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1 **Sequential disturbance effects of hailstorm and fire on vegetation in a Mediterranean-type**  
2 **ecosystem**

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7 **Author Contributions:** NJE, JBF, and KG designed the study; KG and JBF performed the  
8 fieldwork; KG, JBF, and CB analysed the data; KG, JBF, NJE and CB wrote the paper.

9

**10 ABSTRACT**

11 Frequency and intensity of disturbance is projected to increase for many ecosystems globally,  
12 with uncertain consequences, particularly when disturbances occur in rapid succession. We  
13 quantified community response (fifty-two shrub species and the tree *Eucalyptus tottiana*) to a  
14 severe hailstorm followed two months later by prescribed fire for a Mediterranean-type  
15 shrubland in southwestern Australia. Partial overlap of hailstorm path and fire perimeter  
16 provided a unique opportunity to compare storm and fire effects along a storm severity gradient  
17 (high-moderate-none) with and without fire. We quantified disturbance severity (bark and  
18 canopy removal, scorch height) and subsequent response (resprouting type, quantity and quality,  
19 and seedling regeneration) to evaluate evidence for disturbance interactions and implications for  
20 ecosystem recovery. Canopy loss, litter deposition, and tree bark removal increased significantly  
21 with hailstorm severity. Scorch heights in hailstorm + burn were significantly higher than fire  
22 alone, suggesting one disturbance conditioned the effect of the next. Hailstorm severity  
23 interacted with fire such that severely storm-affected shrubs and trees displayed reduced  
24 resprouting quantity and quality (length) after fire, implying resource depletion. Seedling  
25 regeneration was highest in fire-only plots for soil-stored seed species, while for serotinous  
26 species was significantly reduced by the combination of storm and fire. Overall, our results show  
27 strong resilience of this Mediterranean type ecosystem to storm or fire alone, whereas successive  
28 storm and fire reduced resprouting quantity and quality, and selectively filtered recruitment of  
29 serotinous species, potentially altering species composition and structure. These results  
30 underscore the complex effects of linked and compound disturbances and reveal an important  
31 knowledge gap requiring future research.

32

33 **Key words:** defoliation, resprouting, *Eucalyptus*, compound disturbance, linked disturbance,  
34 Mediterranean, Western Australia, kwongan, shrubland

35

## 36 INTRODUCTION

37 The role of disturbance (e.g., from fire, storm, drought, pests, pathogens) as a process central to  
38 ecosystem dynamics, species coexistence and persistence has been widely established for  
39 terrestrial ecosystems globally (Pickett and White 1985), with increasing recognition of the  
40 importance of interactions between successive disturbance events (Harvey and others 2014a). In  
41 refining a conceptual framework to better understand disturbance interactions, Simard and others  
42 (2011) identified two categories of disturbance interaction: compound and linked. Compound  
43 disturbances (sensu Paine and others 1998) describe the biotic response after the second event  
44 and how it is synergistically (negatively or positively) altered relative to individual events,  
45 influencing ecosystem resilience (capacity to return to a pre-disturbance state), and presenting  
46 profound challenges to scientists, managers, and policy makers trying to anticipate future system  
47 states. For example, alterations to conifer regeneration by multiple disturbances has now been  
48 examined in several contexts in North America (Donato and others 2009; Buma and Wessman  
49 2012; Harvey and others 2014a). Linked disturbances pertain to the synergistic effect of the first  
50 event on attributes such as probability, extent, or severity of the second disturbance. For  
51 example, the effect of bark beetle-caused tree mortality on subsequent fire severity and forest  
52 regeneration has received widespread attention (Kulakowski and Veblen 2007; Simard and  
53 others 2011; Donato and others 2013a; Harvey and others 2013) as has the interplay between tree  
54 windthrow, salvage logging, and subsequent fire severity (Kulakowski and Veblen 2007; Buma  
55 and Wessman 2011). Testing the validity of this multiple disturbance framework based on  
56 empirical evidence is critical given projected increases in fire (Moritz and others 2012), storm,  
57 drought (Allen and others 2010), and insect outbreaks (Raffa and others 2008), among others,

58 thereby increasing the frequency of disturbance interactions and attendant uncertainty of future  
59 ecosystem states and resilience.

60         Compound disturbance studies, where biotic response is altered relative to individual  
61 events, have focused mostly on resilience traits such as seedling regeneration. For example,  
62 adult tree mortality may be cumulative across two disturbance events, leading to reduced seed  
63 sources and thus lowered regeneration. However, the nature of seed banks (transient, canopy, or  
64 soil) has been recognized as critical in this context (Buma and others 2013; Harvey and others  
65 2014a). In a Mediterranean type shrubland, Gosper and others (2010) documented the strong  
66 compound effects of vegetation chaining closely followed by prescribed fire (one month later) on  
67 species with canopy stored seeds whose fruits had dried and opened, leaving seeds vulnerable to  
68 fire. Similarly, fire and drought may interact synergistically; seedlings in their first year are  
69 more susceptible to drought than adult plants, thus lowering recruitment and future demographic  
70 resilience when fire and drought coincide (Enright and others 2014). Thus far, application of this  
71 conceptual framework has focused on seedling regeneration in conifer-dominated forests leaving  
72 the other major resilience trait, resprouting, largely unconsidered. Disturbance-prone  
73 Mediterranean-type systems have an extensive legacy of examining resprouting as a persistence  
74 trait (Keeley and others 2012; Pausas and Keeley 2014) and therefore offer ideal systems within  
75 which to evaluate and potentially extend the conceptual framework of compound and linked  
76 disturbances.

77         While fire responses of plants in Mediterranean-type shrublands are well known (Bond  
78 and Van Wilgen 1996; Keith and others 2002; Keeley and others 2012), and these ecosystems  
79 are often characterised by a rapid return to pre-disturbance composition following fire,  
80 understanding of the ecological consequences of other disturbance types (e.g., severe storms),

81 and of multiple disturbances at short interval (e.g., storm and fire), is largely absent (though see  
82 Pratt and others 2014). Rather, a great deal of work has focused on the processes and  
83 mechanisms governing the balance between post-fire regeneration strategies (e.g., evolution of  
84 seeding vs. resprouting; Pausas and Keeley 2014) as well as mechanisms governing prevalence  
85 and strength of resprouting (e.g., Moreira and others 2012). With projected increases in the  
86 frequency of extreme weather events such as drought and wildfire as climate warms and dries,  
87 multiple disturbance scenarios are hypothesised to become increasingly important in  
88 Mediterranean-type ecosystems as drivers of ecosystem change and possible biodiversity loss  
89 (Parry and others 2007; Diffenbaugh and Field 2013).

90         Severe storms and fire have similarities in their effects on vegetation, including removal  
91 of live foliage, twigs, small branches and bark, leading to a resprouting recovery response in  
92 many perennial species (Bellingham and Sparrow 2000; Keeley and others 2012; Moreira and  
93 others 2012). In fire-prone forests and shrublands, vegetative regrowth may occur from buds on  
94 buried stems (lignotubers) and roots insulated from the heat of fire by soil, from epicormic buds  
95 on the stem protected by bark, or from apical buds protected by densely packed leaf-bases  
96 (Clarke and others 2013). Storms may also cause the release of seeds from some serotinous  
97 species where branch death leads to fruit opening (Lamont and others 1991; Enright and others  
98 1999). However, storm effects differ from fire in that there is no heat or smoke released from  
99 combustion of fine fuels, no removal of dead biomass through combustion, and no deposition of  
100 nutrients from burned plant tissues, so that the triggers for germination (e.g., heat, smoke) for  
101 soil seedbank and for serotinous (canopy seedbank) species, as well as for seedling establishment  
102 (increased resource availability), may not be met.

103           In March 2010, severe hailstorms across southwest Western Australia caused extensive  
104 bark and canopy removal to a ~10 km<sup>2</sup> area of Mediterranean-type shrublands near Eneabba  
105 (Figure 1). Two months later, part of the hail-affected area was subjected to prescribed fire. We  
106 used the extent of canopy loss from trees as an index of storm severity, allowing us to identify  
107 continuous gradients from unaffected to severely storm-affected (i.e., plant canopies almost or  
108 completely removed) natural shrubland in adjacent burned and unburned areas, thus providing  
109 the opportunity to compare storm, fire, and storm plus fire effects with unaffected controls.

110           We proposed the following hypotheses in relation to potential linked and compound  
111 disturbance effects on vegetation response:

- 112 1. Linked disturbance effects: the initial disturbance (hailstorm) influences the severity of the  
113 second disturbance (fire) due to altered fire behaviour caused by elevated fine fuel loads  
114 resulting from storm-removed canopy and bark material
- 115 2. Compound disturbance effects on vegetative regrowth: vegetative regrowth (resprouting) is  
116 similar for hail and fire as individual disturbances, but combined disturbance (hail + fire) leads  
117 to compound effects on resprouting quantity and quality since carbon reserves are likely to have  
118 been depleted after the first disturbance event.
- 119 3. Compound disturbance effects on recruitment: seedling recruitment response varies in relation  
120 to disturbance type and seed storage mode (canopy vs. soil). We predicted greatest recruitment  
121 after fire (since many species require heat or smoke for germination) and least recruitment in  
122 unburned control plots (no germination cues), with serotinous species positively affected by  
123 storm alone (due to seed release), but negatively affected by hail + fire (due to fire-induced death  
124 of hailstorm released seeds).

125



## 126 **METHODS**

### 127 *Study Area*

128 The study sites were located in fire-prone Mediterranean-type shrublands on the Eneabba  
129 sandplain, approximately 270 km north of Perth, Western Australia (Figure 1). The sandplain is  
130 characterised by unconsolidated acid sands of varying depth (1-10 m) overlaying lateritic clays.  
131 These low nutrient, poor water-holding capacity soils support a low open heath (< 1m) on  
132 shallow sands, while deeper sands also support taller shrubs and scattered clumps of the small  
133 (to 5 m) tree, *Eucalyptus todtiana* (Hnatiuk and Hopkins 1981). The region is a centre of high  
134 plant biodiversity and endemism within the southwest Australian global biodiversity hotspot  
135 (Hopper and Gioia 2004). The shrublands are particularly rich in representatives of the families  
136 Proteaceae, Myrtaceae, Ericaceae and Restionaceae with >98% of woody species having a  
137 persistent seed bank (approximately a 2:1 ratio of soil stored vs. canopy stored propagules,  
138 Enright and others 2007; Enright and others 2014).

139 Climate is strongly Mediterranean, with the bulk of mean annual rainfall (493mm;  
140 Eneabba climate station, Australian Bureau of Meteorology) falling in the cool winter months,  
141 while the summer is characterised by extended periods of drought and very high day-time  
142 temperatures (mean January and February daily maximum temperatures >35°C). The region is  
143 fire-prone, with an estimated mean fire interval of 12-16 years based on plant demographic data  
144 (Enright and others 1998) and 13-20 years based on analysis of satellite imagery (for the period  
145 1972-2002, Miller and others 2007). Most extant plant species show adaptations to fire,  
146 including persistent seed banks with fire-stimulated germination of soil-stored seeds, release of  
147 seeds from woody fruits (Enright and Lamont 1989; He and others 2011), and the ability to

148 recover vegetatively, with resprouting plants constituting approximately two-thirds to three-  
149 quarters of all species (Enright and others 2014).

150

### 151 *Disturbance Events*

152 On 21-22 March, 2010 a series of severe thunderstorms affected a broad extent of southwestern  
153 Australia. The storms near Eneabba were characterised by large hail (>2cm diameter; Bureau of  
154 Meteorology), destructive winds (gusts >150 km h<sup>-1</sup>), and very heavy rain (up to 40 mm h<sup>-1</sup>) (N.  
155 Enright, unpubl. climate station data). Across the affected area, vegetation was subjected to  
156 mechanical effects by hail and defoliation by both hail and wind ranging from moderate to high  
157 severity.

158         Following the storm event and including portions of the storm-affected area, a scheduled  
159 management burn was conducted by the Western Australian Department of Parks and Wildlife  
160 (DPaW) as part of its fuel hazard reduction program (early May 2010). Management fires in the  
161 region are conducted under mild to moderate fire weather conditions which minimise the risk of  
162 fire escape, typically in spring and autumn. The fire area overlapped partially with the path of  
163 the previous hailstorm due to a railroad line bisecting the area (Figure 1). It was ignited along a  
164 strip and allowed to burn with the wind towards containment lines. Fire ignition time was  
165 approximately mid-day under low wind speed (<10 km h<sup>-1</sup>) and moderate temperature (~ 25°C)  
166 conditions. The fire consumed litter and, consistent with the crown fire regime of the system,  
167 top-killed all shrubs and scorched tree canopies.

168

### 169 *Site location and disturbance history*

170           Given the configuration of hailstorm path and prescribed fire (Figure 1), we took  
171 advantage of the unique opportunity to establish a fully factorial sampling design of burn/no burn  
172 along a storm intensity gradient of high, moderate, or no tree canopy loss. At each of the six sites  
173 we established shrubland and tree plots (N=10 each for a total of 60) to capture dynamics in both  
174 structural elements of the ecosystem. Burned sites were located immediately adjacent to each of  
175 the three unburned, storm-affected sites (range 100-250 m; Figure 1). Disturbance histories of  
176 sites were similar, with moderate and high severity storm sites of equivalent fire age (26 yrs  
177 since last fire) and burned and unburned sites not affected by storm (controls) also of similar fire  
178 age (12 yrs). Local vegetation is typically mature within 10 years of fire (Delfs and others 1987)  
179 with only slow change in biomass and litter cover thereafter (Fontaine and others 2012;  
180 Westcott and others 2014). After sites were chosen and plots established (see below), we visited  
181 them once in winter to assess hail disturbance effects and again in the following spring to  
182 measure fire effects and vegetation response and regeneration.

183

#### 184 *Storm and Fire Severity Assessment*

185           Canopy loss was assessed for ten replicate *E. tottiana* clumps and paired shrubland plots  
186 per site one month after the storm (N=30 each for *E. tottiana* and shrubland plots, respectively).  
187 Within the study area, *E. tottiana* grows in clumps of 3-50 stems/clump representing a single  
188 genetic individual and as such we used the clump as the experimental unit rather than each  
189 individual stem. At each site, one clump was randomly chosen and an additional nine selected  
190 by walking to the nearest-neighbour clump of suitable size (minimum canopy extent  $\geq 5 \times 5$ m).  
191 Canopy loss was visually estimated on a 5-level scale corresponding to 0, 1-24, 25-74, 75-99,  
192 and 100 percent canopy loss. Shrub plots were placed in open shrubland to the north of each tree

193 clump at a distance of at least 2x tree canopy height to ensure no shading effects. The tallest  
194 shrub in each 1 m<sup>2</sup> cell of the ten 4 x 4 m plots was tagged and scored for defoliation (same  
195 categories as for *E. tottiana*), giving a sample size of 16 plants per plot (160 plants per site). The  
196 tallest plant in each cell was sampled on the presumption that larger plants would reflect storm  
197 effects most clearly (See Table A1 in Supplementary Materials for complete list of species and  
198 counts).

199         Bark removal from *E. tottiana* stems at unburned sites was measured three months  
200 following the hailstorm, and in burned plots, six months following fire. In all cases bark  
201 thickness was measured 1.3 m above ground level for both storm-exposed and storm-protected  
202 sides of five *E. tottiana* stems per clump, including at the unaffected control site where the same  
203 stem orientations were sampled (a total of 6 sites x 10 clumps x 5 stems x 2 sides). A steel pin  
204 was pushed into the bark until the bark-wood interface was reached, producing a measurement of  
205 bark thickness (to the nearest mm) which included both dead and live bark (phloem) and  
206 vascular cambium (Cornelissen and others 2003; Lawes and others 2011).

207         Scorch height in burned tree clumps was assessed by measuring char on tree boles to the  
208 nearest cm. To estimate fine fuel (litter) biomass beneath *E. tottiana* clumps and in shrub plots,  
209 percent cover and litter depth were measured one month following the hailstorm. To estimate  
210 biomass from percent cover and litter depth values, additional microplots (four 20 x 20 cm  
211 quadrats per *E. tottiana* clump or 1 m<sup>2</sup> quadrat per 4 x 4 m shrub plot, total N= 60 for trees and  
212 N=50 for shrubs) were established. Percent cover and litter depth were measured, and all litter in  
213 each microplot collected, returned to the laboratory and oven dried at 65°C for 72 hours. Site  
214 specific equations were constructed relating litter volume to mass for each level of storm impact

215 (severe, moderate, none) and cover type (tree, shrub) with  $R^2$  values 0.56-0.69 for shrub litter  
216 and 0.65-0.77 for tree litter.

217

### 218 *Post-disturbance Response*

219 The number of epicormic regrowth shoots from ground level to a height of 1.3 m for five stems  
220 per *E. tottiana* clump was counted in unburned sites three months after the hailstorm and at  
221 burned sites, six months after fire (8 months after storm; late spring). A subsample of stems at  
222 unburned sites were reassessed at six months to ensure no change in epicormic resprout  
223 abundance over the intervening winter months. Stem length to 1.3 m was measured to calculate  
224 the mean number of shoots per lineal metre. Counts of the number of stems per clump with basal  
225 resprouts were made six months after fire at all sites. Magnitude (number of basal regrowth  
226 shoots; 1-10, 11-20, 21-50, 51-100, >100), vigour (length of longest basal shoot), and type  
227 (apical-axillary bud regrowth, epicormic, basal) of shrub recovery was assessed for tagged  
228 shrubs 8 months after the storm. Because fire top-killed all shrub species, post-fire shrub  
229 response is reported for basal resprouting only.

230 The density of seedling recruits establishing over the winter of 2010 was quantified 8  
231 months after the storm (6 months post fire) from seedling counts within 4 x 4 m plots at all sites  
232 (N=60), with species identified and grouped by seed storage type (canopy vs. soil stored; see  
233 Table A2 in Supplementary Materials for complete list of species and their abundance).

234

### 235 *Statistical Analyses*

236 We analysed each of the measured vegetation components (litter, trees, shrubs, seedlings)  
237 separately, first assessing severity of hail and fire in terms of their effects (i.e., canopy loss, stem

238 bark removal, litter biomass increase, scorch height) and then in terms of post-disturbance  
239 response (i.e., incidence, quantity, quality, and type (apical, epicormic or basal) of sprouting),  
240 and seedling recruitment. In all cases we considered an interaction of storm and fire and used a  
241 model selection framework (Burnham and Anderson 2002) to determine whether covariates (e.g.,  
242 stem diameter, shrub height) remained in the final model. We assessed the main and interactive  
243 effects of storm severity and fire disturbance on vegetation using general linear models,  
244 including a random effect where appropriate (e.g., *E. tottiana* clump with respect to epicormic  
245 sprouting when assessing individual stems within clump; Table 1). All data and models were  
246 visually assessed for normality and fit (residuals, homogeneity of variance, overdispersion) and  
247 variables log-transformed where necessary. Covariates such as tree clump size and response to  
248 the initial disturbance were included (see descriptions below). Effect sizes and their 95%  
249 confidence intervals are reported as a measure of disturbance effects and their interactions.

250 Storm and fire effects on trees were estimated at the stem and clump levels depending on  
251 metric. We estimated removal of bark at the level of the individual stem, allowing for a random  
252 effect of clump, while canopy loss was analysed at the clump level. Defoliation of *E. tottiana*  
253 and woody shrub species was recorded as a 5-level ordinal variable. Preliminary analyses  
254 showed similar patterns when analysed as an ordinal versus continuous variable and the results  
255 of analyses treating canopy loss as a continuous variable on a percentage scale are presented.  
256 Covariates included in the full model of bark removal were stem diameter (cm) and clump height  
257 (m). Litter biomass was estimated at the tree clump level and shrub plot scale. Shrub canopy loss  
258 was analysed at the individual plant level with a random effect of species. Fire-related effects  
259 were analyzed as a function of scorch height in burned *E. tottiana* clumps. Mortality for all  
260 species after storm disturbance only, and for resprouter species in fire treatments, was extremely

261 low and was not analysed further (<1% of marked plants across both moderate and high severity  
262 storm sites).

263 Epicormic resprouting in *E. tottiana* was analysed at the individual stem scale allowing  
264 for a random effect of clump. Total epicormic sprouts per lineal meter of stem were  $Ln$ -  
265 transformed prior to analysis. Stem diameter was included as a covariate. Basal sprouting of *E.*  
266 *tottiana* (proportion of stems with basal sprouts) was analysed at the clump level owing to the  
267 diffuse nature of basal sprouting and difficulty in ascribing each sprout to a particular stem when  
268 closely spaced. For shrubs, the frequency and type of resprouting induced by the hailstorm was  
269 assessed by analysing the proportion of shrubs showing apical, epicormic, and basal sprouting as  
270 response variables at the plot scale. We analysed counts of total resprouts (mid-points of ordinal  
271 ranks) and the length of the longest new sprout at the scale of individual plants with a random  
272 effect of species.

273 Seedling densities were low and were pooled by seed storage type (canopy vs. soil-  
274 stored). They could not be considered in relation to species or other functional groupings (e.g.,  
275 resprouter/non-sprouter). Seedling counts were analysed at the plot scale using a generalised  
276 linear model with zero inflated negative binomial distribution. Sparse data prevented estimation  
277 of the interaction of hailstorm and fire, thus only additive effects are presented. Regression using  
278 simple presence/absence per plot (binomial distribution) produced similar results.

279 All analyses were carried out in R 2.12.0 (R Development Core Team 2010) using  
280 standard packages. Models containing random effects were implemented with lme4 (Bates and  
281 others 2010) for mixed effect (fixed + random) modelling. Seedling counts were analysed using  
282 R package pscl (Jackman 2011).

283

284

285 **RESULTS**286 *Canopy Loss and Bark Removal*

287 Canopy loss due to the storm in both shrub and tree layers increased across the storm  
288 severity gradient from <10% at the control site, to 58% for shrubs (pooled for all species) and  
289 70% for *E. tottiana* at the high severity site (Table 1, Figure 2A). Canopy loss due to fire was  
290 100% for all burned shrub plots regardless of site and averaged 75-85% in storm affected *E.*  
291 *tottiana* clumps, with no difference along the storm severity gradient. The hailstorm removed  
292 significant amounts of bark from storm-exposed relative to storm-protected portions of tree  
293 stems, with significant difference from controls for both moderate and high severity conditions  
294 (1.9 and 4.8 mm of bark removed respectively; Table 1). At control sites mean bark thickness  
295 was 9.4 mm (SE=0.5; range 5-20) and at moderate and high severity storm sites 7.9 mm  
296 (SE=0.3; range 4-15) and 6.3 mm (SE=0.4; range 2-15), respectively for storm-exposed stems.

297

298 *Litter Biomass and Scorch Height*

299 Canopy losses due to storm disturbance substantially increased fine fuel loads. Beneath *E.*  
300 *tottiana* clumps, litter mass increased from 8.5 Mg ha<sup>-1</sup> at the unaffected control site to 26.3 and  
301 24.0 Mg ha<sup>-1</sup> at moderate and high severity sites, respectively (Table 1, Figure 2B). Storm  
302 disturbance also increased shrub plot litter, from 1.6 Mg ha<sup>-1</sup> at the control site to 3.4 and 4.5 Mg  
303 ha<sup>-1</sup> at medium and high severity sites, respectively (Table 1, Figure 2B). For both tree and  
304 shrub plots litter mass was not different between moderate and high severity sites with effect  
305 estimates having overlapping 95% confidence intervals.



306           Bole scorch height in *E. tottiana* clumps following fire increased monotonically with  
307 storm severity (Table 1, Figure 2C). Accounting for differing heights of individual *E. tottiana*  
308 clumps, scorch height was significantly higher at the moderately, but not the more severely  
309 affected site, relative to clumps unaffected by the storm (Table 1).

310

### 311 *Resprouting Response*

312           The epicormic response of *E. tottiana* to hailstorm reflected storm intensity with a weak  
313 non-significant response at the moderate severity site and a significant response at high severity  
314 site (increase of 3.2 sprouts m<sup>-1</sup>, Table 1, Figure 3A). The number of epicormic shoots was  
315 greater on hail-affected (storm-oriented) sides of stems and was correlated with both the extent  
316 of canopy loss (Spearman's rank correlation,  $r = 77$ ,  $p < 0.001$ ,  $df = 28$ ) and bark removal  
317 (Pearson's correlation,  $r = -0.23$ ,  $p < 0.005$ ,  $df = 146$ ). At hail + fire disturbance sites, the  
318 interaction of moderate and high-severity storm with fire was not significant, but was suggestive  
319 of a threshold effect being reached in the high-severity site, with a negative interaction narrowly  
320 overlapping zero (Table 1, Figure 3A). Extensive tree canopy recovery occurred in response to  
321 both fire and storm but was not measured.

322           Hailstorm disturbance induced only a weak basal resprouting response in *E. tottiana*,  
323 with the percentage of stems per clump with basal resprouts showing no trend in relation to the  
324 storm severity gradient, although highest shoot occurrence (11%) was at the high severity site.  
325 By contrast, fire induced a strong basal resprout response, occurring in 77% of stems at the  
326 control site, but with a significant negative interaction where fire followed high severity storm  
327 (37% reduction, Table 1, Figure 3B).

328 Strong shrub recovery from storm alone was evident in the increased incidence of all  
329 types of resprouting, (apical, epicormic, and basal; Table 1, Figure 4). Epicormic and basal  
330 sprouting both increased linearly with increasing storm severity from very low values in the  
331 control to > 70% of resprouting plants at high severity (Table 1, Figure 4). Apical sprouting was  
332 more prevalent (owing to its connection with normal annual growth occurring at stem tips) and  
333 showed a threshold effect with no difference between moderate and high storm severity (Table 1,  
334 Figure 4).

335 In contrast to the general absence of basal resprouting in *E. todtiana* in response to storm  
336 disturbance, basal resprouting in shrubs was strong, with the number of sprouts per plant  
337 increasing from < 1 shoot plant<sup>-1</sup> in the control site to 18 shoots plant<sup>-1</sup> at the highest severity site  
338 (Table 1, Figure 5A). Consistent with the crown-fire regime where fire kills all above-ground  
339 tissue of shrubs, fire induced a strong basal resprouting effect with >20 shoots plant<sup>-1</sup> at all sites.  
340 However, basal shoot numbers were significantly reduced at both the moderate and high severity  
341 hail + fire disturbance sites (Table 1).

342 At unburned sites, shrub basal resprout length increased with hailstorm severity and at the  
343 high severity site was triple that of the control (Table 1, Figure 5B). At burned sites, the  
344 response to fire was similarly strong. However, the combination of fire with moderate or high  
345 severity storm effects reduced resprout length by 11.6 and 26.2 cm, respectively (Table 1, Figure  
346 5B). Thus the combination of hail + fire decreased the regrowth capacity of shrubs.

347

#### 348 *Seedling Recruitment*

349 No seedlings established in unburned control plots (no storm effect site) in the first winter-spring  
350 after the storm. Some seedlings, all from soil seed storage species, were recorded at the

351 moderate and high severity storm sites (Tables 1-2), while large numbers of seedlings established  
352 in the burned control (fire, no storm), with serotinous seedlings also present. Fire alone had a  
353 significant positive effect on soil-stored seedling densities while high-severity storm alone had a  
354 negative estimate that overlapped zero (Table 1). Effects of fire alone and storm alone on  
355 serotinous species recruitment followed a similar pattern to soil stored species but with a  
356 negative effect of severe storm not overlapping zero and other estimates overlapping zero in their  
357 95% confidence intervals (Table 1). Interactive effects of fire and storm could not be examined  
358 for seedling recruitment owing to low densities in some treatments (Table 2).

359

## 360 **DISCUSSION**

361 Responses to hailstorm or fire alone were consistent with the broad literature on  
362 individual disturbance events (Wagner 1973; Méndez 2003; Arevalo and others 2009; Fernande  
363 and others 2012). Indeed, the system considered here is considered one of the most fire adapted  
364 systems worldwide (Keith and others 2002). However, when the combined effect of the two  
365 disturbances was analysed, we found evidence for interaction in terms of both effect (linked  
366 disturbance) and response (compound disturbance), and for both modes of regeneration  
367 (resprouting, seedlings). Scorch heights in hail + fire plots were higher than in fire-alone plots  
368 suggesting that increased fuel loads resulting from storm-induced canopy loss elevated fire  
369 intensities, thus providing evidence for the disturbances being linked; notably effects in moderate  
370 and high severity hail plots did not differ. With regard to compound disturbance, quantity and  
371 quality of resprouting was lowered in hail + fire plots relative to single disturbances suggesting  
372 resource depletion (Clarke and others 2013). The increasing magnitude of disturbance  
373 interaction with hailstorm severity for resprouting supports this hypothesis. Seedling

374 regeneration of plants was consistent with the hypothesis that serotinous species are selected  
375 against by mechanical + fire disturbance events (Gosper and others 2010) though caution is  
376 required given our inability to formally estimate interactions.

377

378 *Loss of aboveground biomass and linked disturbances effects*

379 Hailstorm effects on vegetation depend on the physical properties of both storm and  
380 hailstones, such as angle of hail stone impact, size of stones, wind, and also on the structure and  
381 architecture of plants (Houston 1999; Méndez 2003). Data from the March 2010 hailstorm  
382 showed that the size of hailstones was up to 6 cm and the highest daily wind gust on that day was  
383 120 km/h (BOM 2010), and 150 km/h at our climate station near the field sites, indicating storm  
384 severity capable of inflicting considerable damage to vegetation. Our best direct measures of  
385 storm effects were bark loss for hailstones and canopy loss for wind and hail. Bark removal was  
386 consistent with previous reports (e.g., Riley 1953) and overall effects similar in magnitude to  
387 cyclone effects in tropical forests (Metcalf and others 2008), and for hailstorms in other  
388 systems (Houston 1999; Fernande and others 2012).

389 Overall, storm debris increased surface fine fuel loads approximately threefold in shrub  
390 plots across the storm gradient and in storm-affected *E. todtiana* clumps. Litter mass reported for  
391 shrub plots at severely affected sites were higher than those reported for 34 sites measured in a  
392 recent fire behaviour study (Fontaine and others 2012) which found higher fire residence time  
393 and soil heating with increased litter biomass. Similarly, fuel manipulation studies in pine  
394 savannah showed substantial increases in mean maximum fire temperature (300-400°C) with  
395 just two fold increases in fine fuels (Thaxton and Platt 2006), whereas here we observed 2.5-3x  
396 increases in fine litter fuels. Therefore, it is likely that the first disturbance (hailstorm) affected

397 the physical intensity of the second disturbance (fire) via increased litter deposition and resulting  
398 fire intensity, as measured by elevated scorch heights, thereby demonstrating linkage of the two  
399 disturbances.

400 The short period of time between disturbances (< three months) and hot, dry post storm  
401 conditions also meant that litter cured fully, did not decompose, was well aerated and thus  
402 available to burn. Studies of other defoliating disturbances, prominently bark beetles in northern  
403 hemisphere conifer forests, have quantified a strong effect of time interval between disturbances  
404 (Simard and others 2011; Donato and others 2013a; Harvey and others 2014b). When trees are  
405 freshly killed and retaining dead leaves ('red' stage), crown fire potentials may be elevated but as  
406 time passes and leaves begin to drop ('grey' stage), crown fire potentials decrease (Donato and  
407 others 2013a; Donato and others 2013b). Therefore, the degree to which disturbances are linked  
408 and the type of effect is highly contingent on the elapsed time interval and ecosystem type. This  
409 study quantifies linked disturbance effects consistent with prior studies where short-interval  
410 disturbance led to elevated severity though with uncertain ecological ramifications (see below).

411

#### 412 *Response of Extant Vegetation and Compound Disturbance Effects*

413 Trees and shrubs which had resprouted after storm did so again after fire, but the  
414 number and vigour (length) of resprouts was reduced, particularly after combined severe storm  
415 and fire (compound disturbance). Previous work on successive short-interval fires in Brazilian  
416 cerrado (Medeiros and Miranda 2008), and from clipping experiments in Mediterranean  
417 shrublands in SW Australia (Bowen and Pate 1993), and Spain (Moreira and others 2012) have  
418 reported similar effects of reduced resprout vigour as well as increased mortality. Moreira and  
419 others (2012) set out a conceptual framework of the complex process of resprouting,

420 encompassing a single disturbance through to full recovery; here, due to the short interval  
421 between disturbances and lack of mortality, we focus on actual resprouting (creation and  
422 elongation of new tissue) during early regrowth. Fewer resprouts observed after severe hail +  
423 fire may have been due to a reduction in the quantity of available buds and/or other reserves after  
424 initial mobilisation of resources in response to the hailstorm. Resprouting requires a supply of  
425 buds as well carbohydrates (CHO) and sensitivity to multiple disturbance in resprouters has been  
426 variously attributed to depletion of buds and carbohydrates with recovery times estimated at six  
427 months for buds and up to two years for carbohydrates (Chapin and others 1990; Canadell and  
428 others 1991; Bowen and Pate 1993; Paula and Ojeda 2009). In view of the very large effect of  
429 hailstorm + fire on shrub resprout lengths, depletion of CHO reserves is a more likely  
430 explanation for reduced recovery from fire at multiple disturbance sites. Our evidence for trees is  
431 more limited but as previous work has shown elevated mortality attributed to bud limitation after  
432 long fire-free intervals (Enright and others 2011), and no observed mortality in this study, the  
433 more likely reason for reduced tree resprouting is CHO depletion.

434         Given the evidence that fire intensity likely increased due to hailstorm it is important to  
435 consider the consequences of increased fire severity on plant regenerative tissues. For trees and  
436 shrubs, fire following hailstorm likely increased soil heating via increased litter combustion  
437 possibly elevating damage to underground buds; a result repeatedly observed across  
438 Mediterranean shrub systems (Keeley and others 2012). For example, Moreno and Oechel (1991)  
439 found a relationship between fire intensity and resprout number but not resprout length in  
440 California chaparral. Here we found a threshold effect on resprout number (reduced in high  
441 severity hail + fire only) and a monotonic decrease in resprout length for shrubs. Further, scorch  
442 heights on trees (a measure of fire intensity) were higher in both moderate and severe hail + fire

443 sites but resprouting was only reduced for severe hail + fire sites. Therefore, loss of bud reserves  
444 due to elevated soil heating may not have been a major effect. An additional consideration for  
445 trees is that greater fire intensity may have increased damage to stems with reduced bark  
446 protection (due to hail effects). Tree epicormic resprouts after hailstorm alone were concentrated  
447 on the storm-affected side of stems owing to bark removal and tissue damage. Following fire  
448 epicormic sprouts were equally spread on stems including at moderate and high-severity storm  
449 sites. Thus, thin-barked portions of tree stems did not appear to have experienced heating  
450 sufficient to cause differential effects to bud regenerative tissue. Indeed, vegetation in this  
451 ecosystem and particularly *Eucalyptus* spp. are widely recognized for their extraordinary  
452 resprouting capacity (Clarke and others 2013). These observations suggest that, for resprouting,  
453 the physical increase in fire intensity did not lead to loss of bud regenerative potential and  
454 compound effects were manifested via other pathways (resource depletion). It is likely that  
455 effects of plant age, microsite, and resprouting syndrome (epicormic, lignotuber, basal), among  
456 others, interact to generate complex response patterns, warranting further research to extend  
457 existing knowledge of experiments (Moreira and others 2012) and single fires (Enright and  
458 others 2011; Marais and others 2014) to multiple disturbances.

459

#### 460 *Compound Disturbance Effects on Seedling Recruitment*

461 Seedling recruitment was highest at the fire-only site (no storm effect) and negligible at the  
462 storm-only site since many species require heat or smoke to trigger winter germination of soil-  
463 stored seeds (Brown and van Staden 1997; Keith 1997), and heat leads to release of seeds stored  
464 in the canopy. However, recruitment declined as storm severity increased, with seeds of  
465 serotinous species released by the hailstorm subsequently consumed or killed (by lethal

466 temperature) by fire. This parallels similar findings by Gosper and others (2010) who reported  
467 that mechanical + fire treatments separated by ~1 month had a strong negative impact on  
468 serotinous species. The response of serotinous species described here varies markedly from  
469 those reported in studies of serotinous conifers (Donato and others 2009; Harvey and others  
470 2013) where cones are held shut mechanically rather than by live tissue as in most serotinous  
471 species (Lamont and others 1991; Buma and others 2013). Thus, the nature of seed storage (type  
472 of serotiny, soil-stored seed) greatly affects the magnitude and nature of compound disturbance  
473 effects with commensurate flow-on responses in species composition and structure over time.  
474 The importance of seed storage, disturbance size and shape have been previously recognized as a  
475 critical knowledge gap (Halofsky and others 2011; Buma and others 2013), particularly with  
476 changing climate and increased uncertainty of future conditions.

477

#### 478 *Synthesis*

479 In the context of global change effects, where short interval disturbances are expected to  
480 increase, our observations offer insight into persistence and resilience of varying plant growth  
481 forms and functional types. The rich history of studying disturbance effects in Mediterranean-  
482 type climate systems (e.g., Keeley and others 2012) offers a perfect opportunity to extend the  
483 conceptual model of linked and compound disturbances beyond conifer-dominated regions.  
484 Here, we report clear evidence of linked disturbance effects (elevated fire severity after  
485 defoliating hailstorm) and compound disturbance effects (altered vegetation regeneration  
486 dynamics in both resprouting and seedling regeneration). Our results show strong resilience of  
487 this shrubland system to storm or fire alone (although storms may adversely affect seed stores of  
488 some serotinous species), while storm and fire in the same year reduced seedling recruitment and



489 negatively affected subsequent resprouter vigour, with the potential to alter species composition  
490 and competitive relationships. With the number of severe climatic events predicted to increase in  
491 the face of global environmental change (Easterling and others 2000) and with Mediterranean  
492 systems particularly susceptible given predicted rainfall decline (Diffenbaugh and Field 2013),  
493 species-rich communities such as Mediterranean type-shrublands may be negatively affected if,  
494 on average, fires follow more closely in time after severe non-fire disturbances such as  
495 hailstorms. Indeed interaction of fire and drought may strongly filter communities leading to  
496 species losses (Enright and others 2015) and potentially altering species coexistence processes  
497 maintaining the exceptional diversity present in shrublands in southwestern Australia.

498         Order of occurrence, inter-disturbance interval, and number of multiple, short-interval  
499 disturbances are also likely to affect the nature of system response and warrant further  
500 investigation. Better quantification of the magnitude and direction of both linked and compound  
501 disturbance effects may enable prediction of ecosystem dynamics and vegetation resilience and  
502 inform management strategies. For example, fire management for conservation and wildfire risk  
503 mitigation could dynamically respond to windows of elevated ecosystem susceptibility to linked  
504 disturbance effects (e.g., incorporating or excluding fire during wet or dry years; Enright and  
505 others 2014).

506

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512

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681

682 **List of Figures**

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685 **Figure 2.** Mean defoliation for *Eucalyptus todtiana* clumps (n=10 per site) and shrub plots (n =  
686 30, 32 and 30 species at control, moderate and high severity storm sites, respectively)  
687 (A); estimated mean surface litter mass (fine fuel load) under tree (i.e., *E. todtiana*)  
688 clumps and in shrubland plots, n = 10 per site (B) and mean scorch height on *E. todtiana*  
689 stems (C) in shrubland across a hailstorm severity gradient, near Eneabba, Western  
690 Australia. Bars are 95% confidence intervals.

691 **Figure 3.** Mean number of epicormic resprouts m<sup>-1</sup> (n = 50 stems per site, n= 42 at the unburned  
692 control site) on *Eucalyptus todtiana* stems (A) and mean proportion of *E. todtiana* stems  
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694 and burned sites across a storm severity gradient (B) in shrubland, near Eneabba, Western  
695 Australia. Bars are 95% confidence intervals.

696 **Figure 4.** Resprouting response (apical, epicormic, or basal) of shrub species along a hail storm  
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698 **Figure 5.** Mean number of basal sprouts per resprouter shrub (A) and length of the longest  
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700 storm + fire) across a storm intensity gradient in shrubland near Eneabba, Western  
701 Australia, n (left to right) = 134, 159, 131, 160, 148, 155. Bars are 95% confidence  
702 intervals.

703 **Table 1.** Effect (95% confidence interval) of hail storm (moderate, severe effect), prescribed fire, and hail followed by fire (interaction  
 704 term) on tree and shrub species and their response in mixed shrublands in Eneabba, Western Australia. Values in bold  
 705 represent estimates whose 95% confidence intervals do not overlap zero.

IMPACT	Units	STORM SEVERITY		FIRE	INTERACTIONS		Random Effects
		Moderate	High	Burned	Mod*Burn	High*Burn	
Tree defoliation	% canopy loss	12.5 (0, 27.0)	<b>62.5</b> <b>(48.0, 77.0)</b>	na	na	na	None
Shrub defoliation	% canopy loss	<b>22.0</b> <b>(16.8, 27.2)</b>	<b>48.2</b> <b>(43.0, 53.4)</b>	na	na	na	Species, plot
Bark removal (trees)	relative bark thickness (mm)	<b>1.9</b> <b>(0.42, 3.3)</b>	<b>4.8</b> <b>(3.4, 6.3)</b>	na	na	na	Indiv plant
Litter deposition (under trees)	Mg ha <sup>-1</sup>	<b>17.8</b> <b>(9.3, 21.8)</b>	<b>15.5</b> <b>(11.6, 24.0)</b>	na	na	na	None
Litter deposition (shrubs)	Mg ha <sup>-1</sup>	<b>1.8</b> <b>(0.1, 3.5)</b>	<b>2.9</b> <b>(1.2, 4.6)</b>	na	na	na	None
Scorch height	height (m)	Na	na	na	<b>0.11</b> <b>(0.01, 0.21)</b>	0.06 (-0.04, 0.16)	Indiv plant
RESPONSE							
Tree epicormic sprouting	log # sprouts m <sup>-1</sup> of stem	0.26 (-0.21, 0.73)	<b>1.2</b> <b>(0.69, 1.6)</b>	0.40 (-0.07, 0.87)	0.64 (-0.01, 1.3)	-0.61 (-1.3, 0.04)	Indiv plant

Tree basal sprouting	proportion of stems with basal sprouts	0.01 (-0.19, 0.21)	0.11 (-0.09, 0.31)	<b>0.77</b> <b>(0.57, 0.97)</b>	-0.13 (-0.38, 0.12)	<b>-0.37</b> <b>(-0.62, -0.12)</b>	None
Shrub basal sprouting†	proportion of plants plot <sup>-1</sup>	<b>0.50</b> <b>(0.36, 0.63)</b>	<b>0.68</b> <b>(0.54, 0.82)</b>	na	na	na	None
Shrub epicormic sprouting†	proportion of plants plot <sup>-1</sup>	<b>0.57</b> <b>(0.44, 0.70)</b>	<b>0.76</b> <b>(0.63, 0.88)</b>	na	na	na	None
Shrub apical sprouting†	proportion of plants plot <sup>-1</sup>	<b>0.36</b> <b>(0.28, 0.44)</b>	<b>0.38</b> <b>(0.30, 0.46)</b>	na	na	na	None
Shrub sprouting (quantity)	log # basal sprouts per plant	<b>1.1</b> <b>(0.80, 1.3)</b>	<b>1.6</b> <b>(1.3, 1.8)</b>	<b>2.6</b> <b>(2.3, 2.8)</b>	<b>-1.2</b> <b>(-1.5, -0.85)</b>	<b>-1.9</b> <b>(-2.2, -1.6)</b>	Species, plot
Shrub sprouting (quality)	length longest sprout (cm)	<b>9.0</b> <b>(4.1, 13.9)</b>	<b>19.9</b> <b>(15.1, 24.7)</b>	<b>12.2</b> <b>(7.4, 17.0)</b>	<b>-11.6</b> <b>(-17.4, -5.7)</b>	<b>-26.2</b> <b>(-32.0, -20.4)</b>	Species, plot
RECRUITMENT							
Soil-stored seed species	count per plot	0.44 (0.47, -0.47)	-0.92 (0.48, -1.8)	<b>2.9</b> <b>(2.0, 3.7)</b>	na	na	None
Serotinous species	count per plot	-20.2 (-13,421, 13,381)	<b>-2.5</b> <b>(-4.7, -0.28)</b>	11,701 (-11,662, 11,702)	na	na	None

706 †Diversity in shrub resprouting could be measured in hail only plots as the crown-fire regime in shrublands means only basal  
707 sprouting is possible following fire.

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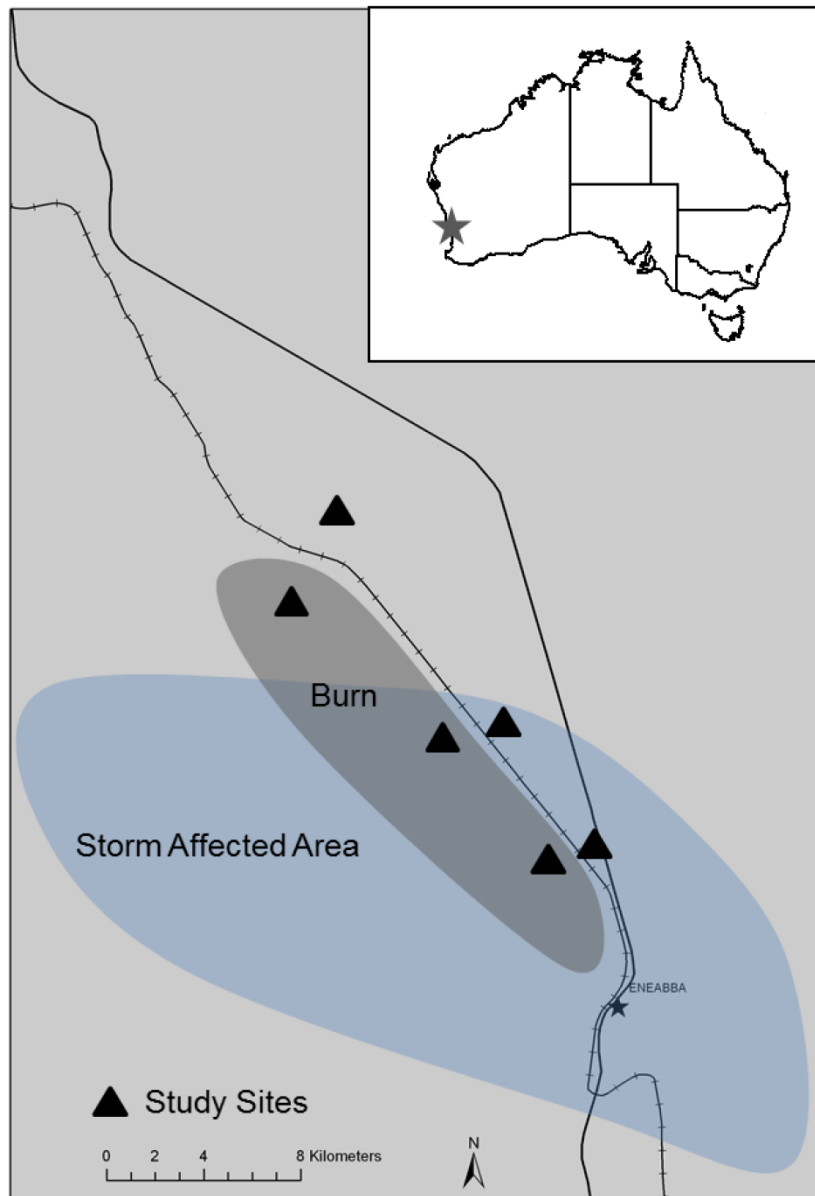
710 **Table 2.** Seedling density  $\text{ha}^{-1}$  ( $\pm\text{SE}$ ) for serotinous and soil-seed bank species after single (storm, fire) and multiple disturbances  
 711 (storm + fire) across a hailstorm intensity gradient (control, moderate and high severity , respectively) in shrubland, near Eneabba,  
 712 Western Australia.

		Control	Moderate severity	High severity
Unburned	Serotinous	0	0	0
	Soil-storage	0	1,563 ( $\pm 553$ )	438 ( $\pm 133$ )
Burned	Serotinous	750 ( $\pm 333$ )	0	63 ( $\pm 63$ )
	Soil-storage	19,938 ( $\pm 5933$ )	12,250 ( $\pm 3277$ )	3,500 ( $\pm 1590$ )

713

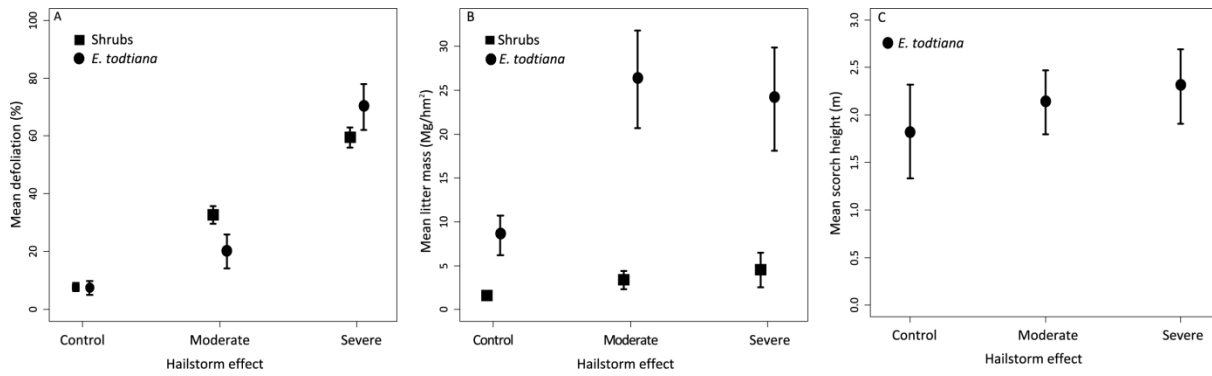
714

**Figure 1.** Study area location near Eneabba, Western Australia, showing storm and burn affected areas and the six study sites.

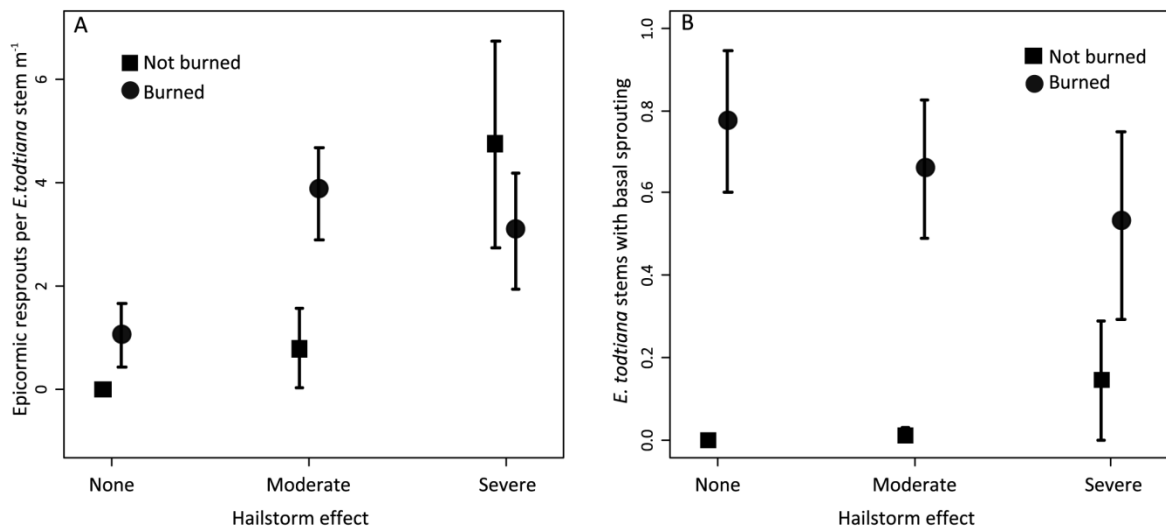




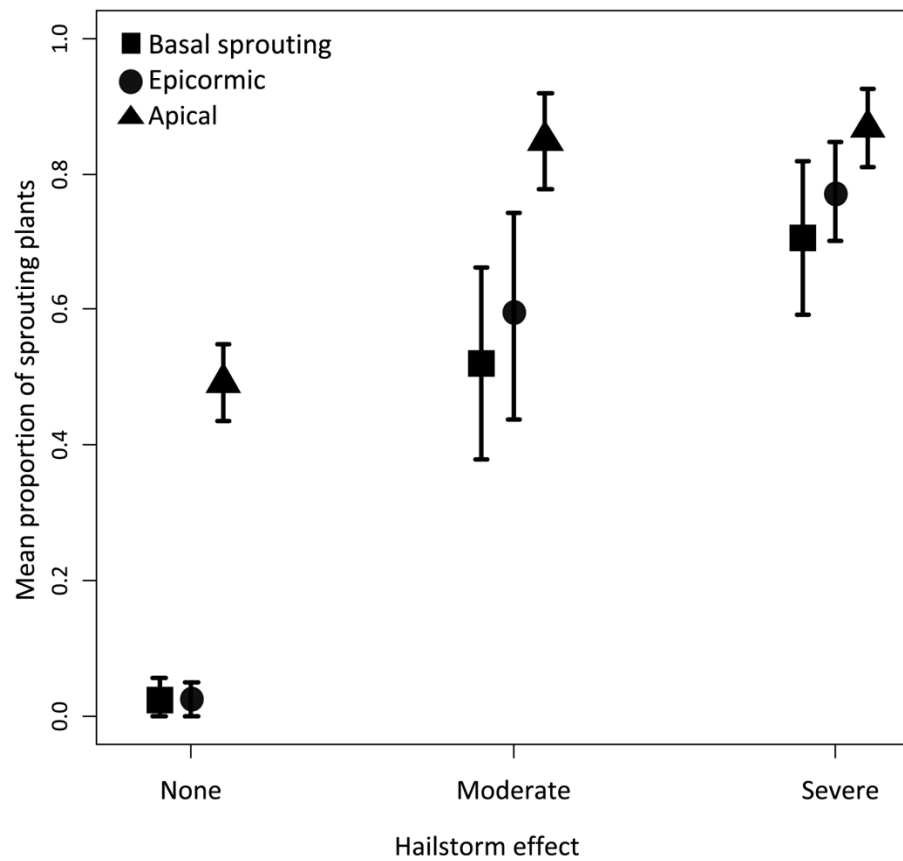
**Figure 2.** Mean defoliation for *Eucalyptus totdtiana* clumps (n=10 per site) and shrub plots (n = 30, 32 and 30 species at control, moderate and high severity storm sites, respectively) (A); estimated mean surface litter mass (fine fuel load) under tree (i.e., *E. totdtiana*) clumps and in shrubland plots, n = 10 per site (B) and mean scorch height on *E. totdtiana* stems (C) in shrubland across a hailstorm severity gradient, near Eneabba, Western Australia. Bars are 95% confidence intervals.



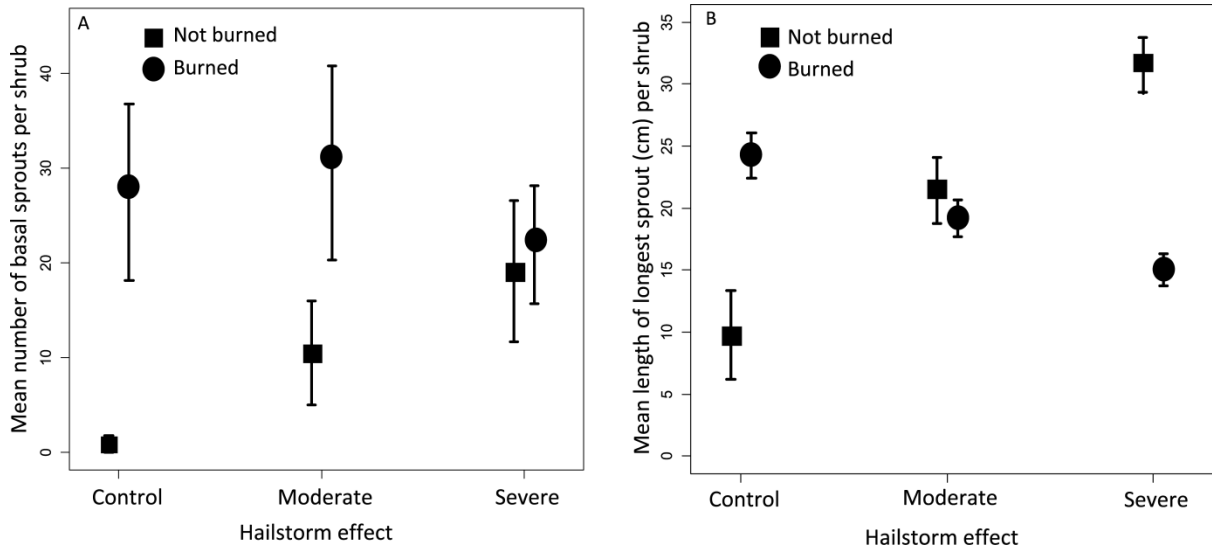
**Figure 3.** Mean number of epicormic resprouts  $m^{-1}$  ( $n = 50$  stems per site,  $n = 42$  at the unburned control site) on *Eucalyptus tottiana* stems (A) and mean proportion of *E. tottiana* stems with basal resprouts in response to hail storm and prescribed fire at matched unburned and burned sites across a storm severity gradient (B) in shrubland, near Eneabba, Western Australia. Bars are 95% confidence intervals.



**Figure 4.** Resprouting response (apical, epicormic, or basal) of shrub species along a hail storm severity gradient near Eneabba, Western Australia. Bars are 95% confidence intervals.



**Figure 5.** Mean number of basal sprouts per resprouter shrub (A) and length of the longest resprout (cm) (B) following single disturbance (hail storm) and multiple disturbance (hail storm + fire) across a storm intensity gradient in shrubland near Eneabba, Western Australia, n (left to right) = 134, 159, 131, 160, 148, 155. Bars are 95% confidence intervals.



**FOR ONLINE PUBLICATION ONLY**

**Supplementary Material, Table A1.** Woody shrub species sampled (number of individuals) in shrubland plots after single and multiple disturbance (hail, fire) near Eneabba, Western Australia. Species are reported with their taxonomy (family, genus + species), regeneration mode (rs: resprouting, ns: nonsprouting), seed storage (s: soil, c: canopy), and the number of individuals sampled in each of six site treatments (control, moderate, high severity hail, each burned or unburned).

Family	Species	Regeneration	Seed storage	Storm only			Storm + Fire			Total N
				Control	Mod	High	Control	Mod	High	
Anthericaceae	<i>Thysanotus dichotomus</i>	rs	s		1	2	3	6	1	13
Casuarinaceae	<i>Allocasuarina humilis</i>	rs	c		5	7		2	2	16
Casuarinaceae	<i>Allocasuarina microstachya</i>	rs	c			2				2
Cupressaceae	<i>Actinostrobus acuminatus</i>	rs	c	1	2	1		10	1	15
Dasyopogonaceae	<i>Calectasia narragara</i>	rs	s					1		1
Dilleniaceae	<i>Hibbertia crassifolia</i>	rs	s	2		1		2		5
Dilleniaceae	<i>Hibbertia hypericoides</i>	rs	s		36	44	4	17	27	128
Dilleniaceae	<i>Hibbertia spicata</i>	rs	s		2			1		3
Ericaceae	<i>Andersonia heterophylla</i>	ns	s	3	1	2				6
Ericaceae	<i>Astroloma microdonta</i>	rs	s				1			1
Ericaceae	<i>Astroloma xerophyllum</i>	ns	s		2	1				3
Ericaceae	<i>Conostephium preissii</i>	rs	s			1				1
Ericaceae	<i>Leucopogon conostephioides</i>	ns	s	2		1				3
Ericaceae	<i>Leucopogon gracillimus</i>	ns	s	1						1
Euphorbiaceae	<i>Monotaxis grandiflora</i>	rs	s					1	1	2
Fabaceae	<i>Daviesia divaricata</i>	rs	s	5			1			6
Fabaceae	<i>Daviesia nudiflora</i>	rs	s	1	2	4		4		11
Fabaceae	<i>Daviesia pedunculata</i>	rs	s			1				1
Fabaceae	<i>Daviesia triflora</i>	rs	s		1			1	1	3

Fabaceae	<i>Jacksonia floribunda</i>	rs	s	9	3	4	6	4	3	29
Fabaceae	<i>Jacksonia hakeoides</i>	rs	s		1		28	1		30
Goodenaceae	<i>Scaevola canescens</i>	ns	s				1			1
Goodenaceae	<i>Verreauxia reinwardtii</i>	rs	s						1	1
Lamiaceae	<i>Hemiandra pungens</i>	rs	s					2		2
Mimosaceae	<i>Acacia barbinervis</i>	rs	s					1		1
Mimosaceae	<i>Acacia lasiocarpa</i>	ns	s				1	1	1	3
Myrtaceae	<i>Babingtonia camphorosmae</i>	rs	s	1						1
Myrtaceae	<i>Beaufortia elegans</i>	ns	c	13	22	7				42
Myrtaceae	<i>Calothamnus hirsutus</i>	rs	c		3	2	9	2		16
Myrtaceae	<i>Calothamnus sanguineus</i>	rs	c	1						1
Myrtaceae	<i>Darwinia neildiana</i>	rs	s		1					1
Myrtaceae	<i>Darwinia speciosa</i>	rs	s					2	3	5
Myrtaceae	<i>Eremaea acutifolia</i>	rs	c		2	1				3
Myrtaceae	<i>Eremaea asterocarpa</i>	rs	c		1					1
Myrtaceae	<i>Eremaea beaufortoides</i>	rs	c	6	2		8	1	2	19
Myrtaceae	<i>Eremaea sp</i>	rs	c	1			2	11	1	15
Myrtaceae	<i>Eremaea violacea</i>	rs	c	1		1	1	1		4
Myrtaceae	<i>Hypocalymma angustifolium</i>	rs	s					1		1
Myrtaceae	<i>Leptospernum oligandrum</i>	rs	s	5	3	3	3			14
Myrtaceae	<i>Leptospernum spinescens</i>	rs	c	1	2	2	1	5		11
Myrtaceae	<i>Melaleuca leuropoma</i>	rs	c	18	12	11	22	22	18	103
Myrtaceae	<i>Phymatocarpus porphyrocephalus</i>	ns	c	13						13
Myrtaceae	<i>Pileanthus filifolia</i>	rs	s	27	7	14	20	21	47	136
Myrtaceae	<i>Scholtzia involucrata</i>	rs	s	6	17	26	9	9	9	76
Myrtaceae	<i>Verticordia aurea</i>	ns	s	1						1
Myrtaceae	<i>Verticordia densiflora</i>	rs	s	6	6	2	5	5	12	36
Myrtaceae	<i>Verticordia grandis</i>	rs	s	5	5	5	2	1		18
Proteaceae	<i>Banksia attenuata</i>	rs	c	1						1
Proteaceae	<i>Banksia candolleana</i>	rs	c					6	8	14

Proteaceae	<i>Banksia dallaneyi</i>	rs	c			2	6	1		9
Proteaceae	<i>Banksia grossa</i>	rs	c		2			2		4
Proteaceae	<i>Banksia shuttleworthania</i>	rs	c		6	5		8	7	26
Proteaceae	<i>Conospermum incurvum</i>	ns	s		2					2
Proteaceae	<i>Conospermum wycherleyi</i>	rs	s	11	2	3	10	1	7	34
Proteaceae	<i>Grevillea eriostachya</i>	rs	c	4						4
Proteaceae	<i>Hakea eneabba</i>	rs	c		3	1	1	5		10
Proteaceae	<i>Hakea flabellifolia</i>	rs	c			1				1
Proteaceae	<i>Hakea polyanthema</i>	ns	c	3						3
Proteaceae	<i>Isopogon tridens</i>	rs	s	6						6
Proteaceae	<i>Petrophile brevifolia</i>	rs	s		1	2	11		1	15
Proteaceae	<i>Petrophile macrostachya</i>	rs	s	2	1		2	1		6
Proteaceae	<i>Stirlingia latifolia</i>	rs	s				1			1
Proteaceae	<i>Synaphea spinulosa</i>	rs	s		2					2
Sterculiaceae	<i>Lasiopetalum drummondii</i>	rs	s	1			2	1	4	8
	<b>Total</b>			<b>157</b>	<b>158</b>	<b>159</b>	<b>160</b>	<b>160</b>	<b>157</b>	<b>951</b>

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**Supplementary Material, Table A2.** Seedlings of woody species sampled (number of individuals) in shrubland plots after single and multiple disturbance (hail, fire) near Eneabba, Western Australia. Species are reported with their taxonomy (family, genus + species), regeneration mode (rs: resprouting, ns: nonsprouting, unk: unknown), seed storage (s: soil, c: canopy), and the number of individuals sampled in each of six site treatments (control, moderate, high severity hail, each burned or unburned).

Family	Species	Regeneration	Seed Storage	Storm Only			Storm + Fire			Total N
				Control	Mod	High	Control	Mod	High	
Anthericaceae	<i>Thysanotus dichotomus</i>	rs	s				4	7		11
Dilleniaceae	Dilleniaceae sp 1	unk	s				5			5
Dilleniaceae	Dilleniaceae sp 2	unk	s				1			1
Dilleniaceae	<i>Hibbertia hypericoides</i>	rs	s					5	1	6
Ericaceae	<i>Ericaceae sp 1</i>	ns	s				23	16		39
Ericaceae	<i>Ericaceae sp 2</i>	ns	s					3		3
Fabaceae	<i>Isotropis cuneifolia</i>	rs	s				43	1		44
Fabaceae	<i>Jacksonia floribunda</i>	rs	s				1	7	3	11
Fabaceae	<i>Jacksonia hakeoides</i>	rs	s				71	39		110
Goodeniaceae	Goodeniaceae sp	rs	s						2	2
Goodeniaceae	<i>Scaevola canescens</i>	ns	s				9			9
Goodeniaceae	<i>Scaevola sp 1</i>	unk	s					5		5
Goodeniaceae	<i>Scaevola sp 2</i>	unk	s				3		3	6
Goodeniaceae	<i>Verreauxia reinwardtii</i>	rs	s					2	3	5
Lamiaceae	<i>Hemiandra pungens</i>	rs	s				1	8	1	10
Mimosaceae	<i>Acacia lasiocarpa</i>	ns	s				46	14		60
Mimosaceae	<i>Acacia sp</i>	ns	s					1		1
Myrtaceae	<i>Darwinia neildiana</i>	rs	s				1			1
Myrtaceae	<i>Beaufortia elegans</i>	ns	c				6			6
Myrtaceae	<i>Calothamnus hirsutus</i>	rs	c				1			1
Myrtaceae	<i>Calothamnus sp</i>	rs	c				2			2
Myrtaceae	<i>Calytrix sp</i>	unk	s				1	3		4
Myrtaceae	<i>Eremaea beaufortioides</i>	rs	c				1			1



Myrtaceae	Myrtaceae sp	unk	s				1		1	
Myrtaceae	<i>Pileanthus filifolia</i>	rs	s			4	6		10	
Myrtaceae	<i>Verticordia densiflora</i>	rs	s					1	1	
Proteaceae	<i>Banksia candolleana</i>	rs	c			2		1	3	
Proteaceae	<i>Conospermum wycherlii</i>	rs	s	11	7	50	18	35	121	
Proteaceae	<i>Daviesia nudiflora</i>	rs	s			4	22		26	
Proteaceae	<i>Daviesia triflora</i>	rs	s			50	1	6	57	
Proteaceae	<i>Stirlingia latifolia</i>	rs	s			2			2	
Proteaceae	<i>Synaphea spinulosa</i>	rs	s	10			35		45	
Rutaceae	<i>Boronia racemosa</i>	ns	s			4	2		6	
	<b>Total</b>			<b>0</b>	<b>25</b>	<b>7</b>	<b>331</b>	<b>196</b>	<b>56</b>	<b>615</b>

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