

Atmospheric change causes declines in woodland arthropods and impacts specific trophic groups

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- Abstract**
- 1 Arthropod assemblages form a fundamental part of terrestrial ecosystems, underpinning ecosystem processes and services. Yet, little is known about how invertebrate communities, as a whole, respond to climatic and atmospheric changes, including predicted increases in carbon dioxide concentrations (CO₂).
 - 2 To date, woodland Free Air CO₂ Enrichment (FACE) studies have focused entirely on northern hemisphere managed plantations. We manipulated atmospheric CO₂ in a mature, native *Eucalyptus* woodland (0.15 ha, >32 000 m³) in Australia, using the *Eucalyptus* FACE ('EucFACE') facility. We used three complementary sampling methods (vacuum sampling, pitfall and sticky trapping) to record invertebrate abundances under ambient and elevated levels of CO₂ (400 versus 550 ppm).
 - 3 Based on the collection of over 83 000 invertebrates, we found significant declines in the overall abundance of ground-dwelling (14.7%) and aerial (12.9%) arthropods under elevated CO₂, with significant decreases in herbivore, omnivore, scavenger and parasitoid functional groups. Even though several groups showed varying declines in abundance, elevated CO₂ did not measurably affect community composition.
 - 4 The results of the present study indicate that atmospheric CO₂ levels predicted within the next 35 years may cause declines in arthropod abundances in *Eucalyptus* woodland. Declines found in several functional groups suggest that elevated atmospheric CO₂ has the potential to affect ecosystem processes, possibly including nutrient cycling by herbivores and omnivores, as well as biocontrol by parasitoids.

Keywords Ecosystem functioning, ecosystem processes, feeding guilds, global change, invertebrate assemblages.

Introduction

With over 1 million described species, arthropods comprise the majority of terrestrial multicellular life on Earth (Mora *et al.*, 2011; Scheffers *et al.*, 2012) and are the main players in the bulk of terrestrial plant-based food webs (Price, 2002). Aside from their impressive contribution to biodiversity, arthropod communities are important in a functional context, underpinning a variety of ecosystem processes (Wilson, 1987). For example, invertebrates perform substantial roles in nutrient cycling through the consumption and breakdown of plant material (Hunter, 2001).

Arthropod communities are shaped by complex combinations of abiotic and biotic factors, as well as biotic interactions,

including trophic associations (Polis, 1998), which are themselves sensitive to environmental change (Tylianakis *et al.*, 2008). Consequently, perturbations occurring in either the biotic or abiotic environment have the capacity to alter the structure of communities, as well as the interactions occurring between the species that form them, by virtue of the fact that not all species in a system will respond to change in the same way (Sanders *et al.*, 2003; Raffaelli, 2004; Pockock *et al.*, 2012).

Although previous community-level studies have shown that the responses of different taxa to environmental change can be highly individualistic and species-specific (Altermatt, 2003; Sanders *et al.*, 2004), invertebrate taxa sharing the same feeding strategy are likely to be affected by change in similar ways to each other, allowing some generalizations to be made (Altermatt, 2003; Hillstrom & Lindroth, 2008). For example, sap-feeding

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invertebrates may be positively affected by changes in the quality of their food plants under elevated CO₂ (Bezemer & Jones, 1998). Conversely, folivores, by virtue of their different feeding habits, tend to have reduced performance under elevated CO₂ (Stiling *et al.*, 2003; Stiling & Cornelissen, 2007), leading to reductions in folivory (Hamilton *et al.*, 2004; Knepp *et al.*, 2005). Organisms at higher trophic levels, including predators, may be more sensitive to environmental perturbations, perhaps as a result of higher metabolic costs and their dependency on the responses of organisms at lower trophic levels (Voigt *et al.*, 2003; Hance *et al.*, 2007). Moreover, specialist species such as endoparasitoid wasps may be more at risk from changes to the environment than generalists because they are dependent on a smaller group of hosts and therefore might be disproportionately affected if they cannot utilize alternative hosts (Hance *et al.*, 2007; Vanbergen *et al.*, 2010).

The concentration of carbon dioxide (CO₂) in the atmosphere now exceeds the range the Earth has seen in the last 800 000 years (IPCC, 2013) and, as such, is considered as an abiotic perturbation with the potential to alter ecological communities. Numerous studies have reported CO₂-induced changes in plant biomass and morphology (Pritchard *et al.*, 1999; Stiling & Cornelissen, 2007; Zhu *et al.*, 2016), as well as altered botanical composition (Vasseur & Potvin, 1998), coupled with reductions in plant quality (Robinson *et al.*, 2012). Elevated CO₂-related changes in plants could therefore have crucial implications for invertebrate herbivores (Hentley *et al.*, 2014) and their arthropod consumers, as well as the ecosystems that these communities support (Tylianakis *et al.*, 2008). Despite their recognized importance, relatively little is known about how invertebrate communities, as a whole, will respond to climatic and atmospheric changes (Jamieson *et al.*, 2012; Facey *et al.*, 2014). To adequately predict the consequences of climatic and atmospheric change on ecosystems, large scale experiments considering community-level responses to change are necessary, complementing work conducted in more controlled settings (Stiling *et al.*, 2003; Facey *et al.*, 2014). Free Air CO₂ Enrichment (FACE) experiments have been invaluable for assessing the impacts of elevated CO₂ for plants and invertebrates in temperate forest systems (Hamilton *et al.*, 2004; Knepp *et al.*, 2005; Stiling & Cornelissen, 2007; Couture & Lindroth, 2012; Couture *et al.*, 2015; Facey & Gherlenda, 2016).

Thus far, however, forest FACE invertebrate community studies have been limited to experiments on relatively young, managed plantation trees in the northern hemisphere. Gaining an adequate understanding of the responses of the terrestrial biosphere to elevated CO₂ will require greater habitat representation among the next generation of FACE experiments (Ainsworth & Long, 2005; Facey & Gherlenda, 2016; Norby *et al.*, 2016). The present study redresses this gap two ways. First, it is the first field-based experiment investigating arthropod responses to atmospheric change in a southern hemisphere forest system, allowing comparisons and generalizations to be made across studies in other systems. Second, it is the first experiment established in native mature natural woodland. The site consists of *Eucalyptus* woodland, which is the second most dominant habitat type in Australia after grasslands. This habitat is estimated to cover over 890 000 km² of the continent (Department of the Environment and Water Resources, 2007). Furthermore, the

Eucalyptus genus is the most widely planted hardwood globally (Frew *et al.*, 2013), yet information concerning the responses of *Eucalyptus* communities to climatic and atmospheric change is scant as a result of a lack of field studies.

The present study aimed to characterize the arthropod community occurring in this woodland study system and to assess the extent to which this community may be affected by rising atmospheric CO₂ concentrations. We used a variety of sampling methods applied from ground-level to the forest canopy to obtain representative samples of the invertebrate community. We focused on how different functional groups (i.e. feeding guilds) responded to elevated CO₂ (i.e. if specialists such as parasitoids were more sensitive than generalist predator groups).

Given the generally negative effects of elevated CO₂ on plant quality, we predicted that (i) folivorous herbivores would decline in abundance under elevated CO₂, whereas those in different feeding guilds including sap-suckers would be positively affected by alterations in food quality; (ii) arthropods at higher trophic levels would show greater declines than groups from lower trophic levels; (iii) specialized taxa (e.g. parasitoids) would be more strongly affected by CO₂ manipulation than generalists; and (iv) as a result of changes in the abundances of different taxa, invertebrate community composition would be altered under elevated CO₂ conditions.

Materials and methods

Experimental site

The present study was carried out at the *Eucalyptus* Free-Air CO₂ Enrichment ('EucFACE') site in western Sydney, Australia (33°36'59"S, 150°44'17"E), as described in Duursma *et al.* (2016). In brief, the site consists of approximately 15 ha within a 167-ha tract of mature, native Cumberland Plain woodland, dominated by *E. tereticornis* (over 90% coverage). There are six 25 m diameter ring arrays; from September 2012 onward, the CO₂ levels have been manipulated in three randomly selected rings [ambient + 150 ppm, corresponding to the concentration predicted by the middle of this century under the emission scenario A1F1 (IPCC, 2007)], with the other three rings receiving ambient CO₂ levels. Diluted CO₂ or air (in ambient plots) is released into the vegetation within the ring from valves in the vertical vent pipes around the outside edge of the ring during the day time.

Invertebrate collections

We collected invertebrates using three different methods across seasons to obtain a broad, representative sample of the arthropod community occupying different niches. Pitfall traps were used to sample ground-dwelling arthropods, with suction sampling to capture invertebrates from understory vegetation and sticky traps to sample aerial (canopy) invertebrates. Suction sampling is a proven quantitative technique for sampling invertebrate populations (Brook *et al.*, 2008). Sticky and pitfall trapping allow for relative comparisons of invertebrate abundance between CO₂ treatments, within sampling method (Buntin, 1993; Woodcock, 2005). Pitfall traps were first used in November 2013; pitfall

and suction sampling was then carried out quarterly from January 2014 to January 2015 (six pitfall campaigns, five suction sampling campaigns). Sticky trapping was carried out six times throughout the experiment, on a monthly basis, between the end of September and the start of December during 2013 and 2014, when most flying arthropods would be active. In each of the three niche-types, sampling was carried out in fixed locations across all sampling dates.

Ground-dwelling arthropods (pitfall sampling). Within each ring, two locations were selected at random on the woodland floor. In each of these, a 500-mL plastic pot (diameter 9 cm) was buried flush with the soil level. Traps were left dry and open for 1 week prior to the initial sampling period in November 2013 to account for digging-in effects (Woodcock, 2005). Thereafter, traps were active for 2 weeks at the beginning of each of the six sampling periods; for this, they were filled to approximately one third full with water, with a droplet of scentless detergent to break surface tension. A piece of chicken-wire mesh was pegged over the mouth of the trap to prevent by-catch of nontarget mammals and reptiles (Woodcock, 2005), while only potentially excluding the very largest of beetle species. A transparent plastic roof was suspended above each trap for protection during rain events. A lid was placed over each trap in between sampling events.

Understorey arthropods (suction sampling). Two plots (1 × 1 m²) (selected at random) within each ring were used on the woodland floor. A petrol-powered vacuum 'G-Vac' device (SH 86C; Stihl AG & Co. KG, Germany) (Bell *et al.*, 2002), fitted with an organza bag to capture dislodged debris and invertebrates, was passed over the understorey herbaceous vegetation in a zig-zag pattern for 20 s during each sampling event. Sampling was carried out when vegetation was dry to the touch.

Aerial arthropods (sticky trapping). In each of the six rings, 16 yellow card sticky traps (Bugs for Bugs, Mundubbera, Australia) were secured to the central scaffold at four height intervals (2, 5, 10 and 20 m) facing each compass direction. This allowed a full range of arthropods occurring at different strata to be sampled. Traps were left in place for 1 week prior to collection.

Identification and processing. Arthropods were counted and identified under a dissecting microscope (SZ51; Olympus, Japan) to at least Order level (except for three groups taken to Subclass only: Acari, Collembola and Chilognatha) and, in some cases, Family level, to more reliably determine functional guild in as many cases as possible (Hamilton *et al.*, 2012) (a full list of identified groups and guild assignments is provided in the Supporting information, Table S1). Psyllidae (Hemiptera) were excluded from the study because they are the focus of a concurrent study occurring at the site (Gherlenda *et al.*, 2016). Better estimations of the energy flow occurring through different trophic levels within communities can be achieved through the assessment of biomass (Saint-Germain *et al.*, 2007). Thus, after abundances were taken, pitfall and suction samples were dried at

60 °C to constant weight before weighing using a microbalance with an accuracy of 1 µg (model XP6; Mettler-Toledo GmbH, Germany).

Statistical analysis

All statistical analyses were performed using R, version 3.2.0 (R Core Team, 2015). To avoid pseudoreplication, the subplots in each ring were pooled for all analyses, giving one sample per ring, per time point ($n = 6$; 36 plot-time samples in total for pitfall and sticky traps, 30 for suction). Separate analyses were carried out on data from each of the three sampling methods to enable assessment of the effect of elevated CO₂ on the arthropod communities in the different niches.

Abundance analysis. Total arthropod abundance, as well as the abundance of individual taxa and functional groups, was analyzed first using generalized linear mixed models (GLMM) with Poisson error distributions using 'glmer'. Models contained CO₂ treatment as a fixed effect and date sampled as a random factor. Model fit was verified by inspection of residual plots and overdispersion parameters from the 'overdisp_fun' function (specified at <http://glmm.wikidot.com/faq>). In the majority of cases, data were overdispersed and so models were refitted using the negative binomial extension of GLMM, 'glmer.nb', in 'lme4' (Bates *et al.*, 2014). The significance of CO₂ treatment as a predictor was assessed using likelihood ratio tests between the full model and a reduced model without the fixed effect of CO₂ treatment (Faraway, 2006).

Orders that were poorly represented (i.e. found in fewer than 10% of samples or had fewer than 50 individuals) were removed from the individual Order analyses. Sanguivores were also not analyzed as a result of the small sample size. In one case (aerial Thysanoptera), a negative binomial model did not adequately fit the data and so an observation-level random effect was included in the model to account for overdispersion (Harrison, 2014).

Biomass analysis. Similar to the abundance analyses, arthropod biomass data (in terms of total sample biomass, not individual biomass) were analyzed for separate functional guilds and Orders, with the same poorly-represented groups removed. Total arthropod biomass across all groups was also analyzed for each sampling method. Data were modelled using linear mixed models (LMM) with the 'lmer' function, with CO₂ treatment as a fixed effect and date sampled as a random factor. In all cases, biomass was rank transformed prior to analysis to meet assumptions of homoscedasticity of residuals. For groups with tied ranks (where zeros were present in the variable), the analysis was iterated 1000 times on retransformed data with randomly broken ties to attain stable average *P* and chi-squared values.

Community composition. To assess the effects of elevated CO₂ on overall community composition, we used permutational multivariate analysis of variance (PERMANOVA) coupled with non-metric multidimensional scaling (NMDS) to visualize

the data (Hillstrom *et al.*, 2014), with the package ‘vegan’ (‘adonis’ and ‘metaMDS’ functions, Oksanen *et al.*, 2015). For community-level analyses, poorly-represented taxa were included. PERMANOVA was carried out on the three niche-types separately, with the fixed effect of CO₂ treatment, on both functional guild and Order-level abundance data. Analyses were carried out on Bray–Curtis dissimilarity matrices, permuted 999 times. The number of dimensions, *k*, used in each NMDS analysis was determined by visual inspection of stress plots and stress values. Stress values were <0.2 across multiple runs for all analyses.

As a result of the low replication inherent in FACE designs, we set a critical *P* value of 0.1 to avoid type II errors, as recommended by Lindroth and Raffa (2016) and consistent with previous studies of this type (Sanders *et al.*, 2004; Villalpando *et al.*, 2009; Hamilton *et al.*, 2012).

Results

A total of 83 528 arthropods from 19 different taxa (16 Orders and three Subclasses) were collected and identified during the experiment (14 459 ground-dwelling, 19 153 understorey and 49 916 aerial arthropods; see Supporting information, Table S1). Total arthropod abundance was lower in elevated CO₂ in all three of the sampled niches; this effect was significant for ground-dwelling and aerial invertebrates (Table 1), which decreased by 14.7% and 12.9%, respectively (ground-dwelling total individuals, mean ± SD: ambient 7803 ± 280.17, elevated 6656 ± 280.11; understorey: ambient 11 362 ± 792.56, elevated 7791 ± 437.55; aerial: ambient 26 672 ± 384.29, elevated 23 244 ± 403.32) (Table 1). Across all groups, total arthropod biomass did not significantly differ between CO₂ treatments (*P* > 0.1) (Table 1).

Ground-dwelling arthropods

The abundance of ground-dwelling chewing herbivores was significantly reduced under elevated CO₂ conditions (Fig. 1b and Table 2), although their biomass remained unchanged (*P* > 0.1). Detritivores and omnivores showed a decrease in biomass under elevated CO₂ but did not show measurable declines in abundance (Fig. 1a,b, Table 2).

The abundances of ground-dwelling Hymenoptera, Isopoda and Orthoptera were significantly reduced under elevated CO₂ (Fig. 1c,d and Table 1), with the latter two groups also showing decreases in biomass (Fig. 1c,d and Table 1). Acarina showed an increase in biomass (Fig. 1c and Table 1), with no evidence of change in abundance (*P* > 0.1).

Understorey arthropods

Declines were also seen in the abundance of certain groups in the understorey, although different groups were affected. Omnivores showed a significant decrease in average abundance and this was coupled with a marked decline in population biomass (Fig. 2 and Table 2). None of the other feeding guilds showed a significant response to elevated CO₂ in this niche (*P* > 0.1).

At Order level, Coleoptera were significantly decreased in abundance under elevated CO₂, although their biomass was not significantly different from ambient CO₂ (Fig. 2d and Table 1). Although the data for understorey Isopoda could not be accurately modelled, this group appeared to show a trend towards lower abundance under elevated CO₂, as found for the same group in ground-dwelling samples (compare Figs 2d and 1c).

Aerial arthropods

Elevated CO₂ generally resulted in decreased abundances of aerial arthropods. At feeding guild level, both scavengers and parasitoids experienced a significant decline in abundance (Fig. 3a,b and Table 2). At Order level, significant decreases were seen for four of the recorded taxa; Hymenoptera, Neuroptera, Acari and Collembola (Fig. 3c,d and Table 1). However, in contrast to these declines, aerial Psocoptera showed a significant increase in abundance under elevated CO₂ (Fig. 3d and Table 1).

Community composition

Although elevated CO₂ resulted in significant changes in the abundances of several different feeding guilds and Orders (summarized in Fig. 4), this did not significantly affect the community composition occurring in any of the three niche types, either in terms of functional guild or Order composition (see Supporting Information, Fig. S1 and Table S2).

Discussion

Elevated CO₂ caused widespread changes in arthropod abundance and biomass

To our knowledge, this is the first study of its kind to find significant declines in the abundance of a wide range of woodland arthropods under elevated CO₂; out of the 21 taxonomic and functional groups that satisfied our analysis criteria, over half (11 groups) experienced significant declines in abundance. Previous work on soil micro-arthropod communities has reported similar decreases (Hansen *et al.*, 2001; Loranger *et al.*, 2004), yet most previous studies looking at aboveground invertebrate communities have revealed no significant changes in abundance as a result of elevated CO₂ (Sanders *et al.*, 2004; Hillstrom & Lindroth, 2008; Hillstrom *et al.*, 2014).

The declines in total arthropod abundance did not translate into overall declines in total biomass, although this is not unexpected because the two metrics are known to not necessarily correlate well (Saint-Germain *et al.*, 2007). However, we did find significant changes in arthropod biomass at the individual functional group/Order level, five out of six of which were negative. This reinforces the findings from the abundance analyses and indicates the potential for changes in ecosystem functioning. Reductions in biomass indicate the loss of larger bodied organisms, especially in groups that did not see a corresponding reduction in abundance, such as ground-dwelling detritivores and omnivores. Larger organisms are likely to be of greater importance for trophic interactions occurring within the ecosystem

Table 1 Results from likelihood ratio tests performed on generalized linear mixed models (GLMM) (abundance) and linear mixed models (LMM) (rank-transformed biomass) with and without the fixed effect of CO₂ treatment, with the abundance or biomass of each of the groups collected over the course of the experiment as the dependent variable

Group	Niche type	Abundance		Biomass	
		χ^2 (d.f. = 1)	<i>P</i>	χ^2 (d.f. = 1)	<i>P</i>
Overall	Ground-dwelling	3.442	0.064	0.190	0.66
	Understorey	2.412	0.12	0.087	0.77
	Aerial	3.878	0.049	—	—
Coleoptera	Ground-dwelling	1.122	0.29	0.219	0.64
	Understorey	3.129	0.077	2.540	0.11
	Aerial	0.493	0.48	—	—
Diptera	Ground-dwelling	0.443	0.51	0.623	0.43
	Understorey	2.002	0.16	2.005	0.16
	Aerial	0.194	0.66	—	—
Araneae	Ground-dwelling	1.546	0.21	0.000	1.00
	Understorey	0.023	0.88	0.338	0.56
	Aerial	0.658	0.42	—	—
Acarina	Ground-dwelling	0.085	0.77	2.783	0.095
	Understorey	1.854	0.17	2.624	0.11
	Aerial	16.486	<0.001	—	—
Hemiptera	Ground-dwelling	0.047	0.83	0.046	0.83
	Understorey	1.188	0.28	0.163	0.69
	Aerial	1.989	0.16	—	—
Hymenoptera	Ground-dwelling	4.646	0.031	0.785	0.38
	Understorey	2.580	0.11	0.941	0.33
	Aerial	3.441	0.064	—	—
Thysanoptera	Understorey	0.367	0.55	0.013	0.91
	Aerial	2.418	0.12	—	—
Orthoptera	Ground-dwelling	11.347	<0.001	5.356	0.021
Isopoda	Ground-dwelling	9.010	0.0027	14.469	<0.001
	Understorey	^a	^a	^a	^a
Blattodea	Understorey	0.205	0.65	0.141	0.71
Collembola	Ground-dwelling	0.824	0.36	0.081	0.78
	Understorey	0.148	0.70	0.014	0.91
	Aerial	2.708	0.10	—	—
Lepidoptera	Aerial	1.190	0.28	—	—
Psocoptera	Aerial	26.389	<0.001	—	—
Neuroptera	Aerial	5.982	0.014	—	—

Significant *P* values are shown in bold ($\alpha = 0.1$).

^aDenotes that, for this taxa, strong variation in the data made analysis unreliable. Those groups with sample sizes too small for analysis in all three niches are not shown.

(Saint-Germain *et al.*, 2007) because energy flow through trophic levels is tied to body mass (Brown *et al.*, 2004). Conversely, in cases where declines in abundance were not reflected by biomass data (e.g. chewing herbivores and Coleoptera), there may be a greater proportion of larger-bodied individuals occurring under elevated CO₂ compared with ambient conditions, suggesting that ecological functionality may be more likely to be maintained for these groups, despite population declines.

Elevated CO₂ had variable effects on feeding guilds

We predicted that chewing herbivores would suffer a decrease in abundance under elevated CO₂ compared with other feeding guilds employing different feeding methods, such as sap-suckers, which may even stand to benefit from such conditions via changes in phloem chemistry (Bezemer & Jones, 1998). We found significant reductions in the abundances of

ground-dwelling chewing herbivores, although this effect was not seen in either the understorey or aerial niches. We found declines in the abundance and biomass of omnivorous taxa in the understorey and at ground level; these animals will also have partially plant-based diets. These findings are consistent with those reported in other studies of this type (Stiling *et al.*, 2002, 2003; Hamilton *et al.*, 2012) and could indicate a reduction in herbivore-pressure and herbivore-mediated nutrient cycling in the system.

Given the decline in parasitoids and stable levels of other predatory taxa, the reduction in the abundance of herbivorous taxa at ground and understorey level is unlikely to be explained by changes in top-down regulation. Our prediction that herbivore abundance would be reduced under elevated CO₂ conditions was based on the widely reported decrease in plant resource quality observed elsewhere under the same conditions (Robinson *et al.*, 2012). However, work carried out at the EucFACE site concurrently with the present study has revealed no change

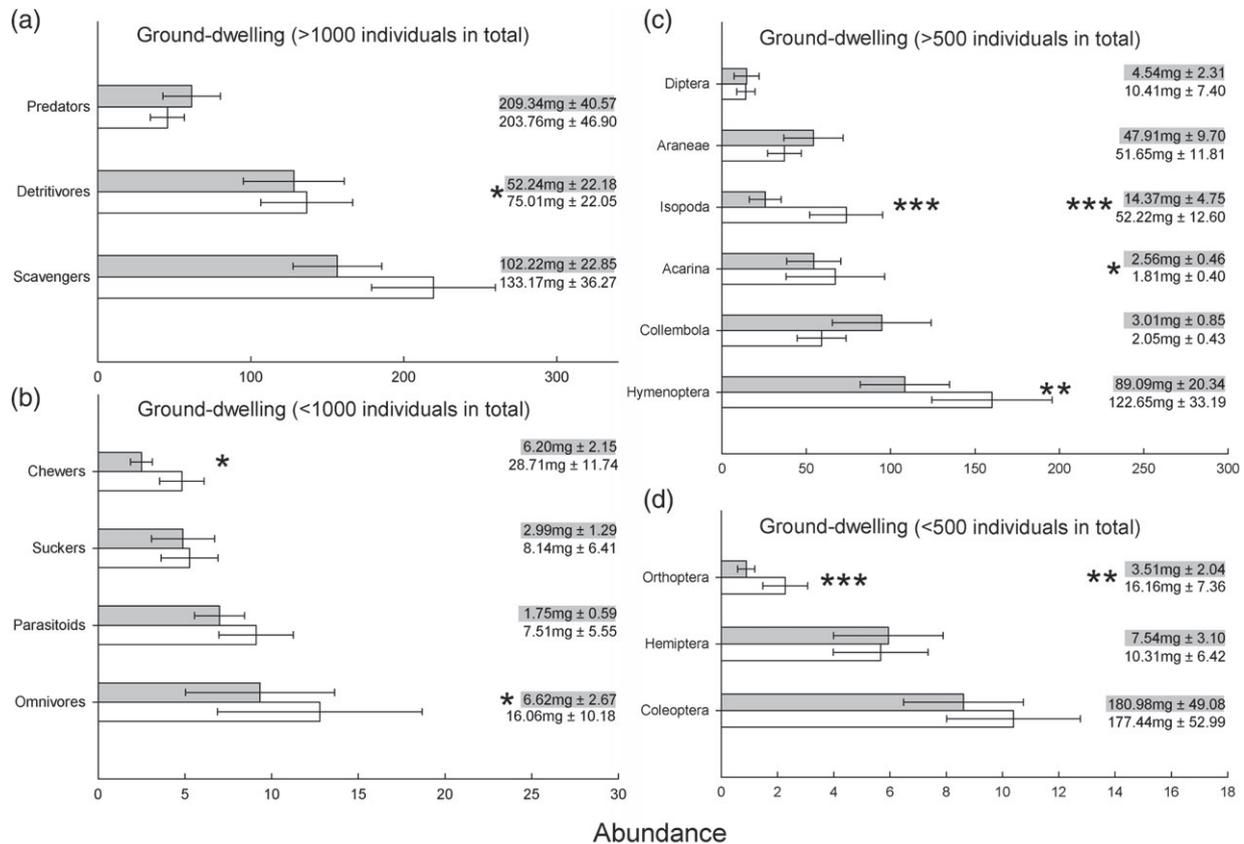


Figure 1 Mean abundance of different functional guilds (a, b) and taxonomic groups (c, d) of ground-dwelling arthropods, split by CO₂ treatment (across all dates). Ambient samples are shown with white bars; those from elevated conditions shown are in grey. To the right of each bar, total mean ± SE biomass is shown for the corresponding group. Significant differences [from generalized liner mixed models (GLMM) (abundance) and linear mixed models (LMM) (biomass)] (Tables 1 and 2) are indicated by asterisks (**P* < 0.1, ***P* < 0.05, ****P* < 0.01). Error bars show the SE.

in various plant quality metrics, including canopy C:N ratios (Gherlenda *et al.*, 2015) and leaf area index (Duursma *et al.*, 2016). This is not entirely unexpected; Hamilton *et al.* (2012) also observed changes in arthropod populations under elevated conditions with no accompanying alteration in C:N ratios of plant tissues. One as yet undetermined plant-mediated mechanism for these declines could be alterations in plant secondary chemistry occurring under elevated CO₂, which have been reported in other studies and are known to affect invertebrate herbivores (Robinson *et al.*, 2012). Further work is needed to link the observed changes in invertebrate abundance with plant quality changes occurring in the woodland at EucFACE.

In contrast to the declines in chewing herbivores and omnivores, sap-sucking herbivores (Order Hemiptera) did not decline in any of the three niche types. However, work by other researchers at EucFACE reported a decrease in the abundance of three species of psyllid under elevated CO₂ (Gherlenda *et al.*, 2016). Although controlled environment studies tend to report an enhanced abundance and performance of sap-feeders, linked with CO₂-induced changes in phloem and sap chemistry (Bezemer & Jones, 1998), these often do not consider natural enemies. Hentley *et al.* (2014) showed that aphid populations under elevated CO₂ were suppressed to population levels at ambient

CO₂ when a predatory ladybird was also included in the experiment. On the other hand, Percy *et al.* (2002) found that the severity of aphid infestations on aspen was increased under long-term CO₂ exposure, as a result of asynchrony between aphid and natural enemy populations. In the present study, given the significant reduction found in parasitoid abundance in the canopy, there is the potential for reduced top-down regulation of sap-feeding insects in the future, and thus population growth. Such growth could increase herbivory levels under elevated CO₂, as found by Couture *et al.* (2015). Long-term monitoring would be needed at the EucFACE experimental site to substantiate this. Presently, however, the decline in chewing herbivores and omnivores and comparable levels of (non-psyllid) Hemiptera suggests that herbivory will decline in *Eucalyptus* woodland as emissions of CO₂ rise, as reported for other northern hemisphere systems (Hamilton *et al.*, 2004; Knepp *et al.*, 2005).

We also found a significant decline in the abundance of scavengers in the canopy, likely driven by the significant decrease in the abundance of mites (Acari) under elevated CO₂. The significant reduction in mites is consistent with previous studies (Hansen *et al.*, 2001; Loranger *et al.*, 2004). However, the same decline was not seen in the ground-dwelling and understorey

Table 2 Results from likelihood ratio tests performed on generalized liner mixed models (GLMM) (abundance) and linear mixed models (LMM) (rank-transformed biomass) with and without the fixed effect of CO₂ treatment, with the abundance of the arthropods in each of the recognized guilds as the dependent variable

Group	Niche type	Abundance		Biomass	
		χ^2 (d.f. = 1)	<i>P</i>	χ^2 (d.f. = 1)	<i>P</i>
Scavengers	Ground-dwelling	2.661	0.10	0.003	0.96
	Understorey	2.619	0.11	1.709	0.19
	Aerial	9.961	0.0016	—	—
Detritivores	Ground-dwelling	1.712	0.19	3.379	0.066
	Understorey	0.116	0.73	1.005	0.32
	Aerial	<0.001	0.98	—	—
Omnivores	Ground-dwelling	1.643	0.11	3.481	0.062
	Understorey	3.448	0.063	8.471	0.0036
	Aerial	1.303	0.25	—	—
Chewing herbivores	Ground-dwelling	2.845	0.092	1.419	0.24
	Understorey	0.091	0.76	0.323	0.57
	Aerial	0.252	0.62	—	—
Sucking herbivores	Ground-dwelling	0.751	0.39	0.800	0.38
	Understorey	1.095	0.30	0.078	0.78
	Aerial	1.989	0.16	—	—
Predators	Ground-dwelling	0.597	0.44	0.069	0.79
	Understorey	0.890	0.35	0.149	0.70
	Aerial	0.535	0.47	—	—
Parasitoids	Ground-dwelling	0.305	0.58	0.296	0.59
	Understorey	0.026	0.87	0.012	0.91
	Aerial	3.422	0.064	—	—

Significant *P* values are shown in bold.

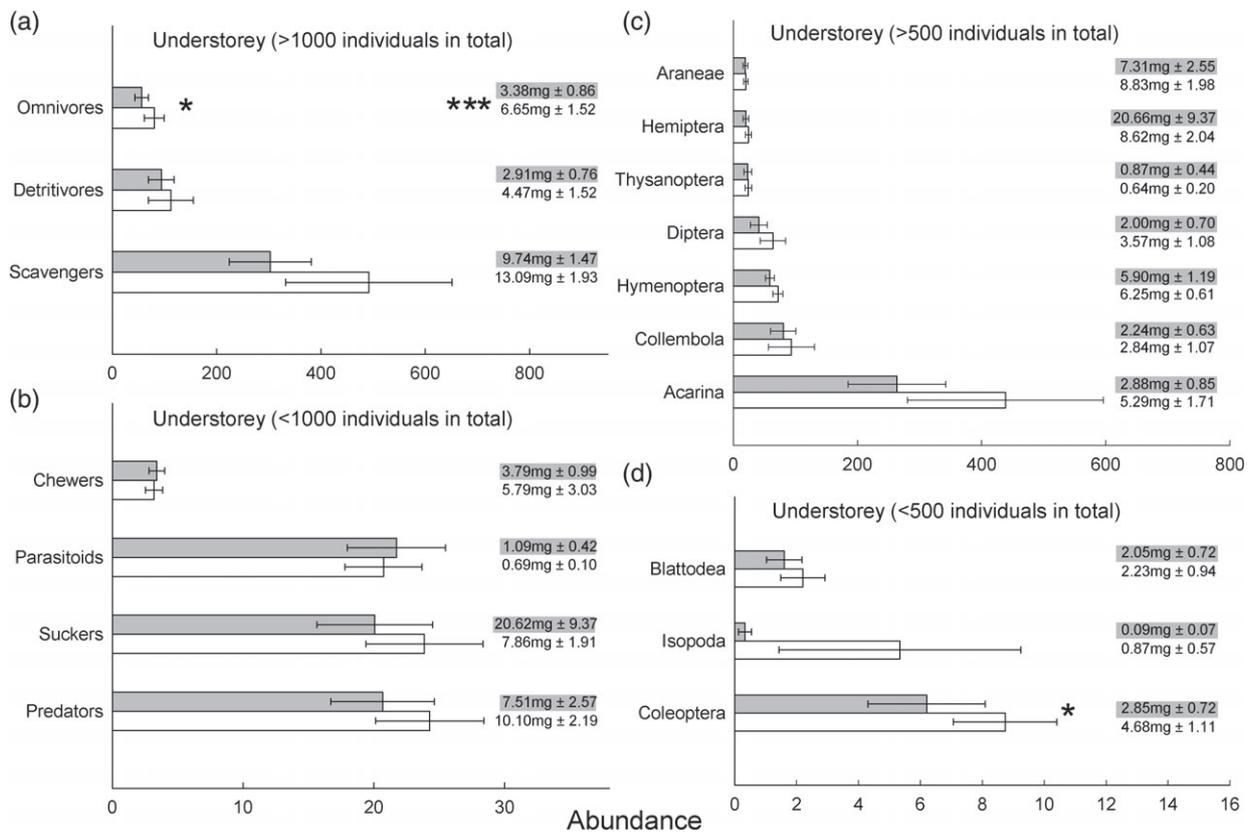


Figure 2 Mean abundance of different functional guilds (a, b) and taxonomic groups (c, d) of understorey arthropods, split by CO₂ treatment (across all dates). Ambient samples are shown with white bars; those from elevated conditions are shown in grey. To the right of each bar, total mean ± SE biomass is shown for the corresponding group. Significant differences [from generalized liner mixed models (GLMM) (abundance) and linear mixed models (LMM) (biomass)] (Tables 1 and 2) are indicated by asterisks (**P* < 0.1, ***P* < 0.05, ****P* < 0.01). Error bars the SE.

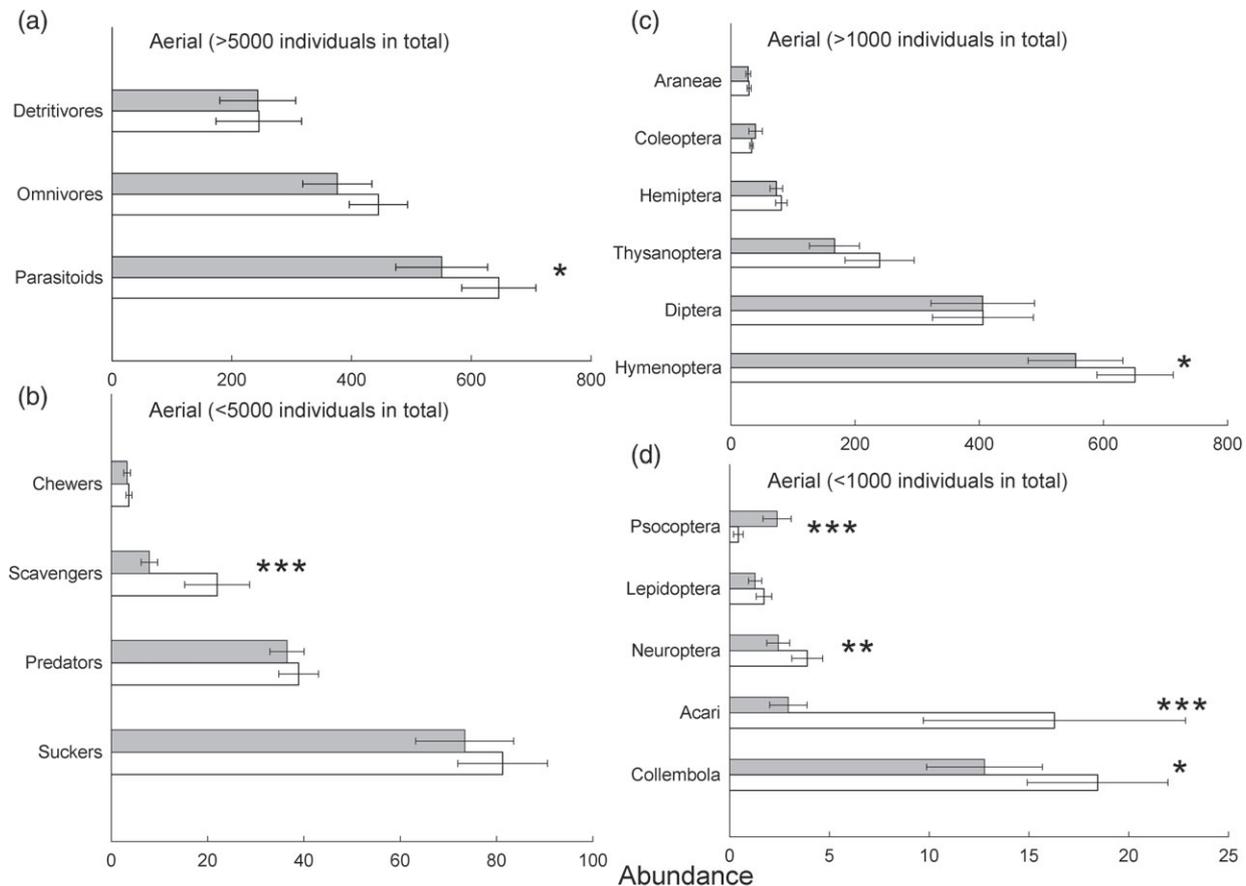


Figure 3 Mean abundances of the different functional guilds (a, b) and taxonomic groups (c, d) of aerial arthropods, split by CO₂ treatment (across all dates, with no biomass data as a result of the sampling method). Ambient samples are shown with white bars; those from elevated conditions are shown in grey. Significant differences [from generalized linear mixed models (GLMM)] (Tables 1 and 2) are indicated by asterisks (* $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$). Error bars show the SE.

samples, which contained far greater abundances of this group; indeed, the total biomass of ground dwelling mites actually increased under elevated CO₂, potentially as a result of larger individuals of greater body size.

Specialist versus generalist natural enemies

We predicted that arthropods at higher trophic levels would show greater declines in abundance than groups from lower trophic levels, given the generally greater sensitivity of higher trophic levels to environmental change (Voigt *et al.*, 2003). We expected this to be particularly true for more specialized feeding groups such as parasitoids because they are more restricted by tightly-coupled relationships with a limited number of host species compared with generalist predators, which can exploit a greater range of prey species. We found significant reductions in the abundance of aerial parasitoid wasps, as expected, and, as such, the present study adds to the body of evidence indicating that specialized taxa may be more susceptible to environmental change (Hance *et al.*, 2007). Conversely, previous studies from similar sites have found increases in the numbers of parasitoids or parasitism rates under elevated CO₂ (Percy *et al.*, 2002; Stiling *et al.*, 2002, 2003; Hillstrom & Lindroth, 2008). Stiling *et al.*

(2003) attributed their findings to host plant quality-mediated increases in the development time of host species, leaving them vulnerable to parasitoid attack for longer periods. In the present study, host species may well be experiencing reduced development rates (this would require further work for confirmation), although the reductions seen in absolute host abundance may be more important for parasitoids. The declines found across a range of groups from lower trophic levels, both in terms of abundance and biomass, could be responsible for the declines seen in parasitoid abundance, as their larval food sources become limited.

In contrast to our expectations, the abundance and biomass of generalist predators such as spiders did not decline in any of the niche types, despite declines in the number of many of the groups likely to constitute their prey. We did find a significant decline in the abundance of aerial Neuroptera, although this was the only predatory Order to show a response. Previous findings concerning the responses of predatory taxa to elevated CO₂ are mixed, with some studies finding increases in the abundance of carnivorous groups (Sanders *et al.*, 2004; Hamilton *et al.*, 2012) and one reporting no change (Hillstrom & Lindroth, 2008). In the present study, it is possible that highly mobile predators, such as ground-walking spiders and carabid beetles, could access prey external to the rings from which they were caught, enabling the

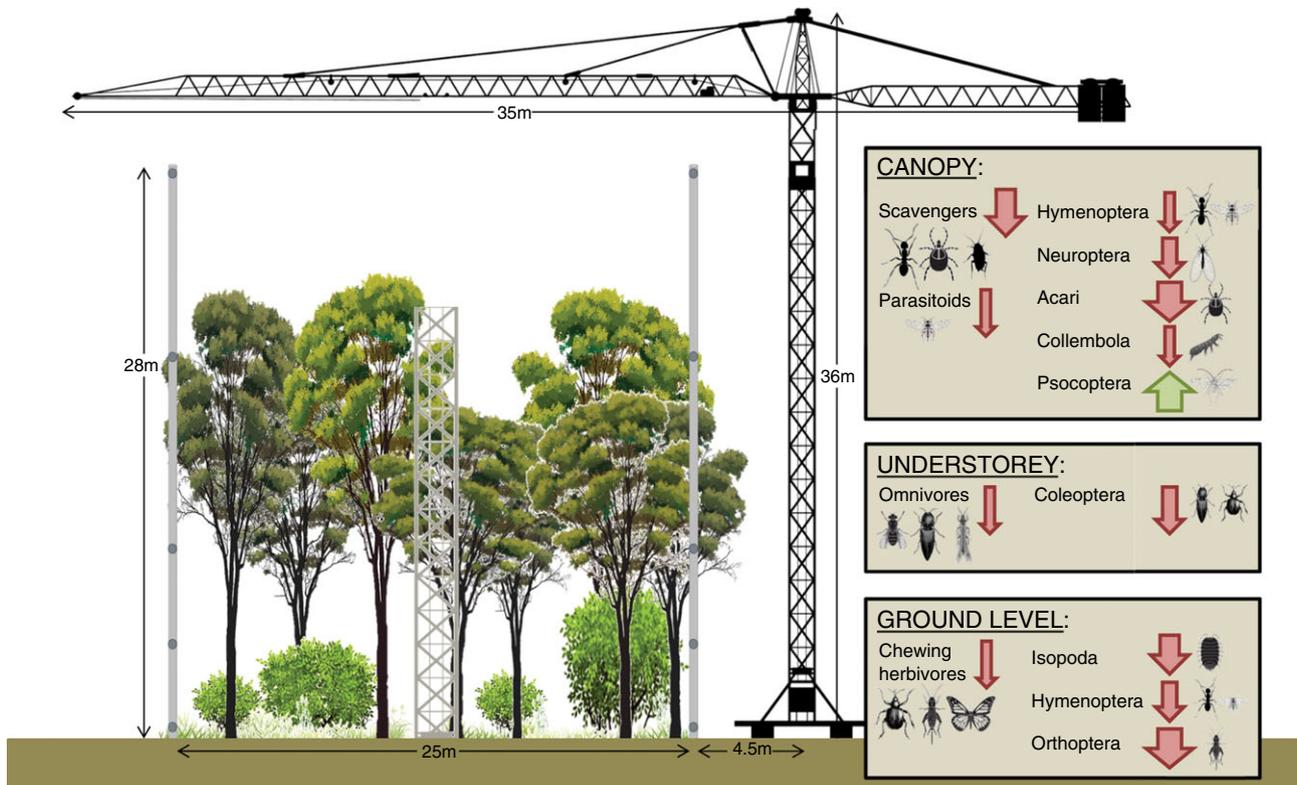


Figure 4 A schematic diagram summarizing the main findings of the present study, and showing a scaled drawing of one of the *Eucalyptus* Free Air CO₂ Enrichment ('EucFACE') arrays. CO₂ (or air in the case of ambient rings) is pumped in to the ring from the vertical vent pipes surrounding each array. The crane is used to access the tree canopy. Arrows show the direction of significant changes in the abundances of the taxa shown, in response to elevated CO₂. The widths of the arrows indicate their level of significance, with wider arrows representing smaller *P* values, thus comprising greater evidence against the null hypothesis.

maintenance of ambient population levels within elevated rings; however, this is also true of winged parasitoids for which we still detected an effect. Alternatively, the effects of elevated CO₂ at the plot level may have deterred certain insects from entering the rings, resulting in the population declines observed for many of the groups studied; this is an inherent issue in plot-level experiments of this type (Moise & Henry, 2010) and needs to be considered when interpreting the results of the present study. Either way, the reduced densities of these invertebrate groups in elevated CO₂ suggest that conditions were less favourable for them than those under ambient CO₂ levels. In addition, it is possible that the predator population is yet to respond to declines in prey availability under elevated CO₂, given the relatively short fumigation time (late 2012 onward).

Our level of taxonomic identification (Order/Family) did not allow for estimations of the abundance of arthropods from the fourth trophic level (intra-guild predators). The inclusion of intra-guild predators within the predator group could potentially mask any CO₂ effects on the abundance of third-level predatory taxa, although we might expect that fourth-level predatory taxa would be negatively impacted by elevated CO₂ over the long term. The design of the present study also did not allow for the level of host specificity of herbivorous arthropods to be determined; this could be an interesting consideration for further studies, particularly with respect to the plant species-rich

understorey, because monophagous specialist herbivores are more strongly negatively affected by increases in CO₂ than polyphagous species (Stiling & Cornelissen, 2007).

Community composition did not change under elevated CO₂

Despite widespread overall declines within individual trophic groups and Orders, we found no evidence for an effect of elevated CO₂ on community composition, in contrast to our predictions. Similarly, other studies of this type have shown weak to non-existent effects of elevated CO₂ on community composition (Sanders *et al.*, 2004; Hillstrom *et al.*, 2014). Given that the majority of the responses of the different groups to elevated CO₂ in the present study, both in terms of abundance and biomass, were negative in nature, this could have resulted in compositionally-similar communities comprising fewer total individuals compared with those under ambient conditions.

The range of sampling methods used in the present study means that we gained a broad, representative sample of the community occurring in *Eucalyptus* woodland. We found many differences in the responses of the individual trophic and taxonomic groups to elevated CO₂ between sampling methods, indicating the potential for studies using only one sampling technique to overlook effects of elevated CO₂. We therefore

stress the importance of using multiple sampling methods in future studies, aiming to ensure that the results more accurately reflect the responses occurring in the system.

Conclusions

There is a growing body of evidence from community-level studies indicating that the responses of invertebrates to climatic and atmospheric change will likely be taxon-specific and idiosyncratic (Sanders *et al.*, 2004; Hamilton *et al.*, 2012; Hillstrom *et al.*, 2014). In support of this, we found differences in the directions and/or strength of change for certain groups between niche types, as well as differences in the responsiveness of the taxa comprising the individual feeding guilds, highlighting the importance of studies conducted across multiple trophic levels (Pocock *et al.*, 2012). However, overall, we found evidence for a consistent decline across a broad range of groups under elevated CO₂. Particularly for those groups showing corresponding declines in biomass such as detritivorous Isopoda and omnivores, these declines could indicate reductions in the energy flow attributed to these organisms in the system. Significant reductions in the abundance and biomass of several groups with roles in nutrient cycling and biocontrol suggest that woodland ecosystem processes could potentially be affected as global concentrations of atmospheric CO₂ continue to rise.

Acknowledgements

We thank V. Kumar, S. Wohl, C. McNamara, C. Barton, G. Lopaticki, B. May and S. Pulumbarit for their assistance. We also thank K. Barnett, J. Powell and R. Duursma for statistical advice. This work was supported by a Hawkesbury Institute for the Environment Higher Degree Research Award to S.L.F. and a British Ecological Society Small Project Grant awarded to L.M.B. EucFACE is supported by the Australian Commonwealth Government through the Education Investment Fund, the Department of Industry and Science, and the Australian Research Council in partnership with Western Sydney University. The facilities at EucFACE were built as part of the Australian Government's Nation-building Economic Stimulus Package.

Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference: 10.1111/afe.12190

Fig. S1. Non-metric multidimensional scaling (NMDS) plots of arthropod community data in each of the three niche types, partitioned by functional guild classification and Order identity. Ambient CO₂ samples are shown in white, with elevated CO₂ indicated in dark grey/black. Ellipses show the SD around each community centroid. All sampling dates were included in the analysis. Pr, Predators; Pa, Parasitoids; Sc, Scavengers; De, Detritivores; Om, Omnivores; Su, Suckers; Ch, Chewers; Sa, Sanguivores; Di, Diptera; Co, Coleoptera; Ar, Araneae; Ac, Acarina; He, Hemiptera; Th, Thysanoptera; Bl, Blattodea; Is, Isopoda; Col, Collembola; Hy, Hymenoptera; Pse, Pseudoscorpiones; Or, Orthoptera; Le, Lepidoptera; Li, Lithobiomorpha;

Ma, Mantodea; Pso, Psocoptera; Ne, Neuroptera; Mi, Millipedes (Chilognatha); Sc, Scolopendromorpha. Stress values remained below 0.2 for all analyses, with $k = 3$ dimensions.

Table S1. A list of the total abundances of the groups identified in the present study and their functional guild classifications (Barker, 2004; CSIRO, 1991; Moran & Southwood, 1982; Zimmer, 2002). Those groups marked with an asterisk were identified to Subclass level only.

Table S2. Results from multivariate permutational analysis (PERMANOVA) of the effect of CO₂ treatment on community data from the three different niche-types, partitioned by Order identity and functional feeding guild classification (FG).

References

- Ainsworth, E.A. & Long, S.P. (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytologist*, **165**, 351–372.
- Altermatt, F. (2003) Potential negative effects of atmospheric CO₂ enrichment on insect communities in the canopy of a mature deciduous forest in Switzerland. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **76**, 191–199.
- Barker, G.M. (2004) Millipedes (Diplopoda) and centipedes (Chilopoda) (Myriapoda) as predators of terrestrial gastropods. *Natural Enemies of Terrestrial Molluscs* (ed. by G. M. Barker), pp. 405–426. CABI Publishing, U.K.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014) *lme4: Linear Mixed-Effects Models Using Eigen and S4*. R package, version 1.1-7 [WWW document]. URL <https://cran.r-project.org/web/packages/lme4/index.html> [accessed on 1 May 2015].
- Bell, J.R., Wheather, C.P., Henderson, R. *et al.* (2002) Testing the efficiency of suction samplers (G-vacs) on spiders: the effect of increasing nozzle size and suction time. *European Arachnology 2000* (ed. by S. Toft and N. Scharff), pp. 285–290. Aarhus University Press, Denmark.
- Bezemer, T.M. & Jones, T.H. (1998) Plant-insect herbivore interactions in elevated atmospheric CO₂: quantitative analyses and guild effects. *Oikos*, **82**, 212–222.
- Brook, A.J., Woodcock, B.A., Sinka, M. & Vanbergen, A.J. (2008) Experimental verification of suction sampler capture efficiency in grasslands of differing vegetation height and structure. *Journal of Applied Ecology*, **45**, 1357–1363.
- Brown, J.H., Gillooly, J., Allen, A., Savage, V. & West, G. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.
- Buntin, G.D. (1993) Developing a sampling program. *Handbook of Sampling Methods for Arthropods in Agriculture* (ed. by L. P. Pedigo and G. D. Buntin). CRC Press, Boca Raton, Florida.
- Couture, J.J. & Lindroth, R.L. (2012) Atmospheric change alters performance of an invasive forest insect. *Global Change Biology*, **18**, 3543–3557.
- Couture, J.J., Meehan, T.D., Kruger, E.L. & Lindroth, R.L. (2015) Insect herbivory alters impact of atmospheric change on northern temperate forests. *Nature Plants*, **1**, 1–5.
- CSIRO (1991) *The Insects of Australia: A Textbook for Students and Research Workers*. Melbourne University Press, Australia.
- Department of the Environment and Water Resources (2007) *Australia's Native Vegetation: A Summary of Australia's Major Vegetation Groups* [WWW document]. URL <https://www.environment.gov.au/resource/australias-native-vegetation-summary-australias-major-vegetation-groups> [accessed on 10 September 2015].

- Duursma, R.A., Gimeno, T.E., Boer, M.M., Crous, K.Y., Tjoelker, M.G. & Ellsworth, D.S. (2016) Canopy leaf area of a mature evergreen *Eucalyptus* woodland does not respond to elevated atmospheric CO₂ but tracks water availability. *Global Change Biology*, **22**, 1666–1676.
- Facey, S.L. & Gherlenda, A.N. (2016) Forest invertebrate communities and atmospheric change. *Global Climate Change and Terrestrial Invertebrates* (ed. by S. N. Johnson and T. H. Jones), in press.
- Facey, S.L., Ellsworth, D.S., Staley, J.T., Wright, D.J. & Johnson, S.N. (2014) Upsetting the order: how climate and atmospheric change affects herbivore–enemy interactions. *Current Opinion in Insect Science*, **5**, 66–74.
- Faraway, J.J. (2006) *Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models*. Chapman & Hall/CRC, Boca Raton, Florida.
- Frew, A., Nielsen, U.N., Riegler, M. & Johnson, S.N. (2013) Do eucalypt plantation management practices create understory reservoirs of scarab beetle pests in soil? *Forest Ecology and Management*, **306**, 275–280.
- Gherlenda, A.N., Crous, K.Y., Moore, B.D., Haigh, A.M., Johnson, S.N. & Riegler, M. (2015) Precipitation, not CO₂ enrichment, drives insect herbivore frass deposition and subsequent nutrient dynamics in a mature *Eucalyptus* woodland. *Plant and Soil*, **399**, 29.
- Gherlenda, A.N., Esveld, J.L., Hall, A.G., Duursma, R.A. & Riegler, M. (2016) Boom and bust: rapid feedback responses between insect outbreak dynamics and canopy leaf area impacted by rainfall and CO₂. *Global Change Biology*. DOI: 10.1111/gcb.13334.
- Hamilton, J.G., Zangerl, A.R., Berenbaum, M.R., Pippen, J., Aldea, M. & DeLucia, E.H. (2004) Insect herbivory in an intact forest understory under experimental CO₂ enrichment. *Oecologia*, **138**, 566–573.
- Hamilton, J., Zangerl, A.R., Berenbaum, M.R., Sparks, J.P., Elich, L., Eisenstein, A. & DeLucia, E.H. (2012) Elevated atmospheric CO₂ alters the arthropod community in a forest understory. *Acta Oecologica*, **43**, 80–85.
- Hance, T., van Baaren, J., Vernon, P. & Boivin, G. (2007) Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Review of Entomology*, **52**, 107–126.
- Hansen, R.A., Williams, R.S., Degenhardt, D.C. & Lincoln, D.E. (2001) Non-litter effects of elevated CO₂ on forest floor microarthropod abundances. *Plant and Soil*, **236**, 139–144.
- Harrison, X.A. (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, **2**, e616.
- Hentley, W.T., Hails, R.S., Johnson, S.N., Jones, T.H. & Vanbergen, A.J. (2014) Top-down control by *Harmonia axyridis* mitigates the impact of elevated atmospheric CO₂ on a plant-aphid interaction. *Agricultural and Forest Entomology*, **16**, 350–358.
- Hillstrom, M.L. & Lindroth, R.L. (2008) Elevated atmospheric carbon dioxide and ozone alter forest insect abundance and community composition. *Insect Conservation and Diversity*, **1**, 233–241.
- Hillstrom, M.L., Couture, J.J. & Lindroth, R.L. (2014) Elevated carbon dioxide and ozone have weak, idiosyncratic effects on herbivorous forest insect abundance, species richness, and community composition. *Insect Conservation and Diversity*, **7**, 553–562.
- Hunter, M.D. (2001) Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. *Agricultural and Forest Entomology*, **3**, 77–84.
- IPCC (2007) *Climate Change 2007: The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, et al.). Cambridge University Press, U.K.
- IPCC (2013) *Summary for Policy Makers. In: Climate Change 2013: The Physical Science Basis: Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by T. F. Stocker, D. Qin, G.-K. Plattner, et al.), pp. 3–29. Cambridge University Press, U.K.
- Jamieson, M.A., Trowbridge, A.M., Raffa, K.F. & Lindroth, R.L. (2012) Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology*, **160**, 1719–1727.
- Knepp, R.G., Hamilton, J.G., Mohan, J.E., Zangerl, A.R., Berenbaum, M.R. & DeLucia, E.H. (2005) Elevated CO₂ reduces leaf damage by insect herbivores in a forest community. *New Phytologist*, **167**, 207–218.
- Lindroth, R.L. & Raffa, K.F. (2016) Experimental approaches for assessing invertebrate responses to global change factors. *Invertebrates and Global Climate Change* (ed. by S. N. Johnson and T. H. Jones), in press.
- Loranger, G.I., Pregitzer, K.S. & King, J.S. (2004) Elevated CO₂ and O₃ concentrations differentially affect selected groups of the fauna in temperate forest soils. *Soil Biology & Biochemistry*, **36**, 1521–1524.
- Moise, E.R.D. & Henry, H.A.L. (2010) Like moths to a street lamp: exaggerated animal densities in plot-level global change field experiments. *Oikos*, **119**, 791–795.
- Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011) How many species are there on earth and in the ocean? *PLoS Biology*, **9**, 1–8.
- Moran, V.C. & Southwood, T.R.E. (1982) The guild composition of arthropod communities in trees. *Journal of Animal Ecology*, **51**, 289–306.
- Norby, R.J., Kauwe, M.G.D., Domingues, T.F. et al. (2016) Model-data synthesis for the next generation of forest free-air CO₂ enrichment (FACE) experiments. *New Phytologist*, **209**, 17–28.
- Oksanen, J., Blanchet, F.G., Kindt, R. et al. (2015) *vegan: Community Ecology Package*. R package, version 2.2-1 [WWW document]. URL <https://cran.r-project.org/web/packages/vegan/index.html> [accessed on 1 May 2015].
- Percy, K.E., Awmack, C.S., Lindroth, R.L. et al. (2002) Altered performance of forest pests under atmospheres enriched by CO₂ and O₃. *Nature*, **420**, 403–408.
- Pocock, M.J.O., Evans, D.M. & Memmott, J. (2012) The robustness and restoration of a network of ecological networks. *Science*, **335**, 973–977.
- Polis, G. (1998) Stability is woven by complex webs. *Nature*, **395**, 744–745.
- Price, P.W. (2002) Resource-driven terrestrial interaction webs. *Ecological Research*, **17**, 241–247.
- Pritchard, S.G., Rogers, H.H., Prior, S.A. & Peterson, C.M. (1999) Elevated CO₂ and plant structure: a review. *Global Change Biology*, **5**, 807–837.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Austria [WWW document]. URL <https://www.R-project.org/> [accessed on 1 May 2015].
- Raffaelli, D. (2004) How extinction patterns affect ecosystems. *Science*, **306**, 1141–1142.
- Robinson, E.A., Ryan, G.D. & Newman, J.A. (2012) A meta-analytical review of the effects of elevated CO₂ on plant-arthropod interactions highlights the importance of interacting environmental and biological variables. *New Phytologist*, **194**, 321–336.
- Saint-Germain, M., Buddle, C.M., Larrivée, M. et al. (2007) Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? *Journal of Applied Ecology*, **44**, 330–339.
- Sanders, N.J., Gotelli, N.J., Heller, N.E. & Gordon, D.M. (2003) Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 2474–2477.
- Sanders, N.J., Belote, R.T. & Weltzin, J.F. (2004) Multitrophic effects of elevated atmospheric CO₂ on understory plant and arthropod communities. *Environmental Entomology*, **33**, 1609–1616.

- Scheffers, B.R., Joppa, L.N., Pimm, S.L. & Laurance, W.F. (2012) What we know and don't know about Earth's missing biodiversity. *Trends in Ecology and Evolution*, **27**, 501–510.
- Stiling, P. & Cornelissen, T. (2007) How does elevated carbon dioxide (CO₂) affect plant–herbivore interactions? A field experiment and meta-analysis of CO₂-mediated changes on plant chemistry and herbivore performance. *Global Change Biology*, **13**, 1823–1842.
- Stiling, P., Cattell, M., Moon, D.C., Rossi, A., Hungate, B.A., Hymus, G. & Drake, B. (2002) Elevated atmospheric CO₂ lowers herbivore abundance, but increases leaf abscission rates. *Global Change Biology*, **8**, 658–667.
- Stiling, P., Moon, D.C., Hunter, M.D., Colson, J., Rossi, A.M., Hymus, G.J. & Drake, B.G. (2003) Elevated CO₂ lowers relative and absolute herbivore density across all species of a scrub-oak forest. *Oecologia*, **134**, 82–87.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- Vanbergen, A.J., Woodcock, B.A., Koivula, M. *et al.* (2010) Trophic level modulates carabid beetle responses to habitat and landscape structure: a pan-European study. *Ecological Entomology*, **35**, 226–235.
- Vasseur, L. & Potvin, C. (1998) Natural pasture community response to enriched carbon dioxide atmosphere. *Plant Ecology*, **135**, 31–41.
- Villalpando, S.N., Williams, R.S. & Norby, R.J. (2009) Elevated air temperature alters an old-field insect community in a multifactor climate change experiment. *Global Change Biology*, **15**, 930–942.
- Voigt, W., Perner, J., Davis, A.J. *et al.* (2003) Trophic levels are differentially sensitive to climate. *Ecology*, **84**, 2444–2453.
- Wilson, E.O. (1987) The little things that run the world (The Importance and Conservation of Invertebrates). *Conservation Biology*, **1**, 344–346.
- Woodcock, B.A. (2005) Pitfall trapping in ecological studies. *Insect Sampling in Forest Ecosystems* (ed. by S. Leather), pp. 37–58. Blackwell Science Ltd, U.K.
- Zhu, Z., Piao, S., Myneni, R.B. *et al.* (2016) Greening of the Earth and its drivers. *Nature Climate Change*, **6**, 791–795.
- Zimmer, M. (2002) Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach. *Biological Reviews of the Cambridge Philosophical Society*, **77**, 455–493.

Accepted 28 August 2016