

Experimental reductions in stream flow alter litter processing and consumer subsidies in headwater streams

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SUMMARY

1. Forested headwater streams are connected to their surrounding catchments by a reliance on terrestrial subsidies. Changes in precipitation patterns and stream flow represent a potential disruption in stream ecosystem function, as the delivery of terrestrial detritus to aquatic consumers and downstream transport are compromised. The potential effect of drying on decomposition is critical to understanding ecosystem processes in these detritus-driven ecosystems.
2. In this study, we experimentally altered stream connectivity to examine how altered water availability would influence litter decomposition. We used three catchments in the Coweeta Hydrologic Lab in North Carolina, U.S.A., establishing sites that were always wet, intermediately wet and completely terrestrial, while also experimentally diverting significant surface flow from downstream locations for several months.
3. The flow manipulation significantly reduced the amount of water available to the three study reaches, leading to drastic changes in organic matter accumulation. Stream temperature and dissolved oxygen changed during the manipulation but only in response to season. Nutrient concentrations remained low or below detection during the experiment, demonstrating no response to the manipulation.
4. Red maple and white oak demonstrated significantly different mass loss during the first few days of the experiment, but by the completion of the experiment, location was a more significant determinant of breakdown rate than leaf identity. Leaves placed in sites that were consistently wet decomposed at a higher rate than those in bank or terrestrial sites.
5. Initially, leaf decomposition varied significantly based on site type and presence of water, which led to disruptions in microbial and macroinvertebrate colonisation and processing. High flows during large winter storms reconnected dried reaches and stimulated rates of decomposition due to colonisation by microbes and macroinvertebrates.
6. Macroinvertebrate densities tracked microbial biomass accumulation on leaves, but were dependent upon location. Leaves in the manipulated reaches had significantly higher macroinvertebrate densities compared to the upstream control in the winter and spring in response to the delayed wetting of large standing stocks of leaves and subsequent colonisation by microbes.
7. Our study demonstrated that even minor disruptions in stream connectivity at key times of the year have community- and ecosystem-level influences that alter decomposition. The resilience of these ecosystems will depend on the frequency of disturbances and the ability of organisms to adapt to changing resource conditions.

Keywords: aquatic–terrestrial linkages, climate change, experimental drying, headwater streams, leaf decomposition

Introduction

Forested headwater streams are strongly connected to their surrounding catchments by a reliance on terrestrial subsidies (Cummins *et al.*, 1989; Wallace *et al.*, 1997). Terrestrial organic matter blown or washed in from riparian areas in the autumn provides a nutritional resource for microbes and macroinvertebrates. The transport of processed organic material to downstream consumers creates an important longitudinal link between larger streams and their headwaters (Vannote *et al.*, 1980; Cummins *et al.*, 1989; Kominoski & Rosemond, 2012). Therefore, disruptions in the linkages between aquatic and terrestrial components of headwater stream ecosystems may alter vital ecosystem processes.

Changes in precipitation patterns and stream flow represent a potential disruption in stream ecosystem function, as the delivery of terrestrial detritus to aquatic consumers and downstream transport are compromised. In studies of streams spanning tropical (Larned, 2000) and temperate (Lugthart & Wallace, 1992; Whiles & Wallace, 1995) forests, significant amounts of detritus (mostly leaves) were retained during severe drought conditions. Accumulated leaves were mostly exported downstream with the arrival of storms (Lugthart & Wallace, 1992; Larned, 2000), suggesting that leaves remain unprocessed during periods of low flows (Hutchens & Wallace, 2002; Robson *et al.*, 2008). In the absence of water, Datry *et al.* (2011) found a nearly 25% decrease in decomposition rate. Flow reductions alter the period of time that leaves are submerged. Studies of leaf decomposition in tropical streams (Encalada *et al.*, 2010), temperate streams (Schlief & Mutz, 2011) and temperate wetlands (Inkley, Wissinger & Baros, 2008) suggest that the amount of time that leaves spend submerged is a significant factor influencing both biotic and abiotic breakdown processes. Langhans *et al.* (2008) further noted that in a heterogeneous landscape of wet, dry and intermittent riverine habitats, decomposition was much faster in permanently wet areas as opposed to those with variable water persistence.

Altered precipitation patterns are a common prediction of climate models (e.g. Bates *et al.*, 2008). Empirical studies of reduced flow in stream ecosystems have generally been conducted in response to natural drying, instead of through targeted experimental reductions in flow. Also, the majority of studies linking lower precipitation and ecosystem function have been performed in regions naturally prone to drought, such as the desert Southwest of the United States (e.g. Dahm *et al.*, 2003) or

Mediterranean regions (e.g. Acuña *et al.*, 2005; Datry *et al.*, 2011, 2012). Studies linking precipitation and ecosystem function in temperate forest ecosystems have shown that these systems may also be vulnerable to drought stress (Lugthart & Wallace, 1992; Whiles & Wallace, 1995). The potential effect of this drying on processes such as decomposition is critical to understanding ecosystem processes in these detritus-driven ecosystems. Drought-related studies in perennial streams (e.g. Lugthart & Wallace, 1992; Whiles & Wallace, 1995) have been more descriptive of changes to populations of macroinvertebrates, but Corti *et al.* (2011) and Datry *et al.* (2011) have shown that decreased water availability can also affect ecosystem processes such as leaf decomposition.

Concurrent with the changes in the timing of precipitation are regional changes to canopy cover due to climate change and species invasion. Recent work has suggested a shift in dominant overstory in the southern Appalachians and the east coast in general (Iverson, Prasad & Matthews, 2008a). Specifically, the southeastern United States will move from a maple-oak-dominated system to one dominated by more xeric oak-pine forests (Iverson *et al.*, 2008b). The generally slower breakdown of oak (relative to maple), combined with the increased probability of more recalcitrant leaf inputs into the streams draining this region (e.g. Morkeski, 2007; Webster *et al.*, 2012), suggest a shift in not only processing rates (Kominoski *et al.*, 2007) but the availability of less labile dissolved and particulate organic matter for downstream consumers (McArthur & Richardson, 2002; Ardón, Pringle & Eggert, 2009).

Given the uncertainties in how ecosystems may function in a future climate of altered precipitation, we chose to experimentally address these issues in perennial streams in the southern Appalachians. These streams are ideal because, in spite of constant stream flow, precipitation frequency and intensity are currently changing relative to past conditions. Most precipitation has shifted to winter and spring, as opposed to the more even annual distribution of rainfall in the past (Wu, Clark & Vose, 2012, 2014). For example, in the last decade, the distribution of storms at Coweeta Hydrologic Laboratory in North Carolina have not only demonstrated a temporal shift away from summer but also an increase in intensity relative to those measured made during the middle of the 20th century (Ford *et al.*, 2011; Laseter *et al.*, 2012). Furthermore, there is a paucity of studies in forested perennial headwaters where targeted reductions in stream flow are used to address predicted future precipitation variability on critical ecosystem functions.

Therefore, our objective in this study was to better understand how leaf decomposition is affected by a targeted experimental reduction in stream flow meant to simulate predicted changes in water availability in the southern Appalachians. Sites of experimental flow reduction were part of a gradient of water availability that we established in and around our study streams to assess leaf decomposition and other biotic responses. The gradient included unmanipulated stream reaches, experimental sites, along with two non-stream locations. Non-stream locations were chosen to represent potential extreme future decomposition outcomes when water is less available. Bank-side sites served as an analogue for a completely dry stream bed, still having moist soils but lacking the consistent inundation common to stream sites. Terrestrial sites were chosen to represent a complete lack of stream water interaction.

We predicted that leaves in sites with some degree of stream flow would decompose faster than those in drier sites. Also, we predicted that patterns of microbial and macroinvertebrate colonisation of leaves would be in response to the location in which they were placed. Red maple leaves were expected to decompose more quickly than white oak due to greater lability of maple leaves noted in prior work in the region (e.g. Webster *et al.*, 1999).

Methods

Site description

This study took place in three catchments (WS 22, 40 and 41) at the Coweeta Hydrologic Laboratory, North Carolina. Three sites on each of the three catchments were established along a natural gradient from the thalweg of the stream up to the hillside directly adjacent (Fig. 1). Upstream sites were located in-stream, bank sites only became wet when intense storms increased the wetted-width of the stream and terrestrial sites were located uphill on the forest floor. Experimental sites had surface flow reduced downstream of established (but non-functional) weirs using experimental diversions (Fig. 1).

With permission of the US Forest Service at Coweeta, we established a 'proof-of-concept' weir diversion on WS 40 on 10 September 2010 followed by the establishment of our other two experimental diversions in 2011 (WS 41 on 26 July and WS 22 on 9 August). Weir ponds were cleared, and a large piece of plywood was inserted behind the weir blade with a piece of landscape piping inserted through the board to drain water from the main

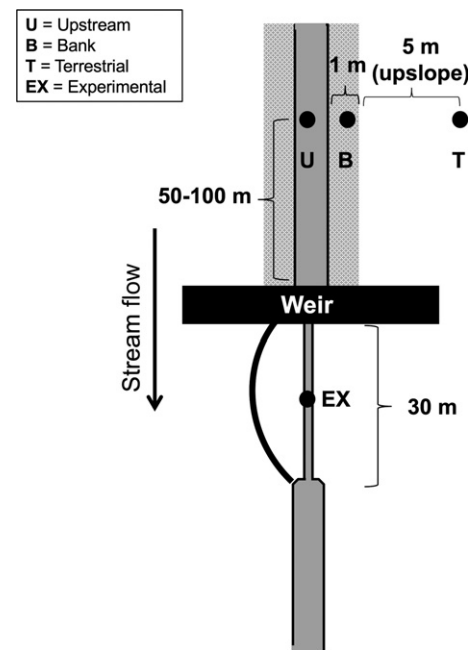


Fig. 1 Experimental design used for this study. This setup was replicated across three catchments in Coweeta ($n = 3$), with each point representing the location of the leaf packs in each of the site types in the catchment. The grey hatched area surrounding bank sites indicates that leaf packs in those locations that only became wet during major storms that increased stream width.

channel. Downstream, experimental sections ranged from 25 to 30 m in length, with water being piped back into the stream below the study reaches (Fig. 1). This resulted in a balanced, replicated design ($n = 3$) for each of the four site types. Experiments were conducted in the three catchments from 7 October 2011 to 4 March 2012 before diversions were removed at the request of the USFS.

Leaf breakdown

Leaf breakdown was assessed at all sites using both red maple [(Aceraceae) *Acer rubrum*] and white oak [(Fagaceae) *Quercus alba*] leaves, which represented a range of decomposition based on previous studies at Coweeta (Webster *et al.*, 1999). Additionally, red maple leaves represent a more labile, deciduous canopy leaf species that is predicted to decrease in the future in favour of more recalcitrant and xeric oaks and pines (e.g. Iverson *et al.*, 2008a,b). Five-gram leaf packs were made for both species using plastic mesh bags (mesh size = 5 mm) and were staked to the sediment or soil at each site. One maple and one oak pack were collected from each site on six occasions from October 2011 to March 2012, for a total experimental time of 150 days. Leaf material was

washed gently with stream water into a pan and small subsamples were taken for microbial analyses (see below). The rest of the leaf material was placed in paper bags for transport and drying in the laboratory. Leaves were oven-dried for 3 days at 60 °C. Dried leaf material was weighed and ground, and a subsample was burned in a muffle furnace at 550 °C for 1 h for calculation of ash-free dry mass (AFDM; Benfield, 2006). Exponential breakdown rates (k ; day^{-1}) were determined by regressing log-transformed AFDM over time (Benfield, 2006).

Biotic collections

Nine leaf subsamples (16-mm diameter discs) were removed from each leaf pack immediately after collection. One of the leaf discs was used as an estimate of mass removed from leaf packs due to subsampling. Four of the discs were preserved in methanol for quantification of ergosterol (Gessner, 2005), while the other four were preserved in 4% formalin for determination of bacterial abundance (Findlay *et al.*, 2002). Ergosterol concentration was determined by saponification and extraction into pentane (Gulis & Suberkropp, 2006). Leaf material preserved for bacterial counts was sonicated at 10 W for 2 min (Findlay *et al.*, 2002), and bacterial aliquots were enumerated on a gridded Petroff-Hausser cell counting chamber using phase-contrast microscopy. Cell densities were calculated as the average number of cells per chamber grid unit (mm^2), standardised to the volume of sample used. Ergosterol and bacteria concentrations were converted to units of C, allowing for direct comparisons of microbial biomass (Findlay *et al.*, 2002).

Macroinvertebrates washed from leaf material were preserved in 95% ethanol for enumeration and identification using keys of Brigham, Brigham & Gniska (1982) and Merritt, Cummins & Berg (2008). Density (number per g leaf AFDM) of macroinvertebrates and functional feeding group (FFG; e.g. Merritt *et al.*, 2008) were determined for each leaf pack collected during the experiment.

Physicochemical stream measures

We used salt slug dilution (Gordon *et al.*, 2004) to measure discharge at all stream sites throughout the sampling period. Wetted cross-sectional stream area was also measured throughout the sampling period. During each of the six sampling days, water was collected and filtered through 0.7- μm GFF filters and frozen for analysis of background nutrient levels in each site. In the

laboratory, ammonium concentrations were determined using the phenate method (American Public Health Association, American Water Works Association & Water Environment Federation (APHA, AWWA, WEF), 2005) with a flow-injection analyser (Lachat Quickchem 8500, Lachat Corporation, Loveland). Nitrate and soluble reactive phosphorus (SRP) concentrations were determined using ion chromatography (Dionex DX500 ion chromatograph, Thermo Fisher Scientific, Inc., Waltham). Specific conductance, stream temperature and dissolved oxygen (DO) were measured using a Hydrolab MS5 multi-parameter mini sonde (Loveland). Stream pH was measured using a YSI 556MPS multi-parameter handheld probe (Yellow Springs).

Organic-matter standing stocks

Coarse particulate organic matter (leaves, twigs and large pieces of material) was randomly sampled (0.25 m^2) from each stream reach ($n = 3$ for upstream and experimental) on each sampling date. Material was placed in paper bags and allowed to dry in an oven at 60 °C for at least 3 days. Mass was measured for each sample and standardised to sampling area.

Statistical analyses

Sites in the three catchments (e.g. Fig. 1) were sampled on seven different occasions from October 2011 to March 2012 for all response variables assessed here. Two-way ANOVA was used to determine differences in background measures (discharge, wetted cross-sectional stream area, conductivity, temperature, DO, pH, nutrients and organic-matter standing stocks) using sites (upstream versus downstream) and sampling date as factors. Differences in leaf breakdown rates among sites were assessed using a two-way ANOVA to assess differences among leaf pack locations for each species, blocking by catchment. A mixed-model ANOVA with repeated measures, blocking by catchment, was used to determine significant differences in leaf species, location and days for a series of response variables: %AFDM remaining, microbial biomass and macroinvertebrate density. Non-significant factors and interactions were removed from the mixed model, and it was re-analysed with Tukey-Kramer corrections for all pairwise comparisons of significant factors and interactions ($\alpha = 0.05$). A three-way ANOVA was also used to determine differences in leaf species, date and location for FFG density (Zar, 1999). All analyses were run with either JMP 9.0 or SAS 9.3 (SAS Institute, Inc., Cary).

Results

Physicochemical measures

Our point measures of discharge generally followed rainfall patterns in Coweeta (Northington, 2013), where a relatively dry summer and autumn were followed by a wet, stormy winter. Weir diversions on each of the three catchments used for this study successfully removed surface flow from experimental reaches when compared to upstream sites ($P = 0.04$). These data indicated that the diversions reduced flow in experimental sites by 40–90% initially, reflecting the ranges of model predictions for regional stream flow reductions in the future (Wu *et al.*, 2012). Over the course of the experiment, the maximum discharge occurred in February and March 2012 ($P < 0.0001$; Fig. 2a). It should be noted that changes in hydrology (e.g. Fig. 2) coincided with changes in leaf litter decay state during this experiment. Differences in wetted cross-sectional area generally

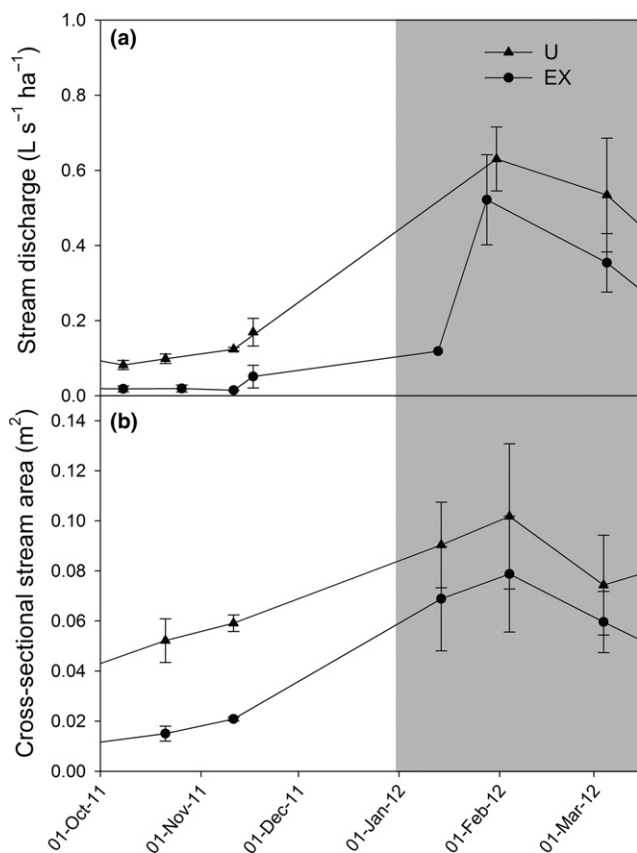


Fig. 2 Stream characteristics during this study, including (a) discharge and (b) wetted cross-sectional area. Points represent means of each site type, and bars represent 1 SE of the mean. Grey shading represents the period of the study where increased storms led to higher stream discharges.

followed patterns in discharge, with greater wetted areas in upstream sites ($P = 0.02$), and the widest stream areas occurred in February and March (Fig. 2b). Leaves in bank sites were wet when cross-sectional areas of the study streams were the widest and were noticeably moist (but not inundated).

Water temperature changed significantly and predictably as the seasons progressed during the experiment (Table 1). In contrast, both conductivity and pH remained relatively similar across all stream reaches over time. Dissolved oxygen also varied significantly over time, generally responding to changes in temperature ($r = -0.93$, $P < 0.001$; Table 1). Background levels of nutrients remained low over the course of the experiment. There were no detectable levels of ammonium or SRP during the study (minimum detection limit = $5.0 \mu\text{g L}^{-1}$). Measurable levels of nitrate were seen but did not exhibit a pattern across experimental and upstream sites (Table 1).

Organic-matter standing stocks significantly differed over time ($P = 0.001$) but not among sites (Fig. 3). There was a trend of greater standing stocks in experimental sites during the autumn when leaves were actually falling into the stream (Fig. 3). The accumulation of organic matter coincided with changes to discharge at each of the sites, with times of higher discharge generally having lower standing stocks of organic matter.

Mass loss of leaves over time

Leaves that were continually wet decomposed faster than those less consistently exposed to water, a pattern seen in both leaf species. With the exception of leaves on the bank, red maple mass decreased significantly after the first day of the experiment in all other sites ($P < 0.02$; Fig. 4). On the last day of the experiment (4 March 2012), the mass in upstream leaf packs was not different from bank and terrestrial sites (Fig. 4) but was significantly greater than in experimental sites ($P < 0.05$). The apparent increase in red maple mass on the last day of the experiment in upstream sites is likely an artefact of the design, where the final leaf packs were buried under stream sediments thereby slowing decomposition.

The trajectory of decomposition for white oak leaves was different than that of red maple (Fig. 4). White oak leaf mass declined from the beginning of the experiment until 12 November 2011 (day 36), where leaf packs in upstream sites had significantly less mass remaining as compared to all others ($P = 0.004$). After January 2012 (day 99), heavy winter storms increased variability in

Table 1 Background abiotic conditions of experimental (EX) and upstream (U) reaches used in this study. Missing data (–) were due to malfunctioning equipment. All ammonium and SRP values were below detection (BD; minimum detection limit = 5.0 $\mu\text{g L}^{-1}$). Day groupings that were significantly different have different letters based on Tukey's *post hoc* analysis ($\alpha = 0.05$).

| Date | Reach | Temperature ($^{\circ}\text{C}$) | | Specific conductance ($\mu\text{S cm}^{-1}$) | | pH | | Dissolved oxygen (mg L^{-1}) | | NO_3^- ($\mu\text{g L}^{-1}$) | |
|-------------|-------|------------------------------------|-----------|--|-----------|-----------|---------|---|-----------|--|----------|
| | | Mean (SE) | Range | Mean (SE) | Range | Mean (SE) | Range | Mean (SE) | Range | Mean (SE) | Range |
| 8 Oct 2011 | EX | 12.7 ^a (0.5) | 11.8–13.3 | 19.7 (4.1) | 13.2–27.3 | – | – | 6.7 ^a (0.5) | 5.8–7.6 | 27.9 (13.9) | 9.5–55.1 |
| | U | 12.7 (0.4) | 11.9–13.2 | 17.0 (2.1) | 12.8–19.3 | – | – | 8.5 (0.5) | 7.6–9.4 | 10.2 (3.2) | 7.1–13.4 |
| 22 Oct 2011 | EX | 10.7 ^b (0.4) | 9.9–11.3 | 20.6 (3.8) | 14.5–27.7 | – | – | 8.0 ^a (0.5) | 6.9–8.6 | 6.0 (0) | |
| | U | 10.5 (0.3) | 10.1–11.2 | 17.7 (2.0) | 13.7–20.0 | – | – | 9.5 (0.3) | 9.0–10.0 | BD | |
| 12 Nov 2011 | EX | 8.7 ^c (0.8) | 7.2–9.8 | 21.4 (2.5) | 16.8–25.6 | 7.2 (0.5) | 6.6–8.1 | 10.9 ^b (0.8) | 9.4–12.3 | 15.9 (7.7) | 6.5–25.4 |
| | U | 8.4 (0.5) | 7.6–9.3 | 19.6 (2.0) | 15.6–21.9 | 7.1 (0.5) | 6.8–7.6 | 11.9 (0.3) | 11.5–12.5 | 20.7 (0) | |
| 14 Jan 2012 | EX | 4.9 ^e (0.2) | 4.4–5.1 | 14.8 (2.5) | 10.0–18.3 | 7.4 (0.2) | 7.1–7.7 | 13.6 ^c (0.2) | 13.3–14.0 | 14.2 (0) | |
| | U | 4.8 (0.2) | 4.5–5.1 | 14.8 (2.5) | 9.9–18.3 | 7.4 (0.1) | 7.2–7.6 | 13.8 (0.2) | 13.5–14.0 | 6.4 (2.0) | BD–8.4 |
| 4 Feb 2012 | EX | 8.2 ^c (0.4) | 7.4–8.7 | 17.0 (2.3) | 12.5–20.4 | 6.9 (0.2) | 6.7–7.2 | 10.6 ^b (0.3) | 10.2–11.1 | 11.2 (0) | |
| | U | 8.3 (0.5) | 7.4–8.8 | 16.9 (2.3) | 12.3–20.1 | 7.0 (0.3) | 6.7–7.6 | 10.8 (0.3) | 10.5–11.3 | 8.5 (3.3) | BD–15.0 |
| 5 Mar 2012 | EX | 7.0 ^d (0.4) | 6.6–7.2 | 15.1 (2.6) | 10.3–19.0 | 6.9 (0.1) | 6.7–7.1 | 11.2 ^b (0.5) | 10.2–11.9 | 8.6 (0.8) | 7.7–9.6 |
| | U | 6.9 (0.2) | 6.6–7.1 | 15.3 (2.6) | 10.1–18.1 | 7.1 (0.2) | 6.8–7.4 | 11.2 (0.1) | 11.0–11.3 | 7.2 (2.1) | BD–11.4 |

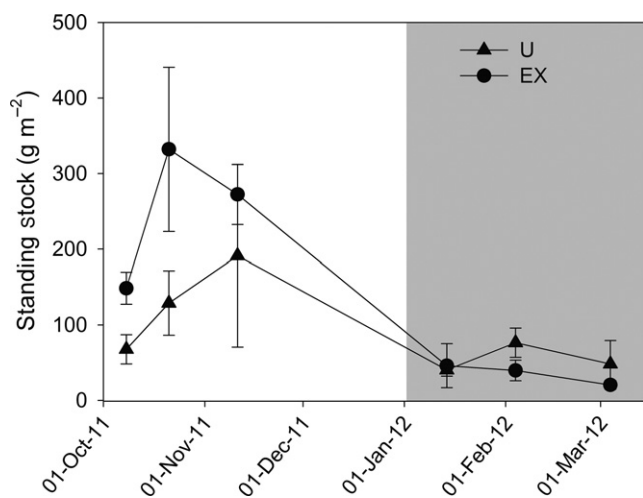


Fig. 3 Coarse particulate organic matter (CPOM) standing stocks over the course of the experiment. Points represent means of each site type, and bars represent 1 SE of the mean. Grey shading represents the period of the study where increased storms led to higher stream discharges.

breakdown rates of white oak at all sites, resulting in almost no further mass loss (c. 70% remaining in bank and terrestrial sites and c. 40% remaining in experimental and upstream sites; Fig. 4). At the conclusion of the experiment, there was a greater mass overall ($F_{1,128} = 41.22$, $P < 0.0001$) of white oak ($73.6 \pm 2.4\%$) than red maple ($66.1 \pm 2.4\%$).

Leaf breakdown rates

In general, red maple decomposed faster than white oak leaves, but the rates greatly depended on the location of

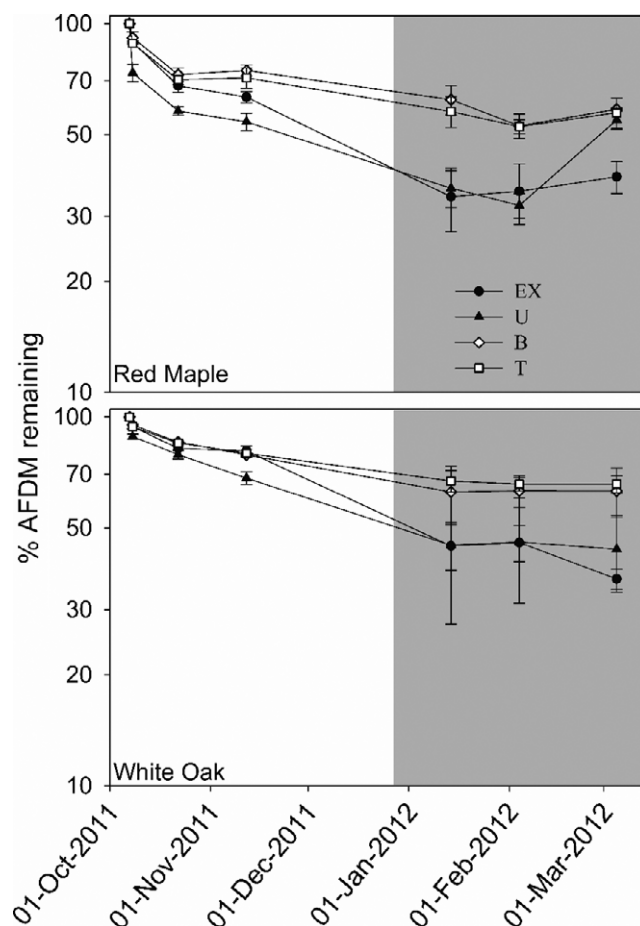


Fig. 4 Patterns in breakdown of leaves over time along a gradient of inundation at streams in Coweeta Hydrologic Laboratory from October 2011 to March 2012. Data points represent means and error bars represent 1 SE of the mean. Grey shading represents the period of the study where increased storms led to higher stream discharges.

the leaves during the experiment. While breakdown rates of red maple and white oak leaves in wet sites (experimental and upstream) varied between 0.0056 and 0.0070 day⁻¹ (Table 2), both leaf species decomposed at essentially the same rates in bank and terrestrial sites ($P < 0.05$; range: 0.0033–0.0035 day⁻¹). Red maple decomposition rates in upstream and experimental sites were significantly greater than those on bank and terrestrial areas (Table 2). In contrast, white oak leaves had faster breakdown in upstream sites only (Table 2), suggesting the importance of permanently wet conditions for leaf decomposition. Heavy winter storms led to higher stream discharge (Fig. 2; Northington, 2013), which increased the variability between upstream and experimental sites (Table 2) as rates of decomposition after day 99 (13 January 2012) were not significantly different ($P < 0.001$, Table 2).

Total microbial biomass

Total microbial biomass increased from the beginning of the experiment until January ($F_{5,87} = 8.02$, $P < 0.0001$), after which biomass remained constant. Although total microbial biomass increased throughout the experiment, significantly more accumulated in all sites during last few sampling periods of the experiment ($P < 0.05$; Fig. 5). By the end of the experiment, a greater accumulation of microbial biomass had occurred on white oak than red maple leaves ($F_{1,87} = 4.30$, $P = 0.04$).

Microbial biomass was dominated by fungi (Fig. 5). Fungal colonisation on leaves in experimental and upstream sites increased over time (Fig. 5). White oak leaves had greater fungal colonisation than red maple ($P = 0.02$) especially at bank and terrestrial sites, otherwise no other sites were significantly different from one another in terms of fungal biomass. Bacterial biomass on leaves was several orders of magnitude lower than

that of fungi (Fig. 5) and demonstrated patterns of accumulation different from that of fungi. Red maple leaves accumulated significantly more bacterial biomass than white oak ($P = 0.04$). Bacterial biomass also increased over the course of the experiment ($P < 0.0001$) but more so in upstream and experimental sites compared to bank and terrestrial ($P < 0.0001$), suggesting that peaks of bacterial biomass generally occurred during or on dates immediately following peaks of fungal biomass (Fig. 5).

Macroinvertebrate colonisation

Macroinvertebrate density was not different between leaf species but did increase significantly over time ($P = 0.02$, Fig. 6). Average macroinvertebrate presence on leaves remained similar (<5.5 per g AFDM) until days 121 and 150 (4 February and 4 March 2012), where density increased to 11.7 ± 2.8 and then 19.4 ± 5.8 per g AFDM respectively (Fig. 6). Major changes in density during the last sampling day were driven by the increase in macroinvertebrates colonising leaves in experimental sites ($P < 0.001$, 38.6 ± 13.2 per g AFDM).

Collector–gatherer and shredding macroinvertebrates were the most commonly found FFGs colonising leaf packs in this study, comprising nearly 80% of the total samples (Fig. 6). Shredders had significantly greater overall density (6.7 ± 1.5 per g AFDM) compared to any other group colonising leaves, followed by collectors (3.8 ± 0.5 per g AFDM).

Stream sites (both upstream and experimental) had similar rates of colonisation by macroinvertebrates from days 15–99 (Fig. 6), with shredders and collectors co-dominating. Shredders began to appear in November, but their greatest increases in density occurred with greater discharge in January in both experimental and upstream sites for both leaf species (Fig. 6).

Table 2 Breakdown rates of leaves (day⁻¹) across different site types in Coweeta catchments. Rates from the first three sampling days (Autumn only; October to November 2011) and the whole experiment (October 2011 to March 2012) are included here. Different letters indicate significant differences based on one-way ANOVA with Tukey's *post hoc* analysis ($\alpha = 0.05$).

| Leaf species | Site | October–November | | Whole experiment | |
|--------------|--------------|-----------------------------|---------------|-------------------------------|---------------|
| | | Mean (SE) | Range | Mean (SE) | Range |
| Red maple | Experimental | 0.0118 (0.001) ^a | 0.0104–0.0137 | 0.0070 (0.001) ^a | 0.0064–0.0076 |
| | Upstream | 0.0136 (0.002) ^a | 0.0112–0.0183 | 0.0056 (0.001) ^a | 0.0043–0.0073 |
| | Bank | 0.0075 (0.001) ^b | 0.0060–0.0090 | 0.0034 (0.000) ^b | 0.0032–0.0037 |
| | Terrestrial | 0.0084 (0.002) ^b | 0.0060–0.0119 | 0.0035 (0.001) ^b | 0.0024–0.0043 |
| White oak | Experimental | 0.0054 (0.001) ^b | 0.0040–0.0070 | 0.0067 (0.001) ^{a,b} | 0.0056–0.0075 |
| | Upstream | 0.0093 (0.001) ^a | 0.0070–0.0112 | 0.0065 (0.003) ^a | 0.0029–0.0125 |
| | Bank | 0.0061 (0.000) ^b | 0.0050–0.0070 | 0.0033 (0.001) ^b | 0.0015–0.0054 |
| | Terrestrial | 0.0057 (0.001) ^b | 0.0040–0.0070 | 0.0035 (0.001) ^b | 0.0019–0.0054 |

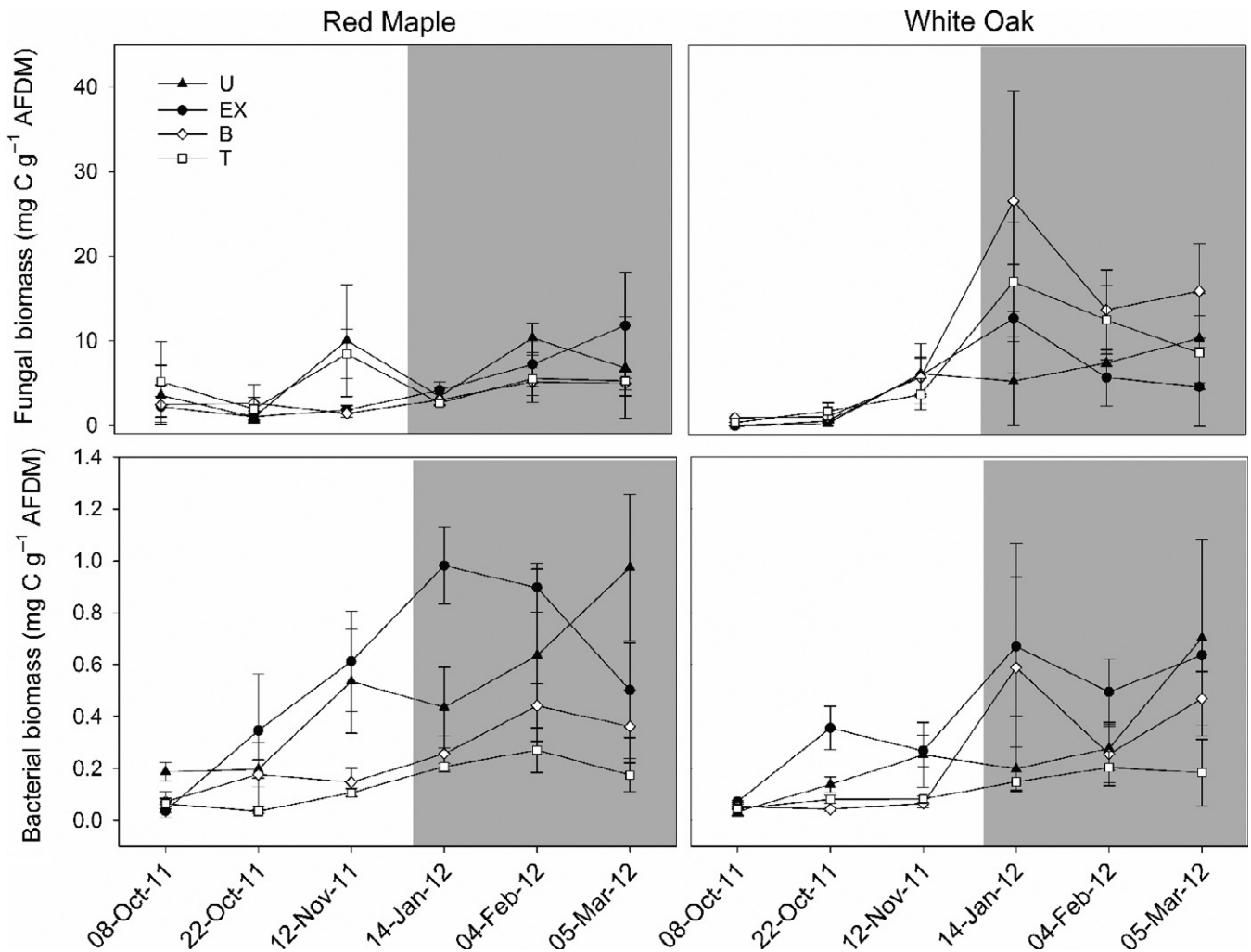


Fig. 5 Patterns in fungal (top panels) and bacterial (bottom panels) biomass accumulation on leaves in the four sites over time at catchments in Coweeta from October 2011 to March 2012. Columns represent means and error bars represent 1 SE of the mean. Note the differences in scale for each type of biomass. Grey shading represents the period of the study where increased storms led to higher stream discharges.

Leaves in the bank sites tended not to be colonised by macroinvertebrates until they became more consistently wet (Fig. 6) with increases in discharge during winter 2012 (collection days 99–150). Densities of FFGs were significantly lower on leaves in the bank sites, which were also dominated by collectors and terrestrial macroinvertebrates, especially in slower decaying white oak (Fig. 6). Leaf packs placed in terrestrial sites were never colonised by aquatic macroinvertebrates nor by substantial numbers of any other invertebrate consumers.

Discussion

Our study demonstrated the importance of hydrology and litter identity on decomposition processes in perennial stream ecosystems. The presence of water within a

stream initiated a cascade of biotic processing, the extent of which may be altered depending on the timing and delivery of that water within the ecosystem. Ultimately, the change to the timing of these decomposition processes may influence both food-web dynamics and downstream delivery of organic matter.

Influence of water availability

Although streams in the southern Appalachians are considered perennial (Sun *et al.*, 2005), there are already noticeable changes to the frequency and intensity of rainfall in the region (Laseter, 2012; Wu *et al.*, 2012, 2014). In this study, we demonstrated that water (as discharge) had a major influence on leaf processes in our streams. The importance of consistent flow on leaf breakdown has been recently shown to be a stronger

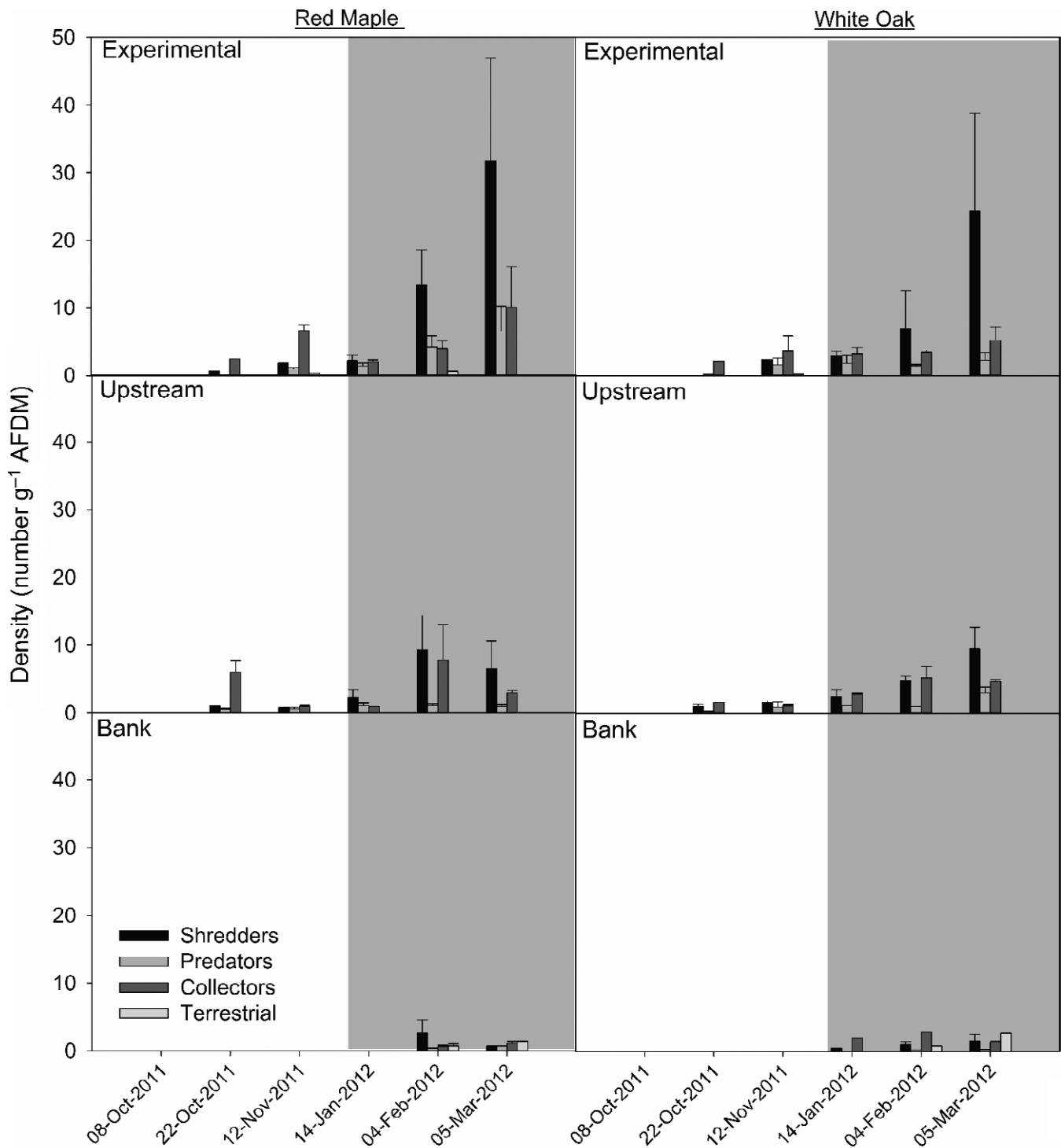


Fig. 6 Density of FFG taxa colonising leaf packs in different sites of inundation throughout the course of the experiment. Columns represent means and error bars represent 1 SE of the mean. Note the differences in scale. Grey shading represents the period of the study where increased storms led to higher stream discharges.

control over the rates of decomposition in streams compared to the importance of macroinvertebrate processing (Leberfinger, Bohman & Herrmann, 2010; Treplin & Zimmer, 2012). However, it is hard to separate these

factors because richness and density of detritivorous macroinvertebrates were greater in streams with consistent flows (Datry *et al.*, 2011) where leaves have been conditioned through wetting (Dieter *et al.*, 2011).

Wet leaves generally lose mass significantly faster than those in any other habitat (e.g. dry or intermittent; Hutchens & Wallace, 2002; Acuña *et al.*, 2005; Corti *et al.*, 2011), although Capps *et al.* (2011) noted faster decomposition at drier sites in some Amazonian streams. Leaves in our upstream sites lost mass at a significantly greater rate than seen at other sites at the beginning of the study due to continual submergence in water (Fig. 4). Leaching loss during the initial stages of decomposition essentially sets the trajectory of mass loss in aquatic ecosystems (Treplin & Zimmer, 2012), and leaves in upstream sites lost significantly more mass due to leaching during the initial 24 h of the study compared to the other sites. Previous work in intermittent systems has demonstrated that exposure to dry conditions and solar radiation appeared to be a more important control over leaching in leaves that are inconsistently wet (Fellman, Petrone & Grierson, 2013), while these same conditions negatively impact microbial degradation and overall mass loss on drier material (Bruder, Chauvet & Gessner, 2011; Dieter *et al.*, 2013).

Even though leaf decomposition in streams is clearly linked to the time of contact between leaves and water, the influence of water permanence on biota is also significant. In a study of leaf decomposition in seasonal wetlands, Inkley *et al.* (2008) demonstrated higher microbial biomass on permanently submerged leaf packs, similar to our results for upstream and experimental sites (Fig. 5). Previous work has demonstrated a clear preference by macroinvertebrates for leaves that had been submerged to some degree (Inkley *et al.*, 2008), which may provide an additional explanation for higher densities of macroinvertebrates initially in upstream packs and eventually in all leaf packs after high winter precipitation (Fig. 6).

Even though increases in water availability brought about major changes in leaf decomposition, so too did the return of stream connectivity between upstream and experimental sites. Physically, increases in winter precipitation homogenised and reconnected these sites as seen by the lack of differences in discharge from January 2012 until the end of the study (Northington, 2013; Fig. 2). More drastically, the reconnection of the streams during winter storms clearly removed standing stocks of leaves that had accumulated in the stream bed (Northington, 2013; Fig. 3), an occurrence much like that seen by Whiles & Wallace (1995) after a severe drought at Coweeta. Renewed connectivity of these stream sections increased the delivery of microbial (Fig. 5) and macroinvertebrate colonists (Fig. 6) from more upstream sites. This pattern was apparent as the biomass of both fungi

and bacteria increased similarly with the return of water to experimental sites, versus the more gradual buildup of bacterial biomass in upstream sites (Fig. 5) as seen in most breakdown studies (e.g. Kaushik & Hynes, 1971).

While increased storms allowed the reconnection of upstream and experimental sites, the widening of stream areas (Fig. 2) also allowed a lateral reconnection with bank sites. The high frequency of *Collembola* colonising leaf packs on the bank (Fig. 6; Northington, 2013) suggested that the lateral connection was incomplete, as this taxon typically is a terrestrial collector (Briones, Ineson & Sleep, 1999), and we observed typical aquatic collectors at upstream and experimental sites (Northington, 2013).

Ecosystem consequences

The loss of complete decomposition in forested headwater streams may alter food availability to downstream consumers (Wallace *et al.*, 1997; Kominoski & Rosemond, 2012). In a study conducted parallel to this one, Currinder *et al.* (2014) demonstrated significant decreases in the presence and total body condition of salamanders in experimental sites compared to upstream sites. The lack of stream connectivity not only altered leaf decomposition and macroinvertebrate colonisation (Figs 4 & 6) but also disrupted an important food source for these top consumers in Coweeta streams (Wyman, 1998; Johnson & Wallace, 2005). Additionally, translocation of unprocessed litter by intense storm flows can shift unprocessed litter to far downstream reaches, where decomposition may be further influenced by anthropogenic and climatic factors (Hagen, Webster & Benfield, 2006; Kominoski & Rosemond, 2012). On a larger scale, the energetic basis of heterotrophic headwater streams may be disrupted from the bottom up, thus altering the stability of the system (Kominoski & Rosemond, 2012).

Combined effects and the future of decomposition

Previous work has suggested that there is a 'drying memory' associated with systems that consistently go through wet-dry or intermittent phases (Datry *et al.*, 2011). Central to this idea is that some organisms are resilient to changes in flow permanence and timing of hydrologic return (Dodds *et al.*, 2010; Datry *et al.*, 2011) and that these species typically occur in intermittent streams. This taxonomic shift may be temporal, with a shift to functionally redundant taxa with different life histories that are better suited to utilise available

resources under changing hydrological conditions (e.g. Gessner *et al.*, 2010). The predicted change in precipitation and generally lower flows during the summer and autumn months (Wu *et al.*, 2012, 2014) suggest that ecosystem processes may not be stimulated at a time when leaf inputs are typically maximal and stream invertebrates would have a large availability of food to fuel their production (Whiles & Wallace, 1995; Wallace *et al.*, 1997).

While water availability does play a key role in decomposition processes, it is not the only factor to consider. At the end of our experiment, decomposition rates did not differ between our stream sites (upstream and experimental), although there were initially changes in hydrology between these sites at the start of the experiment in 2011. Additionally, nitrogen availability and temperature were not different when comparing sampling periods in stream sites. While temperature has been shown to directly affect organic matter decomposition, ecosystem consequences vary. Friberg *et al.* (2009) suggest that decomposition rates increase with temperature due to increasing microbial activity in the absence of key macroinvertebrate groups, while Boyero *et al.* (2011) suggest that no changes in rates may occur but instead, more carbon is lost from the system through higher respiration of leaf microbes. Friberg *et al.* (2009) also suggest nutrient limitation of these microbes as an additional control on decomposition. Therefore, unless changes in water availability are accompanied by changes in dissolved nitrogen or other nutrient concentrations (e.g. Cheever *et al.*, 2013; Rosemond *et al.*, 2015) or temperature, the effects on leaf decomposition will likely be small.

Taken together, the combined effects of climate change, precipitation and forest species change will have important effects on perennial systems. While many studies of perennial headwater streams have shown them to be important processors of organic matter that link aquatic and terrestrial areas (Cummins *et al.*, 1989; Wallace *et al.*, 1997), future scenarios suggest that they may become net retentive (Figs 2 & 3; Acuña *et al.*, 2005). Retention of organic matter will be due to the decreased water availability at key times of annual breakdown, decreased movement of in-stream leaves and wood and the availability of less-palatable leaves and large wood present in the system (Acuña *et al.*, 2005; Morkeski, 2007). The loss of adequate processing of materials has obvious downstream consumer effects (Gessner *et al.*, 2010; Kominoski & Rosemond, 2012; Currinder *et al.*, 2014) but may also alter the quality of exported organic matter (McArthur & Richardson, 2002; Ardón *et al.*, 2009). These potential

shifts thus represent an important switch in ecosystem stable states (e.g. Heffernan, 2008; Dodds *et al.*, 2010) in perennial systems that have no appropriate 'drying memory' to respond to changes to ecosystem processes. Future work in this region will need to address more clearly how all of these changes will not only alter decomposition but also other functional ecosystem components (e.g. biogeochemical cycling).

Leaf decomposition is a vital process in many headwater streams, connecting streams to their landscapes laterally and longitudinally connecting consumers and their resources through stream flow. Globally, flow intermittency is a real possibility for the future in many areas. Headwater stream reaches of the southern Appalachians have not been typically studied as systems prone to intermittency, as they were considered to be resilient and resistant to flow changes and influenced by groundwater inputs. Our study demonstrates that, even over a short time period, reducing stream connectivity and water permanence can alter the timing of decomposition by changing biotic colonisation as a result of hydrologic disturbance. These results, when taken together with changes in annual storm distributions, forest cover and altered food webs will have an important role in structuring mountain streams in the future.

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