OIKOS

Research

Species identity and the functioning of ecosystems: the role of detritivore traits and trophic interactions in connecting of multiple ecosystem responses

Jes Hines and Nico Eisenhauer

J. Hines (https://orcid.org/0000-0002-9129-5179) ✉ (jessica.hines@idiv.de) and N. Eisenhauer, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; and Inst. of Biology, Leipzig Univ., Leipzig, Germany. JH also at: Smithsonian Environmental Research Center, Edgewater, MD, USA.

Oikos
130: 1692–1703, 2021
doi: 10.1111/oik.08333

Subject Editor: Matty Berg
Editor-in-Chief: Dries Bonte
Accepted 17 June 2021

Ecosystems world-wide experience changes in species composition in response to natural and anthropogenic changes in environmental conditions. Research to date has greatly improved our understanding of how species affect focal ecosystem functions. However, because measurements of multiple ecosystem functions have not been consistently justified for any given trophic group, it is unclear whether interpretations of research syntheses adequately reflect the contributions of consumers to ecosystems. Using model communities assembled in experimental microcosms, we examined the relationship between four numerically dominant detritivore species and six ecosystem functions that underpin fundamental aspects of carbon and nitrogen cycling above- and below-ground. We tested whether ecosystem responses to changes in detritivore identity depended upon species trait dissimilarity, food web compartment (aboveground, belowground, mixed) or number of responses considered (one to six). We found little influence of detritivore species identity on brown (i.e. soil-based) processes. Only one of four detritivore species uniquely influenced decomposition, and detritivore species did not vary in their influence on soil nitrogen pools (NO_3^- and NH_4^+), or root biomass. However, changes in detritivore identity influenced multiple aboveground ecosystem functions. That is, by serving as prey, ecosystem engineers and occasionally also as herbivores as well as detritivores, these species altered the strength of aboveground predator–herbivore interactions and plant–shoot biomass. Yet, dissimilarity of detritivore functional traits was not associated with dissimilarity of ecosystem functioning. These results serve as an important reminder that consumers influence ecosystem processes via multiple energy channels and that food web interactions set important context for consumer-mediated effects on multiple ecosystem functions. Given that species are being lost, gained and redistributed at unprecedented rates, we can anticipate that changes in species identity will have additional ecosystem consequences beyond those predicted by species' primary functional role.

Keywords: aboveground–belowground, alternative prey, detritivore, ecosystem engineer, ecosystem multifunctionality, herbivore suppression, predation, trophic interactions, species identity

NORDIC SOCIETY OIKOS

www.oikosjournal.org

Introduction

A major goal in ecological research is to understand the consequences of changes in biological diversity for ecosystem functioning (Cardinale et al. 2012, Tilman et al. 2014, Isbell et al. 2017). Therefore, many scientists have conducted experiments where they manipulated species richness and measured the productivity or resource uptake of focal communities (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006). Cumulatively, these experiments have demonstrated that less diverse communities consistently produce less biomass, and typically support reduced ecosystem process rates (Cardinale et al. 2011).

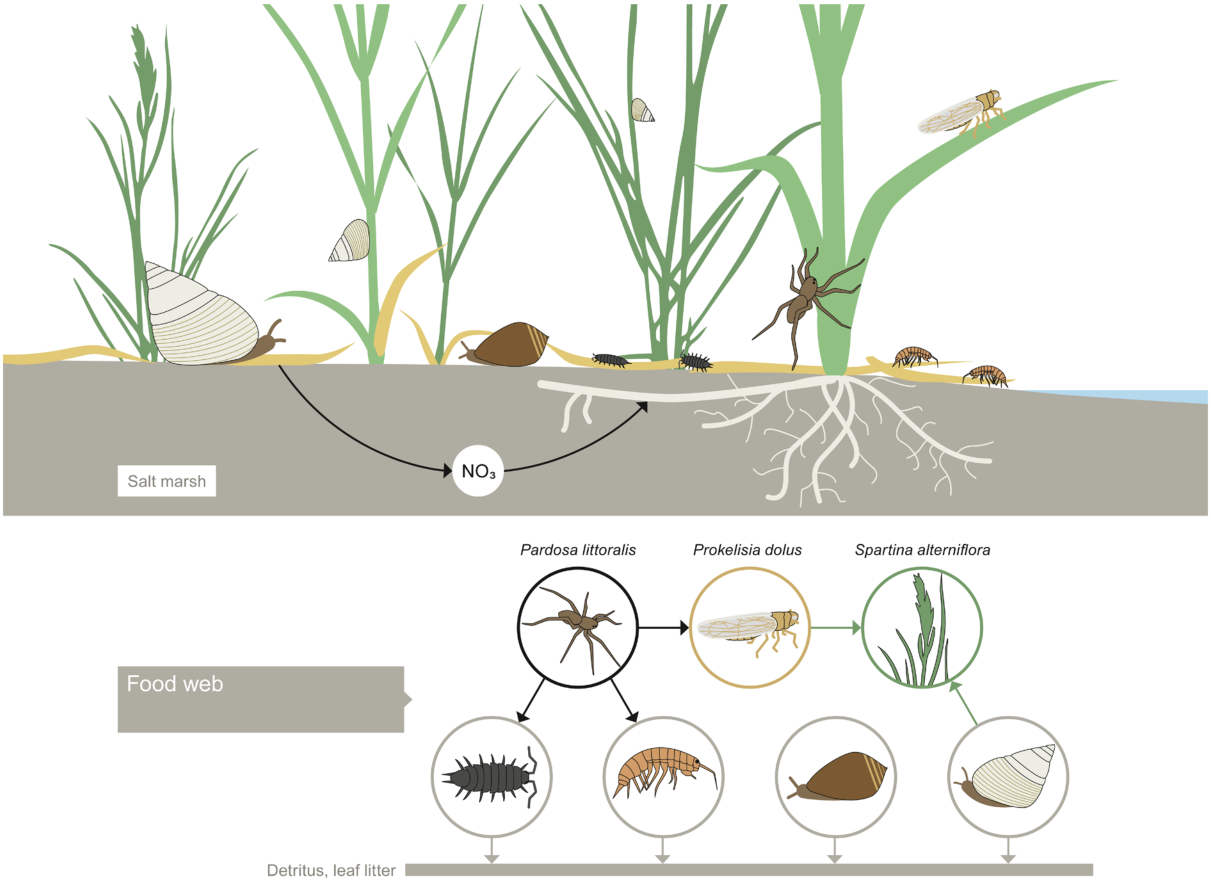
Notably, previous conclusions about the influence of diversity change on ecosystem functioning have been based predominately on plant communities, despite the fact that consumers feeding at higher trophic levels may be relatively more vulnerable to environmental change (Voigt et al. 2003, Hines et al. 2015a). Moreover, in many cases, species losses from ecosystems can be balanced by species gains (Vellend et al. 2013, Dornelas et al. 2014), which has led to skepticism about whether conclusions from classic biodiversity experiments adequately describe ecosystem responses to realistic changes in biological communities (but see Eisenhauer et al. 2016, Wardle 2016). That is, communities often experience high compositional turn-over in species identity (β-diversity) in response to natural and anthropogenic disturbances in environmental conditions, even when there is no change in local species richness (Dornelas et al. 2014). Therefore, it is important to anticipate how changes in species identity will influence the functioning of ecosystems.

One basis for considering species contribution to ecosystems is to identify functional groups of species that share similarities in traits, or groups of traits, that determine the way the group regulates an ecosystem process (Laureto et al. 2015). Such traits can be quantified on axes that describe morphological, physiological, behavioral and life history characteristics (Ellers et al. 2018). Emphasis is often placed on 'effect' traits related to resource use, consumption-based processes (Pla et al. 2012), and to a lesser extent, how species activity may influence the structure of their habitat (Lawton 1994, Jones and Lawton 1995). For example, invertebrate detritivores drive decomposition via direct consumption of detritus, by influencing microbial dynamics, and by physical shredding of litter (Zimmer et al. 2004). In this context, functional group is considered to be synonymous with trophic level. Theory suggests that for a given trophic/functional group, dissimilarity in traits indicates differences in proficiency with respect to a focal ecosystem process (Chapin et al. 1997, Louca et al. 2018).

Although discrete functional groups have a superficial appeal, it has long been recognized that these groupings mask more complex influences of species on multiple processes that sustain an ecosystem (Hines et al. 2015b, Risch et al. 2018). It is tempting to suggest that trait dissimilarity may also be used to predict dissimilarity in multiple ecosystem functions (Heemsbergen et al. 2004). However, hierarchical (Holzwarth et al. 2015) or nonlinear relationships between trait dissimilarity and dissimilarity of single functions (Cadotte 2017) may inhibit detection of multivariate trait–function relationships. Accordingly, it has been suggested that measuring more ecosystem functions (ecosystem multifunctionality), rather than traits, could be used to document species' unique contributions to ecosystems, and could be an informative way to quantify ecosystem responses to biodiversity change (Byrnes et al. 2014).

Unfortunately, measures of ecosystem multifunctionality have not been standardized across study systems or trophic groups, and careful consideration of methods is needed to interpret results (Bradford et al. 2014, Manning et al. 2018, Giling et al. 2019). For example, in a research synthesis describing the consequences of changes in biodiversity on ecosystem multifunctionality of four distinct trophic groups, Lefcheck et al. (2015) found no evidence that changes in detritivore diversity influence ecosystem multifunctionality. Yet, in the seven independent experimental manipulations of detritivore diversity that fit the criteria for their analysis, typically fewer than three functions were reported (mean = 2.5, mode = 2, n = 17) (Lefcheck et al. 2015). Additionally, all of the reported functions describe responses related to decomposition or detritivore growth, which would be more typical of consumer–resource dynamics (Lefcheck et al. 2015). Given that detritivores are notorious omnivores, quantifying their influence on either brown (i.e. soil- and decomposition-based processes) or green (primary producer-based processes) functions in isolation may insufficiently assess their influence on ecosystem functioning (Hines and Gessner 2012, Mulder et al. 2013). Experiments reporting a broader array of ecosystem functions that are more clearly linked to food web dynamics and realistic species changes are needed to assess the multifunctional role of detritivores in ecosystems (Hines et al. 2015b, Mancinelli and Mulder 2015).

Here we use model communities, composed of common salt marsh plant and invertebrate species, to test how changes in detritivore communities influence ecosystem multifunctionality. We quantify six ecosystem functions that serve as proxies for the suite of ecological processes that broadly represent ecosystem functioning (Hector and Bagchi 2007, Gamfeldt et al. 2008). To assess how well classic functional–group assignments capture species' main roles in ecosystems (i.e. how effects of different detritivores extended beyond effects on decomposition), we also test whether effects of detritivores on ecosystem functions are dependent upon food web compartment (belowground, aboveground or combinations of aboveground and belowground functions), or the number of functions considered (1–6). We expect that all detritivores will affect decomposition and subsequent nutrient mineralization, but that the multifunctional role of detritivores will be revealed by examining a broader range of ecosystem functions associated with food web interactions (Fig. 1). Specifically, 1) by consuming and mineralizing leaf litter, detritivore activity may subsidize nutrients available for plant uptake, enhance plant quality for herbivores, and indirectly support herbivore population growth. Additionally,



		Littorophiloscia vittata	*Orchestia grillus*	*Melampus bidentatus*	*Littoraria irrorata*
Food Resource	Detritus	yes	yes	yes	yes
	Live plants	no	no	no	yes
	Microbes	grazing	grazing	farming	farming
Activity	Body size (mm)	4	5.5	<13	<30
	Ecosystem engineer	no	yes	no	yes
	Defense against spiders	chitin	chitin	calcium carbonate	calcium carbonate
	Mobility	walk	jump	crawl	crawl
	Vertical stratification	indifferent	ground	ground	indifferent
Density	Density (Individuals m-2) (upper limit; common)	1000; 400	2000; 150	3000; 400	220; 25
References		(Newell and Porter 2000; Zimmer et al. 2004)	(Graça et al. 2000; Wildish et al. 2011)	(Graça et al. 2000; Zajac et al. 2017)	(Schindler et al. 1994; Silliman and Newell 2003)

Figure 1. Conceptual diagram and paired table showing feeding interactions and functional traits of four numerically dominant salt marsh detritivores: *Littoraria irrorata*, *Melampus bidentatus*, *Orchestia grillus*, *Littorophiloscia vittata*. Feeding interactions are shown as arrows pointing from consumer to resource. Species functional traits related to food sources (detritus, microbes, live plants) and activity (body size, ecosystem engineering and vulnerability to spider predation) characterize functional dissimilarity among four numerically dominant salt marsh detritivore species, while unique combinations of traits can be used to characterize species identity. Throughout the text species are referred to by their genus name.

2) by serving as alternative prey, detritivores can maintain predator populations, and enhance predation on herbivores. However, leaf litter structure provides a component of habitat complexity that is the preferred habitat of spiders, in part, because it provides refuge from cannibalism (Langellotto and Denno 2004). Therefore, 3) by modifying habitat structure (i.e. ecosystem engineering) detritivores can indirectly influence populations of predators and their herbivore prey. Depending on the vulnerability of detritivores to predation, and the strength of their influence on decomposition, some predicted influences on the aboveground community can differentially promote predator populations (1), subsidize herbivore populations (2) or potentially destabilize predator–herbivore dynamics (3). Therefore, the extent to which each effect attenuates or cascades to influence all measured ecosystem functions likely depends on the unique combinations of traits of the detritivores (Fig. 1).

Methods

Study system

Along the Atlantic coast of North America, the single cordgrass species, *Spartina alterniflora*, can form expansive monospecific stands (Valiela et al. 1976, Mendelssohn 1979, Mendelssohn et al. 1981, Bradley and Morris 1991). In the decomposition based 'brown' food web compartment, there are four common detritivorous species: *Littorophiloscia vittata*, *Orchestia grillus*, *Melampus bidendatus*, *Littoraria irrorata* (Fig. 1 for description of traits, abundances and trophic interactions). The aboveground 'green' food web compartment is numerically dominated by the phloem-feeding herbivore *Prokelisia dolus* (Delphacidae: Hemiptera) and the generalist spider predator *Pardosa littoralis* (Araneae: Lycosidae) (Denno et al. 2002). *Prokelisia* herbivores are sensitive to changes in host plant nitrogen, and can reach densities as high as 50 000 individuals m^{-2} in patches of high-quality (high % N) *S. alterniflora* plants (Hines et al. 2006). *Pardosa* wolf spiders have been reported to consume *Prokelisia* (Denno et al. 2002), as well as detritivorous prey, such as isopods and amphipods (Morse 1997, Hines and Gessner 2012) (Fig. 1). *Pardosa* aggregate in areas rich in *Spartina* leaf litter because the structural complexity of the litter provides refuge from cannibalism, allowing for enhanced prey suppression (Langellotto and Denno 2004).

Experimental design

To determine the influence of changes in detritivore species on multiple ecosystem functions, we established five detritivore treatments in microcosms. Species densities were chosen to fall within the range of naturally variable field densities, and also to establish communities with comparable detritivore biomasses (Fig. 1): no detritivore, 50 *Littorophiloscia vittata*, 50 *Orchestia grillus*, 50 *Melampus bidentatus* or 5 *Littoraria irrorata*) (Graça et al. 2000, Zimmer et al. 2002, 2004). These microcosm densities correspond to 52 *Pardosa* m^{-2}, 130 *Littoraria* m^{-2} and 1315 individuals m^{-2} for each the species stocked at 50 individuals per microcosm. To tease apart the influences of detritivores that are realized via nutrient/decomposition pathways from influences on ecosystem functioning that are a consequence of their role as prey (Hines and Gessner 2012, Hines et al. 2015a), the detritivore treatments were crossed with two levels of spider predation (4 *Pardosa littoralis* present or absent). The full experimental was a randomized complete block, 5 × 2 factorial design experiment, which consisted of 10 treatments that were replicated in each of nine spatial blocks, resulting in 90 microcosms. The experiment was located in a common garden habitat, at the Smithsonian Environmental Research Center in Edgewater, MD.

Each microcosm consisted of a sand-filled pot (22 cm diameter × 21 cm deep) with five transplants of small *Spartina* plants, 25 g *S. alterniflora* leaf litter and 30 adult *Prokelisia* herbivores (25 females and 5 males, corresponding to 825 individuals m^{-2}). Potted plants were enclosed in clear plastic tube cages (21.5 cm diameter × 30 cm tall), capped with a mesh top, and pots were placed in plastic pans (30 cm diameter × 10 cm deep) filled with water. Treatments were established in a sequential fashion that approximated the phenology of field interactions. Detritivore species, which remain in meadow habitats year-round, were added on 7 June 2007 and were allowed to settle and feed before herbivores emerged. *Prokelisia* herbivores, which overwinter as nymphs in leaf litter and emerge as adults by the end of June, were added to microcosms on 25–27 June 2007 and allowed to settle for four days, before four juvenile *Pardosa* spiders were added to half of the microcosms.

The experiment was terminated on day 60, when visual counts indicated that the second generation adult planthoppers began a slight natural decline (Denno and Roderick 2003). Because detritivores and spiders were often hidden in the leaf litter, it was not possible to obtain a visual assessment of their densities throughout the course of the experiment. Therefore, final invertebrate densities were obtained by collecting all animals from microcosms using a vacuum sampler fitted with mesh bags. Arthropods were killed using ethyl acetate, transferred into plastic bags, before they were counted in the laboratory.

To assess plant growth and litter mass loss, *S. alterniflora* litter, root and shoot biomass was harvested, washed and sieved through 1.7 mm sieves, freeze-dried and weighed to the nearest 0.01 g. Because damage imposed by phloem feeders can be difficult to detect, we did not distinguish between loss of plant biomass caused by detritivore grazing and phloem feeding herbivores. Instead, herbivore abundance was used as a proxy for herbivory by strict herbivores, which is in line with rationale for energy flux to herbivores (Barnes et al. 2018, Gauzens et al. 2019), but could overlook the potential for non-linear density dependent feeding rates (Hines et al. 2016) or non-consumptive effects of predators (Peckarsky et al. 2008). That is, herbivory was considered as ability of the ecosystem to support two generations of herbivore populations during the course of the experiment, and is a proxy related to secondary production of herbivores. *Pardosa* predators molted to adults but, due to longer generation times, they did not reproduce during the time course of the experiment. Nonetheless, for consistency, we also consider persistence of predators as a measure of predation potential. Soil inorganic soil nitrogen (NH_4^+ and NO_3^-) was extracted using 2.0 M KCl (Mulvaney 1996).

Statistical analysis

We used a mixed model ANOVA (lme Pinheiro et al. 2014) to assess the influence two fixed factors (i.e. detritivore identity and predator presence) on six individual functions as well as ecosystem multifunctionality. For all analyses, the microcosm was considered as the experimental unit in which response variables were reported and spatial block was included as a random factor. To calculate average ecosystem multifunctionality, we used the averaging approach (Byrnes et al. 2014), and included the average of all possible reported response variables in each microcosm (shoot biomass, root biomass, litter decomposition rate k, nutrient concentration [NO_3^-], herbivore abundance, predator abundance). Predator abundance was not included in the calculation when predators were absent. Because standardized nutrient concentrations of NH_4^+ and NO_3^- were similar, and neither molecule was sensitive to treatments in this experiment, we chose to report NO_3^- in the average ecosystem multifunctionality metric and text.

We used another mixed model analysis to consider how two additional factors (i.e. food web compartment, and number of functions included in the average multifunctionality metric) influenced the average multifunctionality responses in the original 2 × 5 factorial experimental. In this analysis, we calculated average multifunctionality for each microcosm using all viable combinations of 1, 2, 3, 4, 5 and 6 standardized functions that filled the criteria of being from aboveground compartment, belowground compartment or mixed compartment multifunctionality metric that included a combination of at least one aboveground and one belowground function. The experimental design was necessarily unbalanced as some combinations of covariate calculations were not possible (e.g. mixed aboveground–belowground compartment with only one function, or aboveground compartment with three functions when predators were absent). For this analysis, we were interested in how the number of functions and/or the focal compartment influenced variation in multi-functionality results, rather than the specific combination of functions included in calculations for each microcosm. Therefore, we included the identity of function combinations in the model as a random factor. Spatial block was also included in the model as a random factor. Following significant ($p < 0.05$) mixed model results, we used pairwise comparisons with Tukey's adjustment for multiple comparisons to identify significant treatment differences (lsmeans: Lenth 2018). All data met assumptions of homogeneity of variance and normality of residuals.

To test whether dissimilarity in species functional traits were associated with dissimilarity in multiple ecosystem functions, we constructed distance matrices both for species traits and for the ecosystem functions performed by model communities with and without predators (Gower 1971). Subsequently, we used a partial mantel test to examine correlations between the three distance matrices (species traits, functioning of communities with or without predators) (Vegan: Legendre and Legendre 1998, Oksanen et al. 2019).

Results

Individual functions

The most rapid decomposition occurred when *Melampus* was present (Fig. 2A). The other two belowground functions, nitrate availability (Fig. 2B) and root production (Fig. 2C) were not influenced by detritivore species either alone (open circles), or when detritivores and predators were present in combination (filled circles). Consequently, only one-of-three belowground ecosystem response variables was sensitive to turnover in detritivore identity (Fig. 2A–C, Table 1).

Aboveground ecosystem functioning was comparatively more sensitive to changes in detritivores, and observed effects were partly moderated by predator–detritivore interactions (Fig. 2D–F). In the absence of detritivores, *Pardosa* spiders survived (Fig. 2D). *Prokelisia* populations were suppressed to low densities in detritivore-free communities when spiders were present compared to when spiders were absent (Fig. 2E). These differences in herbivory (i.e. herbivore abundance) attenuated, leaving plant shoot biomass unaffected by the presence or absence of predators in control treatments (Fig. 2F). Microcosms with *Littorophiloscia* also supported predation (i.e. predator survival; Fig. 2D), but predators did not suppress herbivores as strongly when this source of alternative prey was available (filled circles; Fig. 2E). *Orchestia* was less effective as a source of alternative prey (Fig. 2D–E). That is, there were no differences in predator or herbivore survival when *Orchestia* was present, compared to when detritivores were absent (Fig. 2D–E). Communities where *Melampus* was present had enhanced *Spartina* shoot biomass compared to when *Orchestia* or *Littoraria* were present, but no significant effects on predators, or herbivores (Fig. 2F, Table 1). Microcosms with *Littoraria* were associated with the reductions in all three aboveground ecosystem functions, namely reduced predator survival (Fig. 2D), lower herbivore abundance in the presence and absence of predators (Fig. 2E), and less plant shoot biomass (compared to *Melampus* Fig. 2F).

Ecosystem multifunctionality

Ecosystem multifunctionality (EMF) was sensitive to changes in detritivore identity and the presence of predators (Fig. 3, Table 2). Trait dissimilarity, however, was not associated with dissimilarity in ecosystem functions (partial Mantel test between traits and ecosystem functions with predators:

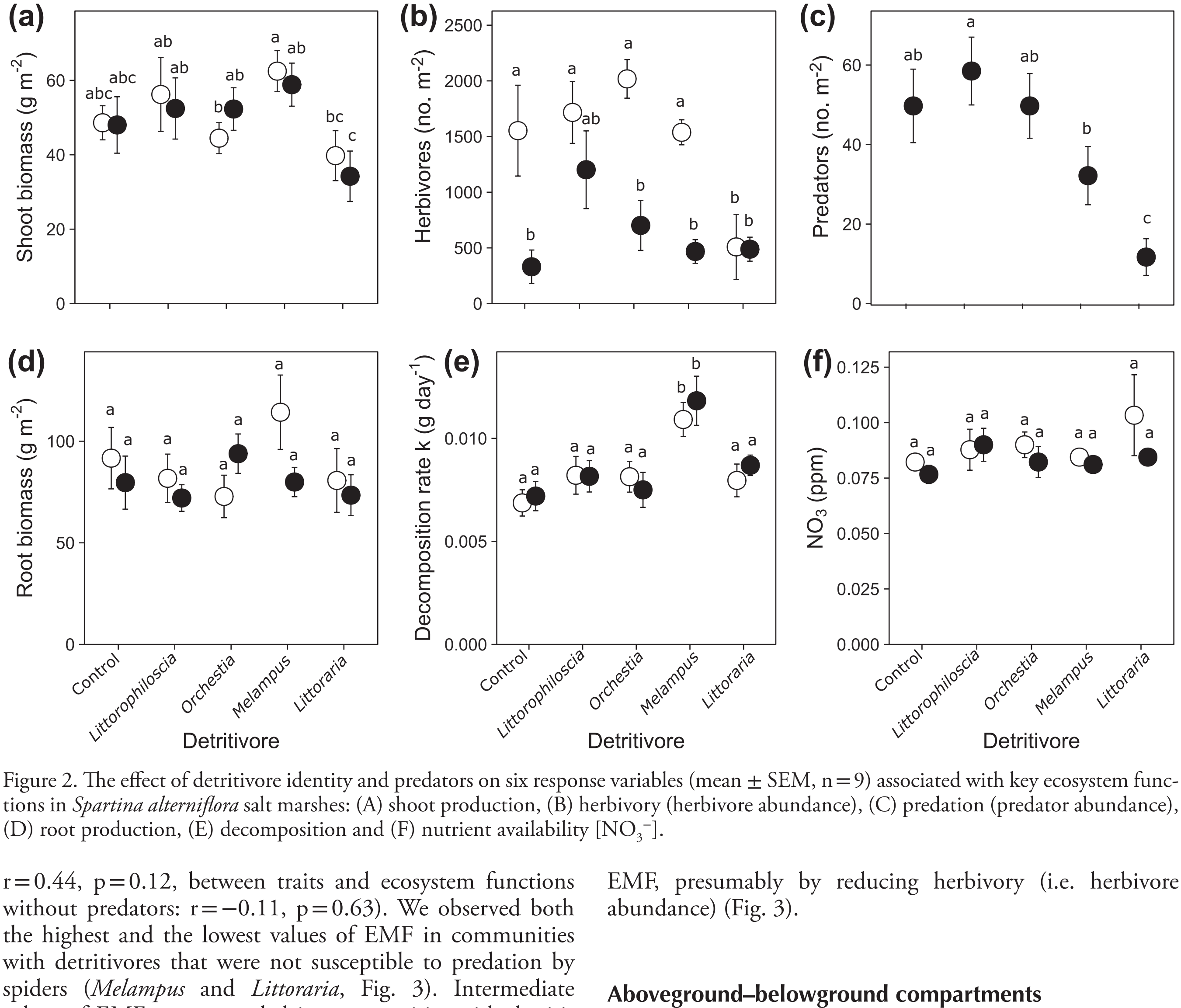


Figure 2. The effect of detritivore identity and predators on six response variables (mean ± SEM, n = 9) associated with key ecosystem functions in *Spartina alterniflora* salt marshes: (A) shoot production, (B) herbivory (herbivore abundance), (C) predation (predator abundance), (D) root production, (E) decomposition and (F) nutrient availability [NO_3^-].

r = 0.44, p = 0.12, between traits and ecosystem functions without predators: r = −0.11, p = 0.63). We observed both the highest and the lowest values of EMF in communities with detritivores that were not susceptible to predation by spiders (*Melampus* and *Littoraria*, Fig. 3). Intermediate values of EMF were recorded in communities with detritivores that were susceptible to predation (*Littorophiloscia* and *Orchestia*) (Fig. 3). Presence of predators typically reduced EMF, presumably by reducing herbivory (i.e. herbivore abundance) (Fig. 3).

Aboveground–belowground compartments

The effects of detritivore identity on EMF were predominately realized via effects in the aboveground compartment,

Table 1. Mixed model ANOVA results show the main and interactive effects of the detritivore identity and predator-addition treatments on ecosystem multifunctionality (EMF) derived from the six individual functions (herbivore abundance, shoot biomass, predator abundance, litter biomass, root biomass and NO_3^- concentrations) measured in common garden microcosms after 60 days exposure to treatments. Significant p-values ($p < 0.05$) appear in bold for clarity.

	Response	Detritivore identity (D)		Predator presence (P)		D × P	
	df*	4, 72		1, 72		4, 72	
Compartment		F	p	F	p	F	p
	Total EMF	**8.12**	**< 0.001**	***7.85***	**0.007**	0.76	0.55
Aboveground	Herbivore abundance	**4.93**	**0.001**	**29.12**	**< 0.001**	**2.55**	**0.04**
	Shoot biomass	**3.75**	**0.008**	0.08	0.78	0.35	0.85
	Predator abundance	**6.06**	**0.001**	NA	NA	NA	NA
Belowground	Litter biomass	**9.83**	**< 0.001**	0.29	0.58	0.34	0.85
	Root biomass	1.04	0.39	1.36	0.24	1.48	0.22
	NH_4^+	0.37	0.82	0.06	0.79	1.06	0.37
	NO_3^-	1.36	0.26	2.44	0.12	0.66	0.61

*df show degrees of freedom (numerator, denominator) for all response variables except predator abundance which is 4, 32.

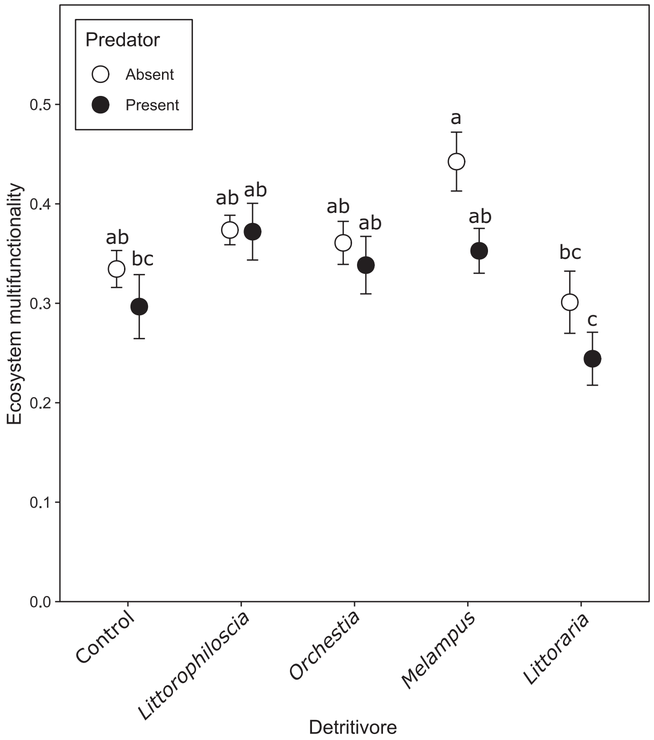


Figure 3. Direct and predator mediated effects of changes in detritivores on average ecosystem multifunctionality based on standardized values of six variable that represent key ecosystem functions above and below the ground: plant shoot biomass, herbivore abundance, predator abundance, plant root biomass, decomposition, nutrient concentration (NO_3^-).

and comparatively few effects were observed for belowground functions or by including combinations of functions from both aboveground and belowground compartments. Moreover, and variability in EMF dampened with increasing number of functions averaged (Fig. 4, Table 2).

Detritivore density

Littorophilosica populations maintained near initial densities in absence of spider predation (1157 ± 392 individuals m^{-2}; mean ± SE, n = 9), and were limited when *Pardosa* predators were present (424 ± 278 individuals m^{-2}; mean ± SE, n = 9). *Orchestia* populations maintained lower population densities overall, and were only weakly suppressed by the presence of spiders (524 ± 36 individuals m^{-2}; mean ± SE, n = 9) compared to the spider-free control (601 ± 52 individuals m^{-2}; mean ± SE, n = 9). All snails survived but none reproduced during the experiment, which resulted in final densities that were consistent with the initial densities stocked in the microcosms.

Discussion

Our results show that changes in detritivore identity influence multiple aspects of ecosystem functioning. Our model communities exemplify three typical pathways by which detritivores' influences on EMF can arise. First, prolific detritivory by *Melampus* enhanced decomposition, and conceivably litter mineralization released nutrient resources that could be available for rapid plant uptake and growth. We did not, however, observe changes in the standing stocks of nutrients in the presence of *Melampus*. This could have been because we chose to assess all six ecosystem functions at the same time, rather than reporting maximum possible influence of detritivores on all ecosystem functions that respond at different rates. That is, nitrate could have been rapidly mobilized within hours or days, whereas effects on predator population growth could be realized only after a full year. Furthermore, the slight trends toward increased plant root and shoot biomass in the presence of *Melampus* were not significant when quantified as individual functions, but they contributed to increased multifunctionality when considered in an aggregated metric (EMF) together with enhanced decomposition. This suggests that multifunctionality may be useful for capturing cumulative effects on ecosystem functioning despite temporal variation of effects for individual functions. Second, detritivorous *Littorophiloscia* served as alternative prey and moderated predator–herbivore interactions. Yet, the observed positive effects on predation and herbivory (measured as predator and herbivore abundance) did not coincide with enhanced

Table 2. Mixed model ANOVA results show the main and interactive effects of detritivore identity, predator addition and number of functions included in ecosystem multifunctionality (EMF) calculated using aboveground functions, belowground functions or mixtures of aboveground and belowground functions (Table 1 for compartment designations of individual functions). Significant p-values ($p < 0.05$) appear in bold for clarity.

	Ecosystem multifunctionality (EMF)								
	Aboveground (AG) EMF			Belowground (BG) EMF			Mixed AG–BG EMF		
	dfn*	F	p	dfn*	F	p	dfn*	F	p
Detritivore identity (D)	4	**4.87**	**< 0.0001**	4	**12.92**	**< 0.0001**	4	**15.9**	**< 0.0001**
Predator presence (P)	1	**14.65**	**< 0.0001**	1	2.73	*0.09*	1	**74.8**	**< 0.0001**
Number of functions (N)	2	0.22	0.80	2	0.00	1.00	4	0.49	0.74
D × P	4	**3.59**	**0.007**	4	0.35	0.87	4	**16.48**	**< 0.0001**
D × N	8	0.30	0.96	8	0.00	1.00	16	0.37	0.98
P × N	1	0.005	0.94	2	0.00	1.00	3	0.32	0.81
D × P × N	4	0.11	0.98	8	0.00	1.00	12	0.12	0.99

*Numerator degrees of freedom. Denominator degrees of freedom approximated with Saitterthwaite's method.

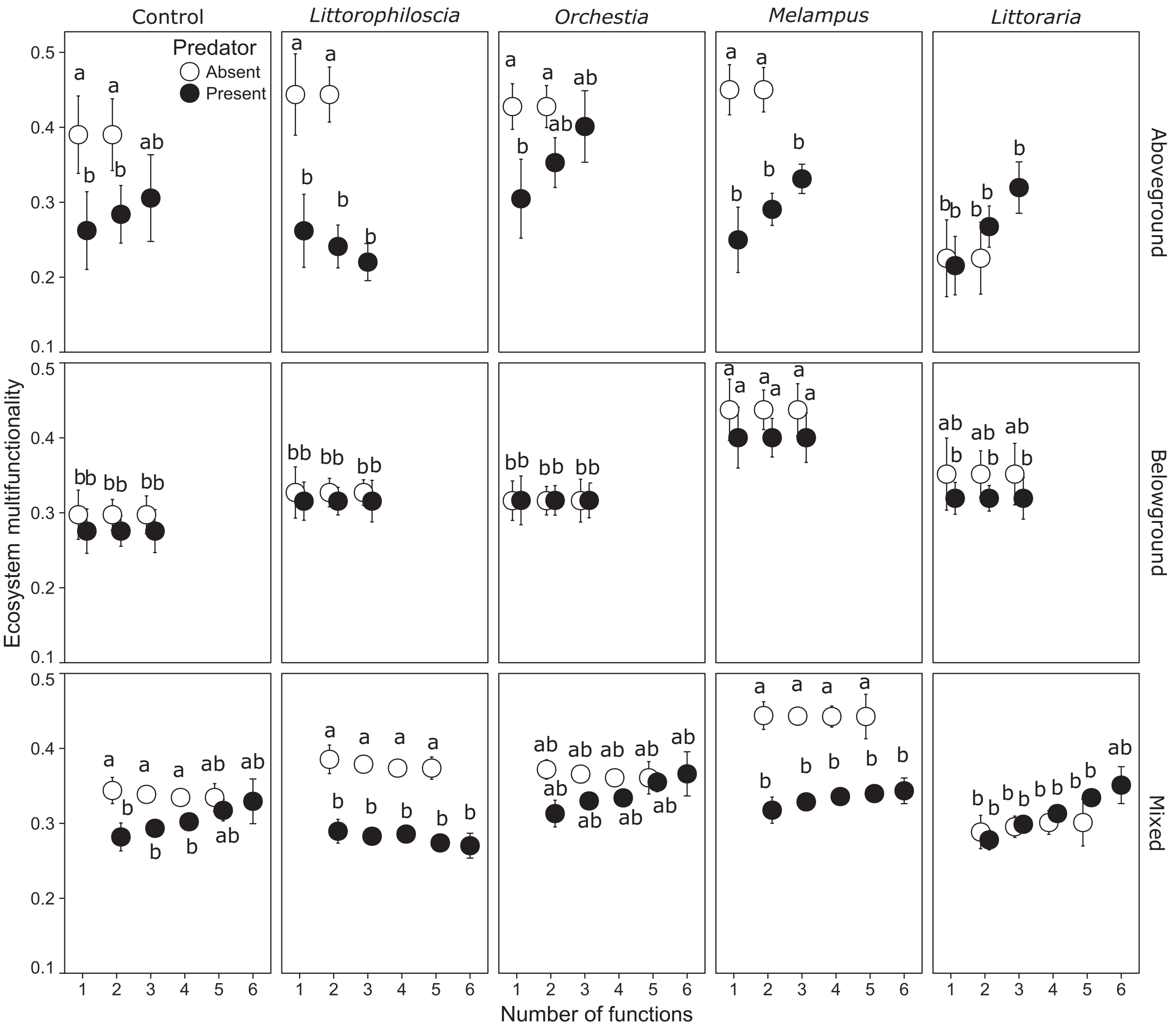


Figure 4. The effects of food web compartment (aboveground, belowground or mixed) and number of ecosystem functions (one to six) on the relationship between detritivore identity and ecosystem multifunctionality when predators are present (black circles) and absent (white circles).

average ecosystem multifunctionality, demonstrating limitation in the utility of the multifunctionality metric. Third, as strong omnivorous grazers *Littoraria* reduced ecosystem multifunctionality by directly consuming multiple resources (i.e. shoots and litter), and we observed reduced abundances of the consumer communities that rely on those resources (i.e. herbivores and predators). Considered together, these results corroborate findings that many detritivores are influential omnivorous species (Hines and Gessner 2012, Mulder et al. 2013, Wolkovich et al. 2014), and suggest that multi-trophic data is needed to draw generalities regarding the influence of detritivores on ecosystem functioning.

Although our results confirm a number of previously reported feeding interactions among the species in our model communities, they also extend several species' ranges of influence across compartments (aboveground–belowground), and in doing so they refute some prior claims of high functional redundancy among detritivores. This finding is consistent with the central claim made by proponents of ecosystem multifunctionality (Byrnes et al. 2014). Namely, expanding the number of functions measured will increase the likelihood of quantifying a unique effect of any given species (Isbell et al. 2011, Meyer et al. 2018). In our analysis, however, averaging an increasing number of functions clearly dampened variation and altered the magnitude of multifunctionality responses, because there are several possible combinations of one or two functions, but only one possible combination that includes all six measured functions in average EMF. This numerical artifact of the average multifunctionality metric has been critiqued openly for obfuscating results (Bradford et al. 2014). Whether it is an attribute, or an artifact, is debatable, and such disputes of multi-function combinations in this response variable echo critiques of multi-species combinations as independent variables in classic biodiversity ecosystem function (BEF) experiments (Huston 1997). For decades, controversy surrounded whether BEF relationships were a real consequence of biodiversity change or whether they were an artifact of classic BEF experimental design that did not account for 'sampling effects' (i.e. a greater chance of including a high functioning species in more diverse mixtures) (Huston 1997, Hooper et al. 2005, Eisenhauer et al. 2016, Wardle 2016). To resolve that debate, post hoc statistical methods were used to determine if a particular species was driving effects (i.e. 'sampling effects'), or if synergistic effects stemmed species interactions (i.e. complementarity or facilitation) (Loreau 1998, Cardinale et al. 2007). Employing somewhat parallel rationale, Byrnes et al. (2014) suggested using threshold values to test if any particular function is driving results, and Manning et al. (2018) suggested that better grouping and naming of functions would be useful to explain which functions would interactively influence ecosystem multifunctionality. Both suggestions focus on number and strength of component processes rather than how they connect and feedback to influence one another. Interpretation of our results, however, hinge upon consideration of trophic interactions, suggesting that a food web, or more systems-based perspective, will provide a useful complement to multifunctionality metrics (Hines 2019).

Indeed, our analysis is part of a convergence of biodiversity–ecosystem function (BEF) research and trophic ecology (Hines et al. 2015b, Wang and Brose 2017). Our results show that detritivores' influences operate across trophic levels, and that the magnitude and the direction of observed effects depend on the presence or absence of predators. Therefore, our findings contribute to a classic debate in trophic ecology about the occurrence of trophic cascades. For many years, scientists argued about whether, and when, predators indirectly benefited plants by consuming herbivores (Schmitz et al. 2000, Shurin et al. 2002, Borer et al. 2005). The outcome of this debate has served as major impetus for predator conservation in agricultural (Tscharntke et al. 2007), and wild ecosystems (Ripple et al. 2014, Stier et al. 2016). Similar to our study, this research has expanding evidence for the ecosystem consequences of direct and indirect species interactions to a wider variety of ecosystems and facets of biodiversity (e.g. species identity and trait-based effects) than some classic BEF research that predominately focused on plant species richness in grasslands and forests. Without overlooking the importance of predators, our results also support the primacy of detritivores as species that can influence multiple ecosystem functions by simultaneously influencing green and brown energetic pathways. An important implication is that species interaction patterns may be more informative than trophic level for establishing conservation priorities. The interpretation that interaction patterns explain important variation in our ecosystem multifunctionality data, is consistent with that of Lefcheck et al. (2015) who suggest that omnivory and multi-channel feeding underpin their finding that herbivores had a stronger diversity–multifunctionality relationships than plants or dead organic matter. Yet, Lefcheck et al. (2015) found remarkably few suitable studies reporting ecosystem consequences of changes in detritivore diversity, highlighting the importance of original empirical studies like this one. Notably, experiments documenting connections among aboveground and belowground sub-systems have historically reported multiple ecosystem responses (Wardle 2002), but these studies did not specifically quantify ecosystem multifunctionality as reported here.

In our experiment, we test the consequences of change in species identity rather than change in species richness. Our results from single-detritivore species do not allow us to evaluate whether co-existing detritivore species would compete with or facilitate each other, and hence whether changes in detritivore-species richness would modify the influences on multiple ecosystem functions that we report. This reflects a recent initiative to emphasize that multiple types of diversity change confront ecosystems, including changes in species traits, dominance and identity (Hillebrand et al. 2018). Despite the prevalence of species turnover in ecosystems around the world (Dornelas et al. 2014, Blowes et al. 2019), the ecosystem consequences of turnover within a given species richness remain an overlooked component of many BEF experiments (Eisenhauer et al. 2016). In the present study, we kept detritivore-species diversity low, which may maximize our ability to detect species-specific influences on ecosystem functioning.

Notably, environmental change often drives changes in biodiversity, whether it be changes in species richness, or species identity. However, we did not impose an environmental change treatment to select for our detritivore communities. Those drivers would likely alter the magnitude of species influence on any given function as well as the strength of feedbacks between functions (Hines and Gessner 2012, Hines et al. 2015a). In our analysis, differences among species were realized as impacts on auxiliary ecosystem functions in addition to species' primary functional role. This finding is likely to hold true for spatial and temporal turnover of many organisms in ecosystems around the world. However, we were not able to attribute species trait dissimilarity to dissimilarity in ecosystem functioning, highlighting the challenges in predicting how diversity change will influence ecosystem functioning. Moreover, we conducted our experiment in closed microcosms which prevent us from assessing the influence of dispersal (i.e. immigration and emigration) on species interactions. Nonetheless, our model communities capture realistic feeding rates and local population dynamics (i.e. invertebrate reproduction and mortality) during the main growing season for several of the major players in Atlantic coastal salt marshes, allowing us to document some baseline influences of detritivore species on multiple ecosystem functions. Notably, individual ecosystem functions need not respond simultaneously, and less is known about timing of belowground interactions compared to aboveground phenology (Eisenhauer et al. 2018). If duration of root production was prolonged or delayed compared to shoot production, examination of an extended belowground growing season may reveal hidden ecosystem functioning that was not detected in this experiment (Abramoff and Finzi 2014, Blume-Werry et al. 2015).

In conclusion, salt marsh detritivores and predators are highly sensitive to environmental variation (Hines et al. 2015a), and we quantify three important ways changes in detritivore species assemblages can influence multivariate ecosystem responses. Our results show that changes in detritivore species composition are likely associated with multiple functional pathways by which detritivores influence aboveground food web interactions. This is especially important when considered in light of mismatches in aboveground and belowground biodiversity patterns (Cameron et al. 2019). That is, although species in the aboveground food web may coexist across environmental gradients in soil conditions, the strength and consistency of their interactions, and their extended influence on multiple ecosystem functions may be contingent upon the identity of the dominant detritivore species. If multifunctionality metrics are used to assess whole ecosystem responses to changes in consumer community composition, then evaluation of food web interactions provide relevant mechanistic underpinnings needed to evaluate responses.

Acknowledgements – Yuri Mori, Hayes Biche and Lilly Owens helped collect animals in the field and maintain the microcosms. John Erickson and members of the SERC crab lab provided valuable EFS. P. Barbosa contributed a d-vac vacuum sampler. R. F. Denno contributed tube cages. D. Craven provided valuable comments on a manuscript draft. Figure 1 was drawn by Gabriele Rada. Open Access funding enabled and organized by Projekt DEAL.

Funding – This work was funded by Garden Club of America wetland fellowship, and EPA-STAR fellowship FP-91648701-1 to JH. Partial support during manuscript revisions was provided by German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118).

Author contributions

Jes Hines: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Nico Eisenhauer**: Conceptualization (equal); Funding acquisition (supporting); Methodology (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.sqv9s4n40> (Hines and Eisenhauer 2021).

References

Abramoff, R. Z. and Finzi, A. C. 2014. Are above- and belowground phenology in sync? – New Phytol 205: 1054–1061.

Balvanera, P. et al. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. – Ecol. Lett. 9: 1146–1156.

Barnes, A. D. et al. 2018. Energy flux: the link between multitrophic biodiversity and ecosystem functioning. – Trends Ecol. Evol. 33: 186–197.

Blowes, S. et al. 2019. The geography of diversity change in marine than terrestrial assemblages. – Science 336: 339–345.

Blume-Werry, G. et al. 2015. The hidden season: growing season is 50% longer below than aboveground along an arctic elevation gradient. – New Phytol. 209: 978–986.

Borer, E. T. et al. 2005. What determines the strength of a trophic cascade? – Ecology 86: 528–537.

Bradford, M. A. et al. 2014. Discontinuity in the responses of ecosystem processes and multifunctionality to altered soil community composition. – Proc. Natl Acad. Sci. USA 111: 14478–14483.

Bradley, P. M. and Morris, J. T. 1991. The influence of salinity on the kinetics of NH_4^+ uptake in *Spartina alterniflora*. – Oecologia 85: 375–380.

Byrnes, J. E. K. et al. 2014. Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. – Methods Ecol. Evol. 5: 111–124.

Cadotte, M. W. 2017. Functional traits explain ecosystem function through opposing mechanisms. – Ecol. Lett. 20: 989–966.

Cameron, E. et al. 2019. Global mismatches in aboveground and belowground biodiversity. – Conserv. Biol. 33: 1187–1192.

Cardinale, B. J. et al. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. – Nature 443: 989–992.

Cardinale, B. J. et al. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. – Proc. Natl Acad. Sci. USA 104: 18123–18128.

Cardinale, B. J. et al. 2011. The functional role of producer diversity in ecosystems. – Am. J. Bot. 98: 572–592.

Cardinale, B. J. et al. 2012. Biodiversity loss and its impact on humanity. – Nature 486: 59–67.

Chapin, F. S. et al. 1997. Biotic control over the functioning of ecosystems. – Science 277: 500–504.

Denno, R. F. and Roderick, G. K. 2003. Population biology of planthoppers. – Annu. Rev. Entomol. 35: 489–520.

Denno, R. F. et al. 2002. Bottom–up forces mediate natural enemy impact in a phytophagous insect community. – Ecology 83: 1443–1458.

Dornelas, M. et al. 2014. Assemblage time series reveal biodiversity change but not systematic loss. – Science 344: 296–299.

Eisenhauer, N. et al. 2016. Biodiversity–ecosystem function experiments reveal the mechanisms underlying the consequences of biodiversity change in real world ecosystems. – J. Veg. Sci. 27: 1061–1070.

Eisenhauer, N. et al. 2018. The dark side of animal phenology. – Trends Ecol. Evol. 33: 898–901.

Ellers, J. et al. 2018. Diversity in form and function: vertical distribution of soil fauna mediates multidimensional trait variation. – J. Anim. Ecol. 87: 933–944.

Gamfeldt, L. et al. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. – Ecology 89: 1223–1231.

Gauzens, B. et al. 2019. Fluxweb: an R package to easily estimate energy fluxes in food webs. – Methods Ecol. Evol. 10: 270–279.

Giling, D. et al. 2019. A niche for ecosystem multifunctionality in global change research. – Global Change Biol. 25: 763–774.

Gower, J. C. 1971. A general coefficient of similarity and some of its properties. – Biometrics 27: 857–871.

Graça, M. A. et al. 2000. Grazing rates of organic matter and living fungal biomass of decaying *Spartina alterniflora* by three species of salt marsh invertebrates. – Mar. Biol. 136: 281–289.

Hector, A. and Bagchi, R. 2007. Biodiversity and ecosystem multifunctionality. – Nature 448: 188–190.

Heemsbergen, D. A. et al. 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. – Science 306: 1019–1020.

Hillebrand, H. et al. 2018. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. – J. Appl. Ecol. 2018: 169–184.

Hines, J. 2019. Ecosystem functioning: how much system do we need to understand function? – Curr. Biol. 29: R1072–R1074.

Hines, J. and Eisenhauer, N. 2021. Data from: Species identity and the functioning of ecosystems: the role of detritivore traits and trophic interactions in connecting of multiple ecosystem responses. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.sqv9s4n40>.

Hines, J. and Gessner, M. O. 2012. Consumer trophic diversity as a fundamental mechanism linking predation and ecosystem functioning. – J. Anim. Ecol. 81: 1146–1153.

Hines, J. et al. 2006. Nutrient subsidies to belowground microbes impact aboveground foodweb interactions. – Ecology 87: 1542–1555.

Hines, J. et al. 2015a. Inter-annual changes in detritus based food chains can enhance plant growth response to elevated atmospheric CO_2. – Global Change Biol. 21: 4642–4650.

Hines, J. et al. 2015b. Towards an integration of biodiversity–ecosystem functioning and food web theory to evaluate relationships between multiple ecosystem services. – Adv. Ecol. Res. 53: 161–199.

Hines, J. et al. 2016. Density constrains cascading consequences of warming and nitrogen from invertebrate growth to litter decomposition. – Ecology 97: 1635–1642.

Holzwarth, F. et al. 2015. Taking a closer look: disentangling effects of functional diversity on ecosystem functions with a trait-based model across hierarchy and time. – R. Soc. Open Sci. 2: 140541.

Hooper, D. U. et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. – Ecol. Monogr. 75: 3–35.

Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. – Oecologia 110: 449–460.

Isbell, F. et al. 2011. High plant diversity is needed to maintain ecosystem services. – Nature 477: 199–203.

Isbell, F. et al. 2017. Linking the influence and dependence of people on biodiversity across scales. – Nature 456: 65–72.

Jones, C. G. and Lawton, J. H. 1995. Linking species and ecosystems. – Chapman & Hall.

Langellotto, G. A. and Denno, R. F. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. – Oecologia 139: 1–10.

Laureto, L. M. O. et al. 2015. Functional diversity: an overview of its history and applicability. – Nat. Conserv. 13: 112–116.

Lawton, J. H. 1994. What do species do in ecosystems? – Oikos 71: 367–374.

Lefcheck, J. S. et al. 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. – Nat. Commun. 6: 6936.

Legendre, P. and Legendre, L. 1998. Numerical ecology, 2nd edn. – Elsevier.

Lenth, R. V. 2018. Least-squares means: The R Package lsmeans. – J. Stat. Software 69, <https://doi.org/10.18637/jss.v069.i01>.

Loreau, M. 1998. Separating sampling and other effects in biodiversity experiments. – Oikos 82: 600–602.

Louca, S. et al. 2018. Function and functional redundancy in microbial systems. – Nat. Ecol. Evol. 2: 936–943.

Mancinelli, G. and Mulder, C. 2015. Detrital dynamics and cascading effects on supporting ecosystem services. – Adv. Ecol. Res. 53: 97–160.

Manning, P. et al. 2018. Redefining ecosystem multifunctionality. – Nat. Ecol. Evol. 2: 427–436.

Mendelssohn, I. A. 1979. Nitrogen metabolism in the height forms of *Spartina alterniflora* in North Carolina. – Ecology 60: 574–584.

Mendelssohn, I. A. et al. 1981. Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. – Science 214: 439–441.

Meyer, S. T. et al. 2018. Biodiversity–multifunctionality relationships depend on identity and number of measured functions. – Nat. Ecol. Evol. 2: 44–49.

Morse, D. H. 1997. Distribution, movement and activity patterns of an intertidal wolf spider *Pardosa lapidicina* population (Araneae, Lycosidae). – J. Arachnol. 25: 1–10.

Mulder, C. et al. 2013. Connecting the green and brown worlds: allometric stoichiometric predictability of above- and belowground networks. – Adv. Ecol. Res. 49: 69–175.

Mulvaney, R. L. 1996. Nitrogen – inorganic forms. – In: Bigham, J. M. (ed.), Methods of soil analysis. Soil Sci. Soc. Am., Madison, Wisconsin, pp. 1183–1184.

Oksanen, J. et al. 2019. vegan: Community ecology package. R package version 2.5-7. – <https://CRAN.R-project.org/package=vegan>.

Peckarsky, B. L. et al. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. – Ecology 89: 2416–2425.

Pinheiro, J. et al. 2014. nlme: linear and nonlinear mixed effects models. R package ver. 3.1-118 – <https://CRAN.R-project.org/package=nlme>.

Pla, L. et al. 2012. Functional groups. – In: Pla, L. et al. (eds), Quantifying functional biodiversity. Springer, pp. 9–25.

Ripple, W. J. et al. 2014. Status and ecological effects of the world's largest carnivores. – Science 343: 1241484.

Risch, A. C. et al. 2018. Size-dependent loss of aboveground animals differentially affects grassland ecosystem coupling and functions. – Nat. Commun. 9: 3684.

Schindler, D. E. et al. 1994. Crab:snail size structure interactions and salt marsh predation gradients. – Oecologia 97: 49–61.

Schmitz, O. J. et al. 2000. Trophic cascade in terrestrial systems: a review of the effects of carnivore removal on plants. – Am. Nat. 155: 141–153.

Shurin, J. B. et al. 2002. A cross-ecosystem comparison of the strength of trophic cascades. – Ecol. Lett. 5: 785–791.

Stier, A. et al. 2016. Ecosystem context and historical contingency in apex predator recoveries. – Sci. Adv. 2: e1501769.

Tilman, D. et al. 2014. Biodiversity and ecosystem functioning. – Annu. Rev. Ecol. Evol. Syst. 45: 471–493.

Tscharntke, T. et al. 2007. Conservation biological control and enemy diversity on a landscape scale. – Biol. Control 43: 294–309.

Valiela, I. et al. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: belowground biomass. – Limnol. Oceanogr. 21: 245–252.

Vellend, M. et al. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. – Proc. Natl Acad. Sci. USA 110: 19456–19459.

Voigt, W. et al. 2003. Trophic levels are differentially sensitive to climate. – Ecology 84: 2444–2453.

Wang, S. and Brose, U. 2017. Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. – Ecol. Lett. 21: 9–20.

Wardle, D. 2016. Do experiments exploring plant diversity–ecosystem functioning relationships inform how biodiversity loss impacts natural ecoystems? – J. Veg. Sci. 27: 646–653.

Wardle, D. A. 2002. Communities and ecosystems: linking the aboveground and belowground components. – Princeton Univ. Press.

Wolkovich, E. M. et al. 2014. Linking the green and brown worlds: the prevalence and effect of multichannel feeding in food webs. – Ecology 95: 3376–3386.

Zimmer, M. et al. 2002. Species-specific patterns of litter processing by terrestrial isopods (Isopoda: Oniscidea) in high intertidal salt marshes ad coastal forests. – Funct. Ecol. 16: 596–607.

Zimmer, M. et al. 2004. Salt marsh litter and detritivores: a closer look at redundancy. – Estuaries 27: 753–769.