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Inter-annual changes in detritus-based food chains can enhance plant growth response to elevated atmospheric CO_2

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Abstract

Elevated atmospheric CO_2 generally enhances plant growth, but the magnitude of the effects depend, in part, on nutrient availability and plant photosynthetic pathway. Due to their pivotal role in nutrient cycling, changes in abundance of detritivores could influence the effects of elevated atmospheric CO_2 on essential ecosystem processes, such as decomposition and primary production. We conducted a field survey and a microcosm experiment to test the influence of changes in detritus-based food chains on litter mass loss and plant growth response to elevated atmospheric CO_2 using two wetland plants: a C_3 sedge (*Scirpus olneyi*) and a C_4 grass (*Spartina patens*). Our field study revealed that organism's sensitivity to climate increased with trophic level resulting in strong inter-annual variation in detritus-based food chain length. Our microcosm experiment demonstrated that increased detritivore abundance could not only enhance decomposition rates, but also enhance plant growth of *S. olneyi* in elevated atmospheric CO_2 conditions. In contrast, we found no evidence that changes in the detritus-based food chains influenced the growth of *S. patens*. Considered together, these results emphasize the importance of approaches that unite traditionally subdivided food web compartments and plant physiological processes to understand inter-annual variation in plant production response to elevated atmospheric CO_2.

Keywords: atmospheric carbon dioxide, decomposition, food chain length, global change, multi-trophic interactions, primary production, soil macrofauna, wetland

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Introduction

Anthropogenic activities currently influence ecosystems worldwide (Steffen *et al.*, 2011). For example, increased combustion of fossil fuels and production of cement since the industrial revolution are associated with concomitant increases in atmospheric CO_2 concentrations from 280 to 380 ppm, and current concentrations are projected to double by 2100 (IPCC, 2013). These increases in atmospheric CO_2 are linked to warming of the earth's surfaces (Shakun *et al.*, 2012), ocean acidification (Orr *et al.*, 2005), and changes in global precipitation patterns (Liu *et al.*, 2007; Solomona *et al.*, 2009). Therefore, the principal objectives of many environmental policies have been to reduce CO_2 emissions into ecosystems, and to enhance the ability of ecosystems to absorb excess CO_2 (Kitzes *et al.*, 2008).

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Plants are the primary link between the atmosphere and biosphere, and rising atmospheric CO_2 is expected to stimulate photosynthesis and plant growth. Evidence from long-term CO_2 enrichment studies suggests that plants can consistently accumulate more carbon in their biomass under elevated compared to current CO_2 conditions (Rasse *et al.*, 2005; Drake, 2014), although these effects are generally more pronounced for plant species that use C_3 compared to C_4 photosynthetic pathways (White *et al.*, 2012; Erickson *et al.*, 2013). This leads to the suggestion that highly productive ecosystems, such as wetlands dominated by C_3 plants, may be a net carbon sink in future atmospheric CO_2 conditions and that wetland conservation may be an effective strategy to mitigate the harmful effects of CO_2 on the global climate (Mcleod *et al.*, 2011). This suggestion has been controversial, however, and much research has focused on environmental factors such as salinity (Erickson *et al.*, 2007), nitrogen deposition (Langley & Megonigal, 2010), and production of methane (Dacey *et al.*, 1994; Bridgham *et al.*, 2013), which may modify, or counteract, the value of wetlands as carbon sinks (Drake, 2014). Notably, the strength of

interactions among animal consumer species may also alter the ability of plants to accumulate carbon in their biomass in the future, but we lack rigorous experimental evidence documenting the magnitude of potential consumer effects on plant growth response to elevated atmospheric CO_2.

Due to their importance for litter decomposition and subsequent mobilization of nutrients that may otherwise limit plant growth (Hines & Gessner, 2012), animals in detritus-based food chains may be particularly important in elevated atmospheric CO_2 conditions when plants have increased nutrient demand (De Graaff *et al.*, 2006; Reich & Hobbie, 2013). Evaluations of the influence of elevated CO_2 on the feedback between decomposition and plant growth, however, have generally focused on litter chemistry as a key rate limiting factor (Strain & Bazzaz, 1983; Norby *et al.*, 2001), and less emphasis has been placed on the role of consumers in the detritus-based food chain. For example, initial hypotheses suggested that if the effect of elevated CO_2 on litter chemistry was similar to its effects on live plant tissue [decreased nitrogen concentrations and increased concentration of lignin (Cotrufo *et al.*, 1998)], then litter chemistry could slow decomposition, and lead to progressive limitation of plant growth in elevated atmospheric CO_2 conditions (Strain & Bazzaz, 1983). However, a meta-analysis showed that efficient nutrient resorption during senescence can minimize the influence of elevated CO_2 on litter chemistry (Norby *et al.*, 2001), which reduces the likelihood that delays in decomposition due to litter chemistry will limit plant growth response to elevated CO_2 in the long term. Yet, without an explicit consideration of the consequences of variation in detritivore abundance, these litter chemistry results reflect only a partial understanding of the influence of decomposition on plant growth in elevated atmospheric CO_2 conditions.

At least two factors may influence the magnitude, and potentially the direction, of detritivore effects on plant growth response to elevated atmospheric CO_2. First, detritivores are sensitive to desiccation, and their survival and fecundity rely on minimizing water loss (Hassall *et al.*, 2010). Abiotic factors, such as precipitation and temperature that limit detritivore populations (Brody & Lawlor, 1984; Carefoot, 1993), also influence plant growth (Drake, 2014), but little is known about the relative magnitude of direct and detritivore-mediated effects of climate on plant growth. Second, climate may have differential effects on detritivores and the predators that consume them (MacLennan *et al.*, 2011; Hansson *et al.*, 2012; Sentis *et al.*, 2013). Long-term monitoring of grassland invertebrate communities has shown that sensitivity of organisms to climatic factors, such as temperature and precipitation, can increase with trophic rank (Voigt *et al.*, 2007). However, elevated atmospheric CO_2 effects on higher trophic levels can be quite variable (Blankinship *et al.*, 2011). Notably, predator–detritivore–litter interactions have predominately been studied in context of understanding decomposition alone (Kajak, 1995; Wardle *et al.*, 1998; Hunter *et al.*, 2003; Lawrence & Wise, 2004). The extent to which these effects will attenuate within the detritus-based food chain, or cascade to affect production of live plant tissue in elevated CO_2 conditions, remains an open question.

We conducted a field plot and microcosm experiment to achieve two main objectives: (i) to determine whether climate influences variation in detritus-based food chains; (ii) to evaluate the effect of variation in detritus-based food chain length on the growth response of plants to elevated CO_2. We hypothesize that organisms at higher trophic levels, namely spiders, will be more sensitive to variation in climate than organisms, such as their detritivorous prey that feed at lower trophic levels. Differential sensitivity of trophic levels to climate results in inter-annual variation in detritus-based food chain length. We hypothesize that variation in food chain length will have stronger influence on plant growth in elevated CO_2 conditions when there is increased plant demand for nutrients that are mobilized from litter by detritivores. By comparing the influence of changes in detrititus-based food chains on decomposition and growth of two important plant functional groups (C_3 vs. C_4 plants), we can start to evaluate the role of consumers in determining wetland ecosystem response to elevated CO_2.

Materials and methods

Study system

This study was conducted in a brackish marsh at the Smithsonian Environmental Research Center in MD, USA (38°53′N, 76°33′W). Plant communities at this site are dominated by *Scirpus olneyi* (a C_3 sedge) and *Spartina patens* (a C_4 grass). The species name of *Scirpus olneyi* has been changed to *Schoenoplectus americanus* (*Persoon*) *Volkart ex Schinz and R. Keller*, but throughout this manuscript, we retain the former name to maintain continuity with previous results published from the long-term open topped chamber experiment which was established at this site in 1987 (Drake *et al.*, 1989). Results to date show that *S. olneyi* has a sustained increase in primary production under elevated CO_2 conditions (Rasse *et al.*, 2005). In contrast, the biomass of *S. patens* is less affected by elevated atmospheric CO_2 conditions (Arp *et al.*, 1993; Drake, 2014).

The numerically dominant predator, *Pardosa littoralis* (Araneae: Lycosidae), forages broadly across *S. olneyi* and *S. patens* communities. These mobile spiders also aggregate in areas

with abundant leaf litter where they feed on a broad variety of invertebrate prey including detritivorous isopods, such as *Littorophiloscia vittata* (Isopoda: Philosciidae) (Hines & Gessner, 2012). This isopod lacks pleopodal lungs, making it poorly adapted to absorbing moisture from the air. Consequently, individuals often aggregate in high densities, which creates more favorable microclimate for the group and intensifies their influence on mineralization of leaf litter (Hassall *et al*., 2010; Hines & Gessner, 2012).

Field experiment

To examine the influence of climate on species in detritus-based food chains, we sampled 0.47 m^2 field plots containing either *S. olneyi* or *S. patens* communities. The open field plots were originally established in 1987 as part of a long-term study examining the effects of elevated CO_2 on plant productivity (Drake *et al*., 1989). Description of the plots and long-term monitoring of plant biomass are described in detail by Erickson *et al.* (2007) and Drake (2014). Here, we focus on the invertebrate sampling, which is reported for the first time. Invertebrates were sampled five times over 6 years (28 June 2004, 20 July 2005, 19 July 2006, 23 July 2007, 27 July 2009), an appropriate temporal resolution because the focal species show relatively low intra-seasonal variation (Hines & Gessner, 2012). On each date, we estimated densities of focal arthropods (*L. vittatta* and *P. littoralis*) using a standard suction sampling method consisting of three, 3-second vacuum suction samples taken with a d-vac® vacuum sampler (Ventura, CA, USA) fitted with a 0.20 m^2 nozzle (Hines *et al*., 2006). Arthropods were killed in the field with ethyl acetate vapor before they were counted in the laboratory.

The effect of atmospheric CO_2 on abundance of *P. littoralis* spiders and *L. vittata* isopods was assessed using repeated measures ANOVA with plant community (*S. olneyi* and *S. patens*) considered as a categorical effect and time considered as a continuous effect. Animal densities were log-transformed to meet assumptions of normality and homogeneity of variances for analysis, and untransformed densities are shown in the figures. To estimate sensitivity of predators, detritivores, and plants to variation in climate, we collected five climatic variables reported at a local weather station (Table 1). The chosen variables reflect overall climate conditions, and climatic stress due seasonal temperature extremes, and water stress. To account for potential correlation among climate variables, we simplified the data into two composite principal component axes, which explained 89% of the variation in the climate data. The fraction of temporal variance in animal density and plant biomass that could be accounted for by two composite climatic variables was estimated using partial redundancy analysis (pRDA), which is a multivariate analog of regression (R package Vegan) (Hammock & Johnson, 2014).

Table 1 Repeated measures ANOVA results showing the influence of plant community (*Scirpus olneyi* or *Spartina patens*), and year on density of *Pardosa littoralis* spiders, *Littorophiloscia vittata* isopods, and predator–prey ratio. Tests with significant results ($p \leq 0.05$) are bolded for clarity

		Spider density		Isopod density		Predator: prey	
	df*	*F*	*p*	*F*	*p*	*F*	*p*
Plant	1,8	1.17	0.31	3.17	0.11	1.55	0.24
Year	1,38	**9.04**	**0.005**	0.89	0.35	**10.76**	**0.002**
Plant × Year	1,38	1.80	0.19	**3.92**	**0.05**	1.19	0.28

*Degrees of freedom: numerator, denominator.

Microcosm experiment

To compare the influence of detritus-based food-chain length on litter mineralization and subsequent wetland plant growth of two plant species (*S. olneyi* and *S. patens*) under elevated as opposed to ambient atmospheric CO_2 concentrations, we conducted a 2 × 4 factorial microcosm experiment with a randomized complete block experimental design. Treatment factors included two levels of atmospheric CO_2 (ambient atmospheric CO_2: 365 ppm, or elevated atmospheric CO_2: 705 ppm) and four food-chain length (FCL) treatments: (i) control-litter withheld, (ii) litter addition (5 g per microcosm corresponding to 525 g m^{-2}), (iii) litter and 10 *L. vittata* isopod addition (corresponding to 1275 isopods m^{-2}), and (iv) litter, isopod and 2 *P. littoralis* spider addition (corresponding to 250 spiders m^{-2}). Due to clumped spatial distribution in the field, ten isopods at the base of a plant is reasonable, if not a slightly lower density than natural aggregations. Nonetheless, these initial species densities were chosen to fall within the range of naturally heterogeneous animal densities in the field, to allow for mortality of animals during experimental setup, and to stay within the carry capacity of the microcosms. Treatments involving predators without prey were not included because starvation of animals for the duration of the experiment would be unnecessarily cruel. All treatments were replicated six times for a total of 96 experimental microcosms (2 CO_2 treatments × 4 food-chain length treatments × 2 plant species × 6 replicates).

Atmospheric CO_2 treatments were established in outdoor chambers (1.5 m long × 1 m wide × 1.5 m tall, wooden enclosures surrounded by polyester film) as described by Wolf *et al.* (2007). Detritus-based food chain treatments were established in microcosms placed within CO_2 chambers. Each microcosm consisted of a sand-filled pot (11 cm diameter × 16 cm deep), inoculated with a slurry of natural microbial community and exposed to constant moisture by seating them within pots (16 cm diameter × 16 cm deep) filled to 12 cm with deionized water. Each microcosm contained either *S. olneyi* grown from field-collected, preweighed rhizome nodes, or *S. patens*, which was propagated from field-collected seeds and grown to the height of 5 cm before the start of the experiment on May 22, 2007. Litter addition treatments were established using leaf litter collected from *S. olneyi* or *S. patens* plants that were grown and allowed to completely senesce under either elevated or ambient conditions in the above chambers during the previous year. Clear plastic tube cages of 10 cm diameter × 1 m tall were sunk

in to the soil to enclose the plants and litter community in each microcosm.

To assess invertebrate survival, decomposition, and plant growth through time, half of the experimental units were harvested on each of two sample dates (day 50 and 84, corresponding to July 11, 2007 and August 14, 2007, respectively). On each sampling date, surviving invertebrates were counted following careful visual inspection of microcosms and sieving of soil. Litter remaining, as well as live root and shoot tissue for each plant species, was harvested, washed, and dried at 50°C before each tissue was weighed. Litter mass loss rate coefficients (k) were calculated using an exponential decay model ($M_t = M_0\, e^{-kt}$), where M_t = mass at time t, M_0 = initial litter mass, and t = elapsed time in days. All data met assumptions of homogeneity of variance and normality of residuals. Therefore, the main and interactive effect of atmospheric CO_2 and detritus-based food chain treatments on response variables (isopod abundance, litter mass loss rate, root biomass, shoot biomass) was assessed using mixed-model ANOVA. Categorical factors included atmospheric CO_2 (elevated or ambient) and detritus-based food chain treatments (control, litter addition, isopod addition, isopod and spider addition), and time was considered a continuous factor for the analysis of animal abundance and live plant biomass. Microcosms were considered independent experimental units because they were not hydrologically connected, and variance associated with chambers was effectively zero.

Results

Field experiment

There was strong inter-annual variation in the density of predatory spiders as well as the ratio of predators to their isopod prey (Fig. 1; significant year effects: Table 1), which was partly explained by climate (Fig. 2; Table 2). The pRDA showed that effects of climate were consistently stronger on higher trophic levels in both plant communities (Fig. 2). That is, the two principle component climate axes explained 70–73% of the variation in spider density, 20–21% of the variation in isopod density, and 0–30% of the variation in *S. olneyi* and *S. patens* plant biomass, respectively (Fig. 2).

Microcosm experiment

Spiders persisted in the microcosms for the duration of the experiment (85 ± 5% survival), with some low initial mortality resulting in significant temporal effects on predator survival (Table 3); nonetheless, predator mortality was not influenced by atmospheric CO_2 or plant community. Similarly, isopod mortality was low, and 75–80% of the isopods survived in the absence of predation (Fig. 3). Spiders consumed isopods, but may have been satiated over the course of the experiment as predation on isopods was greater during the first

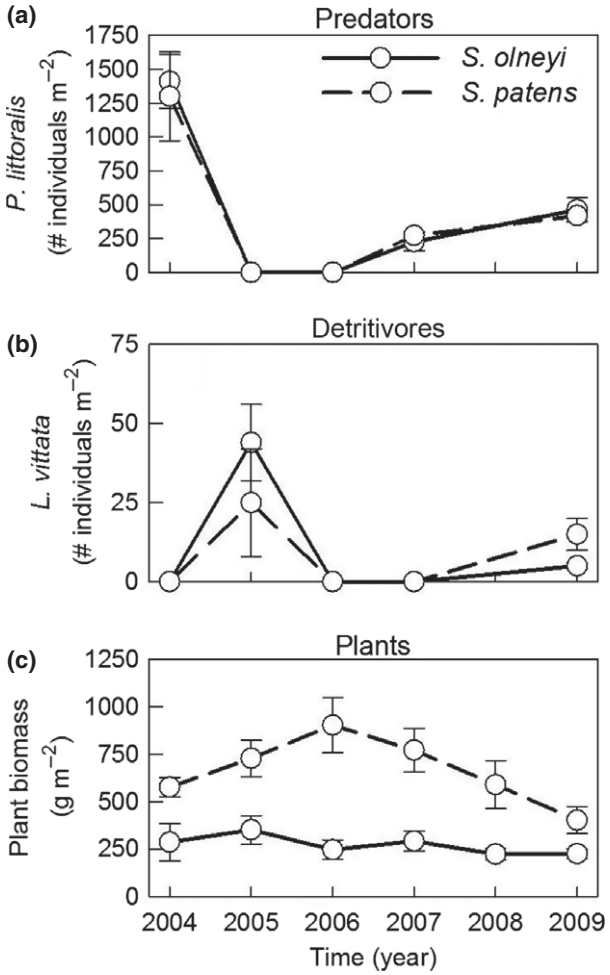

Fig. 1 Inter-annual variation in density (mean ± SEM, n = 5) of (a) *Pardosa littoralis*, (b) *Littorophiloscia vittata*, and (c) primary producers from 6 years (2004–2009) of sampling in 0.47 m^2 open field plots dominated by either *Scirpus olneyi* (dashed lines) or *Spartina patens* (solid lines).

50 days of the experiment (Fig. S1), and prey populations were not reduced further by day 84 (Fig. 3; Table 4). Overall, spiders suppressed isopod populations by 55% compared to isopod populations in spider-free treatments (Fig. 3). Predation was equally effective in both plant communities and was not influenced by atmospheric CO_2 conditions (Table 4, Fig. 3).

Decomposition of both plant species was sensitive to changes in detritivore food chain length, but was not influenced by atmospheric CO_2 (Table 5). That is, decomposition was accelerated by isopods, and there was less litter mass remaining when isopods were present compared to when they were absent (Fig. 4). However, spider predation, which limited isopod abundance (Fig. 3), did not have extended effects on decomposition (Fig. 4).

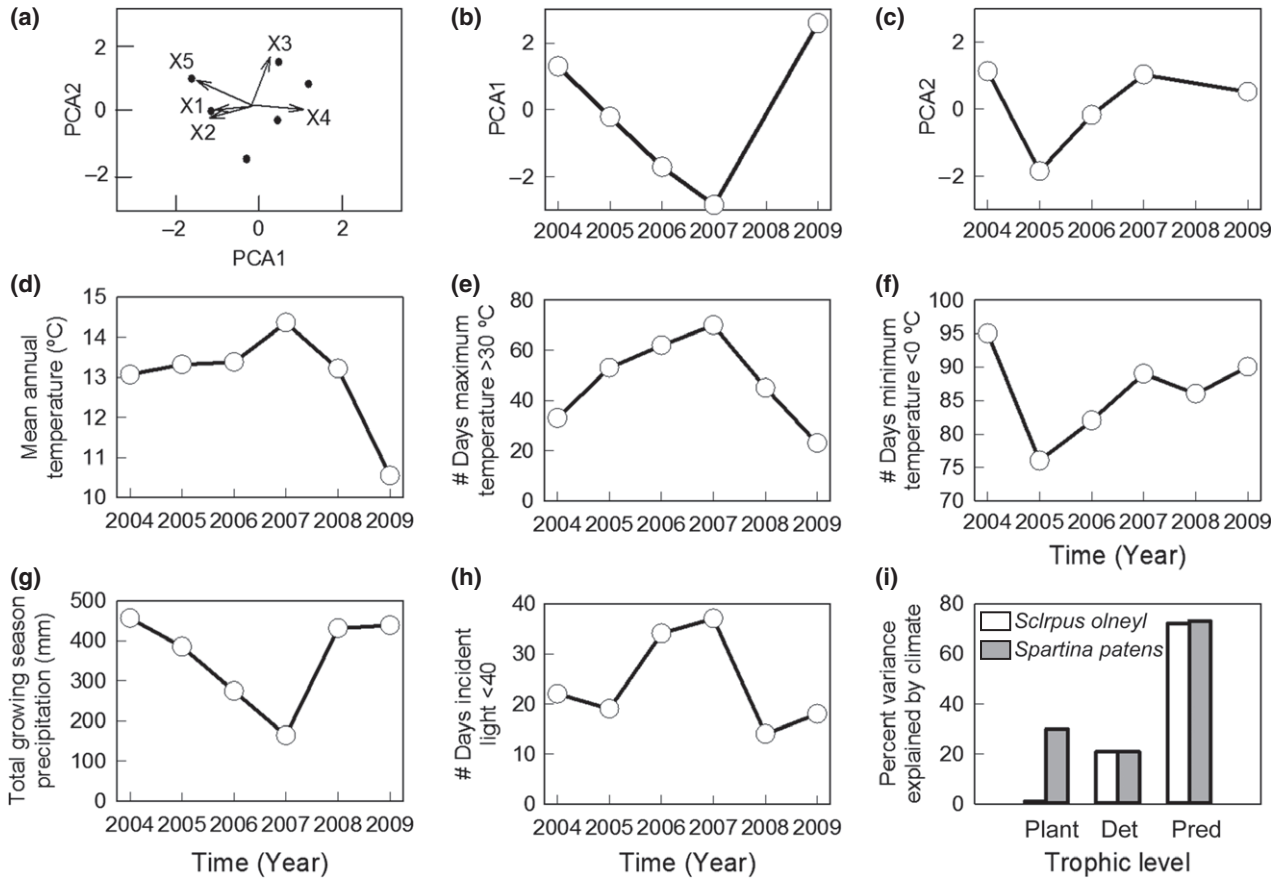

Fig. 2 Inter-annual variation in climate data collected from 2004 to 2009 shown as (a) a principle component bi-plot, (b) first principle component axes, (c) second principle component axis (d–h) five individual climate variables, and (i) the percent of variation of predator (pred), detritivore (det), and plants that can be explained by climate using partial redundancy analysis.

Table 2 Climate variables and the eigenvector coefficients (loadings) of a standardized principal component analysis of climatic variables for 2004–2009

Figure 2 Label	Description	PCA1	PCA2
X1	Mean air temperature, whole year	**−0.452**	
X2	No. days with maximum temperature >30°C	**−0.534**	−0.163
X3	No. days with minimum temperature <0°C (preceding winter)	0.183	**0.879**
X4	No. days incident light <40 mol quanta m^{-2} day^{-1}	**0.510**	−0.191
X5	Total precipitation May–July (mm)	**−0.465**	−0.398

The first two axes explain 89% of total variance. Loadings >0.45 are shown in bold for clarity.

Table 3 ANOVA results showing the effect of elevated atmospheric CO_2 on the survival of *Pardosa littoralis* spiders in microcosms containing *Littorophiloscia vitatta* prey and leaf litter from either *Scirpus olneyi* or *Spartina patens* plants. Significant tests ($p \leq 0.05$) are bolded for clarity

	Scirpus olneyi			*Spartina patens*	
	df*	*F*	*p*	*F*	*p*
CO_2	1,20	0.0	1.00	0.00	1.00
time	1,20	**15.9**	**<0.001**	**8.5**	**0.009**
CO_2 × time	1,20	0.00	1.00	0.24	0.63

*Degrees of freedom: numerator, denominator.

There was an interactive effect of elevated CO_2 and detritus-based food chain on shoot biomass of *S. olneyi* (Table 5, Fig. 5). In elevated CO_2 conditions, the addition of isopods was associated with increased *S. olneyi* biomass, an effect that was not found in ambient atmospheric CO_2 conditions. This positive association

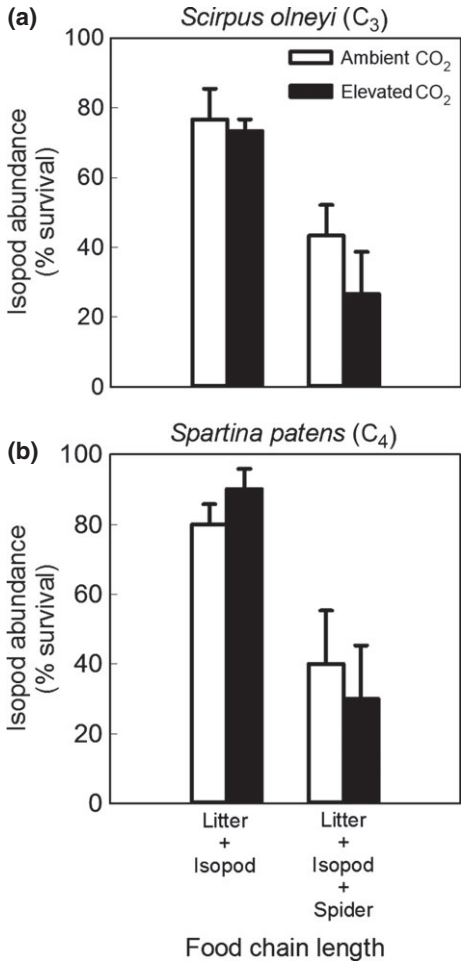

Fig. 3 The influence of atmospheric CO_2 [ambient (□) or elevated (ambient + 345 ppm (■)], and predation by *Pardosa littoralis* spiders on the abundance (mean ± SEM, $n = 3$) of the isopod *Littorophiloscia vittata* after 84 days in outdoor microcosms containing the (a) C_3 sedge *Scirpus olneyi* or (b) the C_4 grass *Spartina patens*.

between *L. vittata* isopods and plant growth was found in the presence and absence of spiders (Table 5, Fig. 5). In contrast, variation in *S. patens* biomass was not explained by atmospheric CO_2 conditions or detritivore food chain treatments (Fig. 5, Table 5).

Discussion

Our 6-year field study shows that an organism's sensitivity to climate increases with its trophic level. In particular, there were strong fluctuations in the relative abundances of *P. littoralis* spiders and *L. vittata* isopods, two numerically dominant species in our detritus-based food chain. This result is consistent with longer-term monitoring studies, which examined larger numbers of species and climate factors (Voigt *et al.*, 2007; Hammock & Johnson, 2014), lending support that our conclusions are not biased by the particular species or climate factors that we included in our analyses. Consequently, it is likely that similar inter-annual variation in detritus-based food chains has the potential to influence decomposition in a wide variety of ecosystems.

Table 4 ANOVA results showing the effect of elevated atmospheric CO_2 and predation by *Pardosa littoralis* spiders on *Littorophiloscia vitatta* prey in microcosms containing leaf litter and either *Scirpus olneyi* or *Spartina patens* plants. Significant tests ($p \leq 0.05$) are bolded for clarity

	Scirpus olneyi			*Spartina patens*	
	df*	*F*	*p*	*F*	*p*
CO_2	1,40	0.42	0.52	0.76	0.39
Predation (FCL)	1,40	**27.2**	**<0.001**	**29.2**	**<0.001**
time	1,40	**121.8**	**<0.001**	**67.1**	**<0.001**
CO_2 × FCL	1,40	0.047	0.083	0.49	0.49
CO_2 × time	1,40	0.86	0.36	0.16	0.70
FCL × time	1,40	**24.1**	**<0.001**	**25.0**	**<0.001**
CO_2 × FCL × time	1,40	0.10	0.75	0.68	0.42

*Degrees of freedom: numerator, denominator.

Our microcosm study shows that variation in detritus-based food chain can have important influences on two important ecosystem processes in wetland ecosystems. Not only did increased *L. vittata* abundance accelerate decomposition, it was also associated with enhanced production of *S. olneyi* biomass in response to elevated CO_2. Specifically, in the presence of litter and isopods, elevated CO_2 enhanced *S. olneyi* shoot growth by 24%, and the effect of elevated atmospheric CO_2 on plant growth was weaker in control microcosms where isopods and litter were absent (Fig. 5). The magnitude of shoot growth response to elevated CO_2 and isopods is consistent with the influence of CO_2 on *S. olneyi* growth in the field, which can range from 0 to 37% depending on variation in environmental conditions (Drake, 2014). The interactive effect of detritivore food chain and elevated atmospheric CO_2 on plant growth that we found was plant species specific (Table 5), whereby *S. olneyi* shoot biomass was enhanced, but no equivalent effect was found for *S. patens*. These results are consistent with our predictions that mineralization of leaf litter by detritivores in elevated CO_2 conditions would be more important for plants with C_3 photosynthetic pathway. A few considerations about linkages between detritus-based food chains and plant production, however, warrant further discussion.

First, spiders consumed isopods in microcosms, but they did not limit the positive effect of isopods on litter

Table 5 ANOVA results showing the direct and interactive influence of atmospheric CO_2 (elevated or ambient) and detritus-based food chain length (control, litter addition, litter and isopod addition, or litter, isopod, and spider addition) on *Scirpus olneyi* and *Spartina patens* (litter mass loss, and shoot biomass). Significant tests ($p \leq 0.05$) are bolded for clarity

	Litter mass					Shoot biomass				
		Scirpus olneyi		*Spartina patens*			*Scirpus olneyi*		*Spartina patens*	
	df*	*F*	*p*	*F*	*p*	df*	*F*	*p*	*F*	*p*
CO_2	1,60	2.8	0.10	1.0	0.3	1,80	1.3	0.3	0.7	0.4
FCL	2,60	**13.7**	**<0.001**	**13.8**	**<0.001**	3,80	1.7	0.18	0.9	0.5
Time	1,60	**620.1**	**<0.001**	**376.4**	**<0.001**	1,80	**249.4**	**<0.001**	**79.9**	**<0.001**
CO_2 × FCL	2,60	0.7	0.5	0.2	0.8	3,80	**5.1**	**0.03**	0.2	0.9
CO_2 × Time	1,60	3.4	0.07	1.6	0.2	1,80	3.3	0.07	0.2	0.6
FCL × Time	2,60	**12.8**	**<0.001**	**13.7**	**<0.001**	3,80	2.3	0.09	1.8	0.2
CO_2 × FCL × Time	2,60	0.5	0.6	0.2	0.8	3,80	1.5	0.2	0.8	0.5

*Degrees of freedom: numerator, denominator.

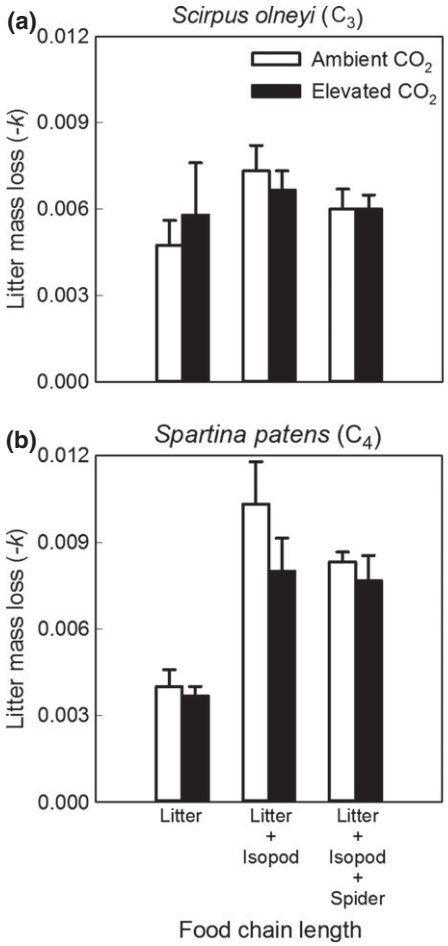

Fig. 4 The influence of atmospheric CO_2 (ambient (□) or elevated [ambient + 345 ppm (■)] and changes in detritus-based food chain length on litter mass loss (k) (mean ± SEM, $n = 3$) of (a) the C_3 sedge *Scirpus olneyi* and (b) the C_4 grass *Spartina patens* in outdoor microcosms for 84 days.

decomposition or *S. olneyi* growth, which demonstrates that trophic interactions can be surprisingly complex, even in tractably simplified experimental food chains. One explanation is that there may be a temporal component to isopod effects on plant growth, whereby isopods mineralized leaf litter, which stimulated *S. olneyi* growth before the isopods were consumed by spiders. That detritivore-mediated effects on plant growth were greater on the first (Fig. S2) compared to the second harvest date (Fig. 5) lends some support to the temporal hypothesis.

Decomposition rate, however, was similar in all microcosms containing isopods (Fig. 4) despite reductions in isopod densities when isopods and spiders were present in combination (Figs 3 and S1). Therefore, it is likely that that per capita feeding rate of *L. vittata* isopods on leaf litter was higher when *P. littoralis* spiders were present, which suggests that higher order (consumer–consumer) interactions may be playing an important role in determining the effects of elevated atmospheric CO_2 on ecosystem processes. Such effects could be due to enhanced isopod metabolism resulting from fear of predation as has been demonstrated in grasshopper–spider interactions (Hawlena & Schmitz, 2010), or due to reductions in interference competition among isopods at lower densities, which would allow for increased foraging time for consumers (i.e. McPeek, 1998). Alternatively, it is possible that spider excretions and decomposition of exsanguinated isopod bodies could have priming effects on soil microbial communities with extended effects on decomposition that rivaled in magnitude the direct consumptive effects of litter by detritivores (MacLennan *et al.*, 2011). This is not an unrealistic possibility as similarly dramatic

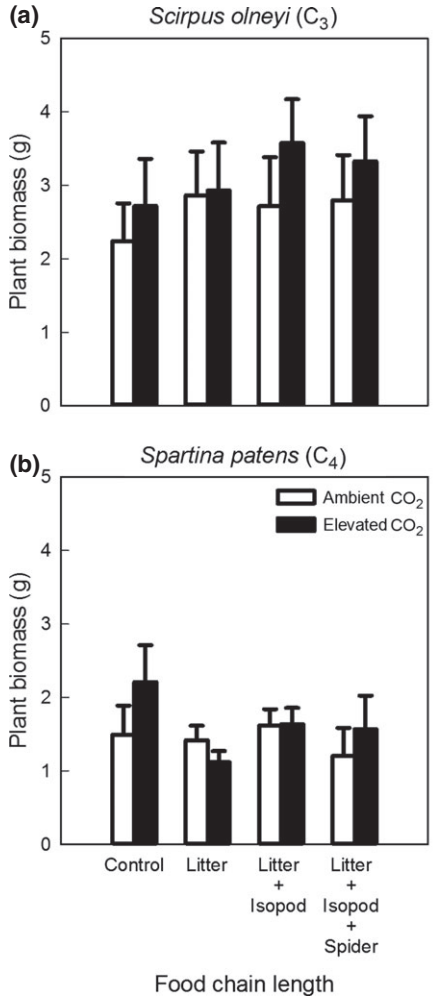

Fig. 5 The influence of altered detritus-based food chain and atmospheric CO_2 conditions [ambient (□) or elevated (ambient + 345 ppm: ■)] on final biomass of (a) the C_3 sedge *Scirpus olneyi*, and (b) C_4 grass *Spartina patens* grown in outdoor microcosms for 84 days.

priming effects have been demonstrated following decomposition of grasshoppers (Hawlena *et al*., 2012).

Although we are not able to isolate the specific interaction pathway by which spider–isopod interactions influence decomposition, our results effectively demonstrate that consumer interactions in the detritus-based food chain influenced *S. olneyi* decomposition, which was also associated with enhanced *S. olneyi* growth response to elevated CO_2. An important caveat is that, contrary to expectation, addition of leaf litter and subsequent feeding by isopods did not result in enhanced shoot biomass in ambient CO_2 conditions for either plant species. This suggests that factors other than nutrients release from litter limited plant growth in these treatments and highlights the importance of context dependency of this interaction pathway. By focusing our microcosm experiment on four different food chain treatments and two abiotic environmental conditions (elevated and ambient atmospheric CO_2), we limited our ability to assess how consistent detritus-based food chain effects will be across a range of climate conditions, such as changes in temperature, salinity, and precipitation. We see much potential for future experiments that follow this line of inquiry.

In conclusion, we find that primary producers and higher trophic levels show differential sensitivity to the effects of inter-annual climate variation and elevated atmospheric CO_2. Although detritivores can be patchily distributed in the field, where present, the magnitude of their influence on litter decomposition and also on shoot biomass can rival in magnitude the interactive effects of elevated CO_2 and other factors of environmental variation, such as precipitation and increased nitrogen deposition (Erickson *et al*., 2007; Reich & Hobbie, 2013; Reich *et al*., 2014). While conservation of habitats that support detritivore consumers may influence the ability of wetlands to absorb some atmospheric CO_2, we do not overlook the potential for other factors, such as methane emissions (Bridgham *et al*., 2013) or competitive exclusion of productive plants (Langley & Megonigal, 2010) to counteract effective carbon sequestration in wetlands. Instead, our results emphasize the importance of approaches that unite traditionally subdivided food web compartments and biogeochemical processes to maximize predictive understanding of ecosystem response to elevated CO_2.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. The effect of atmospheric CO_2 conditions (ambient (□) or elevated (ambient + 345 ppm (■) and predation by *Pardosa littoralis* spiders on percent survival of *Littorophiloscia vittata* isopods after 50 days in microcosms containing either (a) *Scirpus olneyi* or (b) *Spartina patens* plants and leaf litter.

Figure S2. The effect of atmospheric CO_2 conditions (ambient (□) or elevated (ambient + 345 ppm (■) and four different detritus based food chain treatments on biomass of (a) *Scirpus olneyi* and (b) *Spartina patens* plant biomass after 50 days in microcosms.