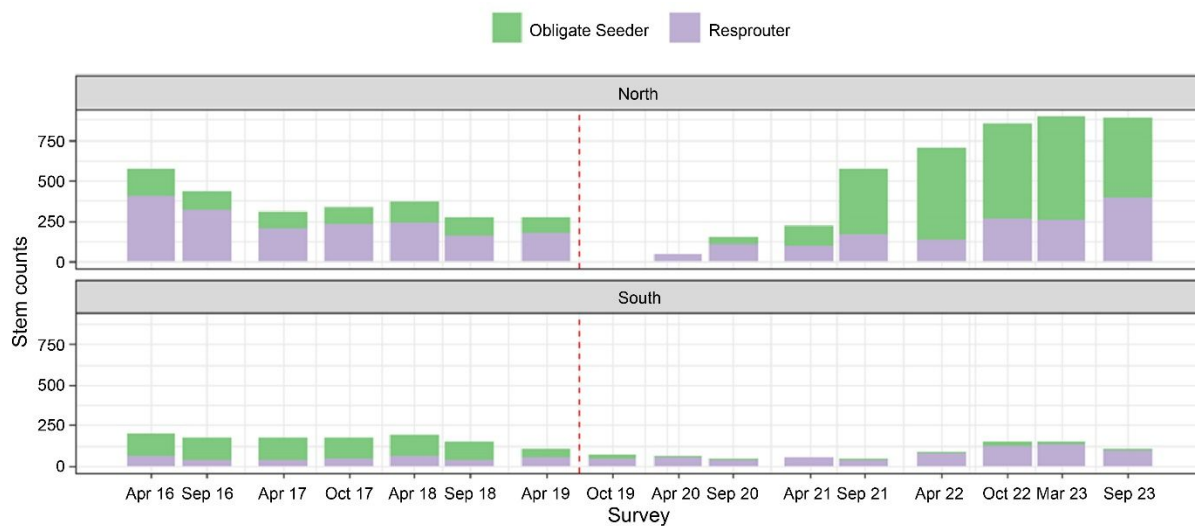
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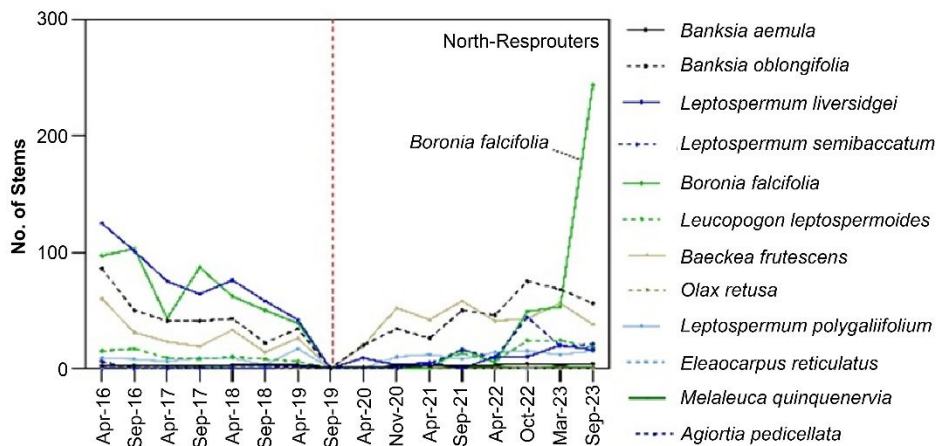
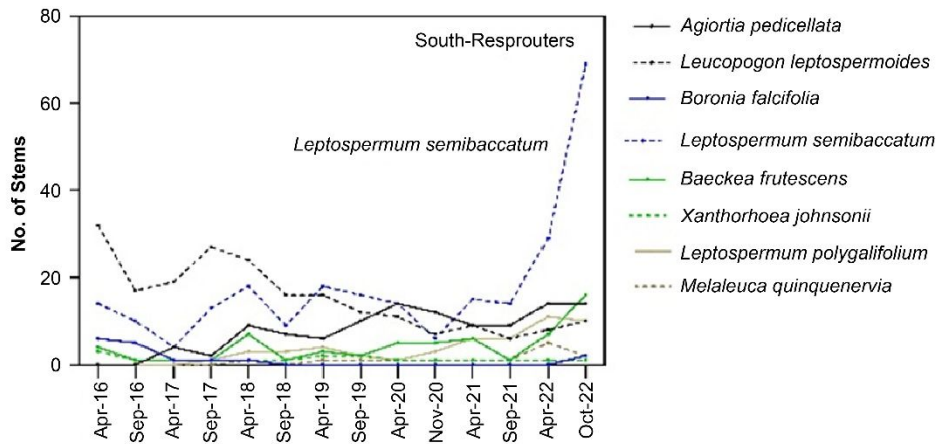
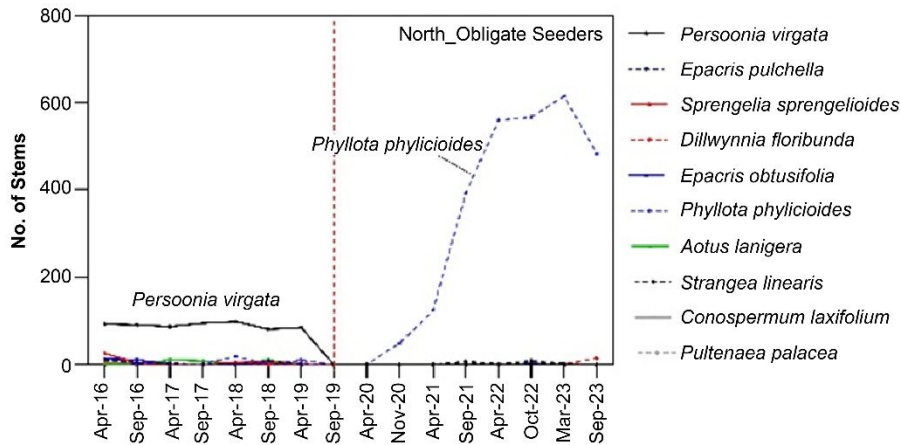
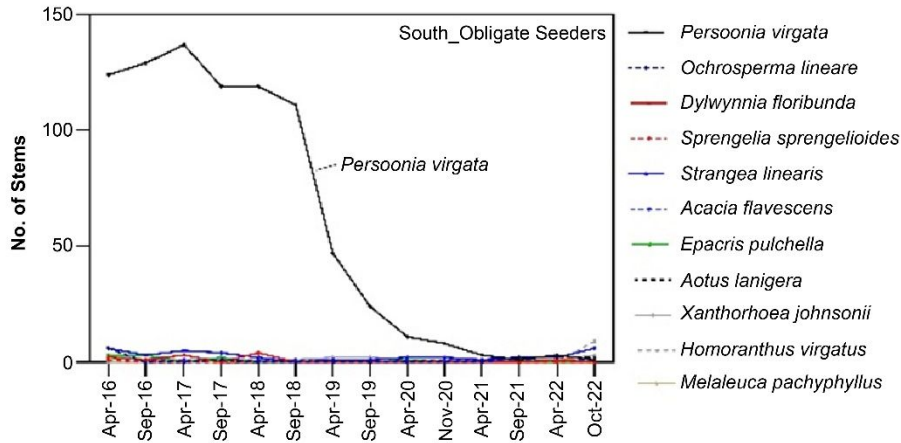
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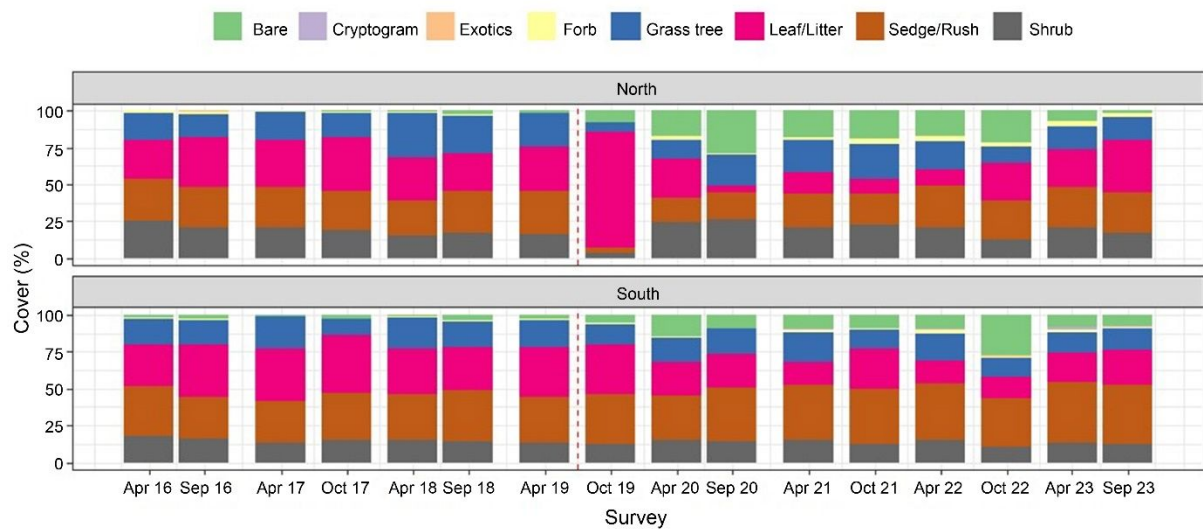
**Figure 6.** Species richness by survey, site, and fire response. The fire event is indicated by the red dashed line.



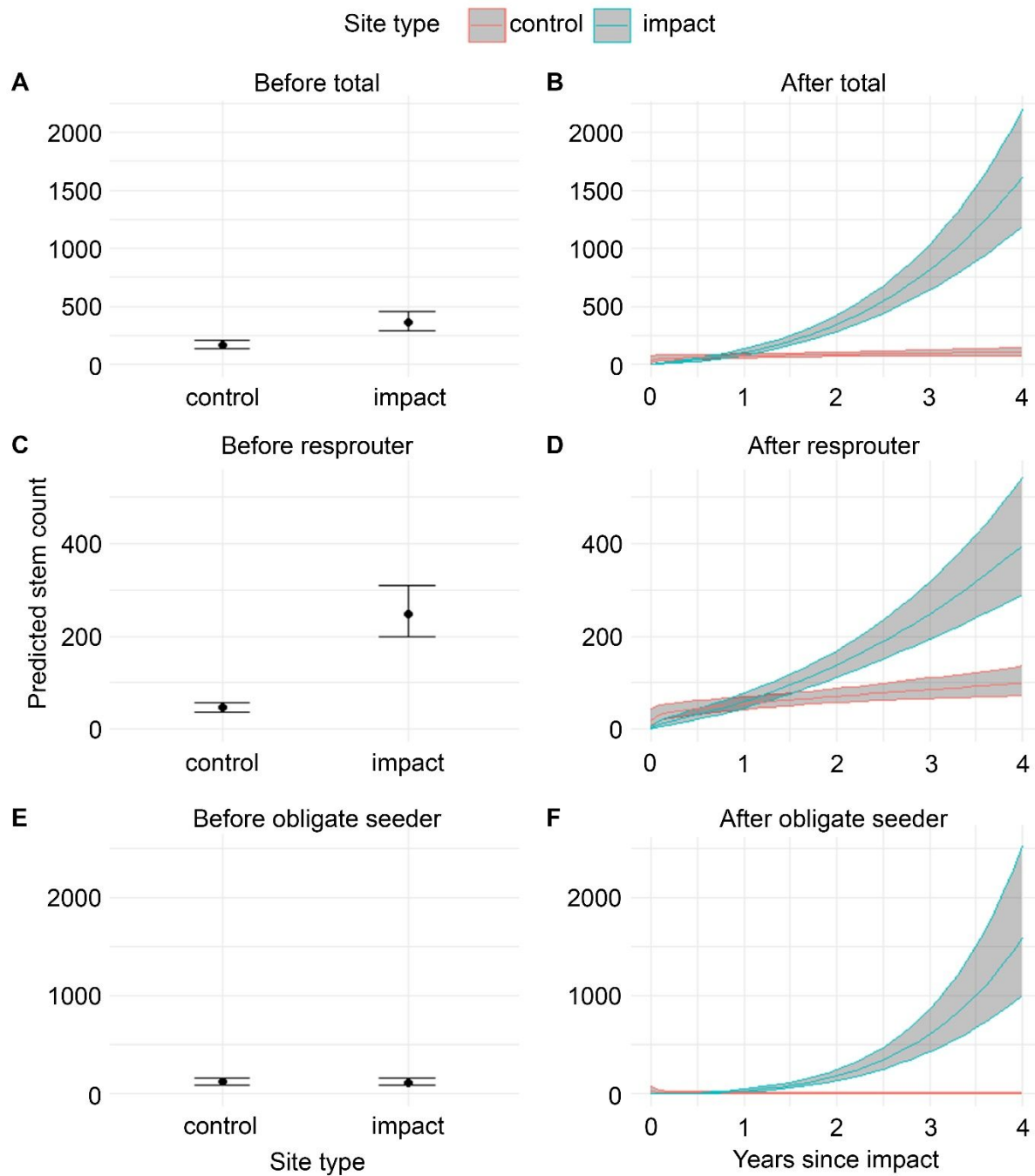
**Figure 7.** Woody (shrub) stem counts by survey, site, and fire response, showing an increase in total stem counts at the North site following fire impact. The counts of obligate seeder species dramatically increased at the North site following the August 2019 wildfire.



**Figure 8.** Trends in shrub stem counts for obligate seeders at the South and North sites (top left and top right, respectively) and resprouter species at the South and North sites (bottom left and bottom right). A large increase in *Phyllota phlycioides* stem counts is evident at the North site following the August 2019 wildfire, while a collapse in *Persoonia virgata* stem counts is evident at the South site after the April 2018 assessment.



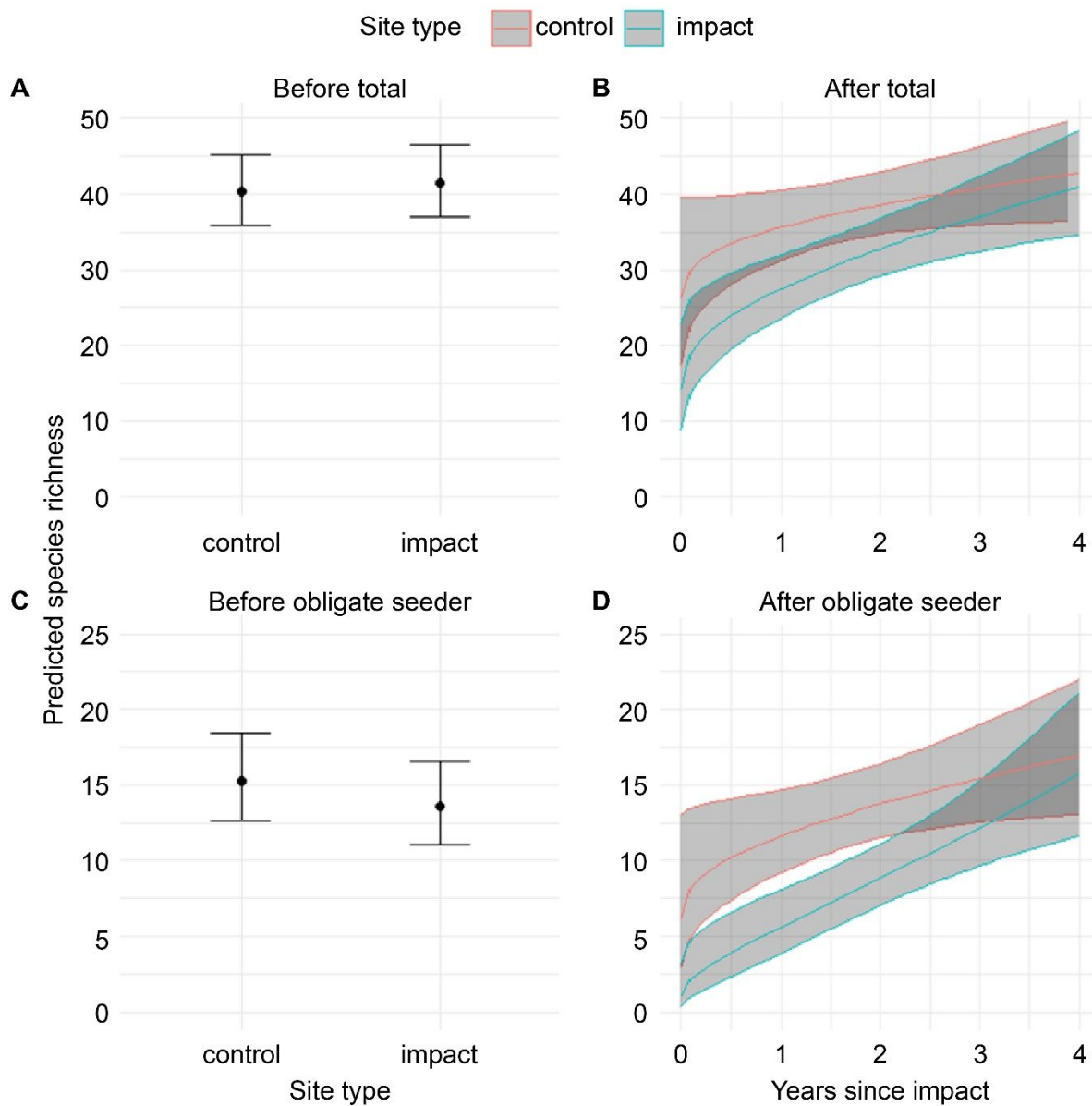
**Figure 9.** Groundcover at the North and South monitoring sites for individual survey events. The red dashed line indicates the fire event.



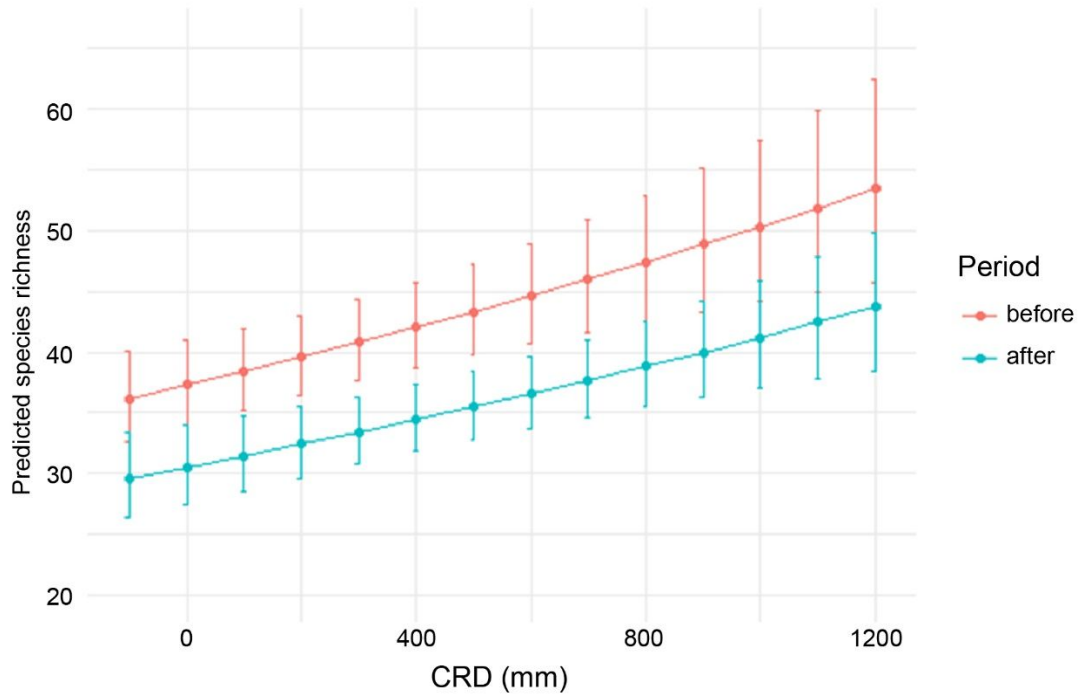
**Figure 10.** Impact of fire on predicted stem counts using the best Before-After-Control-Impact

(BACI) model ( $(t_{\text{years}}^{1/3})$ ) for total mean stem counts (panels A and B), resprouter stem counts (panels C and D), and obligate seeder stem counts (panels E and F). The data illustrates a significant temporal increase in stem counts following fire impact, particularly evident at the South site. Shading represents 95% confidence intervals across all models





**Figure 11.** Impact of fire on predicted mean species richness using the best Before-After-Control-Impact (BACI) model ( $t_{years}^{(1/3)}$ ) for total species richness (panels A and B) and obligate seeder species richness (panels C and D). The data shows no significant temporal effect of fire on total species richness, whereas it demonstrates a significant positive impact on obligate seeder species richness. Shading indicates 95% confidence intervals in all models.



**Figure 12.** Impact of CRD (Cumulative Rainfall Deviation) on predicted mean species richness using the best model incorporating environmental covariates (CRD and Period). Bars represent 95% confidence intervals. CRD values reflect the range between April 2016 and September 2023.

*Table 1: AICc table for stem count model selection. Model split by type (based on BACI design (BACI) and based on environmental covariates (ENV)). The best models for each model type are highlighted in bold.*

Models	Type	K	AICc
<b>~site.type * period + (years.since.impact)**(1/3) * site.type</b>	<b>BACI</b>	<b>7</b>	<b>368.1793</b>
~site.type * period + (years.since.impact)**(1/3) * site.type + CRD	BACI	8	368.5272
~site.type * period + (years.since.impact)**(1/3) * site.type + rainfall	BACI	8	371.6687
~site.type * period + (years.since.impact)**(1/2) * site.type	BACI	7	374.6331
~site.type * period + years.since.impact * site.type	BACI	7	389.5405
<b>~CRD + site.type*period</b>	<b>ENV</b>	<b>6</b>	<b>403.5482</b>
~CRD + site.type + period	ENV	5	404.2672
~CRD + site.type	ENV	4	405.8377
~site.type * period	BACI	5	414.1136
~CRD	ENV	3	421.1776
Null model	NULL	2	427.8103

*Table 2: AICc table for resprouter stem count model selection. Model split by type (based on BACI design (BACI) and based on environmental covariates (ENV)). The best models for each model type are highlighted in bold.*

Models	Type	K	AICc
<b>~site.type * period + (years.since.impact)**(1/3) * site.type</b>	<b>BACI</b>	<b>7</b>	<b>329.1804</b>
~site.type * period + (years.since.impact)**(1/3) * site.type + CRD	BACI	8	331.1148
~site.type * period + (years.since.impact)**(1/2) * site.type	BACI	7	332.1345
~site.type * period + (years.since.impact)**(1/3) * site.type + rainfall	BACI	8	332.6453
~site.type * period + years.since.impact * site.type	BACI	7	339.2239
<b>~CRD + site.type*period</b>	<b>ENV</b>	<b>6</b>	<b>350.3844</b>
~CRD + site.type	ENV	4	351.7741
~CRD + site.type + period	ENV	5	352.9948
~site.type * period	BACI	5	362.6732
~CRD	ENV	3	374.9026
Null model	NULL	2	378.2770

*Table 3: AICc table for obligate seeder stem count model selection. Model split by type (based on BACI design (BACI) and based on environmental covariates (ENV)). The best models for each model type are highlighted in bold.*

Models	Type	K	AICc
<b>~site.type * period + (years.since.impact)**(1/3) * site.type</b>	<b>BACI</b>	<b>7</b>	<b>324.7122</b>
~site.type * period + (years.since.impact)**(1/3) * site.type + CRD	BACI	8	327.5936
~site.type * period + (years.since.impact)**(1/3) * site.type + rainfall	BACI	8	327.9774
~site.type * period + (years.since.impact)**(1/2) * site.type	BACI	7	329.8831
<b>~CRD + site.type*period</b>	<b>ENV</b>	<b>6</b>	<b>359.1969</b>
~site.type * period	BACI	5	362.6732
~CRD + site.type + period	ENV	5	372.3414
~CRD + site.type	ENV	4	373.3258
~CRD	ENV	3	376.7377
Null model	NULL	2	381.0359

*Table 4: AICc table for species richness model selection. Model split by type (based on BACI design (BACI) and based on environmental covariates (ENV)). The best models for each model type are highlighted in bold.*

Models	Type	K	AICc
<b>~CRD + period</b>	<b>ENV</b>	<b>3</b>	<b>208.5826</b>
<b>~site.type * period + (years.since.impact)**(1/3) * site.type</b>	<b>BACI</b>	<b>6</b>	<b>211.3086</b>
~site.type * period + (years.since.impact)**(1/3) * site.type + CRD	BACI	7	211.7705
~site.type * period + (years.since.impact)**(1/2) * site.type	BACI	6	212.8056
~site.type * period + (years.since.impact)**(1/3) * site.type + rainfall	BACI	7	214.4749
~site.type * period + years.since.impact * site.type	BACI	6	216.7190
~CRD	ENV	2	217.4331
~site.type * period	BACI	4	222.2098
Null model	NULL	1	226.4430

*Table 5: AICc table for obligate seeder species richness model selection. Model split by type (based on BACI design (BACI) and based on environmental covariates (ENV)). The best models for each model type are highlighted in bold.*

Models	Type	K	AICc
<b>~site.type * period + (years.since.impact)**(1/3) * site.type</b>	<b>BACI</b>	<b>6</b>	<b>167.5098</b>
~site.type * period + (years.since.impact)**(1/3) * site.type + CRD	BACI	7	168.4819
~site.type * period + (years.since.impact)**(1/2) * site.type	BACI	6	168.8389
<b>~CRD + site.type*period</b>	<b>ENV</b>	<b>5</b>	<b>170.7230</b>
~site.type * period + (years.since.impact)**(1/3) * site.type + rainfall	BACI	7	170.7812
~site.type * period + years.since.impact * site.type	BACI	6	172.7567
~CRD + period	ENV	3	173.5251
~CRD + site.type	ENV	3	178.5767
~CRD	ENV	2	182.5727
~site.type * period	BACI	4	186.7670
Null model	NULL	1	193.8008

*Table 6: AICc table for resprouter species richness model selection.*

Models	K	AICc
Null model	1	184.1780
~CRD + rainfall	3	186.3460
~site.type * period	4	187.7763
~site.type * period + (years.since.impact)**(1/3) * site.type	6	190.6352
~site.type * period + (years.since.impact)**(1/2) * site.type	6	191.2041
~site.type * period + years.since.impact * site.type	6	192.3783
~site.type * period + (years.since.impact)**(1/3) * site.type + CRD	7	193.1472
~site.type * period + (years.since.impact)**(1/3) * site.type + rainfall	7	193.5721