

The β -richness of two detritivore caddisflies affects fine organic matter export

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Abstract We used stream networks as a model system to test whether the ecosystem function, upstream production, and export of fine organic particles, an important subsidy to downstream habitats, would vary between two stream networks with identical detritivore species but different spatial distributions (i.e. high or low β -richness). Our experiment employed artificial stream networks with two simulated tributaries. We used two species of detritivorous caddisflies, *Lepidostoma* sp. and *Pycnopsyche guttifer*, in either sympatry (low β -richness) or allopatry (high β -richness) in the tributaries of each network. The tributaries were given either senesced or green speckled alder (*Alnus incana rugosa*). In the networks with senesced leaves, particle export was more than twice as great when the detritivores were in allopatry whereas interference competition in sympatry reduced particle export. In the networks with green leaves, particle export

did not significantly vary between the allopatric and sympatric distributions because the interference competition was reduced and the two species had similar feeding rates on green leaves. Humans are altering β -richness by homogenizing or differentiating flora and fauna across habitats; however, little is known about how altering this type of biodiversity will affect ecosystem functions. Our experimental manipulation is a simple version of a change in the β -richness of the detritivores in a more complex stream network in nature. These results may indicate that shifts in species distributions across sites may significantly affect ecosystem functions, even when no species are lost from a watershed.

Keywords Meta-ecosystem · Decomposition · Spatial distribution · Network · Subsidy

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Introduction

As global extinctions continue (Sala et al. 2000), understanding how species extinctions are affecting ecosystem functions and services is becoming more important (Grime 1997). There is a rich literature looking at the relationship between α -richness (local) and ecosystem functioning, and, generally, studies find there to be a positive asymptoting relationship between these variables (Hooper et al. 2005; Cardinale et al. 2002). Despite this important body of work, scaling the results of α -richness manipulations up to understanding how species extinction, or reductions in γ -richness, will affect ecosystem functioning has been problematic. At larger spatial scales, there are many more species, habitat heterogeneity may become important (Cardinale 2011), and, interestingly, subsidies move between habitats creating complex networks of interconnected systems (Loreau et al. 2003).

Subsidies are the energy, nutrients, and organic materials that are transported across ecosystem boundaries from a donor patch to a receiving patch (Polis et al. 1997). These spatial subsidies are increasingly recognized as a common feature of ecosystems (Marczak et al. 2007). The production and transfer of subsidies are often mediated by the species present in the producer patch (Ben-David et al. 1998; Reiners and Driese 2001; Baxter et al. 2005). For example, allochthonous leaf inputs subsidizing streams come from primary production in the riparian zone (Webster and Benfield 1986; Tank et al. 2010).

Subsidies add some interesting complexity to the relationship between biodiversity and ecosystem functioning at larger spatial scales. A subsidy, by definition, affects the population dynamics, community composition, and ecosystem functioning in the recipient patch (Huxel et al. 2004). Therefore, when local species diversity exerts control over the production of a subsidy in a donor habitat, that same local diversity will also affect the ecosystem functioning in the habitat receiving the subsidy. In effect, subsidies may increase the spatial extent of the ecosystem functions that communities provide.

In systems where subsidies link together multiple habitats, the community composition and ecosystem functioning in a local habitat may be influenced by community composition and functioning in multiple, spatially separate habitats (Fig. 1). Such interconnected sets of habitats are called meta-ecosystems (Loreau et al. 2003).

When species diversity affects subsidy production in a habitat (Hooper et al. 2005), and multiple subsidy-producing habitats are connected by the flow of materials (Gravel et al. 2010), the spatial turnover of communities

across habitats may then exert considerable control over the total functioning of the meta-ecosystem (Fig. 1). In such a system, two meta-ecosystems with identical species pools but different spatial arrangements of species, i.e. β -richness, may function differently (Massol et al. 2011). Understanding the role of β -richness in the ecosystem functioning of landscapes is particularly important, because humans are rapidly altering the β -richness of many different types of flora and fauna through species movement, increasing connectivity of disparate habitats, and degrading the environment (McKinney and Lockwood 1999; Rahel 2002; Qian and Ricklefs 2006; Smith 2006; Rooney et al. 2007). Often referred to as biotic homogenization and differentiation, this phenomenon has been mainly treated as a conservation concern; however, in the framework we present above, these changes could also be fundamentally impacting ecosystem functions at the landscape level.

Stream networks are an ideal study system for determining if changes to β -richness are affecting ecosystem functions. Streams are ubiquitous systems in which individual habitats are linked together by the flow of organic material carried by water from donor reaches to recipient reaches. Furthermore, streams are one system in which major changes to β -richness have been documented (Patrick and Swan 2011). For the purposes of this conceptual argument, we liken the patch scale of the meta-ecosystem concept to an individual stream reach (Pringle et al. 1988). In meta-ecosystem theory, an individual patch is a spatially explicit ecosystem that is exchanging energy, materials, and organisms with other such ecosystems (Loreau et al. 2003). Stream reaches are spatially explicit sections of similar habitat and coexisting organisms within the greater stream network. In a stream network, the donor stream reaches export organic material downstream (Cummins 1974; Webster and Benfield 1986; Hoover et al. 2010). The rate of materials flow from each donor reach is partially dependent on the feeding activity of the biota in each reach; the biota breaks down coarse particulates into fine particulates that are easily mobilized by water flow (Wallace et al. 1991). The exported organic materials from multiple upstream locations mix together at integration points, or confluences, in the network (Fisher and Welter 2005). Exported organic materials are used by microbial, filter feeding, and collector gathering communities and support secondary production in downstream reaches as well as higher trophic levels (Vannote et al. 1980; Wotton et al. 1998). Locations further downstream in the network receive materials from a greater number of upstream donor reaches than locations higher in the network.

There is a rich body of literature documenting that local shredder community composition exerts considerable control over decomposition rates in stream systems (Ruesink and Srivastava 2001; Jonsson et al. 2002; McKie et al. 2008;

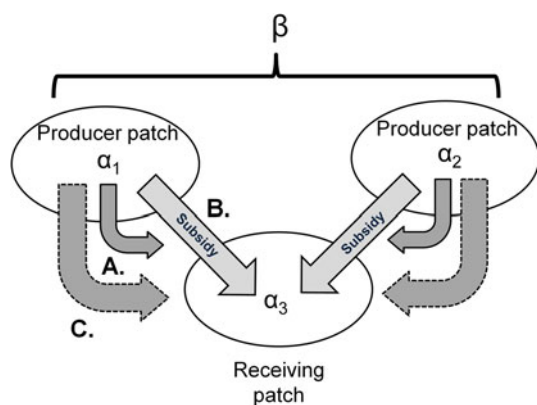


Fig. 1 Theoretical model of an ecological network connected by subsidies where β -richness of the producer communities affects production in the receiving communities. There are two producer patches, each with a local community (α_1 , α_2). Community diversity in each producer patch controls the rate at which the subsidy is produced (a) and exported (b) to the receiving patch. The production of the community in the receiving patch (α_3) is simultaneously affected by the diversity of each producer community (c)

Creed et al. 2009). While some studies have found small variation in decomposition rates between streams (Tiegs et al. 2009), when there are differences between the abundance and identity of shredders between streams, decomposition rates may also differ significantly (Benfield and Webster 1985; Leroy and Marks 2006). The rate of decomposition in turn affects the rate at which fine particles, which originate in large part as fecal pellets (Wotton and Malmqvist 2001), are exported. In an experiment where benthic invertebrates were extirpated with insecticides, fine particulate organic matter (FPOM) export dropped precipitously (Wallace et al. 1997). Additionally, Patrick (2013) found that community composition affects not only the production rate of fine particles but also the size distribution and stoichiometry of those particles. Furthermore, Jonsson and Malmqvist (2005) found that shredder community composition influenced the growth rates of filter feeders.

Using the stream network as a model system, we asked whether the total fine particle production and export should vary between two stream networks with identical detritivore species pools but different distributions of detritivore species, i.e. β -richness, across the headwater tributaries. We set up artificial stream networks to investigate whether shifts in the β -richness of detritivores in a stream network would impact particle production and export. To simulate changes to β -richness, we placed two shredding caddisfly species in either sympatry (low β -richness) or allopatry (high β -richness) across two tributaries in artificial stream networks. We held γ constant between treatments and thus average α varied inversely with β -richness. We simultaneously ran this experiment with two different leaf stages (senesced leaves and green leaves) that are present in the natural streams during the time the experiment was performed. We hypothesized that: (1) network decomposition rates will be higher in sympatry because each tributary will have more species and therefore the potential for complementarity and facilitation; (2) fine particle stoichiometry and particle size distributions will vary significantly between the sympatric and allopatric treatments because the two species have different assimilation efficiencies, different sized fecal pellets, and species feeding rates may change due to interspecific interactions when in sympatry; and (3) particles produced in green leaf treatment will have a higher N content and particle production rates will be faster because green leaves are more nutrient rich.

Materials and methods

Study site

Experiments were carried out in the Upper Peninsula of Michigan at UNDERC (University of Notre Dame

Environmental Research Center, 46°13'N, 89°32'W), the NEON core site for the Great Lakes Domain (Domain #5). Experimental systems were modeled upon streams sampled in the surrounding Ottawa National Forest (ONF). Sampled streams were first and second order, with a forested riparian zone, and a full canopy. We selected two shredders for the experiment, *Pycnopsyche guttifer* and *Lepidostoma* sp., because they were numerically dominant within sites, occurred in the majority of streams, and occurred both alone and together within leaf packs in streams. *Pycnopsyche guttifer* was found in densities ranging from 10 to 130 ind. m⁻² and *Lepidostoma* sp. was observed in densities ranging from 33 to 178 ind. m⁻² via surber sampling and >1,000 ind. m⁻² when specifically sampling debris dams. Both species are generalist shredders and were observed to be most common in leaf packs located between large woody debris or in backwaters on the margins of the stream. Members of these two genera are considered to contribute significantly to leaf processing rates in streams where they are present (Grafius and Anderson 1979, 1980; Herbst 1980, 1982; Eggert and Wallace 2007; Creed et al. 2009). They are univoltine species and overwinter as 1st instar larvae and emerge as adults between late July and September (Grafius and Anderson 1979, 1980; Smith 1984). Speckled alder (*Alnus incana rugosa*) was the dominant riparian tree species found across sites, and in many cases it was present in monoculture in the riparian zone. Speckled alder was selected as the leaf resource.

Experimental set-up

All shredders were collected in May 2010 after ice out in several collecting trips within 1 week of the start of the experiment. *P. guttifer* were collected from Pomeroy Creek (46°17'N, 89°34'W,) and *Lepidostoma* sp. from Emeline Creek (46°14'N, 89°29'W). Collected individuals were kept in separate containers (one for each species) of aerated filtered stream water and provided senesced speckled alder leaves to feed on until the experiment began. Fifty individuals of each species were separated, dried, and weighed to estimate average dry mass per individual. *P. guttifer* was estimated to weigh 0.019 ± 0.001 g (±SE) and *Lepidostoma* sp. was estimated to weigh 0.0014 ± 0.0001 g. Twenty-four hours before the start of the experiment shredders were moved to containers with no leaf litter to void their guts.

Senesced speckled alder leaves were collected at leaf fall in October 2009 at UNDERC. Green speckled alder leaves were collected in June 2009 from the same stand of trees and allowed to air dry. Green leaves were used as a second leaf treatment because they have a different chemical composition than senesced leaves (Lecerf and Chauvet 2008), and are a significant summer input to

streams in this region making them an alternate food source that is present in these streams while the study organisms are developing (Maloney and Lamberti 1995). Furthermore, by late June, most of the deciduous leaf packs have been completely broken down (personal observation) and green leaf inputs from summer storms may provide an important food resource when senesced leaves are scarce.

The experiment was performed in outdoor artificial streams. Each artificial stream was 15 cm wide and the water was 6 cm deep. Depth was maintained with a standpipe where water flowed out. Velocity was maintained at 0.18 m/s using a paddle wheel situated beyond the in-flow (Fig. 2). We used well water to minimize organic particles coming in from outside the system. Water temperature was 9 °C, pH was 8, conductivity was 200 μ s, and dissolved oxygen was 7.5 mg/L. Each stream was covered with a shade cloth to mimic shaded forest conditions (Fig. 2). Each stream was set-up with two upstream habitat patches, meant to simulate upstream reaches in a bifurcated network, as well as a downstream particle collection trap fitted with a 63 μ m drift net that all water moving down stream had to pass through (Fig. 2). Each habitat patch was suspended 1 cm above the stream bed and was composed of a circular plastic cage 12.5 cm across with solid walls extending above the water line affixed with a 1-mm mesh floor to allow water to freely exchange and to allow particles to escape through the bottom.

Experimental design

The experiment was set up as a 2 (senesced or green leaf) \times 3 (allopatric, sympatric, no-shredder) ANOVA design (6 treatments \times 4 replicates = 24 streams) (Appendix E). The total biomass of shredders was the same across stream networks (0.16 ± 0.001 g dry weight) and tributaries (0.08 ± 0.001 g dry weight) (Number per tributary: allopatry: 56 *Lepidostoma* sp., or 4 *Pycnopsyche guttifer*; sympatry: 28 *Lepidostoma* sp. and 2 *Pycnopsyche guttifer*). These numbers were within the range of densities found in real leaf packs in the field and these two taxa were found to co-occur in leaf packs in the field. Both tributaries in a stream network received either 1.2 g of senesced or green speckled alder.

Every 4 days, we collected the particles from each particle collection trap. Collected particles were separated into three size classes: >250, 250–125, and 125–63 μ m, by sieving, dried at 60 °C for 48 h, and then weighed. Dried particles were then saved for elemental analysis to determine C:N using a Costech Elemental Analyzer (Costech Instruments, Valencia, CA, USA). At the end of the experiment we collected the remaining leaves. Remaining leaves from each tributary were dried for 48 h at 60 °C, weighed, then ashed at 550 °C for 2.5 h, then weighed again to determine remaining ash free dry mass (AFDM).

To measure the intra- and interspecific interactions occurring in each tributary, we filmed the individual shredders in a subset of the tributaries described above using a Sony Handycam DCR-DVD digital video camera (Sony, Minato-ku, Tokyo, Japan) fitted with a $\times 0.5$ magnification macro-scale lens and an additional $\times 4$ magnification filter. Filming allowed us to directly observe the mechanism by which our experimental treatments affected FPOM production and leaf decomposition. We filmed in a 2 (senesced or green leaf) \times 4 (*Lepidostoma* sp. allopatry, *P. guttifer* allopatry, *Lepidostoma* sp. sympatry, *P. guttifer* sympatry) design (8 treatments \times 4 replicates = 32 tributaries). For 5 days between days 11 through 17 of the experiment, we filmed all the selected replicates between 1000 and 1600 hours. Each species was filmed for a total of 13 h.

The filming order each day was determined by random selection. For each tributary each day, we filmed a randomly selected focal individual of each species present in the tributary for 10 min. If a focal individual became obscured by leaf material, it was given 30 s to re-appear. If a focal individual remained obscured after 30 s, a new focal individual was selected. Videos were analyzed using BEAST Student 2005 behavioral analysis software (Windward Technology, Kaneohe, Hawaii, USA). We measured the time spent feeding and moving, as well as number of detailed interaction types between species and conspecifics (Appendix A).

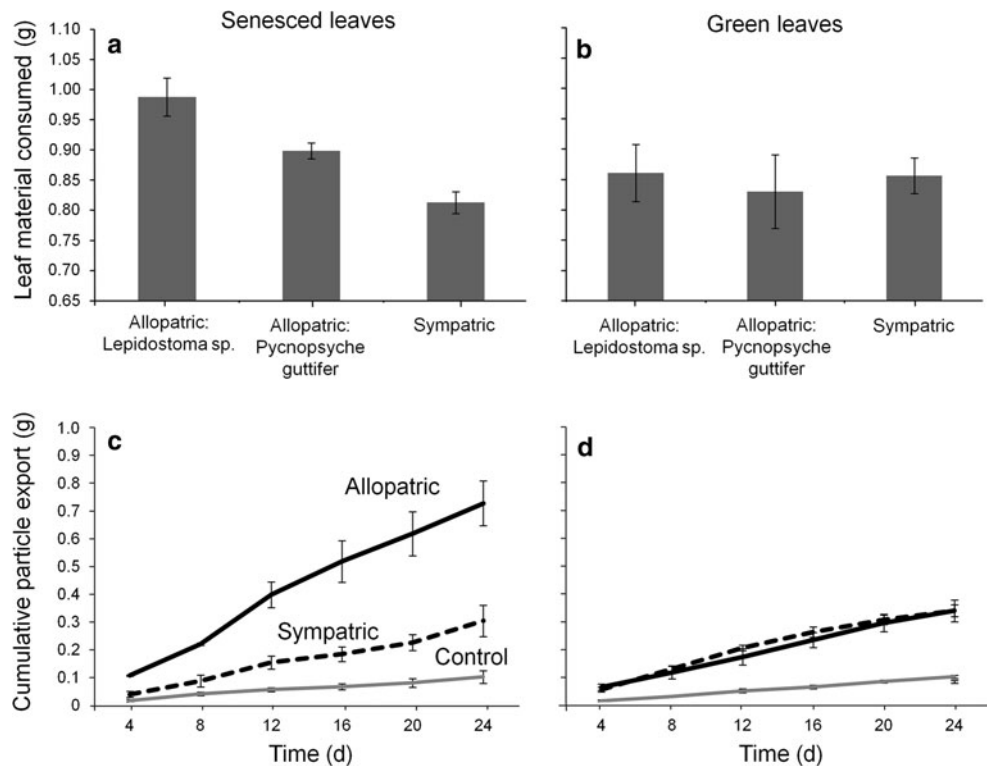
Statistical methods

Particle production rates for each treatment were estimated by calculating the rate, r , in the logarithmic growth model for particle production:

$$M_t = r \ln t - b$$

M_t is the mass of particles produced up to time t and b is a fitted constant. Coefficients were estimated using the glm function in the statistical program R v.2.12.2 (R Development Core Team). Data were checked for normality and log transformed if necessary. The rates for the individual replicates were analyzed in a 2-way ANOVA (analysis of variance). Particle size distribution was expressed as the proportion (arcsin transformed) of particles in the large (>250 μ m) and medium (250–125 μ m) particle size classes and analyzed in a 2-way multivariate analysis of variance (MANOVA). The C:N ratio of particles, Chla, and remaining leaf mass were analyzed in a 2-way MANOVA. The 5 days of film data for each patch were pooled, and we used 2-way ANOVAs for each observed behavior (Dunn–Sidak adjusted $\alpha = 0.0064$). All univariate and multivariate statistical analyses were performed in SYSTAT v.10 (SYSTAT, Karnakata, India).

Fig. 2 **a, b** Leaf material consumed and **c, d** cumulative particle export on each collection day for three treatments with senesced or green leaves of speckled alder (*Alnus incana rugosa*) (mean \pm SE). In the senesced leaf treatment, cumulative particle production is higher in allopatry (high β -richness, *solid line*) than it is in sympatry (low β -richness, *dashed line*) ($P < 0.001$). There is no difference between the shredder treatments in the green leaf treatment. Control is a no-shredder treatment to measure baseline particle export in the absence of shredders



Results

Particle production

Production of particles from senesced leaves was faster than production of particles from green leaves (Table 1; Fig. 2). Particle production in the shredder treatments was faster than in the controls (Table 1; Fig. 2). There was a significant interaction between shredder treatment and leaf stage such that the allopatric treatment had faster particle production compared to the sympatric treatment when the shredders were eating senesced leaves (Table 1; Fig. 2), but there was no difference between the rate of particles produced from green leaves in the allopatric and sympatric treatments.

Particle size distribution

Shredder treatment had a significant effect on particle size distribution, but leaf stage did not significantly affect particle size distribution and there was no interaction between leaf and shredder treatment (Table 2; Fig. 4). Treatments with shredders had a larger percentage of particles in the medium size class (125–250 μm) whereas the control treatment was characterized by a more uniform particle size distribution (Fig. 3). The sympatric senesced leaf treatment had more medium sized particles ($t = 6.7729$, $df = 3.345$, $P = 0.004$) and fewer large sized particles

($t = -3.926$, $df = 4.312$, $P = 0.015$) than the allopatric senesced leaf treatment. There was no observable difference in the particle size distributions between the allopatric and sympatric green leaf treatments.

Particle stoichiometry

The particles formed in the green leaf treatment had significantly lower C:N (17.8 ± 1.5) than the particles formed in the senesced leaf treatments (19.8 ± 1.2) suggesting that relative N content of particles is higher when the shredders are feeding on green leaves (Appendix A). There was no difference in the C:N between the shredder treatments. In the control treatment the green leaf particles had higher C:N than the corresponding shredder treatments, and the senesced leaf particles had lower C:N than the corresponding shredder treatments (Appendix B).

When we looked at % carbon and % nitrogen remaining separately, we found that % nitrogen was significantly higher in the particles produced from green leaves, significantly higher in the shredder treatments versus the control (Table 1; Fig. 4). Percent nitrogen also showed an interaction between leaf and shredder treatment. Nitrogen in particles produced from the sympatric treatment was higher when produced from green leaves, but in the allopatric treatment leaf stage did not affect % nitrogen (Table 1; Fig. 4a). The % carbon was significantly higher in the particles produced from green leaves, and a little

Table 1 ANOVA results for the production of particles, % N and % C present in the particles, and the time *Lepidostoma* sp. and *Pycnopsyche guttifer* spent feeding in each of the experimental treatments

	Source	df	Mean square	F ratio	P
Particle production	Leaf	1	0.019	7.438	0.016
	β-Treatment	2	0.085	30.158	<0.001
	β-Treatment × leaf	2	0.03	11.526	0.001
	Error	18	0.003		
% N	Leaf	1	0.0001	17.9693	0.0004
	β-Treatment	2	0.00002	4.6393	0.023
	β-Treatment × leaf	2	0.00003	5.617	0.012
	Error	19	0.000006		
% C	Leaf	1	0.007	5.199	0.034
	β-Treatment	2	0.004	3.322	0.058
	β-Treatment × leaf	2	0.02	15.515	<0.001
	Error	19	0.001		
<i>Lepidostoma</i> sp. feeding time	Leaf	1	72589.83	37.715	<0.001
	β-Treatment	1	7961.10	4.136	0.065
	β-Treatment × leaf	1	26969.85	14.012	0.003
	Error	12	1924.71		
<i>Pycnopsyche guttifer</i> feeding time	Leaf	1	18184.52	11.796	0.005
	β-Treatment	1	6569.10	4.261	0.061
	β-Treatment × leaf	1	2120.60	1.376	0.264
	Error	12	1541.60		

Leaf refers to the effect of leaf stage (green or senesced) and β-treatment refers to the effect of the shredder manipulation (high β-diversity, low β-diversity, no-shredder control)

Table 2 MANOVA results for the proportion of particles produced and the C:N of particles in each each treatment

	Wilk's Lambda	Value	F stat	df	P
Particle proportion	Leaf	0.787	2.295	2.17	0.13
	β-Treatment	0.473	3.861	4.34	0.011
	β-Treatment × leaf	0.749	1.319	4.34	0.28
	Error				

Refer to Table 1 for explanation of treatments

higher in the shredder treatments (Table 1; Fig. 4b). Leaf stage and shredder treatment significantly interacted with one another with particles from senesced leaves having more carbon in the allopatric treatment, but less carbon in the sympatric and control treatments (Table 1; Fig. 4b).

Leaf mass loss

At the end of the experiment, there was more senesced leaf material consumed (0.76 ± 0.04 g) than green leaf

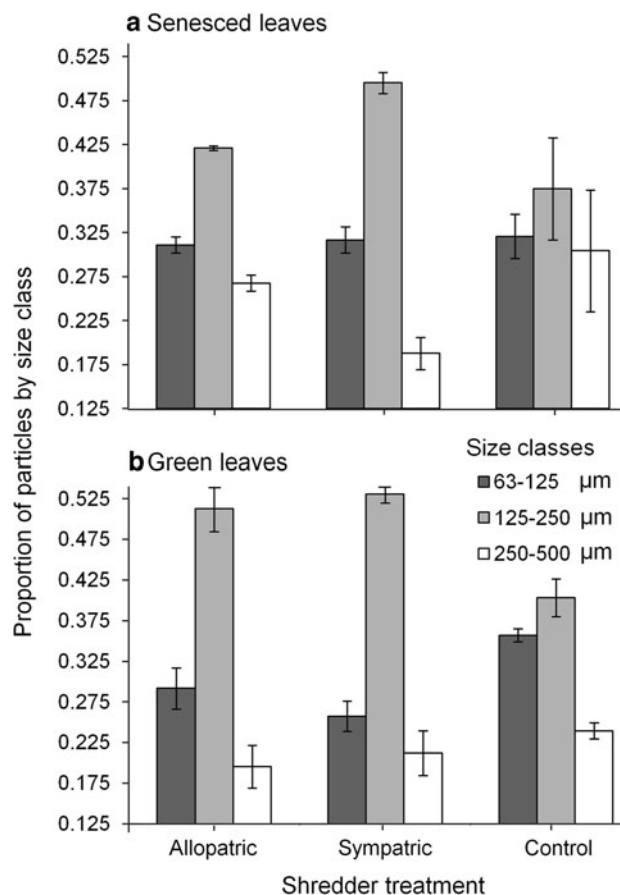


Fig. 3 Particle distribution displayed as the proportion of particles in each of three size classes (63–125 μm dark gray, 125–250 μm light gray, 251–500 μm white) for **a** senesced and **b** green leaves of *Alnus incana rugosa*, mean ± SE. The MANOVA results (Table 2) show that shredder treatments significantly impacted particle size distribution ($p = 0.011$)

material (0.73 ± 0.04 g) in the individual tributaries (Appendix C). More leaf material was lost in tributaries with shredders (0.86 ± 0.02 g) than in tributaries without shredders (0.49 ± 0.01 g) (Appendix C). In the senesced leaf treatment, the leaf mass consumption pattern was: *Lepidostoma* sp. patches > *P. guttifer* patches > sympatric patches; however, there was no difference in green leaf mass consumption between the shredder treatments.

Behavior results

In order to draw inferences about how feeding time affects particle production, we assumed that time spent feeding is a proxy for the amount of food ingested. This assumes that the rate of ingestion per unit time among individuals and on the different food types is constant. We believe this is justified because we observed that more time spent feeding correlates with less remaining leaf mass and higher particle production rates across all treatments.

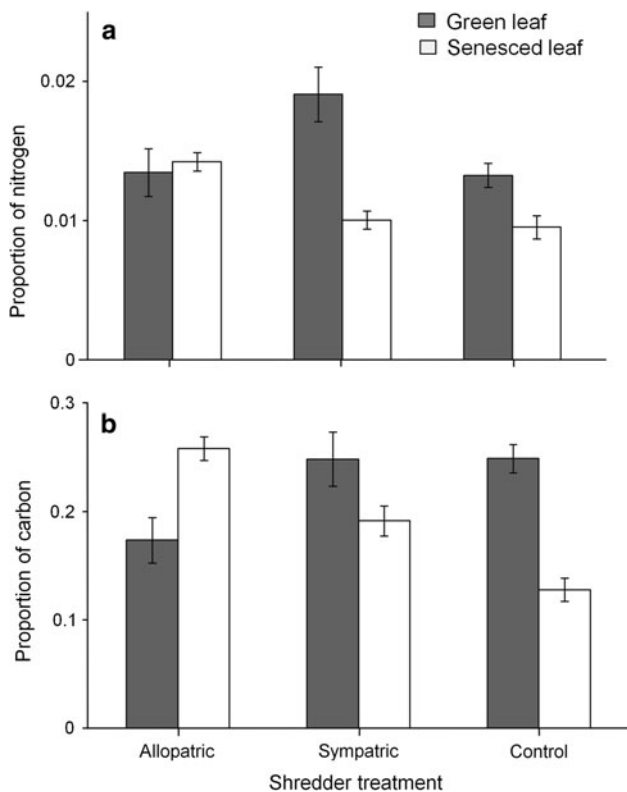


Fig. 4 Proportion of **a** nitrogen and **b** carbon particles produced from senesced (white) or green (gray) leaves in allopatric, sympatric, and control shredder treatments (mean \pm SE). Particles produced from green *Alnus incana rugosa* leaves were higher in nitrogen ($p = 0.012$) and carbon ($p < 0.001$) in the sympatric treatment, but not allopatric treatment

Fig. 5 Proportion of time spent during the observation days by an individual **a, b** *Lepidostoma* sp. or **c, d** *Pycnopsyche guttifer* moving (black), feeding (light gray), interacting (white), and being inactive (dark gray) on senesced or green leaves in allopatric or sympatric shredder treatments (mean \pm SE). *Lepidostoma* sp. spends more time feeding on senesced leaves than green leaves, and more time feeding in allopatry than in sympatry (see Table 1). *Pycnopsyche guttifer* spends more time feeding on green leaves than senesced leaves and spends a little more time feeding when in allopatry than in sympatry (see Table 1)



Both shredder species spent more time feeding when alone in allopatry than when in the presence of the other in the sympatric treatment (Table 1; Fig. 5). *Lepidostoma* sp. spent more time feeding in a given 10-min period on senesced leaves (393.3 ± 18.2 s) than it spent feeding on green leaves (266.6 ± 28.6 s) in the absence of *P. guttifer* in the allopatric treatment. *Lepidostoma* sp. spent less time feeding on senesced leaves than green leaves when in the presence of *P. guttifer* in the sympatric treatment (Table 1; Fig. 5a). As feeding time decreased, the time spent interacting, sitting still, or moving around the mesocosm increased.

When feeding together on the senesced leaves, both caddisflies reduced the time they spent feeding (Fig. 5), indicating interference competition. The magnitude of the decline for *P. guttifer* (38 %) was far less than that experienced by *Lepidostoma* sp. (55 %). When feeding on the alternate food source, green leaves, there was still interference competition, although the absolute effect measured in minutes (senesced leaves: 22 min less per hour spent feeding vs. green leaves: 5 min less per hour spent feeding), as well as the relative effect on *Lepidostoma* sp. (senesced leaves 56 % decline in time spent feeding vs. green leaves 18 % decline in time spent feeding) was much less.

In the sympatric treatment, the decrease that each species exhibited in time spent feeding was made up for by increases in time spent moving or sitting still. There were small increases in the number of interactions in the

sympatric treatments and several events were captured where *Pycnopsyche guttifer* grabbed and bit *Lepidostoma* sp. Such attacks were often met with defensive case waves and hasty retreats by *Lepidostoma* sp. These events, while dramatic, were very rare, and we observed no events that ended in the mortality of a caddisfly. Time spent moving, interacting, or sitting still varied between treatments (Fig. 5), but none of this variation was significant at the Dunn–Sidak adjusted α of 0.006 (Appendix D).

Discussion

Our experimental results provide the first evidence for β -richness being important for ecosystem functioning. We experimentally demonstrate that a shift in β -richness in a meta-ecosystem can affect the production and transport of ecological subsidies. This finding is particularly relevant because humans are rapidly and extensively altering β -richness, as well as homogenizing or differentiating the flora and fauna of many different types of habitats (McKinney and Lockwood 1999; Rahel 2002; Qian and Ricklefs 2006; Smith 2006; Rooney et al. 2007). Furthermore, this result may provide an important piece linking our understanding of the relationship between α -richness and ecosystem functioning to the effect of biodiversity alterations on ecosystem functioning at larger spatial scales than individual ecosystems.

In our experimental system, a model of a stream network meta-ecosystem, changing the spatial distribution of two caddisfly detritivores in the tributaries of an artificial stream network from allopatry, high β -richness, to sympatry, low β -richness, significantly impacts the export of FPOM, an important subsidy in streams, to the downstream channel. This relationship was context-dependent on the stage of the leaf that the detritivores were eating. When feeding on senesced speckled alder, the total particle export increased in the allopatric, high β -richness treatment. When feeding on green speckled alder, there was no difference between the total particle export of the high and low β -richness treatments. These results are counter to our major prediction that total particle export would be higher when the detritivores were in sympatry in the low β -richness.

Our behavioral observations clarify the mechanism for the observed particle export patterns. The two caddisflies feed similarly on green leaves, feed differently on senesced leaves, and experience asymmetric interference competition when together in sympatry that varies in strength according to the leaf upon which they are feeding. In sympatry, *Pycnopsyche guttifer* has a larger negative effect on *Lepidostoma* sp. feeding rates than *Lepidostoma* sp. has on *Pycnopsyche guttifer*. Similar negative impacts of

caddisflies in the genus *Pycnopsyche* on other shredders have been observed by Creed et al. (2009); however, our results differ from Creed et al. in that, while *Pycnopsyche* is still the competitive dominant, it is functionally inferior to its competitor *Lepidostoma* sp. when breaking down leaves. In Creed et al. 2009's experiments, *Pycnopsyche gentilis* was found to be both a competitive and functionally dominant shredder.

These results are very interesting in that they document how mutable species interactions can be. The interaction between *Lepidostoma* sp. and *Pycnopsyche guttifer* is strongly affected by the food resource for which they are competing. Similar results documenting how changes in context can modify the interaction between species have been shown in the modification from a mutualism to a parasitic relationship (Johnson et al. 1997; Johnstone and Bshary 2002). This result is novel in demonstrating that context-dependent changes in species feeding and interacting behavior can have major consequences for the ecosystem function these species provide.

The difference between the particle size distributions of the allopatric and sympatric senesced leaf treatments are a subtle, but important, effect of β -richness on subsidy production in this experiment. The FPOM subsidy is used by filter feeders with different size preferences (Schroder 1987; Wotton 1977). Shifts in particle size spectra could be advantageous to some filter feeders and disadvantageous to others. Furthermore, particle size affects the mobility of the FPOM subsidy. Small particles are more easily moved, and shifts toward smaller particles could increase FPOM export rates from small streams (Wotton et al. 1998; Minshall et al. 2000; Thomas et al. 2001).

Our initial prediction that the C:N ratio would be different between the two β -richness treatments was not supported by our results. The reason the C:N ratio of the particles does not vary between the β -richness treatments was because percent carbon and percent nitrogen are changing at a similar rate and so maintain a similar constant ratio. While the C:N did not change, the total percentages of carbon and nitrogen were higher in the low β -richness treatment potentially increasing their quality as a food resource.

An issue to consider is whether the outcome of the experiment was influenced by the difference in the relative abundance of the two shredder species that were employed in the experiment. We employed the widely used substitutive design and so relative abundance varied between treatments while shredder biomass remained constant (Hooper et al. 2005; Spehn et al. 2005). In substitutive designs, there is a risk that the increased per species density in low diversity treatments will lead to increases in intra-specific competition (Byrnes and Stachowicz 2009); however, we found no evidence for increasing intra-specific

competition in the behavior and process rate data we collected. Density is an important factor that can affect the outcome of biodiversity–ecosystem function experiments, including ones using shredder richness and leaf decomposition (McKie et al. 2008; Creed et al. 2009). While it is possible that changing densities could have affected the results presented here, the experimental treatment densities reflect what exists in the real streams on which we modeled the experiment.

We contend that manipulating the spatial distribution of two detritivores from allopatry to sympatry in an artificial stream network is akin to changing the β -richness of a more species-rich and complex stream network in the field. A valid concern in making that comparison is determining whether our experiment accurately approximates the dynamics we would expect to see in real stream networks. Our experimental organisms were carefully selected because they co-occur at the microhabitat scale, the leaf pack. They also did not always occur in the same streams, so our spatial configuration treatments do occur in nature. Despite our efforts at realism, our experiment lacked the spatial size, species diversity, network complexity, and temporal hydrologic variation that would occur in a real stream network. In terms of network complexity, had we included more upstream reaches, we could have featured a gradient of treatments between zero and high β -richness. Using these same two detritivore species and senesced alder leaves, we expect we would still observe decreased network scale functioning as β -richness declined, because the tributary scale dynamics that provide the mechanism for the patterns we observed would remain unchanged.

The experiment only employed one species combination each for high and low β -richness, in doing so the experiment was un-replicated in regards to the β -richness manipulation. Therefore, we present this experimental result as a case study of one particular ecological scenario of how shredder β -richness can impact ecosystem functioning. Real stream invertebrate communities are much more complex than those we used, but similar results to those we observed at the tributary scale of our experiment have been empirically observed in complex shredding assemblages (McKie et al. 2008; Creed et al. 2009), as well across many different taxonomic groups (Hooper et al. 2005). However, other dynamics in shredder diversity experiments have found facilitation and complementarity between shredders, the opposite of our tributary-scale pattern (Reusink and Srivastava 2001; Jonsson and Malmqvist 2005). We hypothesize that the relationship between shredder β -richness and net particle export is dependent on whether the shredders facilitate one another or interfere with one another at the stream reach scale. Assuming that the total shredder species pool for a network remains intact, when shredders facilitate one another, a

shift toward lower β -richness (homogenization) in a network would increase particle subsidy export. When shredders interfere with one another, a shift toward higher β -richness (differentiation) would increase particle subsidy export. It is the sign of the local-scale interaction that determines how β -richness affects ecosystem processes at larger scales, provided that other factors such as the γ species pool remains unchanged as it did in this experiment. In this experiment, our single manipulation resulted in interference competition at a local scale, and so a positive effect of β -richness at the larger scale; however, other groups of species could result in a neutral or even negative effect of β -richness at large scales. Another area of uncertainty is how environmental variability and hydrology might affect these processes in the field (Lamberti and Steinman 1993).

There has been a recent surge of interest in the dynamics of communities at scales that include multiple spatial locations and communities (Leibold et al. 2004; Brown et al. 2011). While much has been said about the measurement of and mechanisms by which dispersal, predation, and other factors affect local community dynamics and β -richness across communities (Chase et al. 2009; Matthiessen et al. 2010; Anderson et al. 2011; Patrick and Swan 2011), less attention has been given to the consequences of changes to β -richness. Our experiment provides one scenario: a dendritic network meta-ecosystem with uni-directional subsidy flows, where β -richness could affect ecosystem functioning. While our experiment is limited to a single situation in an artificial setting, it is one of the only experiments to demonstrate a link between β -richness and functioning. There are many other kinds of meta-ecosystems with reciprocal flows of subsidies and more complex dynamics (Loreau et al. 2003; Gravel et al. 2010). Notable examples include anadromous fish runs subsidizing streams (Helfield and Naiman 2002), aquatic insects subsidizing terrestrial environments (Gratton et al. 2008), fish predation in ponds influencing terrestrial pollinator abundance (Knight et al. 2005), and seabirds subsidizing island plant productivity (Fukami et al. 2006). Given the wealth of meta-ecosystem types, this experiment suggests that more attention should be given to the role of β -richness in ecosystem processes. The need for more research into how β -richness affects ecosystem processes is pressing, given the documented declines in β -richness (homogenization) of many different types of taxa across regions (McKinney and Lockwood 1999; Rahel 2002; Qian and Ricklefs 2006; Smith 2006; Rooney et al. 2007). Only by understanding the circumstance under which β -richness matters for ecosystem processes can we determine when and where species spatial distributions should be conserved or preserved when managing ecosystems for ecosystem functioning.

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