

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

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Received: 21 August 2014 / Accepted: 15 April 2015 / Published online: 3 May 2015  
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**Abstract** Altered disturbance regimes are a major driver of biodiversity loss worldwide. Maintaining or re-creating natural disturbance regimes is therefore the focus of many conservation programmes. A key challenge, however, is to understand how co-occurring disturbances interact to affect biodiversity. We experimentally tested for the interactive effects of prescribed fire and large macropod herbivores on the web-building spider assemblage of a eucalypt forest understorey and investigated the role of vegetation in mediating these effects using path analysis. Fire had strong negative effects on the density of web-building spiders, which were partly mediated by effects on vegetation structure, while negative effects of large herbivores on web density were not related to changes in vegetation. Fire amplified the effects of large herbivores on spiders, both via vegetation-mediated pathways and by increasing herbivore activity. The importance of vegetation-mediated pathways and fire–herbivore interactions differed for web density and richness and also differed between web types.

Communicated by Raphael Didham.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00442-015-3323-5) contains supplementary material, which is available to authorized users.

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Our results demonstrate that for some groups of web-building spiders, the effects of co-occurring disturbance drivers may be mostly additive, whereas for other groups, interactions between drivers can amplify disturbance effects. In our study system, the use of prescribed fire in the presence of high densities of herbivores could lead to reduced densities and altered composition of web-building spiders, with potential cascading effects through the arthropod food web. Our study highlights the importance of considering both the independent and interactive effects of disturbances, as well as the mechanisms driving their effects, in the management of disturbance regimes.

**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 re-creating appropriate disturbance regimes is therefore the focus of many conservation and restoration programmes (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 altered 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 they can occur in a number of ways. For example, patterns and intensity of herbivory can affect fuel loads and hence modify the spatial extent or intensity of fire (Wisdom et al. 2006; Kimuyu et al. 2014). Similarly, as many herbivores are attracted to the new growth available in recently burnt areas, fire can affect the spatial distribution and intensity of herbivory (Allred et al. 2011). Fire and herbivory also can interact via what is termed an interaction modification, where fire changes the mode of action or per-unit effect of herbivory on organisms (*sensu* Didham et al. 2007). For example, Royo et al. (2010) found that moderate levels of deer browsing increased understorey plant richness in burnt deciduous forest, but not in unburnt forest. Interactions between disturbance drivers can be synergistic [i.e. effects magnified (e.g. Barton et al. 2011)] or antagonistic [i.e. effects diminished or reversed (e.g. Matlack et al. 2001)], and by definition, they differ from what would be predicted from the additive effects of each driver occurring in isolation (Didham et al. 2007; Crain et al. 2008).

Most studies of fire  $\times$  large herbivore interactions have investigated effects on vegetation (e.g. Royo et al. 2010; Kerns et al. 2011), and to date only a small number of studies have investigated how these interactions affect animal assemblages. Among the latter studies, there appears to be a consistency between vegetation and animal responses; most studies which report interactive effects on animals also report interactive effects on vegetation (e.g. Matlack et al. 2001, deer mice; Bailey and Whitham 2002, arthropods), while studies which find no interactive effects on animals also find no interactive effects on vegetation (e.g. Jonas and Joern 2007, grasshoppers; Underwood and Christian 2009, ants).

Web-building spiders are a group of animals that have been found to respond to both fire (Buddle et al. 2000) and large herbivores (Miyashita et al. 2004; Warui et al. 2005), but the responses of these spiders to fire–herbivore

interactions have not previously been studied. Web-building spiders respond strongly to changes in vegetation structure (Langellotto and Denno 2004) and are the dominant invertebrate predators in terrestrial food webs (Riechert and Lockley 1984; Carter and Rypstra 1995). Therefore, disturbance-induced changes in vegetation structure may modify spider densities, which could have important consequences for trophic dynamics (Schmitz 2008). In addition, different types of web-builders may differ in their response to habitat complexity; for example, Halaj et al. (2000) found that sheet-weaving spiders, which build complex three-dimensional webs, responded more negatively to habitat simplification than orb-weaving spiders. As different types of web-builders target different prey items (Nyffeler 1999), changes in vegetation structure also may affect food web structure by altering the composition of the predator guild. As disturbance effects can cascade through ecosystems via both trophic and non-trophic pathways (Ohgushi 2005), it is important to understand the extent to which disturbance effects are mediated by changes in vegetation, and whether managing disturbances to maintain vegetation condition will also cater for the requirements of fauna (Clarke 2008).

In this study, we tested for the effects of fire, large macropod herbivores and their interaction on the web-building spider assemblage of a eucalypt forest understorey. We used a randomised, blocked experiment, combining prescribed fire and herbivore exclusion treatments, to address three questions: (1) Do large herbivores and fire interact to affect the density or richness of web-building spiders? (2) To what extent are the effects of these disturbances mediated by changes in vegetation? (3) Do these effects differ between different types of web-builders? We predicted that both fire and large herbivores would reduce web-building spider density and richness by reducing the structural complexity of vegetation, with sheet web-builders responding most strongly to vegetation simplification.

## Materials and methods

### Study site

We conducted our study in Booderee National Park (BNP), which is an approximately 6500-ha peninsula in south-eastern Australia [35°10'S, 150°40'E; see Electronic Supplementary Material (ESM) 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 programme 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 enclosure 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 the 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 enclosure) and two levels of burning treatment (burnt and unburnt) in a factorial design. Each of these six treatment combinations was replicated across four experimental blocks to give a total of 24 sites (ESM 1). We created the herbivore treatments by using enclosure fences to reduce the density of macropods within 0.125-ha ( $25 \times 25$  m) plots, to produce three treatments: full herbivory (open treatment), intermediate herbivory (partial treatment—plots were fenced but gates opened and closed at 2-month intervals to create a lower browsing pressure) and no herbivory (enclosure treatment). Enclosure fences were constructed in June 2012 using 1.1-m-tall wire fencing, which we found to be effective at excluding macropods (see section “Results”). Smaller animals were observed to move freely through the fence and as other large animals are rare in the park, the effects of enclosure fences were assumed to occur primarily via their effect on macropods. For the burning treatments, small ( $50 \times 50$  m), low-intensity burns were conducted across half of the herbivory treatment sites in August 2012.

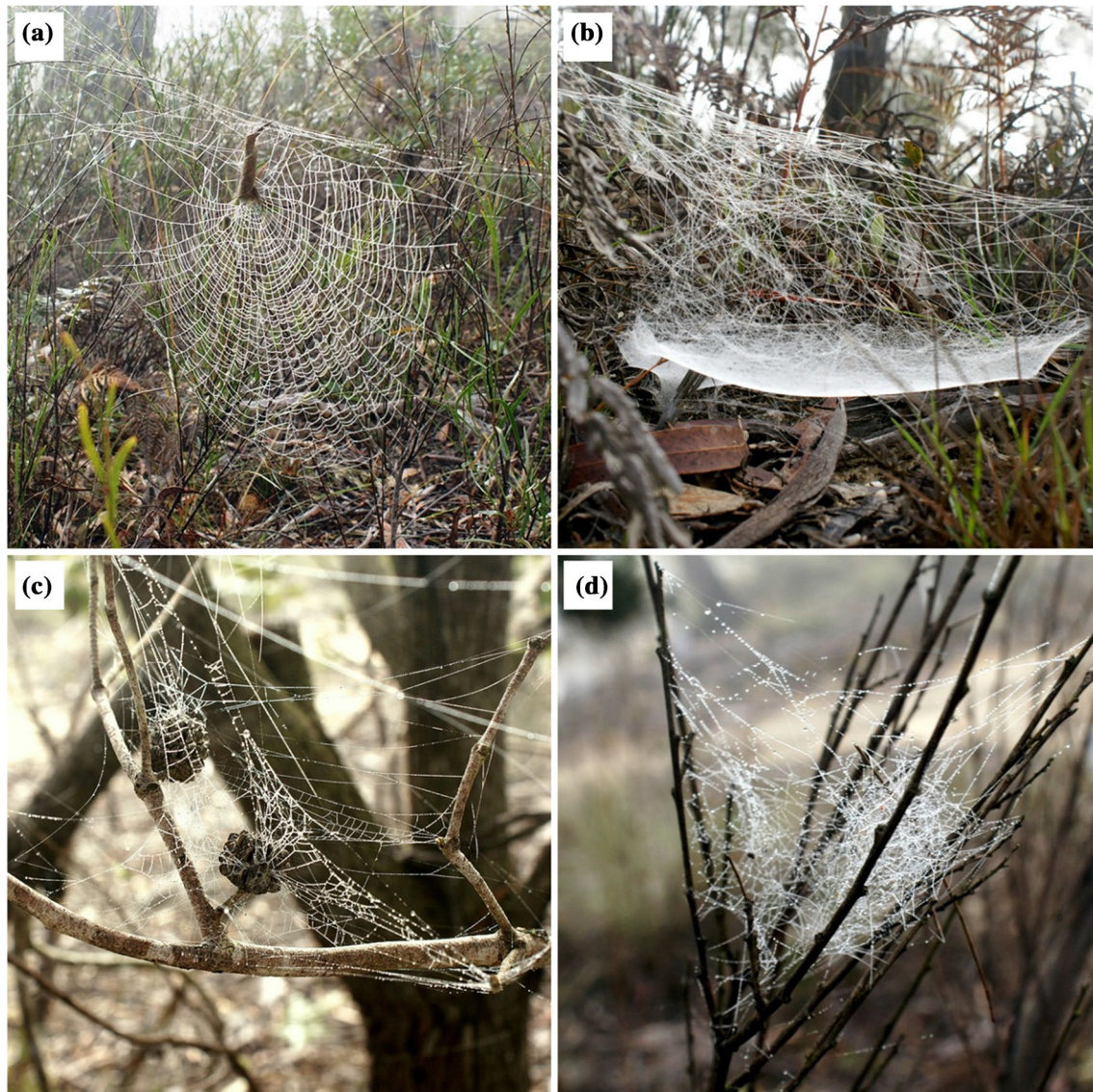
### Data collection

We sampled spider webs and vegetation within four  $3 \times 3$ -m plots within each site (one in each of the four quarters of the site). Data were collected 3 months post-fire (November 2012) and 15 months post-fire (November 2013). Plots were established at least 1.5 m from the edge of the site.

We counted spider webs as a surrogate measure for the web-building spider assemblage. This method was described and tested by Gollan et al. (2010), who found that the diversity of web types (based on web architecture) was strongly correlated with the diversity of spider genera in a site. As the richness of spider genera can be a viable surrogate for the species richness of spiders (Foord et al. 2013), this method allowed us to assess compositional and diversity responses of spiders, in addition to density responses. We used vaporised water, applied with a pressurised spray mister, to assist in locating webs, and counted and identified all spider webs within each of the four plots in each site. Each web was assigned to one of 32 web types based on their architecture, according to the key of Smith (2008) (see Fig. 1 for examples). From this categorisation, we generated measures of web density (number of webs per  $3 \times 3$ -m plot), web richness (the number of different web types per plot) and web composition (the assemblage composition of web types) for each plot. To minimise variation due to weather conditions, surveys were delayed for 48 h following strong wind or rain to allow spiders to rebuild damaged webs.

We recorded the following vegetation variables from each plot; total understorey foliage projective cover (the proportion of ground area covered by foliage held vertically above it; Specht and Morgan 1981), foliage projective cover of vascular plants by life-form, understorey height (measured at 10 evenly spaced locations per plot using the stick and foam disc method of Smit et al. (2001) with a disc diameter of 100 mm and overall weight of 4.7 g), litter depth (measured at 10 evenly spaced locations per plot) and stem density (number of live woody stems at ground level within a  $1 \times 1$ -m sub-plot). Life-forms were grouped into the broad structural categories of ferns, grasses (Poaceae), herbs (including forbs and climbers), sedges (which included grass-like perennial herbs) and shrubs (including sub-shrubs and tree seedlings).

We measured the effects of burning and the herbivory treatments on herbivore activity using scat (pellet) counts. Scat counts are a commonly used method to assess the comparative density of macropod herbivores between sites (e.g. Howland et al. 2014; Pedersen et al. 2014). We counted the number of macropod scats along two  $25 \times 2$ -m transects ( $100 \text{ m}^{-2}$ ) in each site approximately every 2 months from August 2012 to December 2013. Counts from the two transects were summed to give one count per site. Scats were removed from transect lines on each sampling event to avoid double counting. For each site, we summed the count preceding and that following the spider web counts to give an approximate index of herbivore activity in each site at the time of the web count.



**Fig. 1** Examples of web types encountered in the 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, **d** web 32—a tangle web

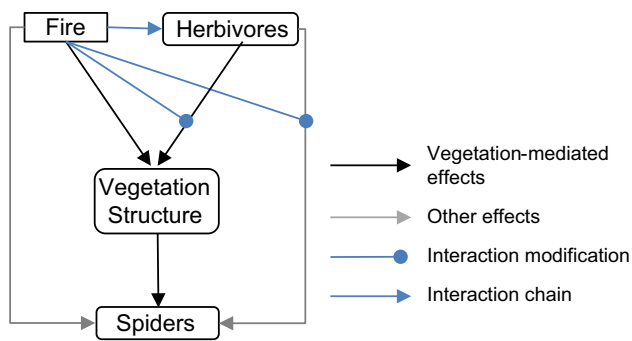
## Data analysis

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

We used generalised multi-level path models (Shiple 2009) to test the effects of fire and large herbivores on spider web density and richness, as well as the extent to which these effects were mediated by vegetation changes. Generalised multi-level path analysis uses directional-separation (d-sep) tests to assess the goodness of fit of a hypothesised causal diagram to the patterns of dependence and independence within a dataset (Shiple 2002). This analysis is based on a structural equation modelling framework but has been

generalised to accommodate hierarchical designs and non-normal response variables (Shiple 2009).

We hypothesised that the effects of fire, herbivores and their interaction on spiders would be largely vegetation-mediated, but would also occur via other mechanisms that operate independently of vegetation structure (Fig. 2). Our rationale for the construction of this causal model was as follows: fire can affect spiders through changes in vegetation structure (Brennan et al. 2006) or via other mechanisms that operate independently of vegetation (the direct fire–spider pathway in Fig. 2), such as fire-induced mortality (Bell et al. 2001) or changes in prey availability (York 1999). Similarly, large herbivores have been found to affect spiders by modifying vegetation structure (Miyashita et al.



**Fig. 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)

2004), but the former could also affect spiders through other mechanisms (the direct herbivore–spider pathway in Fig. 2), such as physical disturbance of webs (Chmiel et al. 2000) or changes to key resources such as arthropod prey (Foster et al. 2014). We also identified three possible pathways by which fire could interact with large herbivores to affect spiders: (1) a chain effect, where fire attracts herbivores to burnt areas, increasing the level of herbivore activity in burnt sites (Allred et al. 2011); (2) an interaction modification, where fire alters plant traits, modifying the effect of herbivores on vegetation (Augustine and McNaughton 1998); (3) an interaction modification, where fire increases the vulnerability of web spiders to other impacts of large herbivores (e.g. by reducing prey availability, increasing the likelihood of spiders abandoning webs after physical disturbance, Chmiel et al. 2000).

Confirmatory path analysis does not allow for reciprocal effects among variables (Shipley 2009), but a number of vegetation variables we measured were likely to be reciprocally related (for example, high grass cover would lead to low average understorey height and low stem density in a site). Therefore, we selected three vegetation variables that were not correlated with each other, but which constituted a large component of the vegetation and were correlated with other vegetation variables, to include in the path analysis (cover of shrubs, sedges and ferns). While this approach avoided reciprocity between variables, in excluding some vegetation variables, we potentially omitted variation in vegetation structure that could explain spider responses to disturbance. Therefore, we also conducted a sensitivity analysis (sensu Ruffell et al. 2014) to test whether including additional vegetation variables in our path model would increase the extent to which disturbance effects were mediated by vegetation (ESM 2). To do this, we used principal

components analysis to reduce our nine vegetation variables to seven orthogonal components, and used these as the measures of vegetation structure in our path analysis. We did not use principal components in the main analysis as principal components are less correlated than would be expected by chance, and including them in the path analysis would reduce our chance of rejecting an incorrectly specified path model (Ruffell et al. 2014).

For each of web density and web richness, we constructed two causal diagrams, one for each year of the study, with the cover of shrubs, sedges and ferns as measures of vegetation structure (each with their own node). For each of these diagrams, we tested goodness of fit using d-sep tests (Shipley 2009). Once we had tested the goodness of fit of the full path model, we simplified the model to a more parsimonious one using a backward selection approach (sensu Ruffell et al. 2014). Backward selection based on minimising the Akaike information criterion was used to simplify each sub-model within the full model (Zuur et al. 2009). Each sub-model was a mixed-effects model fitted with maximum likelihood estimation and included an endogenous variable as the response and its direct causal parents as predictors. Once all sub-models had been simplified, they were grouped back into a single path model, and the fit of this model was tested using generalised multilevel path analysis and d-sep tests as described above.

All analyses were completed using (R Core Team 2013). For the generalised linear mixed models (GLMMs) we used the `glmer` function in the package “lme4”, using a Poisson distribution and log-link function (Bates et al. 2014), while for the LMMs we used the `lme` function in the package “nlme” (Pinheiro et al. 2014). Random effects for all GLMMs and LMMs were sites within blocks (block/site). When used as predictors, count variables were ln-transformed, and continuous variables were centred on their means. Response variables were checked for overdispersion, and model residuals were inspected to verify that the data met model assumptions (Zuur et al. 2009). After deciding upon the final model for both web abundance and richness, we calculated path coefficients as the estimated slopes of the variables within each of the sub-models (Shipley 2009). Unstandardised path coefficients can be interpreted as the change in the response variable for a 1-unit change in the predictor variable (Aiken and West 1991). However, in the presence of an interaction, these path coefficients are conditional effects. Because all predictors were centred, the conditional effects can be interpreted as the effect of the predictor on the response variable when the interacting predictor is held at its mean value or, as in the case of categorical predictors (fire and herbivore enclosure treatments), at the control value (unburnt and open treatments, respectively). The interaction term indicates

the amount of change in the slope of the regression of the response on the predictor with a 1-unit change in the value of the interacting predictor.

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

To test whether different types of webs responded differently to large herbivores and fire, we estimated unstandardised regression coefficients when the density of that web type was substituted for overall web density in the full path diagram. As mentioned above, each of the individual web types was assigned to one of four groups based on similarity of web characteristics—orb webs, sheet webs, lace webs and tangle webs (Fig. 1; ESM 3). Such groupings are commonly used in studies of web-building spiders, and while there is some overlap, these categories broadly sort spiders into groups of families (e.g. Halaj et al. 2000). Orb weavers are generally in the families Araneidae, Tetragnathidae and Uloboridae, sheet weavers in the families Linyphiidae, Theridiidae and Stiphidiidae, lace weavers belong to Desidae and tangle web spinners are generally in the family Theridiidae (ESM 3). We used a separate GLMM for each web-type grouping in each year with a Poisson distribution and log-link function and random effects of block/site. Backward selection was used as described above to simplify the model for each web type in each year.

We also analysed the effect of our treatments on the composition of individual web types using partial (or conditioned) canonical correspondence analysis (CCA) in (R Core Team 2013), using the “cca” function in the package “vegan” (Oksanen et al. 2013), as well as the Bray–Curtis dissimilarity measure. This analysis allowed us to partial out the spatial variation associated with the experimental blocks, before analysing the variation in web type composition that was associated with our experimental treatments (herbivory  $\times$  fire  $\times$  year) (Borcard et al. 1992). We then ran permutation tests using the function “anova.cca” to test the significance of our constraints (treatment combinations) using 10,000 permutations of the data. To reduce the incidence of zero values in the data caused by rare web types, we pooled web counts to the site level for this analysis and excluded web types occurring at two or fewer sites.

## Results

### Density and richness of spider webs

A total of 3687 spider webs were counted across the two sampling periods, representing 28 different web types (ESM 3). Generalised multilevel path analysis indicated that herbivores and fire affected spider web density via both vegetation-mediated and other pathways, but effects on

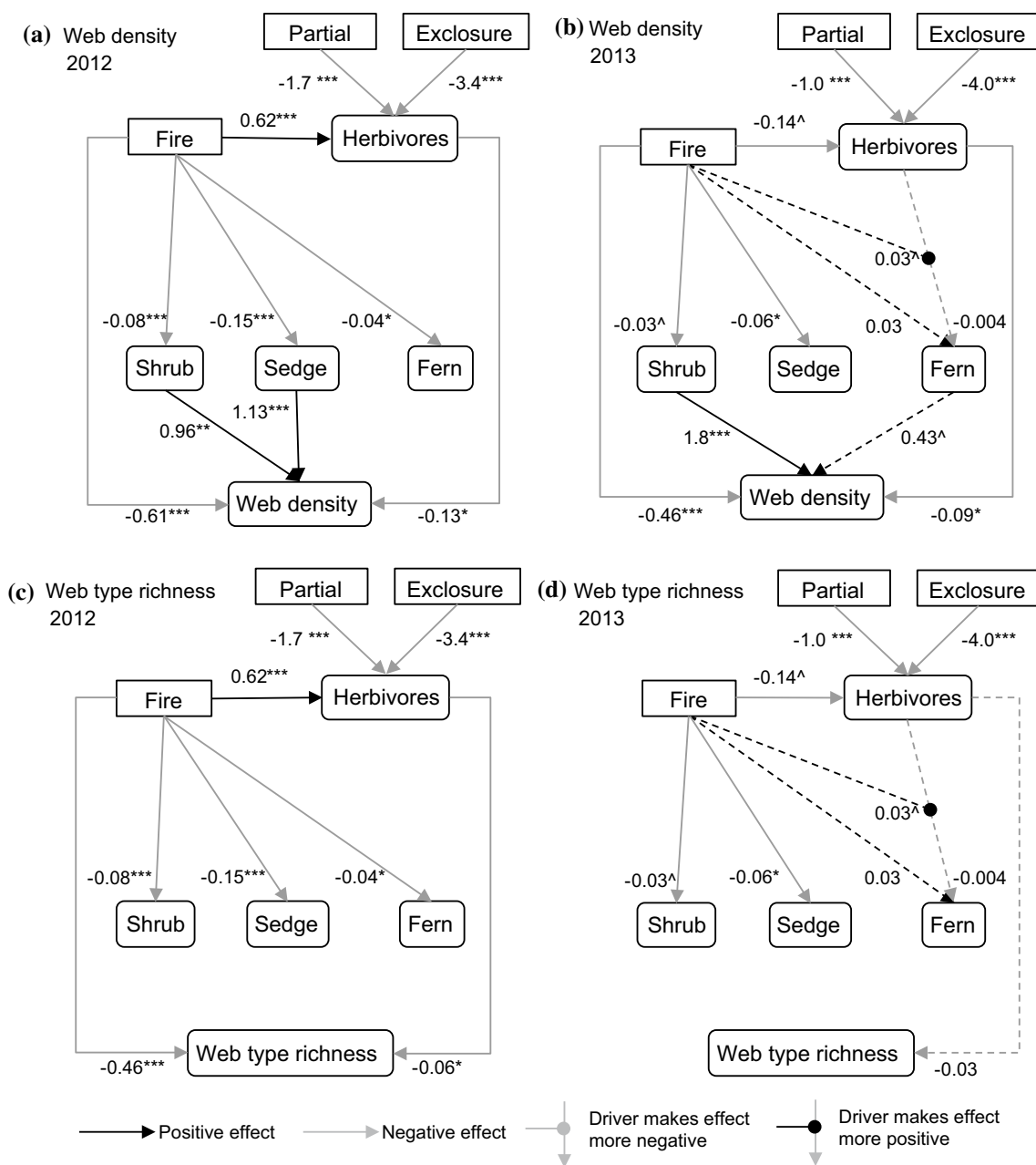
web type richness were of short duration and not mediated by changes in vegetation.

For web density, the simplified path models (2012:  $\chi^2 = 34.7$ ,  $df = 30$ ,  $P = 0.25$ ; 2013:  $\chi^2 = 29.0$ ,  $df = 28$ ,  $P = 0.41$ ) gave as good a fit as the full models (2012:  $\chi^2 = 25.9$ ,  $df = 22$ ,  $P = 0.26$ ; 2013:  $\chi^2 = 28.5$ ,  $df = 22$ ,  $P = 0.16$ ) in both years. The simplified model for web density in 2012 indicated that fire had a strong negative effect on web density, which was partly mediated by negative effects of fire on vegetation cover (Fig. 3a). In contrast, the small, but significant, negative effect of large herbivores on web density was not mediated by changes in vegetation structure. By 2013, the effects of fire on vegetation variables were weaker, which was associated with a recovery in vegetation (Fig. 3b). Both the vegetation-mediated effects and the other effects of fire on web-density were reduced in 2013 compared with 2012. While the effect of fire on shrub cover was reduced in 2013, shrub cover remained a strong determinant of web density in 2013. In 2013 there also was a marginally significant interaction between fire and herbivores, where herbivore activity was positively associated with fern cover in burnt—but not in unburnt—sites (Fig. 3b; ESM 2: Fig. 3a, b). High fern cover was associated with higher web density in the path model (Fig. 3a). As in 2012, in 2013 there was a small negative effect of herbivores on web density which was not explained by vegetation structure. Sensitivity analysis indicated that including all vegetation variables in the path model did not increase the amount of variation in web density that was explained by vegetation-mediated pathways (ESM 2).

Model fits for web-type richness were similar to those for web density, where our simplified 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 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 both years of the study. The simplified path models indicated that the effects of disturbance on web-type richness were not mediated by changes in vegetation structure (Fig. 3c, d). Fire had a short-term negative effect on web-type richness which was no longer evident in 2013 (15 months after fire). Large herbivores had a small negative effect on web-type richness in both years, and this effect was strongest in 2012, when herbivore activity was elevated in burnt sites (Fig. 3c, d). As with web density, including all vegetation variables in the path analysis did not increase the strength of vegetation-mediated effects on web type richness (ESM 2).

### *Responses of different web types*

Substituting different web-type groupings into the full model in place of web density revealed key differences in the factors affecting different types of webs. Orb web



**Fig. 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

unstandardised 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

density was higher on sites with higher shrub cover, a relationship which mediated the negative effects of fire on orb webs in both years (Table 1). In 2013, orb webs also were positively associated with higher fern cover. In contrast, while some of the effects of fire on sheet webs were vegetation-mediated, there was a strong negative effect of fire on sheet webs in both 2012 and 2013, which was not vegetation-mediated (Table 1). Sheet webs also

responded negatively to herbivore activity on both years, a response which was also not explained by changes in vegetation. Tangle webs and lace webs showed only weak or inconsistent responses to the experimental treatments, with tangle webs showing a shrub-mediated negative response to fire and a negative response to herbivore activity in 2012, but no responses to disturbance in 2013 (Table 1).

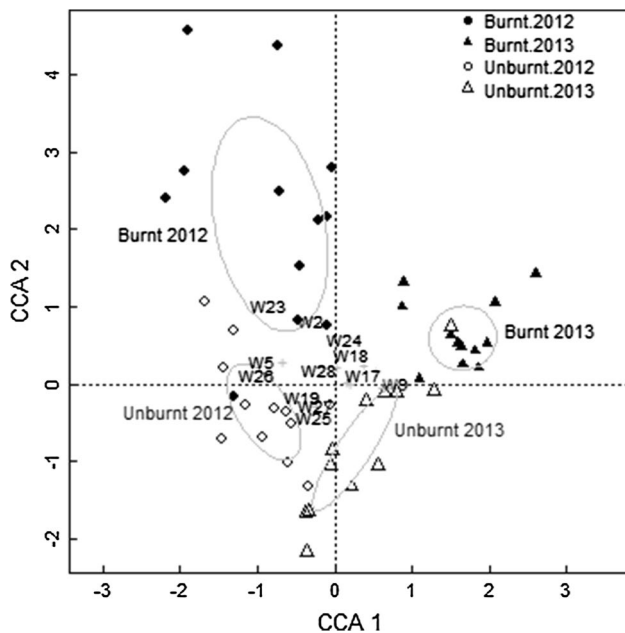
**Table 1** Estimated coefficients of parameters for the four different types of webs, when substituted for overall web density in the path diagrams for 2012 and 2013

Model term	Estimate							
	Orb webs		Sheet webs		Tangle webs		Lace webs	
	2012	2013	2012	2013	2012	2013	2012	2013
Shrub cover	1.23 (0.64) <sup>^</sup>	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) <sup>^</sup>	–	–0.19 (0.07)**	–0.19 (0.08)*	–0.17 (0.05)***	0.02 (0.05)	–	–
Fire × herbivores	–	–	–	–	–	–0.12 (0.07)	–	–

All models included the blocking structure of block/site as a random effect

Data represent the estimated coefficients with the standard error (SE) given in parenthesis

Significance levels: <sup>^</sup>  $P \leq 0.1$ ; \*  $P \leq 0.05$ ; \*\*  $P \leq .01$ ; \*\*\*  $P \leq 0.001$



**Fig. 4** Site scores (linear combinations of variable scores) for axis 1 and 2 of the partial canonical correspondence analysis (CCA) on the distribution of individual web types with respect to the experimental treatments (burning × herbivory × year), after blocking effects had been partialled 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 lace webs, 25–29 sheet webs, 30–32 tangle webs (see ESM 3 for individual descriptions). Overlapping web numbers are replaced with points (+)

Compositional differences in web types reflected the strongest effects in the analysis of web types. The first two axes of the partial CCA analysis accounted for 14.8 and 12.4 % of the variation in web-type composition, respectively. There was a significant interaction between year and burning treatment ( $P = 0.03$ , Fig. 4). There were also

significant differences in web-type composition between burning treatments ( $P < 0.01$ ) and years ( $P < 0.01$ ), but not between herbivory treatments or any of its interaction terms (all  $P > 0.05$ ). The composition of burnt sites appeared to be a sub-set of unburnt sites, with the two most common sheet webs (web 25 and 27, belonging to the families Theridiidae and Linyphiidae, respectively) strongly associated with unburnt sites (Fig. 4).

## Discussion

We used a combination of burning and herbivore exclusion treatments to test the combined effects of fire and large herbivores on web-building spiders in a forest understorey. Fire and large herbivores interacted via a chain effect, where fire increased herbivore activity, which in turn affected the web-building spider assemblage. Fire and large herbivores also interacted via vegetation-mediated pathways to affect spiders, although this interaction was only marginally significant. The extent to which vegetation structure mediated disturbance effects and the importance of interactive effects differed for web density and richness, and also between web types. Strong effects of disturbance on web-building spiders that were not mediated by vegetation indicate that managing disturbances to maintain vegetation structure is unlikely to adequately address the needs of fauna in this system.

### Fire—but not herbivore—effects on web density were vegetation-mediated

Web density was most strongly affected by fire, and much of this effect was mediated by changes in vegetation structure. The loss and subsequent recovery of vegetation after



fire (Fig. 3) was mirrored by a loss and partial recovery of spider web density, with spiders likely responding to changes in web-site availability and litter accumulation that occurred with changes in vegetation cover (Brennan et al. 2006; Podgaiski et al. 2013). However, fire also had strong effects on web density that were not explained by vegetation responses, and these effects persisted in the second year of the study (Fig. 3a, b). As our experimental burns were small (50 × 50 m), and many spiders are able to rapidly disperse via aerial ballooning (Bell et al. 2005; Langlands et al. 2011), this strong residual effect of fire is unlikely to be limited by re-colonisation ability. We suggest that other changes that can occur after fire, but which were not measured this study, such as reduced soil/litter moisture or reduced abundances of arthropod prey, may have limited the re-establishment of high densities of spiders following fire (Neumann and Tolhurst 1991; York 1999).

Fire and large herbivores interacted to increase the cover of ferns, which had a weak positive effect on web density. This interaction likely occurred due to selective browsing by herbivores allowing the less palatable bracken to dominate in burnt, browsed environments (Augustine and McNaughton 1998). This increased cover of ferns was positively associated with web density, with fern cover likely providing suitable web sites in an environment where cover of other lifeforms remained low (ESM 4). Overall, very little of the effect of large herbivores on spiders was mediated by vegetation, which contrasts with the results of a number of previous studies which attributed the observed negative effects of large herbivores on spiders to changes in vegetation structure (e.g. Miyashita et al. 2004; Warui et al. 2005).

Path analysis revealed that large herbivores negatively affected web density (and also web-type richness) via non-vegetation-mediated pathways, likely through the physical disturbance of webs. Web damage is one of the main triggers for a spider to abandon a web site (Chmiel et al. 2000). Repeated web disturbance may therefore have reduced web density by causing spiders to move out of sites with high herbivore activity or by reducing spider fitness, as spiders which move web sites must expend considerable energy in web reconstruction (Rypstra 1983; Chmiel et al. 2000) and are more vulnerable to predation when moving between sites (Lubin et al. 1993). The effect of herbivores on web density was greatest in 2012 (Fig. 3a), and this was likely due to the chain interaction between fire and herbivores, where herbivore activity was higher in burnt sites. This type of interaction has been reported in many previous studies where burning focussed herbivore activity in burnt patches (Klop et al. 2007; Allred et al. 2011). This greater level of herbivore activity in recently burnt sites would have led to greater rates of web disturbance, and hence the stronger negative effects on spiders.

### Disturbance effects on web type richness were not vegetation-mediated

In contrast to web density, the effects of disturbance on web-type richness were of short duration and were not mediated by effects on vegetation structure (Fig. 3c, d). The short-lived effect of fire suggests that spiders were able to rapidly re-colonise sites as the vegetation recovered from fire, a result that is not surprising given the small scale of the burns in our study (50 × 50 m) and the high capacity of spiders to disperse via both ground movement and aerial ballooning (Bell et al. 2005; Langlands et al. 2011). Such short-term effects of fire on spider richness are consistent with the results reported in previous studies on fire-prone environments, where post-fire recovery of spiders can be rapid (e.g. Brennan et al. 2006; Podgaiski et al. 2013). Spider richness was also directly affected by herbivore activity, where sites with higher herbivore activity had slightly (but significantly) lower web richness (Fig. 3a). This is likely due to a few web types being particularly vulnerable to physical disturbance, causing them to occur only rarely on sites with high herbivore activity.

### Responses differed between web types

Different web types showed clear differences in their response to fire, large herbivores and their interaction. Orb web weavers showed a strong post-fire recovery which was largely mediated by vegetation, while sheet web weavers showed a strong negative response to fire, with little recovery after 15 months. These differences are attributable to key differences in the ecology of these different types of web spinners. Firstly, orb weavers tend to build their webs in higher strata of the vegetation than sheet weavers (Janetos 1982) and are therefore more likely to be able to escape being killed by a low-intensity fire. Second, orb weavers tend to have high dispersal capabilities, allowing them to re-colonise rapidly following disturbance (Bell et al. 2005). Third, sheet weavers often have a high proportion of litter arthropods in their diets, compared with orb weavers which target aerial prey (Harwood et al. 2003). Therefore, the dry litter conditions which usually occur after fire may have supported low abundances of the decomposers which are key prey items for sheet weavers (Neumann and Tolhurst 1991; York 1999). Fourth, orb webs are more efficient at prey capture than sheet webs (Zschokke et al. 2006), and so orb web weavers may be able to persist with low post-fire prey densities than sheet web builders. Finally, orb web builders may be better able to use the post-fire vegetation than sheet web builders. Orb weavers responded positively to the recovery of fern cover in burnt sites in 2013, which likely allowed their rapid recovery after fire. In contrast, sheet web density was negatively related to the cover of

ferns. An abundance of ferns may provide suitable structure for orb weavers to build webs spanning open spaces (Rypstra 1983; Halaj et al. 2000), but may not provide sufficient ground-level structure for sheet webs (Janetos 1982 and personal observation).

While orb weavers, sheet weavers and tangle weavers all responded negatively to the high level of herbivore activity in burnt sites in 2012, sheet weavers were the only group to show a consistent negative response in 2013, when herbivore activity was lower. Many sheet webs are larger than tangle and lace webs, are constructed between—rather than within—plants and are built close to the ground (e.g. web 28; Fig. 1b), all characteristics which would make the former vulnerable to trampling and physical disturbance by herbivores. Further, sheet webs have lower rates of prey capture than orb webs, as well as greater costs of initial web construction (Zschokke et al. 2006), which may cause sheet weavers to be more likely to abandon a site after web disturbance (Chmiel et al. 2000). Sheet web-building spiders were more strongly affected by disturbance and were slower to recover than other types of web builders; consequently, disturbance caused a shift in the composition of this important predator guild. As different types of webs target different types of arthropod prey (Nyffeler 1999; Harwood et al. 2003), these compositional changes to the spider assemblage could have important cascading effects through the arthropod food web. Understanding how the effects we observed for spiders affect the rest of the arthropod community therefore remains a key area for future research.

## Conclusions

Our study has shown that fire and large herbivores can interact both via vegetation-mediated pathways, and via chain effects, to affect web-building spiders, an important component of the forest understorey fauna. In our study system, the use of prescribed fire in areas with high densities of native herbivores could lead to reduced densities and altered composition of web-building spiders, with potential cascading effects through arthropod food webs (Riechert and Lockley 1984; Carter and Rypstra 1995). Managing the ecosystem to reduce the effects of herbivores on vegetation post-fire (i.e. managing the interaction modification) may be ineffective in mitigating the combined effects of disturbance, as the chain effect of fire on herbivore activity also had important short-term effects on spiders. Our results reinforce the importance of considering both independent and interactive effects, as well as the different types of interactions, when managing disturbance regimes (Wisdom et al. 2006; Didham et al. 2007; Crain et al. 2008).

The differing strengths of vegetation-mediated pathways between web types observed in our study revealed the importance of understanding the mechanisms driving effects for both predicting interactions and managing disturbance effects (Didham et al. 2007; Crain et al. 2008). In this system, monitoring and managing the effects of disturbance on vegetation [a common approach to management of disturbances such as fire (Clarke 2008)] are unlikely to detect or prevent important changes in the spider assemblage. An understanding of mechanistic pathways is also essential if studies are to be used to inform management in un-studied locations (Ruffell et al. 2014). To identify the mechanisms driving disturbance interactions, long-term, multi-taxon studies, which simultaneously address multiple stressors, will be needed (Tylianakis et al. 2008; Foster et al. 2014). When applied to such studies, analytical approaches, such as path analysis, will give valuable insights into the importance of different interaction pathways. This mechanistic understanding will be useful, not only in predicting the outcomes of interacting disturbance drivers, but also in identifying appropriate actions to manage their effects on biodiversity (Didham et al. 2007; Crain et al. 2008).

**Author contribution statement** CNF, DBL, PSB and JTW designed the experiments. CNF collected data. CNF, PSB and JTW analysed the data. CNF drafted the manuscript, all authors contributed to revisions.

**Acknowledgements** Staff at Booderee National Park conducted prescribed burns. Chris Macgregor assisted with fence construction and plant identification. Many volunteers assisted with data collection. Chloe Sato provided valuable feedback on the manuscript. The Margaret Middleton Fund, The Norman Wettenhall Foundation and the Long Term Ecological Research Network provided financial support. The experiments comply with the current laws of Australia where the research was performed (ANU Animal Ethics Protocol A2012/24 and Booderee National Park Research Permit BDR12/00005).

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