Consumer trophic diversity as a fundamental mechanism linking predation and ecosystem functioning

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Summary

1. Primary production and decomposition, two fundamental processes determining the functioning of ecosystems, may be sensitive to changes in biodiversity and food web interactions.

2. The impacts of food web interactions on ecosystem functioning are generally quantified by experimentally decoupling these linked processes and examining either primary production-based (green) or decomposition-based (brown) food webs in isolation. This decoupling may strongly limit our ability to assess the importance of food web interactions on ecosystem processes.

3. To evaluate how consumer trophic diversity mediates predator effects on ecosystem functioning, we conducted a mesocosm experiment and a field study using an assemblage of invertebrates that naturally co-occur on North Atlantic coastal saltmarshes. We measured the indirect impact of predation on primary production and leaf decomposition as a result of prey communities composed of herbivores alone, detritivores alone or both prey in combination.

4. We find that primary consumers can influence ecosystem process rates not only within, but also across green and brown sub-webs. Moreover, by feeding on a functionally diverse consumer assemblage comprised of both herbivores and detritivores, generalist predators can diffuse consumer effects on decomposition, primary production and feedbacks between the two processes.

5. These results indicate that maintaining functional diversity among primary consumers can alter the consequences of traditional trophic cascades, and they emphasize the role of the detritus-based sub-web when seeking key biotic drivers of plant production. Clearly, traditional compartmentalization of empirical food webs can limit our ability to predict the influence of food web interactions on ecosystem functioning.

Key-words: above-ground, below-ground, food web complexity, nutrient cycling, trophic cascade

Introduction

One of the central challenges in ecology is to identify factors that affect essential ecosystem processes such as primary production and decomposition (Borer *et al*. 2005; Reiss *et al*. 2009; Gessner *et al*. 2010; Isbell *et al*. 2011). Because of the concern that rapid population declines and species extinctions will compromise the functioning of ecosystems, an increasing number of studies have examined the sensitivity of particular ecosystem processes to changes in biodiversity and trophic structure (Schmitz, Hämback & Beckerman 2000; Reiss *et al*. 2009). Most studies have focused on the role of species diversity within a particular trophic level such as primary producers (Isbell *et al*. 2011), consumers (Srivastava *et al*. 2009) or predators (Schmitz 2007). However, the topology of real food webs is far more complex than simplified trophic levels suggest, but it currently remains unclear how much of the complexity is needed to understand the effects of species interactions on ecosystem processes (Duffy *et al*. 2007; Hillebrand & Matthiessen 2009; O'Gorman *et al*. 2009).

Trophic cascades, the indirect effects of predators on non-adjacent trophic levels, have been found to affect ecosystem processes in both green sub-webs consisting of predators–herbivores–plants (Schmitz 2007) and brown sub-webs composed of predators–detritivores–detritus (Santos, Phillips & Whiford 1981; Rosemond *et al*. 2001) (Fig. 1a). Despite evidence that generalist predators often feed on both herbivores and detritivores, the effects of predator–prey

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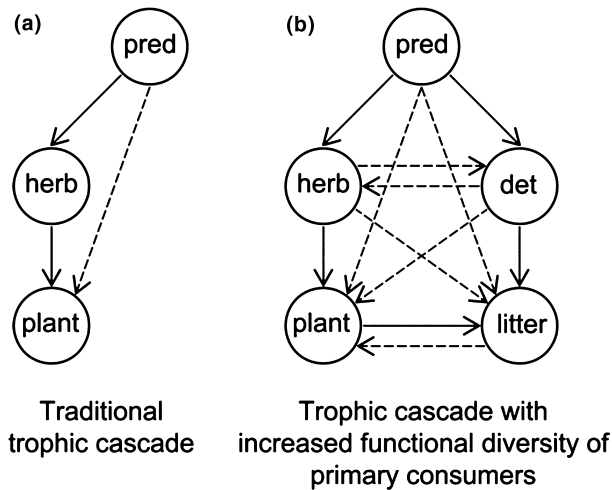
Fig. 1. Conceptual model of possible direct (solid lines) and indirect (dashed lines) interactions in two food webs: (a) The traditional trophic cascade demonstrates the indirect positive effect of predators on plants by consuming herbivores, (b) generalist predators that feed on functionally diverse prey assemblages, composed of both herbivore and detritivores, can have indirect effects on plant production and decomposition, with feedbacks between the two ecosystem processes.

interactions on ecosystem processes have generally been quantified by experimentally decoupling these linked processes and focusing on either green or brown sub-webs in isolation. As a result, the ecosystem consequences of trophic diversity among primary consumers (herbivores and detritivores) have been largely ignored (Knops, Wedin & Tilman 2001; Sylvain & Wall 2011) (Fig. 1b). Specifically, increased trophic diversity within the consumer assemblages could affect persistence of species in each sub-web (Holt & Lawton 1994), and have extended the effects on feedbacks between decomposition and primary production (Wardle *et al.* 2004). These effects have not been explicitly assessed in experiments involving concomitant manipulations of both herbivorous and detritivorous consumers.

Here, we experimentally examine how trophic diversity of primary consumers mediates predator effects on ecosystem functioning, using an assemblage of invertebrates that naturally coexist on *Spartina alterniflora* saltmarshes along the Atlantic coastline of North America (Denno *et al.* 2002; Hines, Megonigal & Denno 2006). An herbivorous planthopper, *Prokelisia dolus* and a detritivorous isopod, *Littorophiloscia vittata*, are among the dominant arthropods in high-marsh habitats (Denno *et al.* 2002; Zimmer *et al.* 2002, 2004). The two consumers share a large hunting spider (*Pardosa littoralis*) as a common predator (Denno *et al.* 2002). Spatial variability in plant productivity and decomposition rate, as well as physical disturbances such as drought and tidal inundation, can lead to a patchy distribution of plant litter across the landscape in these marshes (Denno *et al.* 2002). This situation provides an opportunity to investigate variation in feedbacks between food web structure and ecosystem processes (primary production and decomposition) depending on the

amount of detritus that accumulates at the base of *S. alterniflora* plants (Hines, Megonigal & Denno 2006).

Thus, two main objectives motivated this study: (i) to determine the relative strength of trophic cascades for litter decomposition as opposed to primary production and (ii) to determine the strength of feedbacks between green and brown sub-webs associated with these two ecosystem processes. We test how predation on herbivores and detritivores both alone and in combination affects plant production and litter decomposition. Because the factors that constrain herbivore populations may differ from those constraining detritivore populations (Wu *et al.* 2011), we examined the strength and ecosystem consequences of species interactions in two common saltmarsh habitats, those receiving a litter subsidy and those deprived of a litter subsidy. By identifying species interactions that can influence both decomposition and plant production, this study highlights the importance of examining functionally complete food webs when seeking to identify biotic drivers of ecosystem processes.

Materials and methods

CASCADING EFFECTS OF FOOD WEB STRUCTURE AND LITTER SUBSIDIES ON PLANT PRODUCTION

We conducted an outdoor mesocosm experiment to examine the influence of consumer trophic diversity on the ability of predators to elicit a trophic cascade and affect ecosystem functioning. We measured two ecosystem processes, primary production and litter decomposition, in response to a factorial manipulation of food web structure. Treatments included the presence and absence of predators (*P. littoralis*: 72 m^{-2}; 3 individuals per mesocosm), detritivores (*L. vittata*: 480 m^{-2}; 20 individuals per mesocosm) and herbivores (*Pr. dolus*: 480 m^{-2}; 20 individuals per mesocosm) in all but one of the eight possible combinations. A treatment involving predators without prey was omitted to avoid long starvation of the predators for the experimental duration of nearly 3 months. Initial arthropod densities were chosen to meet four requirements: (i) to fall within the range of field densities (Denno *et al.* 1987, 2002; Zimmer *et al.* 2002), (ii) to allow for possible initial mortality, (iii) to allow for population growth within the carrying capacity of the mesocosms (Finke & Denno 2004), and (iv) to establish equal initial densities of detritivore and herbivore prey. Because the patchy distribution of leaf litter on saltmarshes has the potential to alter feedbacks between primary producer- and decomposer-based food webs, we also established a leaf litter addition treatment by hand-picking fully senesced smooth cordgrass (*S. alterniflora*) litter from the field and adding 25 g of litter dry mass to half of the mesocosms. This corresponds to 600 g m^{-2} or the high end of the range of naturally patchy litter. Thus, there were 14 treatments in total (seven leaf litter withheld and seven leaf litter subsidized), each replicated five times for a total of 70 mesocosms.

Mesocosms were designed to mimic field conditions. They consisted of sand-filled pots (23 cm diameter and 15·5 cm depth) with five transplants of *S. alterniflora* hand-picked from a high-marsh meadow near Tuckerton, NJ, USA (39° 30·8′N, 74° 19·0′W), where the plants were growing at similar densities (21 culms per m^{2}) in the early growing season before tillering occurred. Plants were grown to 10 cm height (*c*. 10 g dry mass per m^{2}) before the experiment started. Standardised pre-experimental growth conditions ensured that initial

shoot biomass varied little and random assignment of treatments to mesocosms precluded effects of any small initial differences. The plants in each mesocosm were enclosed in clear plastic cylinders (cellulose butyrate, 21·5 cm diameter, 30 cm height), capped with a mesh top (0·6-mm mesh, 85% light transmission) and placed in plastic wading pools (120 cm diameter and 15 cm depth) permanently flooded by filling to 13 cm depth with 30 p.p.t. artificial salt water (Instant Ocean, Blacksburg VA, USA). Treatment combinations were blocked by wading pool and located at the Smithsonian Environmental Research Center in Edgewater, MD, USA (38° 53′N, 76° 32′W).

The experiment started on 10 June 2004 and ran for 11 weeks to determine the consequences of food web structure on plant production and litter decomposition. To determine the effect of the food web treatments on plant production, we measured dry mass of *S. alterniflora* shoots in each mesocosm when plants had reached peak biomass at the end of the growing season. To determine decomposition rates, all leaf litter remaining in each mesocosm was removed when the experiment was terminated, dried to constant weight (48 h at 50°C) and weighed to the nearest 0·01 g. Because we could distinguish between the very small amounts of recently senesced leaf litter and experimentally added leaf litter, estimates of litter mass loss were not confounded by the addition of any new litter material. The herbivores (*Pr. dolus*) had reached adult stage in the second of two generations by the end of the experiment. The detritivores (*L. vittata*) reproduced in some mesocosms and were near peak densities at the end of the experiment. The predatory *P. littoralis* moulted to adults but did not reproduce. All animals were collected from mesocosms with a Shop-vac® vacuum sampler (Williamsport, PA, USA) before visually inspecting mesocosms and collecting any remaining arthropods by hand. Arthropods were killed with ethyl acetate vapour, transferred into glass jars containing 70% ethanol and counted in the laboratory.

ARTHROPOD DENSITIES IN TWO COMMON FIELD HABITATS

To compare the final arthropod densities in the mesocosms with natural densities in the field, we conducted a field experiment in a high-marsh meadow near Tuckerton, NJ, USA (39° 30·8′N, 74° 19·0′W), for two consecutive growing seasons (2000, 2001). We chose a completely randomised design using two habitat treatments (ambient leaf litter and twice ambient leaf litter: 600 g m^{-2}) established in a total of twelve 4-m^2 field plots. Litter additions mimicked high and low litter accumulation conditions commonly found in naturally patchy salt-marsh meadows, which include habitat patches nearly devoid of litter. We estimated densities of focal arthropods [herbivores (*Pr. dolus*), detritivores (*L. vittata*) and predators (*P. littoralis*)] on six dates at 3- to 5-week intervals in both years (2001: 31 May, 19 June, 10 July, 31 July, 20 August, 10 September; 2002: 24 May, 19 Jun, 11 July, 25 July, 27 August, 15 September) using a standard sampling procedure (Hines, Megonigal & Denno 2006). Briefly, each sample consisted of three 3-second vacuum suction samples taken with a d-vac® (Ventura, CA, USA) fitted with a 0·20 m^2 nozzle. Arthropods were killed in the field with ethyl acetate vapour before they were transferred to sample jars containing 70% ethanol for counting in the laboratory.

STATISTICAL ANALYSIS

The direct and interactive influence of predators, herbivores and detritivores on decomposition was assessed by three-way ANOVA.

Four-way ANOVA was used to assess the main and interactive effects of the three arthropods and litter addition on plant production (PROC MIXED and SAS, SAS Institute, Cary NC, USA 2001). To assess differences in the final density of each focal arthropod in turn, we used three-way ANOVAs with direct and interactive effects of leaf litter and the two non-focal arthropods in each model. Plastic wading pool was included as a blocking factor with a random source of variation in all models. When overall ANOVA results were significant, treatment means were compared using *t*-tests with a Tukey–Kramer adjustment for multiple means comparisons.

To assess variation in field densities of focal arthropod species, we used mixed-model repeated-measures ANOVA with litter addition, sampling date and the interactive effect of litter × sample date as fixed factors and year (2001 and 2002) as a random factor. A first-order autoregressive covariance structure was selected, because it resulted in the best fit according to Akaike's information criterion (AIC). Arthropod density data were $\log_{10}(x + 1)$-transformed before all analyses to meet the assumptions of homogeneity of variance and normal distribution of residuals.

Results

POPULATION GROWTH OF ARTHROPODS IN MESOCOSMS

In the mesocosm experiment, the two prey species responded differentially to leaf litter and predator subsidies (Fig. 2, Table S1, Supporting information). Detritivore populations did not grow in habitats devoid of litter; detritivore densities after 2 months were roughly the same as the initial densities (final density = 635 ± 286 individuals per m^2, mean ± SEM, $n = 20$; initial density = 480 individuals per m^2; Fig. 2a). Herbivores and predators alone or in combination did not influence detritivore density in mesocosms devoid of leaf litter (herbivore × predator × litter: $F_{1,28} = 0·29$, $P = 0·50$; Table S1, Supporting information; Fig 2a). However, litter addition had a positive effect on detritivore populations ($F_{1,28} = 37·8$, $P < 0·0001$), resulting in three- to sixfold increases from the initial detritivore density (Fig. 2b). Herbivores did not significantly affect detritivore density either interactively with litter ($F_{1,28} = 0·25$, $P = 0·62$) or directly ($F_{1,28} = 0·81$, $P = 0·37$). However, there was an interactive effect of litter and spider predation on detritivore abundance ($F_{1,28} = 4·55$, $P = 0·04$). Predators consumed three times more detritivores in habitats supplemented with leaf litter compared to habitats with no added leaf litter, where detritivores were less abundant overall (Fig. 2b).

In contrast to detritivores, herbivores were not directly affected by the presence of litter ($F_{1,28} = 0·20$, $P = 0·67$; Fig. 2c,d). There was no direct effect of detritivores on herbivore density in mesocosms either with or without litter added (detritivore × litter: $F_{1,28} = 1·73$, $P = 0·20$; detritivore: $F_{1,28} = 0·01$, $P = 0·97$; Fig. 2c,d). In habitats with no added litter, where isopod populations were reduced, predatory *P. littoralis* suppressed *Pr. dolus* herbivores by 43% independent of the presence or absence of *L. vittata* detritivores (Fig. 2c). However, in habitats with added litter, the presence
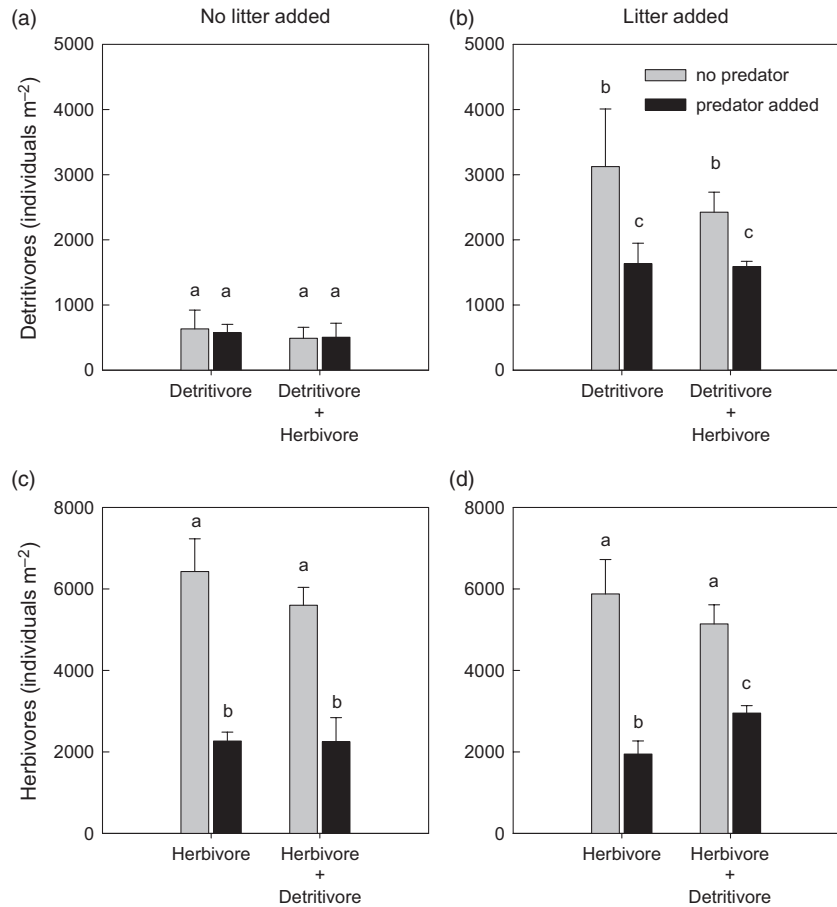
Fig. 2. Final density (mean ± SEM) of detritivore, *Littorophiloscia vittata* (a and b) and herbivore *Prokelisia dolus* (c and d) in mesocosms as a function of food web structure, and leaf litter addition (b and d).

of *L. vittata* alternative prey relaxed predation on herbivores (Fig. 2d; predator × detritivore × litter: $F_{1,28} = 9.26$, $P = 0.005$; predator × detritivore: $F_{1,28} = 5.16$, $P = 0.03$).

Although predators were observed feeding on both prey species during the experiment, predator survival was not sensitive to prey diversity or litter addition in mesocosms. Neither prey species alone nor both in combination significantly affected predator survival (detritivores: $F_{1,24} = 3.00$, $P = 0.09$; herbivores: $F_{1,24} = 0.75$, $P = 0.39$; detritivore × herbivore: $F_{1,24} = 2.04$, $P = 0.18$; Table S1, Supporting information). Litter addition had no interactive (litter × herbivore: $F_{1,24} < 0.01$, $P = 1.00$; litter × detritivore: $F_{1,24} = 0.75$, $P = 0.39$) or direct ($F_{1,24} = 2.53$, $P = 0.12$) effect on *P. littoralis* survival (Table S1, Supporting information).

LITTER DECOMPOSITION AND PLANT PRODUCTION IN MESOCOSMS

Food web structure had cascading consequences on litter decomposition (Fig. 3) and plant production (Fig. 4). Specifically, detritivores enhanced litter decomposition ($F_{1,24} = 27.3$, $P < 0.0001$), with the least litter remaining in mesocosms containing only *L. vittata* detritivores (26.1 ± 9.79 g m^{-2}, mean ± SEM, $n = 5$, Fig. 3a; Table S1, Supporting information). There was an interactive effect of detritivores and herbivores (detritivore × herbivore interac-
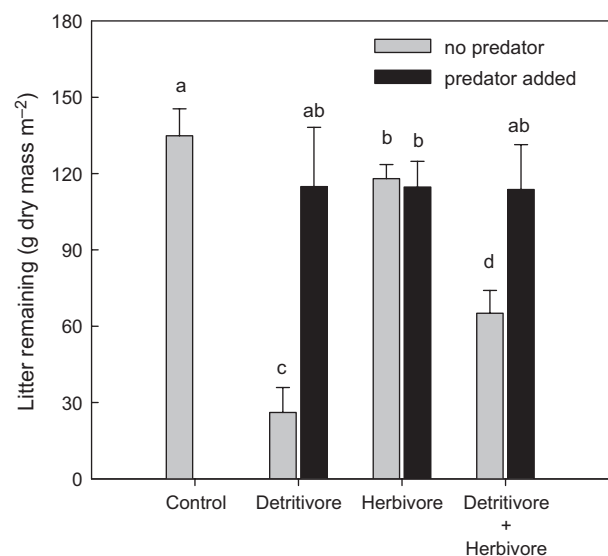

Fig. 3. Direct (a) and predator mediated (b) effects of detritivores and herbivores or both on litter decomposition of *Spartina alterniflora*.

tion: $F_{1,24} = 8.23$, $P = 0.009$; Fig. 3a), whereby herbivores enhanced rates of decomposition on their own (117.9 ± 5.6 g m^{-2}, mean ± SEM, $n = 5$), but diminished the effects on detritivores on leaf litter when both species were present in combination (69.0 ± 9.01 g m^{-2}, mean ±
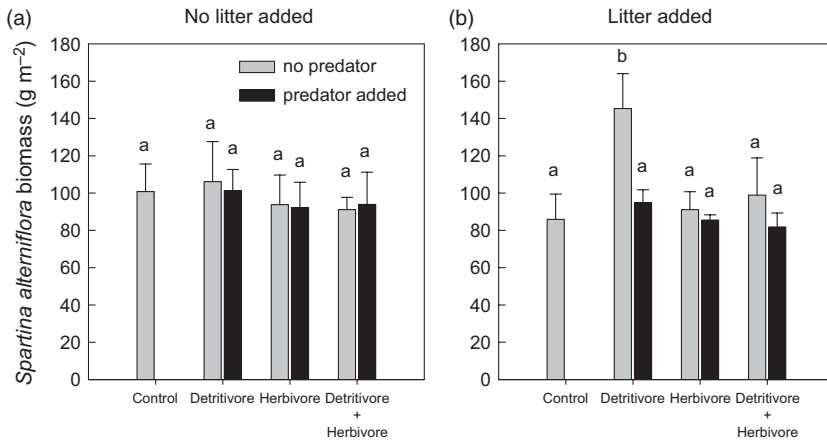
Fig. 4. Direct and indirect effects of herbivores, detritivores and a shared predator on *Spartina alterniflora* biomass production in mesocosms with no leaf litter (a and c) or leaf litter added (b and d).

SEM, $n = 5$). The presence of predators led to a significant increase in leaf litter irrespective of whether herbivores or detritivores were present alone or in combination (detritivore × predator: $F_{1,24} = 2·97$, $P = 0·09$; herbivore × predator: $F_{1,24} = 2·51$, $P = 0·13$; predator: $F_{1,24} = 13·3$, $P = 0·001$; Fig. 3b). Thus, decomposition was influenced by all three arthropod species in this study, either interactively or directly (Fig. 3). Consumer effects on plant production were less pronounced (Fig. 4). Direct feeding pressure by phloem-feeding herbivores did not influence final plant biomass ($F_{1,52} = 1·45$, $P = 0·34$; Fig 4a), and detritivores affected plant production only in litter addition mesocosms

$(145·3 \pm 18·8$ g m^{-2}; Fig. 4b) in the absence of predators (detritivore × predator × litter: $F_{1,52} = 3·89$, $P = 0·05$; Fig. 4d).

ARTHROPOD DENSITIES IN THE FIELD

Final densities of arthropods in mixed species treatments in mesocosms were consistent with peak densities of consumers in open field plots for both litter addition and no litter addition treatments (Figs 3 and 5). However, time of year contributed to variation in density of some invertebrates in the field (Fig. 5, Table S2, Supporting information), an effect we
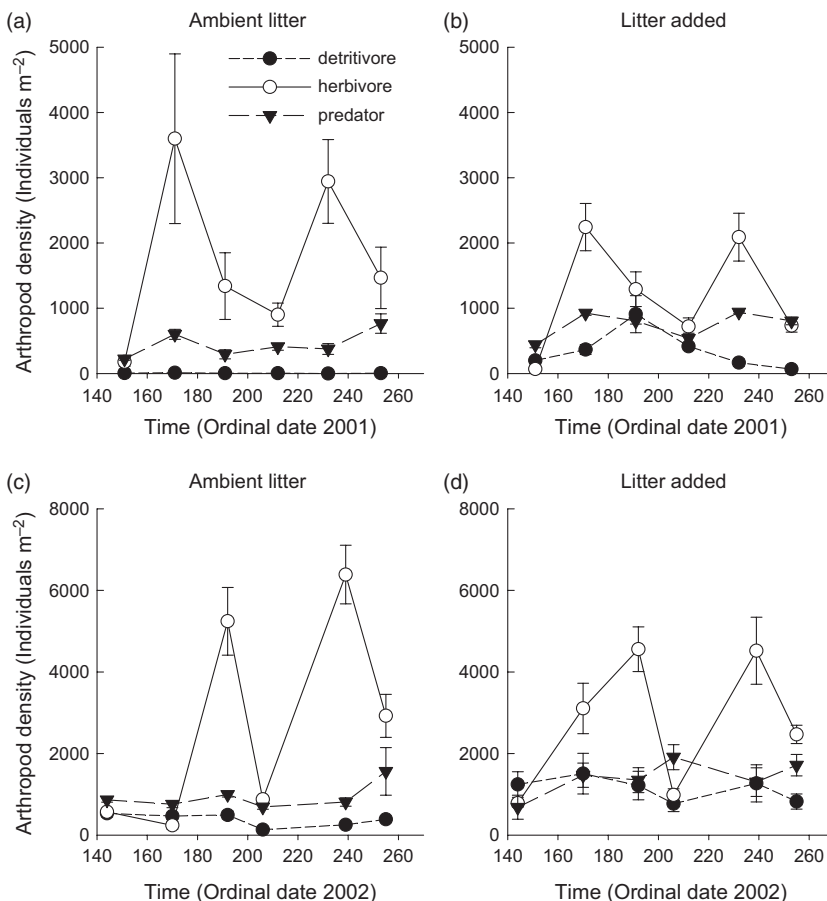

Fig. 5. Dynamics of numerically dominant detritivores (*Littorophiloscia vittata*), herbivores (*Prokelisia dolus*) and predators (*Pardosa littoralis*) in cordgrass (*Spartina alterniflora*) field plots that were either unmanipulated (a and c) or received leaf litter (b and d) in 2001 (a and b) and 2002 (c and d).

could not accurately assess in our mesocosm study. Densities of *Pr. dolus* herbivores with short generation times were most variable throughout the season ($F_{1,115} = 13{\cdot}8$, $P < 0{\cdot}001$; Fig. 5). Detritivores showed a seasonal peak in densities only in litter addition plots in July 2001 ($F_{1,115} = 4{\cdot}07$, $P = 0{\cdot}05$; Fig 5). Season did not explain variation in predator density ($F_{1,115} = 2{\cdot}33$, $P = 0{\cdot}13$). Consistent with the results of our mesocosm study, herbivore densities remained unaffected by litter addition ($F_{1,113} = 0{\cdot}26$, $P = 0{\cdot}61$; Fig. 5c,d). Also consistent with the mesocosms study, detritivores were absent or rare in habitats without leaf litter added and abundant in habitats receiving litter subsidies ($F_{1,113} = 35{\cdot}17$, $P < 0{\cdot}0001$, Fig. 5c,d, Table S2, Supporting information), where predatory *P. littoralis* were also more abundant ($F_{1,113} = 17{\cdot}45$, $P = 0{\cdot}0001$).

Discussion

This study demonstrates asymmetric indirect effects of predation on two fundamental processes in ecosystems, primary production and decomposition, brought about by a generalist predator that consumes both herbivores and detritivores. Specifically, as detritivores (*L. vittata*) strongly affected the amounts of leaf litter in mesocosms (up to 80% resource depletion), with the least litter remaining in mesocosms containing only *L. vittata* detritivores, consumption of detritivores by predacious spiders (*P. littoralis*) suppressed decomposition by over 50% compared to spider-free mesocosms (Fig. 3). Strong predator–detritivore–litter interactions match a classic species-level trophic cascade model (Fig. 1a) and are further supported by results from our field plots where spiders showed a strong aggregative response to litter subsidies accompanied by abundant detritivore prey (Fig. 5).

Plant production was much less sensitive to changes in food web structure than litter decomposition (Fig. 4). Only one of the 14 treatments significantly influenced plant production (Fig. 4). Predators consumed more herbivores than detritivores overall, suggesting that herbivores are preferred prey (Fig. 3). However, because herbivore–plant interactions were weak (Fig. 4a), the strong consumptive effect of predation on herbivores in mesocosms (Fig. 2c,d) did not cascade to influence plant biomass (Fig. 4). The mechanisms (i.e. resource competition and predation) by which species interactions can influence ecosystem processes are equally likely in primary producer- and detritus-based sub-webs (Borer *et al.* 2005; Duffy *et al.* 2007). However, the asymmetric cascade observed in our experiment reveals that particular patterns of strong and weak consumer–resource interactions in the two sub-webs do not necessarily parallel each other. Furthermore, consumer–resource feedbacks do not necessarily operate on the same time-scale in both sub-webs. Plant compensatory growth following herbivory may dampen the effects of herbivores on plant production over the course of a season, but similar increases in litter mass following detritivory would not occur.

Our results show that strong effects of individual consumer species can extend beyond classic sub-web level effects to influence ecosystem process rates in adjacent sub-webs. Increased detritivore density not only enhanced decomposition rates in our mesocosm experiment, but also resulted in almost 40% greater plant biomass by the end of the growing season (Fig. 4b). This result is consistent with studies that demonstrate that mineralization of nutrients from plant litter by detritivores can stimulated plant production (Bardgett & Chan 1999; Laakso & Setälä 1999). Accordingly, plant production was highest where detritivores were most abundant (Fig. 2b) and litter mass loss was greatest (Fig. 3a). The large increase in plant production in the presence of detritivores reflects a realistic scenario given that detritivore densities in the field plots receiving litter subsidies were within the range of those that had a positive effect on plant biomass in the mesocosms (Fig. 5). Therefore, this study lends robust support to the idea that feedbacks through the detritus-based food web and the strength of detritivore–litter interactions can be strong enough to result in changes in live plant biomass in natural field conditions. However, both direct effects of predation and indirect effects of herbivores (see discussion below) can reduce the strength of detritivore–litter interactions and eliminate the positive effect of detritivores on plant production (Fig. 4b,d). This demonstrates that, when placed in a food web context, effects of biodiversity on ecosystem processes can occur via multiple mechanisms (Eisenhauer 2012).

Increased consumer trophic diversity dampened the effects of individual species on both decomposition and primary production, because of reticulate indirect effects between consumers. While these striking effects are evident even in the absence of predation, their interpretation is relatively complex. Decomposition was enhanced not only by litter-consuming detritivores, but also by herbivores when detritivores were absent. That is, herbivores alone enhanced decomposition (Fig. 3a), but diminished the decomposition caused by detritivores when both consumers were present concomitantly (Fig. 3a). Because the phloem-feeding *Prokelisia* herbivores consume neither detritivores nor leaf litter, these context-dependent effects of herbivores on decomposition may result from herbivore-mediated effects on microbial processes, directly via excretions or indirectly as a result of altered detritivore behaviour. Indeed, consistent with our results, a summary of 24 studies showed that arthropods stimulate decomposition more through various indirect effects on microbes than by direct litter consumption (Mikola, Bardgett & Hedlund 2002). Thus, by demonstrating that herbivores can indirectly affect decomposition, our results reveal that classically divided green and brown sub-webs can fail to capture important biotic effects on ecosystem processes. Furthermore, by increasing the number of indirect interactions in reticulate food webs, trophically diverse consumer assemblages (i.e. both herbivorous and detritivorous consumers) can diffuse direct effects of consumers on ecosystem functioning.

Our results also highlight the importance of litter availability as an important component of environmental context for predicting the ecosystem consequences of species interactions in food webs. Habitats without leaf litter subsidies failed to support detritivore population growth; detritivores were absent or rare in habitats without leaf litter and abundant in habitats receiving litter both in mesocosms (Fig 2) and in the field (Fig. 5). Although detritivorous isopods (*L. vittatta*) were often found at the ligules between live stems and senescing *S. alterniflora* leaves where ascomycetes fungi grow, the nutrition provided by senescing litter apparently was insufficient for isopods to reproduce (Zimmer *et al.* 2002). However, increased detritivore densities in litter-rich habitats could have intensified herbivore–detritivore interference competition for ligule space and mediated consumer impacts on plant production and decomposition. In addition, leaf litter subsidies can modify the physical environment, which could reduce isopod exposure to desiccation or provide a refuge that protects juveniles from cannibalism (Zimmer *et al.* 2002). In contrast to detritivores, herbivores were not directly affected by the presence of litter in either the mesocosms (Fig. 2c,d) or the field (Fig. 5c,d). Herbivore populations in mesocosms grew rapidly, with up to 12-fold increases in both the presence and absence of leaf litter (Fig. 2c,d). These differences in the dynamics of consumer densities reveal strong differences in habitat requirements between the two consumer functional groups, providing evidence that the outcome of coupled dynamics between detritivores and herbivores can depend upon environmental context.

Finally, the strength of predation on each consumer was dependent on leaf litter availability. Detritivores were not affected by predation in mesocosms without leaf litter, habitats that failed to support detritivore population growth. This implies that predation on detritivores at low densities of adults was ineffective. Furthermore, in habitats without litter subsidies, where isopod populations were naturally reduced, predatory *P. littoralis* suppressed *Pr. dolus* herbivores by 43% independent of the presence or absence of adult *L. vittata* detritivores (Fig. 2c). In contrast, in habitats containing litter, the presence of juvenile detritivores relaxed the predation pressure on *Pr. dolus* herbivores, as indicated by 40% greater herbivore abundance in mesocosms where detritivores were available as alternative prey (Fig. 2d). Because isopods are on average larger than planthoppers, detritivores may comprise a larger portion of predator diet than suggested by the numbers of individuals alone. However, we were unable to quantify the size class distribution of detritivore prey consumed. Therefore, we cannot discount density-dependent foraging and predator habitat preference as mechanisms by which leaf litter presence can influence the outcome of multispecies interactions.

Because *Spartina* marshes have naturally low plant species diversity, this ecosystem lends well to tests of ecological theory using a mesocosm approach (Benton *et al.* 2007). Nonetheless, it is still possible that the observed effect of predation on herbivore density in our mesocosm experiment was influenced by the closed nature of the mesocosms and by the timing of sampling (Holt & Lawton 1994). However, we could evaluate both of these potential effects by concomitantly tracking invertebrate field densities for two consecutive years. In mesocosms, in the absence of predation and heterospecifics, prey populations grew rapidly and were consistent with the highest densities of animals found during our field study. Notably, animal densities in the field were comparatively high overall during these 2 years (Denno *et al.* 1987). In the field, detritivores served as consistent food resource, and the density of *L. vittata* varied little over the season (Fig. 5), a peak being observed only in July 2001 in field plots receiving additional litter (Fig. 5b), while densities in 2002 were fairly constant (Fig. 5c,d). In contrast, the density of *Pr. dolus* herbivores showed important seasonal variation in the field, with our sampling schedule capturing two distinct peaks in adult densities (Fig. 5). Predatory *P. littoralis* also showed relatively low seasonal variability in the field (Fig. 5). Notably, populations of this predator in mesocosms were not sensitive to either prey functional diversity (i.e. presence of both herbivores and detritivores) or litter addition, as neither primary consumer alone nor both in combination significantly affected predator survival. However, predatory *P. littoralis* were more abundant in habitats receiving litter subsidies in the field. This suggests that spider immigration plays an important role in predator population dynamics in the field, an effect that we did not capture in our mesocosm experiment. The range of final consumer densities in the mesocosms were consistent with the range of species densities observed in the field, suggesting that our treatment combinations in mesocosms reflect potential consumer effects on ecosystem process rates in natural conditions. These results point to the importance of considering population dynamics and trophic complexity in tandem to understand how consumer diversity influences ecosystem functioning.

In conclusion, our results from a reticulate, yet tractably simple food web, demonstrate that by feeding on trophically diverse prey communities generalist predators can buffer plants from strong consumer-mediated effects of both herbivore and detritivore functional groups. Although the strength of species interactions in both green primary producer-based and brown detritus-based food webs may be strong enough to cascade to non-adjacent trophic levels, increases in consumer trophic diversity can result in indirect species interactions that reduce the net impact of generalist predators on key ecosystem processes (i.e. plant production and decomposition). Therefore, including detritivore prey in primary producer-based food webs can alter the strength and pathways of trophic cascades, with consequences for both suppression of herbivores and production of new plant biomass. Clearly, traditional subdivisions of consumer species into sub-webs based on their primary trophic role (detritivore or herbivore) do not sufficiently capture the range of biotic effects on ecosystem functioning.

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Author contributions

JH designed research, JH performed research, JH analysed data, JH & MOG wrote the paper.

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Supporting Information

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

Table S1. ANOVA results for the main and interactive effects of four factors [detritivores (D), herbivores (H), predators (P), and leaf litter (L) presence] on invertebrate density, litter decomposition, and above-ground production of *Spartina alterniflora* in outdoor mesocosms.

Table S2. Repeated-measures ANOVA results showing the response of salt marsh invertebrate species to litter addition in 2-m^2 *Spartina alterniflora* field plots on six dates in 2001 and 2002.

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