Dendritic network location mediates detritivore community structure and associated processing of leaf litter in a riverine ecosystem

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Abstract

Historically, studies have examined how local habitat, resources and species interactions influence community structure in stream ecosystems. Increasingly, though, attention has turned to understanding how regional factors (e.g. dispersal) interact with local conditions to influence communities. Often dispersal of organisms occurs in spatially constrained habitats, which can drastically influence community assembly. Dendritic networks are an example, and have a branching spatial configuration with some branches of the system more connected to others, making dispersal easier, while other locations are more isolated. As interest in multi-scale community assembly mechanisms has increased, less work has focused on the relationship between community assembly and ecosystem processes. Here, we sought to understand how consumer-resource interactions unfold in river networks. We predicted that stream network location would mediate detritivore (shredder) richness and abundance, and in turn would be associated with a shift in decomposition of organic matter (leaf litter). To examine this, we manipulated leaf litter species in isolated (headwaters) and connected (mainstem) stream reaches. We found that shredder richness and abundance were influenced by both leaf litter quality and network location. Headwater environments supported a stronger consumer-resource relationship, and shredder communities were further richer and more abundant. This was not the case in mainstem locations. In these relatively harsher environments, we offer that shredders did not appear to be actively feeding on the resources, but rather utilizing leaf litter more for habitat. Our results suggest river network position has important implications for how ecosystem function changes across spatially constrained environments.

ABRSRACT

Historically, studies have examined how local habitat, resources and species interactions influence community structure in stream ecosystems. Increasingly, though, attention has turned to understanding how regional factors (e.g. dispersal) interact with local conditions to influence communities. Often dispersal of organisms occurs in spatially constrained habitats, which can drastically influence community assembly. Dendritic networks are an example, and have a branching spatial configuration with some branches of the system more connected to others, making dispersal easier, while other locations are more isolated. As interest in multi-scale community assembly mechanisms has increased, less work has focused on the relationship between community assembly and ecosystem processes. Here, we sought to understand how consumer-resource interactions unfold in river networks. We predicted that stream network location would mediate detritivore (shredder) richness and abundance, and in turn would be associated with a shift in decomposition of organic matter (leaf litter). To examine this, we manipulated leaf litter species in isolated (headwaters) and connected (mainstem) stream reaches. We found that shredder richness and abundance were influenced by both leaf litter quality and network location. Headwater environments supported a stronger consumer-

resource relationship, and shredder communities were further richer and more abundant. This was not the case in mainstem locations. In these relatively harsher environments, we offer that shredders did not appear to be actively feeding on the resources, but rather utilizing leaf litter more for habitat. Our results suggest river network position has important implications for how ecosystem function changes across spatially constrained environments.

Key words: dendritic network, shredders, ecosystem processes, dispersal, resource quality, consumer-resource interactions

INTRODUCTION

Historically, community ecologists have investigated the relationship between habitat, spatial structure, and ecological patterns and processes (Dunning et. al. 1992, Rahbek 2005, Simanonok and Burkle 2014). As such, consumer-resource interactions likely vary depending on location in spatially-constrained environments as different structuring mechanisms may influence biodiversity patterns differentially with spatial (Anderson and Hayes 2018). Dendritic networks exhibit linear branching, with habitats isolated as the edges of branches linked to more well-connected habitats (Fagan 2002, Grant et al. 2007). This branching configuration can mean that environmental factors influencing community composition vary depending on location within the network (Brown and Swan 2010, Altermatt et al. 2013, Morán-Ordóñez et al. 2015). As the factors influencing communities change with location, community assembly also shifts (Patrick and Swan 2011), which could lead to stronger consumer-resource associations than other locations across the network. By investigating the effect of spatial factors on community structure, we may provide a better understanding of the spatial dependence of relevant ecosystem functions associated with consumer guilds in such spatially structured environments.

In riverine ecosystems, headwater streams are isolated from the rest of the network when compared to higher order reaches, influencing community structure (Clarke et al. 2008). Compared to headwaters, mainstems are more connected to the regional species pool and dispersal between local communities is relatively more important in structuring communities as local processes (Wilson and McTammany 2014). Therefore, it is hypothesized that regional factors in headwater reaches, such as dispersal, are limited while local conditions, such as resource gradients and species interactions, shape community structure (Poff 1997, Leibold 2004, Chase et al. 2005). In contrast, mainstem (e.g., 3rd or higher order) stream reaches are hypothesized to be structured by a combination of local and regional processes (Economo and Keitt 2008). While it is hypothesized that regional and local factors can influence communities differently depending on stream network location (Kitto et al. 2015, Brown et al. 2018), it is unknown if these factors in any way regulate stronger consumer-resource associations in headwaters, and thus implications for any such consumer-driven ecosystem function. The majority of the leaf litter from deciduous trees falls to the ground and decomposes in soils (Binkley and Giardina 1998). However, some leaf litter falls or is blown into adjacent water bodies, such as streams, ponds and wetlands, and can act as a significant source of energy and nutrients for aquatic food-webs (Anderson and Sedell 1979, Cummins et al. 1989). Leaf breakdown in aquatic systems describes, in part, the energy liberated to higher trophic levels via consumer feeding. It is primarily controlled by environmental conditions (climate, flow, water chemistry), organisms (invertebrates, fungi and bacteria) and foliar chemistry (Ostrofsky 1997, Gessner et al. 1999, Royer and Minshall 2003). Benthic macroinvertebrate consumers, also known as shredders, when present, can contribute substantially to breakdown rates (Hieber and Gessner 2002). These consumers feed on coarse particulate organic matter (large particles $>$ 1mm; Merritt and Cummins 1996) and serve to link terrestrial and aquatic systems by breaking down terrestrial leaf litter, supporting secondary production (Graça 2001). Furthermore, there is some evidence that the generation of fine particulate organic matter (FPOM) as a by-product of shredder feeding can serve as a resource for other particle-feeding stream organisms (Cummins and Klug 1979, Wallace and Webster 1996). In addition to creating FPOM for the aquatic food web, shredders are an important food source for other macroinvertebrates and fish, mediating the transfer of energy from terrestrial environments to aquatic systems (Moore et al. 2004). In this study, we asked if there is a relationship between network structure and ecological function, and if the association differs depending on network location and resource quality. To address this, we examined the

association between leaf-shredding consumers and litter breakdown in different reaches of the stream network. Headwaters offer a more favorable environment for strong consumer resource associates to develop (Freeman et al. 2007, Richardson and Danehy 2007) however, in mainstems, environmental conditions, such as a more intense hydrological regime, may blur the role invertebrate consumers play in regulating resource dynamics (Swan and Brown 2011). This shift in conditions will influence community structure differently, with respect to headwaters, and the interaction between consumers and resources may vary because the environment is less favorable for strong consumer-resource interactions. Therefore, as community composition varies, the function and processing within the stream could be expected to change as well (Royer and Minshall 2003).

We hypothesized consumer-resource interactions would vary depending on location in the stream network as the magnitude of regional and local influences on communities varies. In environments that allow for strong consumer resource interactions, a positive relationship between consumers and resources is expected (Peckarsky et. al. 2006), but in less favorable environments the relationship may change. To investigate the relationship between network position and ecosystem function we replicated local food resources, taken as high and low quality leaf litter, in multiple headwater and mainstem stream sites. We then measured invertebrate consumer community structure and resource dynamics, taken as leaf litter breakdown. Based on previous research (Peckarsky et. al. 2006, Grant et al. 2007, Brown and Swan 2010, Brown et al. 2011, Swan and Brown 2011) we propose the following predictions: (1) consumer richness and abundance will be higher in headwater streams relative to mainstems, (2) resource quality will support stronger consumer-resource relationship, with the relationship between consumer abundance and breakdown rate stronger for the high quality resources in both headwater and mainstems, and (3) resource loss will vary with consumer richness/abundance, which is mediated by position within the river network.

METHODS AND MATERIALS

Study Area

All stream sites were located within Patapsco State Park, Maryland USA. We selected six stream locations at which to test our hypotheses; three headwater streams (1st order) and three mainstem streams (3rd or 4th order). We ground truthed prior to the study to select suitable streams, to confirm had rich invertebrate communities and limited human influence, taken as having low impervious surface and/or low conductivity. Environmental measurements (discharge, L s^{-1}; conductivity, µS; dissolved oxygen, mg L^{-1}; temperature, ^{o}C; latitude/longitude, light availability, µmol $m^{-2}s^{-1}$; percent canopy cover, water quality) were collected for each location. ArcGIS was used to estimate watershed size (ha) using a modified AGREE algorithm; distance to next downstream confluence, distance to next downstream increase in stream order, and percent impervious surface cover within each watershed. Percent impervious surface cover was calculated using 30x30m USGS 2006 NLCD percent developed impervious layer.

Water Quality

Major anions, NO_3-N, PO_4-P, SO_4, were quantified using a DIONEX ICS-5000 ion chromatograph. Samples were filtered through a 0.45µm syringe filter prior to analysis. Replicates of at least two samples were used in each sample batch to ensure internal reproducibility. Additionally, calibration standards, a check standard (SPEX CertiPrep, Inc.), and deionized water blanks were analyzed to ensure the accuracy of the instrument (Gallagher et al. 2011).

Litter Breakdown

To test the hypothesis that the relationship between consumer community structure and ecosystem processing of detritus was mediated by network location, we placed leaf litter bags at different locations in the stream network. Additionally, to test for the effects of local resource quality on consumer community composition we selected two leaf species; one consisted of a high quality food resource (*Fraxinus pennsylvanica* , Green Ash) while the other is a lower quality food resource (*Fagus grandifolia* , American Beech; Table 1).*Fraxinus pennsylvanica* is a fast decomposing species relative to*F. grandifolia* with higher N content; C:N ratio for *F. pennsylvanica* was 29.66 while *F. grandifolia* was higher at 48.47 (Elemental analyzer isotope

ratio mass spectrometry (EA-IRMS)). We constructed litter bags composed of senesced leaves from trees in early November 2012 from a forested area about 3 km from the streams sites. We collected freshly fallen leaves from target tree species during autumn to avoid any potential decomposition on the ground. Coarse mesh bags (7 x 11 mm mesh size) were used to contain the leaves yet allow colonization by invertebrates. Litter bags were filled with ˜5 g of leaves from one species, and eighteen litter bags were deployed at each location (n=9 per species). Our treatment design was 2 leaf species x 2 reaches (headwater, mainstem) x 3 stream networks x n=9 per species = 108 leaf litter bags deployed.

We deployed litter bags from 22 January 2013 to 25 January 2013. Litter bags were exposed to the streams for 40 days. We removed bags in the same order and manner as placement to ensure all bags were treated for the same amount of time. When deploying bags in the streams, we positioned them in reaches where water was flowing (i.e. runs or riffles), while pools were avoided if possible. Bags were attached to a line of galvanized wire and fixed to the streambed using large galvanized nails, approximately 20 cm long. We ran wire through the middle of the stream and bags were located approximately 1 meter apart. We checked bags periodically through the study to make sure they were still anchored to the streambed. General methods followed Swan et al. (2009).

At the completion of the study, we cut each litterbag from the line and immediately placed it in a re-sealable plastic bag. Removing bags was done in a manner to prevent the loss of invertebrates or leaf litter, and to not disturb adjacent bags on the line. Re-sealable plastic bags were transported back to the lab in a cooler for processing. Upon returning to the lab, we rinsed leaves free of sediments and organisms with tap water into a 500 micron sieve before drying them. Insects were preserved in 80% ethanol for eventual identification. The remaining leaf material was dried in a drying oven at 75° C for 24 hours and the dry weight recorded. We then combusted leaves in a muffle furnace at 550° C for an hour, and re-weighed to determined ash-free dry mass remaining (AFDM, Swan and Palmer 2004).

We enumerated and identified invertebrates under a dissecting scope to the lowest possible level, typically genus (Merritt and Cummins 1996), and counted. Functional feeding group classifications were assigned using Merritt and Cummins (1996), and published data (Poff et. al., 2006). The entire macroinvertebrate community from each litterbag was identified, however only the leaf-consuming invertebrates (hereafter, consumers) were used in the analysis.

Data Analysis

We reported breakdown rate as ash-free dry mass lost per gram of initial litter ash-free dry mass per day. We performed a two-way analysis of variance (ANOVA) to examine the variability in resource loss rates between leaf species and stream reach (2 leaf resource types x 2 stream reaches). Additionally, a two-way ANOVA was also used to examine the variability in consumer richness and abundance, across all treatments. We related resource loss to consumer abundance using a simple linear regression for headwater and mainstem network locations separately. When examining consumer abundance against resource loss, abundances were skewed (more litter bags with low abundances than high abundances). As such, consumer abundances were log transformed to improve normality. We preformed all analyses in R statistical software version 3.1.2. All statistical tests were evaluated at α=0.05.

RESULTS

Environmental Results

Headwater and mainstem reaches varied in terms of physical attributes. The mainstem reaches had larger watersheds, higher discharge, and increased impervious surface cover when compared to headwater reaches (Table 2). As watershed area and percent impervious surface cover increased, so did conductivity. Percent canopy cover was typically higher in headwaters than mainstems, except in the Cascade drainage where percent canopy cover was the same for both reaches (Table 2).

Water chemistry varied between stream networks and across stream reaches. Total nitrate (NO_3-N) showed less variability among mainstem reaches relative to headwater sites (Table 3). Total phosphate (PO_4-

P) concentrations were undetectable in all headwater reaches, but the mainstems reaches had detectable concentrations and the sites were similar (Table 3). Sulfate (SO_4) concentrations in all headwater reaches were higher than any of the mainstem reaches, and exhibited higher variability (Table 3).

Leaf Litter Quality

The difference in resource quality between *F. pennsylvanica* and*F. grandifolia* is evident in the leaf chemistry. As stated above,*F. pennsylvanica* had lower carbon:nitrogen (C:N) content than*F. grandifolia* , and that was accompanied by a higher percent N in*F. pennsylvanica* . Percent nitrogen and percent phosphorus (P) varied between resources, and concentrations of both N and P were higher in *F. pennsylvanica* relative to *F. grandifolia* (Table 1). Conversely, *F. grandifolia* contained higher amounts of phenols and tannins than *F. pennsylvanica* , and toughness was higher in*F. grandifolia* relative to *F. pennsylvanica* (Table 1).

Consumer Richness and Abundance

Network location significantly influenced consumer richness (Fig. 1). Consumer richness was higher in headwaters for both resources (f-value = 58.01, $p < 0.001$). In headwaters, *F. pennsylvanica*litter bags contained the highest number of consumer taxa, while*F. grandifolia* litter bags contained ˜1.46 times fewer than that of *F. pennsylvanica* (Fig. 1). The mean consumer richness decreased in litter bags located in mainstems reaches.*Fraxinus. pennsylvanica* litter bags in mainstem reaches contained ˜2.02 times fewer consumer taxa than *F. pennsylvanica* litter bags in headwaters. The same can be concluded about *F. grandifolia* litter bags. Mean consumer taxa in *F. grandifolia* litter bags decreased ˜1.97 times from headwaters to mainstems (Fig. 1). In addition to network location, resource quality had a significant effect on consumer richness (f-value = 17.56, $p < 0.001$; Fig. 1). *F. pennsylvanica* supported significantly higher richness than *F. grandifolia* when compared to one another within the same reach treatment. There was no significant interaction when resources were examined across both reach treatments.

Similar to consumer richness, network location had a significant effect on consumer abundance (f-value = 40.34, $p < 0.001$; Fig. 2). Consumer abundance was higher in headwater reaches for both resource types. Headwater reaches with *F. pennsylvanica* litter bags attracted the most consumers, while *F. grandifolia* litter bags contained ˜1.45 times fewer consumers per litter bag than *F. pennsylvanica* (Fig. 2). In mainstem reaches, the abundance of consumers decreased for both resources. Mainstem reaches with *F. pennsylvanica* litter bags attracted ˜3.35 times fewer consumers than in headwaters (Fig. 2). Additionally,*F. grandifolia* litter bags in mainstems contained ˜3.4 times fewer consumers than that of headwaters (Fig. 2). While stream reach had the greatest influence on consumer abundance, resource quality also significantly affected consumer abundance (f-value = 4.70, $p = 0.03$; Fig. 2). When we examined resources across reaches there was no significant interaction.

Litter Breakdown

Resource quality and network location significantly explained variation in litter breakdown. Resource quality had the most significant effect on breakdown (f-value = 490.11, $p < 0.001$, df = 1; Fig. 3).*F. pennsylvanica* decomposed faster than *F. grandifolia* in both headwaters and mainstems. Mean loss for *F. pennsylvanica* in headwaters was the highest of any treatment (Fig. 3). In mainstems, resource loss for *F. pennsylvanica* litter bags decreased by ˜21% relative to headwaters (Fig. 3). Resource loss for*F. grandifolia* litter bags was essentially the same across stream reaches, though it was slightly higher in mainstems. In headwaters, mean resource loss for *F. grandifolia* litter bags was ˜3% less than in mainstem reaches. Stream reach did have a significant effect on litter breakdown (f-value = 7.04, $p < 0.01$), and there was a significant interaction between resource quality and stream reach (f-value = 9.58, $p < 0.01$; Fig. 3).

Consumer Abundance and Litter Breakdown

The relationships between consumer abundance and litter breakdown were influenced by stream network location. Headwaters demonstrated significant relationships with both resource quality and resource loss (Fig. 4A and 4B). As the abundance of consumers within litter bags increased, litter breakdown increased as well. The relationship between consumer abundance and breakdown in headwaters was stronger for *F.*

pennsylvanica (t-value = 2.22, p = 0.04; Fig. 4A) than *F. grandifolia* (t-value = 2.29, p = 0.03; Fig. 4B). However, this relationship was not observed in mainstem reaches. For *F. pennsylvanica,* there were no significant relationships between consumer abundance and breakdown (t-value = -0.25, p = 0.81). As the abundance of consumers increased, resource loss slightly decreased but remained fairly consistent (Fig. 4C). However, there were significant interactions between *F. grandifolia* loss rate and consumer abundance in mainstems (t-value = -4.17, $p < 0.001$; Fig. 4D), though the interaction between consumer abundance and breakdown was not the same as in headwaters. As consumer abundance increased in the litter bags, breakdown decreased, suggesting consumers are aggregating on *F. grandifolia* but not consuming the resource (Fig. 4D).

DISCUSSION

The purpose of this study was to assess local patterns in consumer community structure, the relationship between these patterns and ecosystem function, and how such potential interactions vary with location in a dendritic network. In locations where local environmental conditions are hypothesized to influence consumer community composition greater than regional (i.e. dispersal-driven) factors, we expected to see stronger consumer-resource relationships (Peckarsky et. al. 2006). In stream reaches where regional and local factors are known to influence consumer community composition (mainstem reaches) environmental constraints should be less amenable for consumer-resource relationships to develop (Fagan 2002, Grant et al. 2007, Brown and Swan 2010, Swan and Brown 2011). Since network position can make the environment more or less suitable for consumer-resource interactions (Poff 1997, Leibold 2004, Chase et al. 2005), resource loss could vary depending on network location.

In this study we found that consumers preferred headwater reaches and high quality resources. We were able to determine this based on results showing that consumer richness and abundances were higher in headwaters than mainstems, and within each reach the high quality local resource contained richer and more abundant consumer communities (Fig. 1 and 2). This was the case even though composition of consumers were similar (Fig. 4). Resource loss due to consumer activity was also higher for *F. pennsylvanica* at both stream network reaches (Fig. 3). However, the relationship between consumers and resources seemed to change with network location. In headwaters, there was a positive relationship between consumer abundance and resource loss, and in mainstems the interaction shifted for both resources (Fig. 4). It appears headwaters created more favorable environments for consumer-resource interactions to develop. The decrease in stream width and discharge may increase retention time for leaves (Graça and Canhoto 2006) and possibly promote consumer mobility (Gjerløv et. al. 2003).

Local environmental conditions varied between headwater and mainstem streams. Mainstem reaches had larger watersheds, discharge, percent impervious surface, and conductivity when compared to headwater streams (Table 2). Differences in local environmental conditions, in addition to increased influence from regional factors, may have created less favorable conditions for strong consumer-resource relationships in mainstem streams when compared to headwater streams (Rosemond et. al 2000). For example, coral reef environments can influence consumer-resource interactions by creating more favorable conditions for species interactions by providing refuge from harsh environmental conditions (i.e. tidal flows; Stachowicz 2001). However, the loss or decrease of these features would make the environment less suitable for strong consumer-resource interactions to develop (Munday 2004). Mallory and Richardson (2005) found consumer-resource interactions varied as environmental factors shifted. Changes in environmental conditions (e.g., light penetration, nutrient concentrations, habitat size) influenced the production of resources (e.g., algae, periphyton) and consumer (e.g., tailed frog tadpoles) growth rates (Mallory and Richardson 2005). When the environment (e.g., unshaded stream reaches) favored resource production, consumer growth rate increased by 14%, relative to unfavorable environmental conditions. Consumer-resource dynamics may also be influenced by temperature (i.e. climate change). Vasseur and McCann (2005) modeled that a warming environment could negatively affect resource and consumer biomass, with consumer biomass possibly being more sensitive to these changing conditions.

Local resource quality also significantly influenced consumer community richness and abundance (Fig. 1

and 2). When comparing resource types within the same network position, consumers preferred high quality resource (Fig. 1 and 2). We found *F. pennsylvanica* litter bags contained more abundant and richer consumer communities than *F. grandifolia* . We contend the consumers were attracted to the more nutrient rich resource and would aggregate in those high quality litter bags to exploit the fast decomposing resource (Hladyz et al. 2009, Yue et al. 2022). In a previous unpublished study, we found similar results. We exposed individual consumer taxa to the same resources and measured consumer feeding rates. When consumers were presented with *F. pennsylvanica* all consumers increased feeding rates relative to*F. grandifolia* .

The relationship between consumers and resources appeared to change with network location. In headwaters, consumer abundance and mass loss were positively related for both resources, though the relationship was stronger for *F. pennsylvanica* (Fig. 4A and 4B). As consumer abundance increased resource loss increased as well, suggesting the environment was suitable for strong consumer-resource interactions. However, in mainstems the consumer-resource relationship changed and was not positive for either resource (Fig. 4C and 4D). For *F. pennsylvanica,* resource loss did not change with increased consumer abundance. *F. grandifolia* actually had a strong negative relationship, with decreased resource loss as consumer abundance increased. This suggests that the mainstem environment was not as suitable for strong consumer-resource interactions, and that consumers used the resources differently when in unfavorable environments. In preferred environments, consumers were abundant with diverse communities and actively feeding on resources, however in unfavorable environments consumer processing and use of the resources changed. The consumer communities found in mainstem reaches consisted of the same consumer taxa as headwaters, thus this shift in resource use was not due to different consumer taxa. We contend the shift in resource use was due to consumers utilizing the resource for habitat from the harsher environment, rather than consuming the resource. This mechanism seems apparent with *F. grandifolia* where we saw a strong negative relationship between abundance and resource loss, and this may be explained by the higher amount of structural compounds found in *F. grandifolia* . With *F. pennsylvanica* the interactions between resource loss and consumer abundance were neutral, implying consumers used the resource for habitat as well. The consumer-habitat interactions were not as strong for *F. pennsylvanica* , compared to *F. grandifolia* , and this may be explained by the lower amounts of structural compounds found in *F. pennsylvanica* .

Our findings of more diverse and abundant consumer communities in the presence of a high quality resource were similar to findings from other studies (Motomori et al. 2001, Kominoski and Pringle 2009). Kominoski and Pringle (2009) found higher consumer abundance in litter bags containing a high quality resource (*Liriodendron tulipifera*), and when the low quality resource (*Rhododendron maximum*) was present in litter bags consumer abundance decreased. In addition to increased consumer diversity and abundance with high quality resources, other studies examined consumer preference by studying feeding rates with different resource qualities (Motomori et al. 2001, Ratnarajah and Barmuta 2009). Motomori et al. (2001) found that as resource C:N decreased the concentrations of macroinvertebrate consumers,*Goerodes satoi* and *Hydatophylax festivus* , increased. Then in a lab setting they found that the same consumers increased feeding activity when offered resources that had lower C:N ratios, higher concentrations of N and P, and lower amounts of structural compounds (Motomori et al. 2001).

Previous research hypothesized local processes influence riverine communities in isolated headwater reaches, while in connected mainstem reaches both regional and local processes influence community composition (Grant et al. 2007, Brown and Swan 2010, Brown et al. 2011). By examining how the consumer-resource interactions changed with network location we were able to test for the relative influence of local and regional processes. In areas where local conditions are more influential than regional processes (headwaters) we saw positive relationships between consumers and resources. In reaches where regional and local processes both influence communities the consumer-resource interaction changed suggesting the processes controlling that interaction changed (Mallory and Richardson 2005, Vasseur and McCann 2005).

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Table 1: Leaf chemistry data for the high quality resource (*Fraxinus pennsylvanica*) and low quality resource (*Fagus grandifolia*).

Species	C:N	Toughness (g)	Toughness (g)	Phenolics (μg g^{-1})	% P	% N	Tannins (% by wt.)
Fraxinus pennsylvanica	29.66	53.54	12.08	12.08	0.115	1.099	0.004
Fagus grandifolia	48.47	64.08	29.257	29.257	0.033	0.656	0.043

% Imp. Surface cover	0.03	4.9	0.11	6.61	0	5.48
Watershed Area (ha)	24.8	203.54	31.17	971.1	19.58	808.14
% Canopy Cover	90	90	98	84	95	90
Discharge (L s^{-1})	4.53	106.38	1.57	83	1.76	78.75
Conductivity (µS)	85.2	181.4	85.5	202	61.7	196.9
Dissolved O_2 (mg l^{-1})	11.13	13.14	13.41	14.58	12.42	14.18
Latitude	N 39°14'9.96"	N 39°14'25.64"	N 39°13'55.51"	N 39°13'29.59"	N 39°13'23.68"	N 39°13'1
Longitude	W 76°45'32.70"	W 76°45'0.29"	W 76°44'40.44"	W 76°43'10.93"	W 76°44'9.34"	W 76°44'5
Stream Order	1	3	1	4	1	4
Reach	HW	MS	HW	MS	HW	MS
Site	Cascade	Cascade	Patapsco	Patapsco	Rockburn	Rockburn

Table 3: Anion concentrations (mg/L) for stream sites. Includes total nitrates (NO_3-N), total phosphate-P (PO_4-P) and sulfate (SO_4). Sample name refers to stream network and reach. HW=headwater reaches and MS=mainstem reaches. When the anion concentration was too low to be detected n.a. was listed.

Site, Reach	NO_3-N	PO_4-P	SO_4
Cascade HW	1.59	n.a.	18.8
Cascade MS	0.89	0.33	16.8
Rockburn HW	1.10	n.a.	17.3
Rockburn MS	0.80	0.30	15.2
Patapsco HW	0.22	n.a.	21.2
Patapsco MS	0.76	0.33	17.2

FIGURE LEDGENDS

Figure 1. The effect of network reach and resource quality on consumer richness. Bars represent the mean number of consumer taxa per litter bag with 95% confidence intervals.

Figure 2: The influence of network reach and resource quality on consumer abundance. Bars represent the mean number of consumers per litter bag with 95% confidence intervals.

Figure 3: The result of network reach and resource quality on resource loss. Bars represent the mean resource loss (AFDM Loss per Gram of Initial Leaf Litter per Day) per litter bag with 95% confidence intervals.

Figure 4: Resource loss plotted against log-transformed abundance. A=high quality resource in headwater reaches, B=Low quality resource in mainstem reaches, C=High quality resource in mainstem reaches, D=Low quality resource in mainstem reaches. Line of best fit added to demonstrate the relationship. Resource loss was calculated as AFDM loss/gram initial litter/day.