Interactive effects of fire and large herbivores on web-building spiders

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1 **Abstract**

2 Altered disturbance regimes are a major driver of biodiversity loss worldwide. Maintaining or

3 recreating natural disturbance regimes is therefore the focus of many conservation programs.

4 A key challenge, however, is to understand how co-occurring disturbances interact to affect

5 biodiversity. We experimentally tested for the interactive effects of prescribed fire and large

6 macropod herbivores on the web-building spider assemblage of a eucalypt forest understorey,

7 and investigated the role of vegetation in mediating these effects using path analysis. Fire had

8 strong negative effects on the density of web-building spiders, which was partly mediated by

9 effects on vegetation structure, while negative effects of large herbivores on web density were

10 not related to changes in vegetation. Fire amplified the effects of large herbivores on spiders,

11 both via vegetation-mediated pathways, and by increasing herbivore activity. The importance

12 of vegetation-mediated pathways and fire-herbivore interactions differed for web density and

13 richness, and also differed between web types. Our results demonstrate that for some groups

14 of web building spiders, the effects of co-occurring disturbance drivers may be mostly

15 additive, whereas for other groups, interactions between drivers can amplify disturbance

16 effects. In our study system, the use of prescribed fire in the presence of high densities of

17 herbivores could lead to reduced densities and altered composition of web-building spiders,

18 with potential cascading effects through the arthropod food web. Our study highlights the

19 importance of considering both the independent and interactive effects of disturbances, as

20 well as the mechanisms driving their effects, in the management of disturbance regimes.

21

22 **Keywords:** Araneae, browsing, disturbance interaction, grazing, synergistic effects

Introduction

Disturbance regimes drive the structure and function of ecosystems worldwide, and altered disturbance regimes are an important cause of biodiversity loss (Sinclair and Byrom 2006). Maintaining or recreating appropriate disturbance regimes is therefore the focus of many conservation and restoration programs (Hobbs and Huenneke 1992; Halme et al. 2013).

Two of the most common and widely studied disturbance drivers in terrestrial systems are herbivory and fire (Bond and Keeley 2005; Danell et al. 2006). Browsing or grazing by large mammalian herbivores has been shown to shape the structure and function of ecosystems, from plant and animal communities, through to nutrient cycles and even climate (Côté et al. 2004; Danell et al. 2006; Foster et al. 2014). Fire is an episodic disturbance, and the frequency, intensity and spatial extent of fires also drives the structure and function of ecosystems (Thonicke et al. 2001; Bond and Keeley 2005). Both of these disturbances can affect biota either directly (e.g. through direct mortality), or indirectly (e.g. by modifying habitat), or both (Thonicke et al. 2001; Côté et al. 2004). A key mechanism linking both large herbivores and fire to effects on biological communities is via changes in vegetation structure and complexity (Bond and Keeley 2005; Foster et al. 2014).

As disturbances rarely occur in isolation, understanding how disturbance drivers interact to affect biota is critical for effective conservation management (Wisdom et al. 2006; Didham et al. 2007; Mantyka-pringle et al. 2012). Although the ecological effects of disturbance have been widely studied, investigations of the interactive effects of disturbance drivers are much less common (Wisdom et al. 2006; Didham et al. 2007; Foster et al. 2014). Interactions between fire and herbivory have been reported in a range of ecosystems, and can occur in a number of ways. For example, patterns and intensity of herbivory can affect fuel loads and

48 hence modify the spatial extent or intensity of fire (Wisdom et al. 2006; Kimuyu et al. 2014).

49 Similarly, as many herbivores are attracted to the new growth available in recently burnt

50 areas, fire can affect the spatial distribution and intensity of herbivory (Allred et al. 2011).

51 Fire and herbivory also can interact via what is termed an interaction modification, where fire

52 changes the mode of action or per-unit effect of herbivory on organisms (*sensu* Didham et al.

53 2007). For example, Royo et al. (2010) found that moderate levels of deer browsing increased

54 understorey plant richness in burnt deciduous forest, but not in unburnt forest. Interactions

55 between disturbance drivers can be synergistic (i.e. effects magnified, e.g. Barton et al. 2011)

56 or antagonistic (i.e. effects diminished or reversed, e.g. Matlack et al. 2001), and by

57 definition, differ from what would be predicted from the additive effects of each driver

58 occurring in isolation (Didham et al. 2007; Crain et al. 2008).

59

60 Most studies of fire × large herbivore interactions have investigated effects on vegetation (e.g.

61 Royo et al. 2010; Kerns et al. 2011), and to date only a small number of studies have

62 investigated how these interactions affect animal assemblages. Among these studies, there

63 appears to be a consistency between vegetation and animal responses; most studies which

64 report interactive effects on animals also report interactive effects on vegetation (e.g. Matlack

65 et al. 2001, deer mice; Bailey and Whitham 2002, arthropods), while studies which find no

66 interactive effects on animals also find no interactive effects on vegetation (e.g. Jonas and

67 Joern 2007, grasshoppers; Underwood and Christian 2009, ants).

68

69 Web-building spiders are a group of animals that have been found to respond to both fire

70 (Buddle et al. 2000) and large herbivores (Miyashita et al. 2004; Warui et al. 2005), but the

71 responses of these spiders to fire-herbivore interactions have not previously been studied.

72 Web-building spiders respond strongly to changes in vegetation structure (Langellotto and

73   Denno 2004), and are the dominant invertebrate predators in terrestrial food webs (Riechert

74   and Lockley 1984; Carter and Rypstra 1995). Therefore, disturbance-induced changes in

75   vegetation structure may modify spider densities, which could have important consequences

76   for trophic dynamics (Schmitz 2008). In addition, different types of web-builders may differ

77   in their response to habitat complexity, for example, Halaj et al. (2000) found that sheet

78   weaving spiders, which build complex three-dimensional webs, responded more negatively to

79   habitat simplification than orb-weaving spiders. As different types of web-builders target

80   different prey items (Nyffeler 1999), changes in vegetation structure also may affect food web

81   structure by altering the composition of the predator guild. However, as disturbance effects

82   can cascade through ecosystems via both trophic and non-trophic pathways (Ohgushi 2005), it

83   is important to understand the extent to which disturbance effects are mediated by changes in

84   vegetation, and whether managing disturbances to maintain vegetation condition will also

85   cater for the requirements of fauna (Clarke 2008).

86

87   In this study, we tested for the effects of fire, large macropod herbivores and their interaction

88   on the web-building spider assemblage of a eucalypt forest understory. We used a

89   randomised, blocked experiment, combining prescribed fire and herbivore exclusion

90   treatments, to address three questions: (1) Do large herbivores and fire interact to affect the

91   density or richness of web-building spiders? (2) To what extent are the effects of these

92   disturbances mediated by changes in vegetation? And (3) Do these effects differ between

93   different types of web-builders? We predicted that both fire and large herbivores would

94   reduce web-building spider density and richness by reducing the structural complexity of

95   vegetation, with sheet web-builders responding most strongly to vegetation simplification.

96

Materials and methods

Study site

We conducted our study in Booderee National Park (BNP); a ~6 500 ha peninsula in south-eastern Australia (35°10′S, 150°40′E, see Online Resource 1). We established sites within the *Eucalyptus pilularis* forest of BNP, which is the most widespread vegetation type in the park (Barton et al. 2014). An intensive baiting program targeting the introduced red fox (*Vulpes vulpes*) has been in place in BNP since 1999 to protect native small and medium-sized mammal species from predation (Dexter et al. 2012). Loss of native predators and a lack of human hunting mean that without foxes, predation pressure on native macropod herbivores is low (Lindenmayer et al. 2014). Over the last decade, there has been a tenfold increase in the numbers of these herbivores in BNP (predominantly *Wallabia bicolor*, a generalist browser and *Macropus giganteus,* a grazer, Family Macropodidae) (Dexter et al. 2012; Lindenmayer et al. 2014). A short-term exclosure trial has indicated that this high abundance of native herbivores could be driving a shift in vegetation composition (Dexter et al. 2013). As prescribed fire is commonly used in eucalypt forests to reduce the risk of high intensity wildfire, promote regeneration of senescing vegetation, and/or increase habitat heterogeneity (Williams et al. 1994), it is important to understand how fire interacts with high abundances of herbivores to affect biodiversity.

Study design

We tested the interactive effects of prescribed fire and large herbivores on understorey vegetation and web-building spiders using a randomised blocked experiment. We combined three levels of herbivore treatment (open, partial and exclosure) and two levels of burning treatment (burnt and unburnt) in a factorial design. We replicated each of these six treatment combinations across four experimental blocks to give a total of 24 sites (Online Resource 1).

122   We created the herbivore treatments by using exclosure fences to reduce the density of

123   macropods within 0.125 ha (25 m × 25 m) plots, to produce three treatments: full herbivory

124   (open treatment), intermediate herbivory (partial treatment – plots were fenced but gates

125   opened and closed at two month intervals to create a lower browsing pressure) and no

126   herbivory (exclosure treatment). Exclosure fences were constructed in June 2012 using 1.1 m

127   tall wire fencing, which we found to be effective at excluding macropods (see Results).

128   Smaller animals were observed to move freely through the fence, and other large animals are

129   rare in the park, so effects of exclosure fences were assumed to occur primarily via their effect

130   on macropods. For the burning treatments, small (50 × 50 m), low-intensity burns were

131   conducted across half of the herbivory treatment sites in August 2012.

132

133   ***Data collection***

134   We sampled spider webs and vegetation within four 3 × 3 m plots within each site (one in

135   each of the four quarters of the site). Data were collected three months post-fire (November

136   2012) and 15 months post-fire (November 2013). Plots were established at least 1.5 m from

137   the edge of the site.

138

139   We counted spider webs as a surrogate measure for the web-building spider assemblage. This

140   method was described and tested by Gollan et al. (2010), who found that the diversity of web-

141   types (based on web architecture) was strongly correlated with the diversity of spider genera

142   in a site. As the richness of spider genera can be a viable surrogate for the species richness of

143   spiders (Foord et al. 2013), this method allowed us to assess compositional and diversity

144   responses of spiders, in addition to density responses. We used vaporised water, applied with

145   a pressurised spray mister, to assist in locating webs, and counted and identified all spider

146   webs within each of the four plots in each site. Each web was assigned to one of 32 web types

147 based on their architecture, according to the key of Smith (2008) (see Fig. 1 for examples).

148 From this, we generated measures of web density (number of webs per 3 x 3 m plot), web

149 richness (the number of different web types per plot) and web composition (the assemblage

150 composition of web types) for each plot. To minimise variation due to weather conditions,

151 surveys were delayed for 48 hours following strong wind or rain to allow spiders to rebuild

152 damaged webs.

153

154 We recorded the following vegetation variables from each plot; total understorey foliage

155 projective cover (the proportion of ground area covered by foliage held vertically above it,

156 Specht and Morgan 1981), foliage projective cover of vascular plants by life-form,

157 understorey height (measured at 10 evenly spaced locations per plot using the stick and foam

158 disc method of Smit et al. (2001), disc 100 mm diameter, 4.7 g weight), litter depth (measured

159 at 10 evenly spaced locations per plot) and stem density (number of live woody stems at

160 ground level within a 1×1 m sub-plot). Life-forms were grouped into the broad structural

161 categories of ferns, grasses (Poaceae), herbs (including forbs and climbers), sedges (which

162 included grass-like perennial herbs) and shrubs (including sub-shrubs and tree seedlings).

163

164 We measured the effects of burning and the herbivory treatments on herbivore activity using

165 scat (pellet) counts. Scat counts are a commonly used method to assess the comparative

166 density of macropod herbivores between sites (e.g. Howland et al. 2014; Pedersen et al.

167 2014). We counted the number of macropod scats along two 25×2 m transects (100 m^{-2}) in

168 each site approximately every two months from August 2012 to December 2013. Counts from

169 the two transects were summed to give one count per site. We removed scats from transect

170 lines on each sampling event to avoid double counting. For each site, we summed the count

171 preceding and that following the spider web counts to give an approximate index of herbivore

172 activity in each site at the time of the web count.

173

174 ***Data analysis***

175 *Effects of fire and large herbivores on web density and richness*

176 We used generalised multi-level path models (Shipley 2009) to test the effects of fire and

177 large herbivores on spider web density and richness, and the extent to which these effects

178 were mediated by vegetation changes. Generalised multi-level path analysis uses directional-

179 separation (d-sep) tests to assess the goodness of fit of a hypothesised causal diagram to the

180 patterns of dependence and independence within a dataset (Shipley 2002). This analysis is

181 based on a structural equation modelling (SEM) framework, but has been generalised to

182 accommodate hierarchical designs and non-normal response variables (Shipley 2009).

183

184 We hypothesised that the effects of fire, herbivores and their interaction on spiders would be

185 largely vegetation-mediated, but would also occur via other mechanisms that operate

186 independently of vegetation structure (Fig. 2). Our rationale for the construction of this causal

187 model was as follows: Fire can affect spiders through changes in vegetation structure

188 (Brennan et al. 2006), or via other mechanisms that operate independently of vegetation (the

189 direct fire-spider pathway in Fig. 2), such as fire-induced mortality (Bell et al. 2001), or

190 changes in prey availability (York 1999). Similarly, large herbivores have been found to

191 affect spiders by modifying vegetation structure (Miyashita et al. 2004), but could also affect

192 spiders through other mechanisms (the direct herbivore-spider pathway in Fig. 2) such as

193 physical disturbance of webs (Chmiel et al. 2000), or changes to key resources such as

194 arthropod prey (Foster et al. 2014). We also identified three possible pathways by which fire

195 could interact with large herbivores to affect spiders; (1) a chain effect, where fire attracts

9

196 herbivores to burnt areas, increasing the level of herbivore activity in burnt sites (Allred et al.

197 2011), (2) an interaction modification, where fire alters plant traits, modifying the effect of

198 herbivores on vegetation (Augustine and McNaughton 1998), or (3) an interaction

199 modification where fire increases the vulnerability of web spiders to other impacts of large

200 herbivores (e.g. by reducing prey availability, increasing the likelihood of spiders abandoning

201 webs after physical disturbance, Chmiel et al. 2000).

202

203 Confirmatory path analysis does not allow for reciprocal effects among variables (Shipley

204 2009), but a number of vegetation variables we measured were likely to be reciprocally

205 related (for example, high grass cover would lead to low average understory height and low

206 stem density in a site). Therefore, we selected three vegetation variables that were not

207 correlated with each other, but made up a large component of the vegetation and were

208 correlated with other vegetation variables, to include in the path analysis (cover of shrubs,

209 sedges and ferns). While this approach avoided reciprocity between variables, in excluding

210 some vegetation variables, we potentially omitted variation in vegetation structure that could

211 explain spider responses to disturbance. Therefore, we also conducted a sensitivity analysis

212 (*sensu* Ruffell et al. 2014) to test whether including additional vegetation variables in our path

213 model would increase the extent to which disturbance effects were mediated by vegetation

214 (Online Resource 2). To do this, we used principal components analysis to reduce our nine

215 vegetation variables to seven orthogonal components, and used these at the measures of

216 vegetation structure in our path analysis. We did not use principal components in the main

217 analysis as principal components are less correlated than would be expected by chance, and

218 including them in the path analysis would reduce our chance of rejecting an incorrectly

219 specified path model (Ruffell et al. 2014).

220

221 For each of web density and web richness, we constructed two causal diagrams, one for each

222 year of the study, with the cover of shrubs, sedges and ferns as measures of vegetation

223 structure (each with their own node). For each of these diagrams, we tested goodness of fit

224 using d-sep tests (Shipley 2009). Once we had tested the goodness of fit of the full path

225 model, we simplified the model to a more parsimonious one using a backward selection

226 approach (*sensu* Ruffell et al. 2014). Backward selection based on minimising AIC was used

227 to simplify each sub-model within the full model (Zuur et al. 2009). Each sub-model was a

228 mixed-effects model fitted with maximum likelihood estimation, and included an endogenous

229 variable as the response and its direct causal parents as predictors. Once all sub-models had

230 been simplified, they were grouped back into a single path model and the fit of this model was

231 tested using generalised multilevel path analysis and d-sep tests as described above.

232

233 All analyses were completed using R (R Core Team 2013). For GLMMs we used the glmer

234 function in the package lme4, using a Poisson distribution and log-link function (Bates et al.

235 2014), while for LMMs we used the lme function in the package nlme (Pinheiro et al. 2014).

236 Random effects for all GLMMs and LMMs were sites within blocks (block/site). When used

237 as predictors, count variables were ln-transformed and continuous variables were centred on

238 their means. Response variables were checked for over-dispersion and model residuals were

239 inspected to verify that the data met model assumptions (Zuur et al. 2009). After deciding on

240 the final model for both web abundance and richness, we calculated path coefficients as the

241 estimated slopes of the variables within each of the sub-models (Shipley 2009).

242 Unstandardized path coefficients can be interpreted as the change in the response variable for

243 a one unit change in the predictor variable (Aiken and West 1991). However, in the presence

244 of an interaction, these path coefficients are conditional effects. Because all predictors were

245 centred, the conditional effects can be interpreted as the effect of the predictor on the response

246 variable when the interacting predictor is held at its mean value, or in the case of categorical

247 predictors (fire and herbivore exclosure treatments) at the control value (unburnt and open

248 treatments respectively). The interaction term indicates the amount of change in the slope of

249 the regression of the response on the predictor with a one-unit change in the value of the

250 interacting predictor.

251

252 *Effects of fire and large herbivores on different web types*

253 To test whether different types of webs responded differently to large herbivores and fire, we

254 estimated unstandardized regression coefficients when the density of that web type was

255 substituted for overall web density in the full path diagram. Each of the individual web types

256 was assigned to one of four groups based on similarity of web characteristics - orb webs,

257 sheet webs, lace webs and tangle webs (Fig. 1, Online Resource 3). Such groupings are

258 commonly used in studies of web-building spiders, and while there is some overlap, these

259 categories broadly sort spiders into groups of families (e.g. Halaj et al. 2000). Orb weavers

260 are generally in the families Araneidae, Tetragnathidae, and Uloboridae, sheet weavers in the

261 families Linyphiidae, Theridiidae and Stiphidiidae, lace weavers belong to Desidae, and

262 tangle web spinners are generally in the family Theridiidae (Online Resource 3). We used a

263 separate GLMM for each web type grouping in each year with a Poisson distribution and log-

264 link function and random effects of block/site. We used backward selection as described

265 above to simplify the model for each web type in each year.

266

267 We also analysed the effect of our treatments on the composition of individual web types

268 using partial (or conditioned) canonical correspondence analysis in R (R Core Team 2013),

269 using the "cca" function in the package "vegan" (Oksanen et al. 2013), and using the Bray-

270 Curtis dissimilarity measure. This analysis allowed us to partial out the spatial variation

271 associated with the experimental blocks, before analysing the variation in web type

272 composition that was associated with our experimental treatments (herbivory × fire × year)

273 (Borcard et al. 1992). We then ran permutation tests using the function "anova.cca" to test the

274 significance of our constraints (treatment combinations) using 10 000 permutations of the

275 data. To reduce the incidence of zero values in the data caused by rare web types, we pooled

276 web counts to the site level for this analysis and excluded web types occurring at two or fewer

277 sites.

278

279 **Results**

280 *Density and richness of spider webs*

281 We counted 3687 spider webs, representing 28 different web types, across the two sampling

282 periods (Online Resource 3). Generalised multilevel path analysis indicated that herbivores

283 and fire affected spider web density via both vegetation-mediated and other pathways, but

284 effects on web type richness were of short duration and not mediated by changes in

285 vegetation.

286

287 For web density, the simplified path models (2012: $\chi^2 = 34.7$, df = 30, P = 0.25, 2013: $\chi^2 =$

288 29.0, df = 28, P = 0.41) gave as good fit as the full models (2012: $\chi^2 = 25.9$, df = 22, P = 0.26,

289 2013: ($\chi^2 = 28.5$, df = 22, P = 0.16) in both years. The simplified model for web density in

290 2012 indicated that fire had a strong negative effect on web density, which was partly

291 mediated by negative effects of fire on vegetation cover (Fig. 3a). In contrast, the small, but

292 significant, negative effect of large herbivores on web density was not mediated by changes in

293 vegetation structure. By 2013, the effects of fire on vegetation variables were weaker, which

294 was associated with a recovery in vegetation (Fig. 3b). Both the vegetation-mediated effects,

295 and the other effects, of fire on web-density were reduced in 2013 compared with 2012.

13

296   While the effect of fire on shrub cover was reduced in 2013, shrub cover remained a strong

297   determinant of web density in 2013. In 2013 there also was a marginally significant

298   interaction between fire and herbivores, where herbivore activity was positively associated

299   with fern cover in burnt, but not in unburnt sites (Fig. 3b, Online Resource 2 - Figs. OR3a,b).

300   High fern cover was associated with higher web density in the path model (Fig. 3a). As in

301   2012, in 2013 there was a small negative effect of herbivores on web density which was not

302   explained by vegetation structure. Sensitivity analysis indicated that including all vegetation

303   variables in the path model did not increase the amount of variation in web density that was

304   explained by vegetation-mediated pathways (Online Resource 2).

305

306   Model fits for web type richness were similar to those for web density, where our simplified

307   model (2012: $\chi^2 = 35.6$, df = 34, P = 0.39, 2013: $\chi^2 = 30.2$, df = 34, P = 0.65) gave as good a

308   fit as the full model (2012: $\chi^2 = 23.8$, df = 22, P = 0.35, 2013: $\chi^2 = 25.0$, df = 22, P = 0.30) in

309   both years of the study. The simplified path models indicated that the effects of disturbance

310   on web-type richness were not mediated by changes in vegetation structure (Fig. 3c,d). Fire

311   had a short-term negative effect on web-type richness which was no longer evident in 2013

312   (15 months after fire). Large herbivores had a small negative effect on web-type richness in

313   both years, and this effect was strongest in 2012, when herbivore activity was elevated in

314   burnt sites (Fig. 3c,d). As with web density, including all vegetation variables in the path

315   analysis did not increase the strength of vegetation-mediated effects on web type richness

316   (Online Resource 2).

317

318   *Responses of different web types*

319   Substituting different web type groupings into the full model in place of web density revealed

320   key differences in the factors affecting different types of webs. Orb web density was higher

321 on sites with higher shrub cover, a relationship which mediated the negative effects of fire on

322 orb webs in both years (Table 1). In 2013, orb webs also were positively associated with

323 higher fern cover. In contrast, while some of the effects of fire on sheet webs were vegetation-

324 mediated, there was a strong negative effect of fire on sheet webs in both 2012 and 2013,

325 which was not vegetation mediated (Table 1). Sheet webs also responded negatively to

326 herbivore activity on both years, a response which was also not explained by changes in

327 vegetation. Tangle webs and lace webs showed only weak or inconsistent responses to the

328 experimental treatments, with tangle webs showing a shrub-mediated negative response to fire

329 and a negative response to herbivore activity in 2012, but no responses to disturbance in 2013

330 (Table 1).

331

332 Compositional differences in web-types reflected the strongest effects in the analysis of web

333 types. The first two axes of the partial CCA analysis accounted for 14.8 % and 12.4 % of the

334 variation in web type composition, respectively. There was a significant interaction between

335 year and burning treatment ($P = 0.03$, Fig. 4). There were also significant differences in web

336 type composition between burning treatments ($P < 0.01$), and years ($P < 0.01$), but not

337 between herbivory treatments or any of its interaction terms (all $P > 0.05$). The composition

338 of burnt sites appeared to be a sub-set of unburnt sites, with the two most common sheet webs

339 (web 25 and 27, belonging to the families Theridiidae and Linyphiidae respectively), strongly

340 associated with unburnt sites (Fig. 4).

341

342 **Discussion**

343 We used a combination of burning and herbivore exclusion treatments to test the combined

344 effects of fire and large herbivores on web-building spiders in a forest understory. Fire and

345 large herbivores interacted via a chain effect, where fire increased herbivore activity, which in

346 turn affected the web-building spider assemblage. Fire and large herbivores also interacted via

347 vegetation-mediated pathways to affect spiders, although this interaction was only marginally

348 significant. The extent to which vegetation structure mediated disturbance effects and the

349 importance of interactive effects differed for web density and richness, and also between web

350 types. Strong effects of disturbance on web-building spiders that were not mediated by

351 vegetation indicate that managing disturbances to maintain vegetation structure is unlikely to

352 adequately address the needs of fauna in this system.

353

354 *Fire, but not herbivore effects on web density were vegetation-mediated*

355 Web density was most strongly affected by fire, and much of this effect was mediated by

356 changes in vegetation structure. The loss and subsequent recovery of vegetation after fire

357 (Fig. 3) was mirrored by a loss and partial recovery of spider web density, with spiders likely

358 responding to changes in web-site availability and litter accumulation that occurred with

359 changes in vegetation cover (Brennan et al. 2006; Podgaiski et al. 2013). However, fire also

360 had strong effects on web density that were not explained by vegetation responses, and these

361 effects persisted in the second year of the study (Fig. 3a,b). As our experimental burns were

362 small (50 x 50 m), and many spiders are able to rapidly disperse via aerial ballooning (Bell et

363 al. 2005; Langlands et al. 2011), this strong residual effect of fire is unlikely to be limited by

364 recolonization ability. We suggest that other changes that can occur after fire, but were not

365 measured this study, such as reduced soil/litter moisture, or reduced abundances of arthropod

366 prey, may have limited the re-establishment of high densities of spiders following fire

367 (Neumann and Tolhurst 1991; York 1999).

368

369 Fire and large herbivores interacted to increase the cover of ferns, which had a weak positive

370 effect on web density. This interaction likely occurred due to selective browsing by

371 herbivores allowing the less palatable bracken to dominate in burnt, browsed environments

372 (Augustine and McNaughton 1998). This increased cover of ferns was positively associated

373 with web density, with fern cover likely providing suitable web sites in an environment where

374 cover of other lifeforms remained low (Online Resource 4). Overall, very little of the effect of

375 large herbivores on spiders was mediated by vegetation, which contrasts with a number of

376 previous studies, which have attributed negative effects of large herbivores on spiders to

377 changes in vegetation structure (e.g. Miyashita et al. 2004; Warui et al. 2005).

378

379 Path analysis revealed that large herbivores negatively affected web density (and also web

380 type richness) via non-vegetation-mediated pathways, likely through the physical disturbance

381 of webs. Web damage is one of the main triggers for a spider to abandon a web site (Chmiel

382 et al. 2000). Repeated web disturbance may therefore have reduced web density by causing

383 spiders to move out of sites with high herbivore activity, or by reducing spider fitness, as

384 spiders which move web sites must expend considerable energy in web reconstruction

385 (Rypstra 1983; Chmiel et al. 2000), and are more vulnerable to predation when moving

386 between sites (Lubin et al. 1993). The effect of herbivores on web density was greatest in

387 2012 (Fig. 3a) and this was likely due to the chain interaction between fire and herbivores,

388 where herbivore activity was higher in burnt sites. This type of interaction has been reported

389 by many previous studies, where burning focusses herbivore activity in burnt patches (Klop et

390 al. 2007; Allred et al. 2011). This greater level of herbivore activity in recently burnt sites

391 would have led to greater rates of web disturbance, and hence the stronger negative effects on

392 spiders.

393

394   *Disturbance effects on web type richness were not vegetation-mediated*

395   In contrast to web density, the effects of disturbance on web type richness were of short

396   duration and were not mediated by effects on vegetation structure (Fig. 3c,d). The short-lived

397   effect of fire suggests that spiders were able to rapidly re-colonise sites as the vegetation

398   recovered from fire, a result that is not surprising given the small scale of the burns in our

399   study (50 x 50 m) and the high capacity of spiders to disperse via both ground movement and

400   aerial ballooning (Bell et al. 2005; Langlands et al. 2011). Such short-term effects of fire on

401   spider richness are consistent with previous studies from fire-prone environments, where post-

402   fire recovery of spiders can be rapid (e.g. Brennan et al. 2006; Podgaiski et al. 2013). Spider

403   richness also was directly affected by herbivore activity, where sites with higher herbivore

404   activity had slightly (but significantly) lower web richness (Fig. 3a). This is likely due to a

405   few web types being particularly vulnerable to physical disturbance, causing them to occur

406   only rarely on sites with high herbivore activity.

407

408   *Responses differed between web types*

409   Different web types showed clear differences in their response to fire, large herbivores, and

410   their interaction. Orb web weavers showed a strong post-fire recovery which was largely

411   mediated by vegetation, while sheet web weavers showed a strong negative response to fire,

412   with little recovery after 15 months. These differences are attributable to key differences in

413   the ecology of these different types of web spinners. Firstly, orb weavers tend to build their

414   webs in higher strata of the vegetation than sheet weavers (Janetos 1982), and so are more

415   likely to be able to escape being killed by a low intensity fire. Second, orb weavers tend to

416   have high dispersal capabilities, allowing them to re-colonise rapidly following disturbance

417   (Bell et al. 2005). Third, sheet weavers often have a high proportion of litter arthropods in

418   their diets, compared with orb weavers which target aerial prey (Harwood et al. 2003).

419   Therefore, the dry litter conditions which usually occur after fire may have supported low

420   abundances of the decomposers which are key prey items for sheet weavers (Neumann and

421   Tolhurst 1991; York 1999). Fourth, orb webs are more efficient at prey capture than sheet

422   webs (Zschokke et al. 2006), and so orb-web weavers may be able to persist with low post-

423   fire prey densities than sheet web builders. Finally, orb web builders may be better able to use

424   the post-fire vegetation than sheet web builders. Orb weavers responded positively to the

425   recovery of fern cover in burnt sites in 2013, which likely allowed their rapid recovery after

426   fire. In contrast sheet web density was negatively related to the cover of ferns. An abundance

427   of ferns may provide suitable structure for orb weavers to build webs spanning open spaces

428   (Rypstra 1983; Halaj et al. 2000), but may not provide sufficient ground-level structure for

429   sheet webs (Janetos 1982, pers. obs.).

430

431   While orb weavers, sheet weavers and tangle weavers all responded negatively to the high

432   level of herbivore activity in burnt sites in 2012, sheet weavers were the only group to show a

433   consistent negative response in 2013, when herbivore activity was lower. Many sheet webs

434   are larger than tangle and lace webs, are constructed between, rather than within, plants, and

435   are built close to the ground (e.g. web 28, Fig. 1b), all of which would make them vulnerable

436   to trampling and physical disturbance by herbivores. Further, sheet webs have lower rates of

437   prey capture than orb webs, as well as greater costs of initial web construction (Zschokke et

438   al. 2006), which may cause sheet weavers to be more likely to abandon a site after web

439   disturbance (Chmiel et al. 2000). As sheet web building spiders were more strongly affected

440   by disturbance and were slower to recover than other types of web builders, disturbance

441   caused a shift in the composition of this important predator guild. As different types of webs

442   target different types of arthropod prey (Nyffeler 1999; Harwood et al. 2003), these

443   compositional changes to the spider assemblage could have important cascading effects

444   through the arthropod food web. Understanding how the effects we observed for spiders affect

445   the rest of the arthropod community therefore remains a key area for future research.

446

447   *Conclusions*

448   Our study has shown that fire and large herbivores can interact both via vegetation-mediated

449   pathways, and via chain effects, to affect web-building spiders, an important component of

450   the forest understory fauna. In our study system, the use of prescribed fire in areas with high

451   densities of native herbivores could lead to reduced densities and altered composition of web-

452   building spiders, with potential cascading effects through arthropod food webs (Riechert and

453   Lockley 1984; Carter and Rypstra 1995). Managing the ecosystem to reduce the effects of

454   herbivores on vegetation post-fire (i.e. managing the interaction modification) may be

455   ineffective in mitigating the combined effects of disturbance, as the chain effect of fire on

456   herbivore activity also had important short-term effects on spiders. Our results reinforce the

457   importance of considering both independent and interactive effects, as well as the different

458   types of interactions, when managing disturbance regimes (Wisdom et al. 2006; Didham et al.

459   2007; Crain et al. 2008).

460

461   The differing strength of vegetation-mediated pathways between web types observed in our

462   study revealed the importance of understanding the mechanisms driving effects for both

463   predicting interactions and managing disturbance effects (Didham et al. 2007; Crain et al.

464   2008). In this system, monitoring and managing the effects of disturbance on vegetation (a

465   common approach to management of disturbances such as fire (Clarke 2008)), is unlikely to

466   detect or prevent important changes in the spider assemblage. Understanding of mechanistic

467   pathways is also essential if studies are to be used to inform management in un-studied

468   locations (Ruffell et al. 2014). To identify the mechanisms driving disturbance interactions,

469   long-term, multi-taxon studies, which simultaneously address multiple stressors, will be

470   needed (Tylianakis et al. 2008; Foster et al. 2014). When applied to such studies, analytical

471   approaches such as path analysis will give valuable insights into the importance of different

472   interaction pathways. This mechanistic understanding will be useful, not only in predicting

473   the outcomes of interacting disturbance drivers, but also in identifying appropriate actions to

474   manage their effects on biodiversity (Didham et al. 2007; Crain et al. 2008).

475

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484

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652

Tables

Table 1. Estimated coefficients (and SE) of parameters of the four different types of webs, when substituted for overall web density in the path diagram for 2012 and 2013. All models included the blocking structure of block/site as a random effect. Significance levels: ^ $P \leq 0.1$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Model term	Estimate (se)							
	Orb webs		Sheet webs		Tangle webs		Lace webs	
	2012	2013	2012	2013	2012	2013	2012	2013
Shrub cover	1.23 (0.64)^	2.87 (0.63)***	-	-	2.18 (0.77)**	-	-	-11.1 (4.0)**
Sedge cover	-	-	2.11 (0.37)***	-1.34 (0.49)**	-	-	-	-2.9 (1.9)
Fern Cover	-1.42 (0.90)	1.55 (0.41)***	-	-1.25 (0.45)**	-	-	-	-
Fire	-0.76 (0.24)**	-	-1.6 (0.23)***	-1.84 (0.29)***	-	-0.07 (0.12)	-	-
Herbivores	-0.13 (0.08)^	-	-0.19 (0.07)**	-0.19 (0.08)*	-0.17 (0.05)***	0.02 (0.05)	-	-
Fire * herbivores	-	-	-	-	-	-0.12 (0.07)	-	-

Figures

Figure 1. Examples of web types encountered in surveys. One example of each of the four groups of web types is shown: (a) web 9, an orb web, (b) web 28, a sheet web, (c) web 23, a lace web and (d) web 32, a tangle web.

Figure 2. Hypothesised causal diagram of the effects of fire and large herbivores on web-building spiders. We predicted that the effects of fire and herbivores on spiders would be largely vegetation-mediated, but may also occur via other mechanisms that operate independently of vegetation structure. We also predicted that fire may potentially interact with large herbivores by increasing herbivore activity (an interaction chain), or by modifying the effects of large herbivores (an interaction modification).

Figure 3. The effects of fire, herbivores and their interaction on web-building spider density (a,b) and richness (c,d), and the extent to which these effects were mediated by vegetation. Arrows represent causal paths between the experimental treatments (square boxes) and plant and animal responses (rounded boxes). Path coefficients are unstandardized partial regression coefficients. Dashed arrows indicate non-significant relationships, significance levels of path coefficients: ^ $P \leq 0.1$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. Herbivore activity was ln transformed when used as a predictor.

Figure 4. Site scores (linear combinations of variable scores) for axis 1 and 2 of the partial canonical correspondence analysis on the distribution of individual web types with respect to the experimental treatments (burning × herbivory × year), after blocking effects had been partialed out. Ellipses indicate one standard deviation from the centroid of each burning × year treatment combination. Numbers identify individual web types: 1-20 – orb webs, 21-24

678   lace webs, 25-29 sheet webs, 30-32 tangle webs (see Online Resource 3 for individual

679   descriptions). Overlapping web numbers are replaced with points (+).
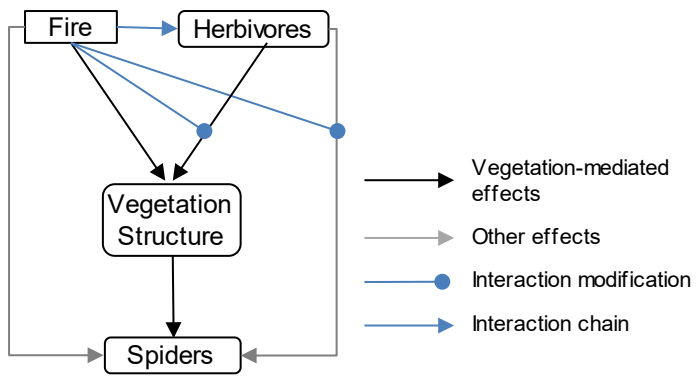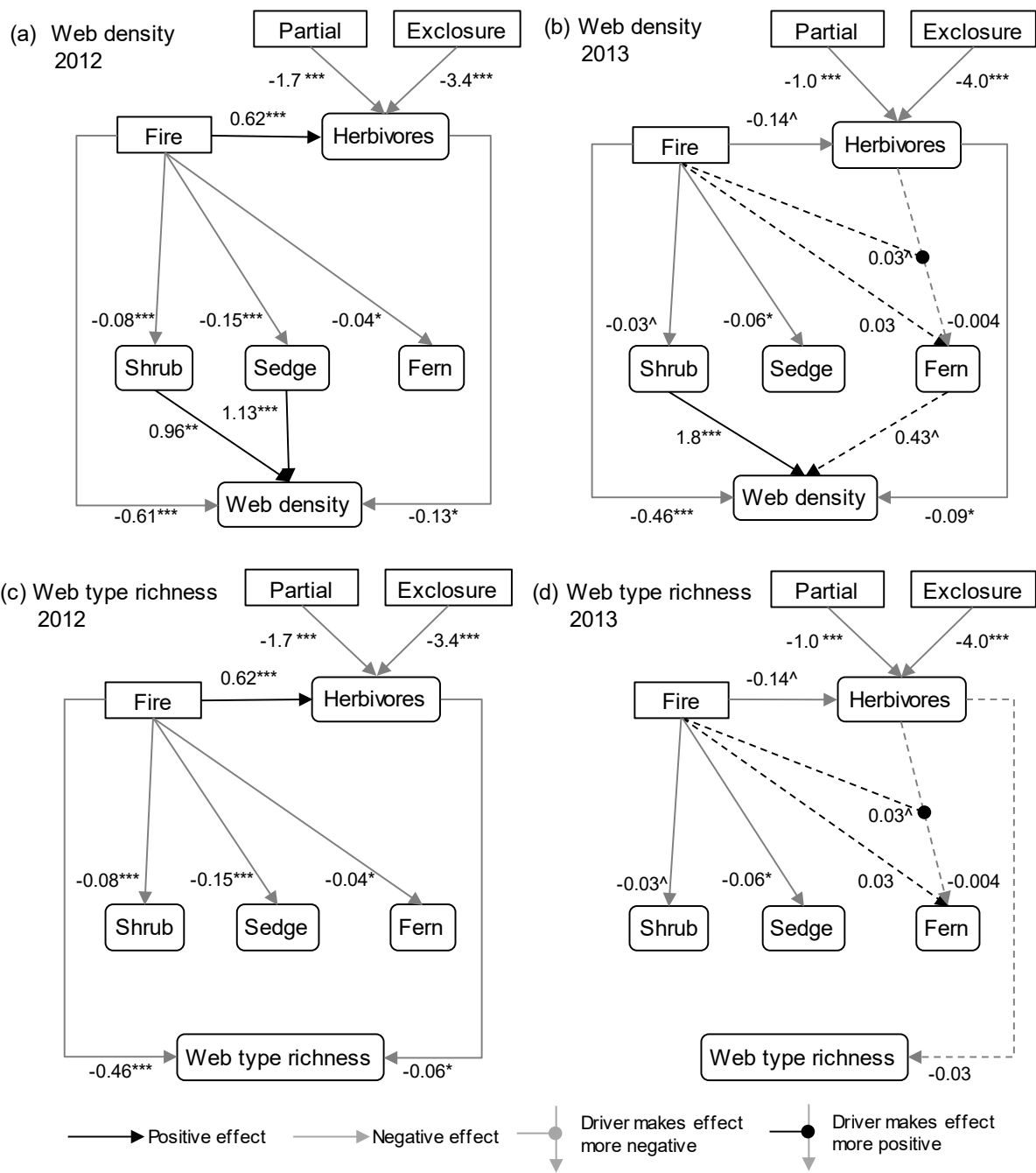
Figure 1.

Figure 2.

Figure 3.

Figure 4.