

Stream invertebrate productivity linked to forest subsidies: 37 stream-years of reference and experimental data

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Abstract. Riparian habitats provide detrital subsidies of varying quantities and qualities to recipient ecosystems. We used long-term data from three reference streams (covering 24 stream-years) and 13-year whole-stream organic matter manipulations to investigate the influence of terrestrial detrital quantity and quality on benthic invertebrate community structure, abundance, biomass, and secondary production in rockface (RF) and mixed substrates (MS) of forested headwater streams. Using a mesh canopy covering the entire treatment stream, we examined effects of litter exclusion, small- and large-wood removal, and addition of artificial wood (PVC) and leaves of varying quality on organic matter standing crops and invertebrate community structure and function. We assessed differences in functional feeding group distribution between substrate types as influenced by organic matter manipulations and long-term patterns of predator and prey production in manipulated vs. reference years. Particulate organic matter standing crops in MS of the treatment stream declined drastically with each successive year of litter exclusion, approaching zero after three years. Monthly invertebrate biomass and annual secondary production was positively related to benthic organic matter in the MS habitats. Rockface habitats exhibited fewer changes than MS habitats across all organic matter manipulations. With leaf addition, the patterns of functional group distribution among MS and RF habitats returned to patterns seen in reference streams. Secondary production per unit organic matter standing crop was greatest for the leaf addition period, followed by the reference streams, and significantly less for the litter exclusion and wood removal periods. These data indicate that the limited organic matter remaining in the stream following litter exclusion and wood removal was more refractory than that in the reference streams, whereas the added leaf material was more labile and readily converted into invertebrate production. Predator production and total production were tightly coupled in reference and treatment streams, indicating strong relationships between predators and their prey. Results from the artificial wood addition demonstrate that physical structure alone will not restore invertebrate productivity without detrital resources from the riparian forest. Our long-term studies conducted over three decades at the ecosystem scale unequivocally show the necessity of maintaining and restoring aquatic–terrestrial linkages in forested headwater streams.

Key words: *allochthonous inputs; Coweeta Hydrologic Laboratory, North Carolina, USA; detritus; functional groups; invertebrate assemblages; organic matter quality; predator–prey relationships; riparian connectivity; secondary production; substratum relationships; whole-stream experiment; woody materials.*

INTRODUCTION

Many ecosystems exhibit exchanges of nutrients and detritus to adjacent ecosystems (e.g., Odum and de la Cruz 1963, Caraco and Cole 2004, Pace et al. 2004). Polis et al. (1997, 2004) provided many examples of how these fluxes or subsidies influence community- and ecosystem-level processes in recipient habitats and systems. Examples of such subsidies include terrestrial inputs to lakes (e.g., Pace et al. 2004, Bartels et al. 2012) and subsidies from lake to terrestrial systems (Hoekman

et al. 2011), surface inputs to caves (Schneider et al. 2011) and cave streams (Venarsky et al. 2012), and detrital subsidies from offshore kelp beds to intertidal invertebrates (Bustamante and Branch 1996).

As much as 70–80% of all primary production from forests (O'Neill and Reichle 1980) and streams (Wetzel 1995) enters the detrital food web. The terrestrial detritus consumption by lentic- and lotic-dwelling invertebrate animals has long been recognized as a food resource to these aquatic systems (e.g., Lloyd 1921, Hynes 1941, Brinck 1949). Hynes (1963) and Ross (1963) recognized that some headwater stream food webs relied on terrestrial detritus, especially leaves. Linkages between allochthonous inputs, detrital pro-

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cessing, and detritivores have been well documented in headwater streams (e.g., Fisher and Likens 1973, Cummins 1974, Anderson and Sedell 1979, Wallace and Webster 1996, Hieber and Gessner 2002, Kominoski et al. 2011).

Few studies have assessed the influence of subsidies to headwater streams by curtailing subsidies from the donor to the recipient ecosystem over decadal time periods or at the ecosystem level. Richardson (1991) showed that detritivores were food limited in artificial streamside channels, as higher levels of coarse particulate organic matter (CPOM) resulted in greater abundances of fine particulate organic matter (FPOM) feeding groups such as collectors. They also observed nonsignificant increases in predators in high-CPOM channels (Richardson and Neill 1991). In a three-year ecosystem-level study, Wallace et al. (1997) showed that exclusion of terrestrial litter to a headwater stream resulted in significant differences in abundances and biomass of CPOM- and FPOM-feeding detritivores and predators when compared to a nearby reference stream.

The effects of subsidies on recipient ecosystems may differ among heterogeneous habitats within the recipient system (Cadenasso et al. 2004), especially if those habitats display physical differences. Habitats in headwater streams at Coweeta Hydrologic Laboratory in North Carolina, USA display striking differences in physical characteristics within a given stream: steep-gradient bedrock outcrop substrates vs. lower-gradient mixed substrate reaches. The moss-covered bedrock outcrops are characterized by higher current velocities, less particle retention, and lower standing crops of CPOM and FPOM. These differences result in very different functional characteristics of the invertebrate assemblages with filterers, followed by scrapers and gatherers, reaching greatest abundances on rockface habitats. In contrast, mixed substrates have greater retention of both CPOM and FPOM and are dominated by shredders, gatherers, and predators (Huryn and Wallace 1987, Lugthart and Wallace 1992). The scale of our experiment was large enough to contain these two physically diverse habitats, which may be important in ecosystem-level studies because diverse habitats may respond differently to the same manipulation (Carpenter 1998, Peterson et al. 1998).

The type of allochthonous subsidy may also influence recipient communities because of temporal changes in its availability as food or habitat within the system. Leaves of various tree species vary greatly in their breakdown rates in streams (Webster and Benfield 1986) and hence in their availability as food to consumers. Fast-breakdown leaf species are available for consumption by detritivores for short periods of time after litterfall. Slowly processed leaf litter is the primary component of leaf resources available during the summer months (Fisher and Likens 1973, Huryn and Wallace 1987, Grubbs and Cummins 1996).

To date, most resource diversity–ecosystem function research in stream ecosystems has focused on short-term consumer diversity and leaf decomposition responses (e.g., Kominoski and Pringle 2009, Gessner et al. 2010, Lecerf and Richardson 2010). Our objectives here were to examine long-term and large-scale responses of benthic invertebrate communities to altered terrestrial subsidies in forested headwater streams. We examine long-term manipulations of leaf detritus and wood to quantify effects of detrital quantity and quality on relationships between benthic assemblages and organic matter. Initially, we planned only litter exclusion; however, after three years, it appeared that some taxa could persist on wood and associated biofilms. Thus, we followed litter exclusion with small- and large-wood removal and finally addition of artificial devices to serve as structure for the experimental addition of leaf litter differing in breakdown rates. Our analyses focus on differences in macroinvertebrate functional feeding group abundances, biomass, and production. In addition to a before vs. after paired stream approach, we also use 24 stream-years of data from forested reference streams to examine natural patterns of abundance, biomass, and secondary production of the invertebrate assemblages by functional feeding group. Long-term multiyear reference conditions are important in that they offer a range of temporal variability within ecosystems (Carpenter 1998); furthermore, such experiments must be large enough to include diverse habitats and physical, chemical, and biotic information to detect how the experiment may be influenced by the physical effects of habitat (Carpenter 1998, Peterson et al. 1998).

MATERIALS AND METHODS

All work was conducted in first-order, forested streams within the Coweeta Hydrologic Laboratory (U.S. Forest Service) in the southern Appalachian Mountains of western North Carolina. Vegetation in the 1625-ha drainage basin consists of mixed hardwoods (oak, hickory, maple, tulip poplar) with a dense understory of rhododendron. Elevation, drainage area, discharge, aspect, substrate, and thermal regime were similar among the three study streams draining catchments 53, 54, and 55 (C53, C54, C55; Lugthart and Wallace 1992, Wallace et al. 1999). We examined data collected from C53, C54, and C55 during years when no experimental manipulations took place, resulting in 24 stream-years of reference data from 1984 to 2006 (Wallace et al. 1982, 1997, 1999, Cuffney et al. 1985, 1990, Lugthart and Wallace 1992, Whiles and Wallace 1992, 1995) and data collected from C55 during a 13-yr experimental manipulation of litter exclusion (LE; 1993–1995), small-wood removal (SWR; 1996–1998), large-wood removal (LWR; 1998–2000), PVC pipe addition (PVC; 2000–2001), fast-leaf addition (FLA; 2001–2003), slow-leaf addition (SLA; 2003–2005), and mixed-leaf addition (MLA; 2005–2006; Table 1). The period from 1984 to 2006 included the second-driest and second-

TABLE 1. Invertebrate and organic matter 37-yr data sets for reference and treatment periods for catchments 53, 54, and 55.

Catchment	Stream-years	Treatment	Description
C53	1984–1985 and each year from 1992–1993 to 2005–2006	reference years	natural detrital inputs to stream
C54	1984–1985, 1989–1990, 1998–1999, 1999–2000	reference years	natural detrital inputs to stream
C55	1984–1985, 1985–1986, 1988–1989, 1989–1990, 1992–1993	reference years	natural detrital inputs to stream
C55	1993–1994, 1994–1995, 1995–1996	litter exclusion	canopy and lateral fence to exclude organic matter
C55	1996–1997, 1997–1998	small-wood removal	litter exclusion and all small wood removed
C55	1998–1999, 1999–2000	large-wood removal	litter exclusion and all large wood removed
C55	2000–2001	PVC pipe addition	litter exclusion and PVC pipe and plastic branches added
C55	2001–2002, 2002–2003	fast-leaf addition	litter exclusion, PVC, plus fast-leaf species
C55	2003–2004, 2004–2005	slow-leaf addition	litter exclusion, PVC plus slow-leaf species
C55	2005–2006	mixed-leaf addition	litter exclusion, PVC plus mixed-leaf addition

Notes: Stream-years included the period from 1 September of the first year to 31 August of the following year. Small wood was <10 cm diameter, large wood was >10 cm diameter. Fast-leaf addition was a one-third-each mixture of tulip poplar (*Liriodendron tulipifera*), dogwood (*Cornus florida*), and sweet gum (*Liquidambar styraciflua*); slow-leaf addition was a one-third-each mixture of rhododendron (*Rhododendron maximum*), white pine (*Pinus strobus*), and northern red oak (*Quercus rubra*); mixed-leaf addition was a one-third-each mixture of tulip poplar, rhododendron, and red maple (*Acer rubrum*).

wettest years on record, based on the 70-yr precipitation record from Coweeta Hydrologic Laboratory (Laseter et al. 2012).

Direct-fall and lateral organic matter inputs were excluded from the top 170 m of the treatment stream from 1993 to 2006 using 1.2-cm mesh gill netting and bird netting along the stream banks. Small and large wood was manually removed from the treatment stream in 1996 and 1998, respectively. Prior to adding leaves back to the stream, we added PVC pipe and plastic tubing to mimic structural complexity previously provided by small and large wood (also see Wallace et al. 1999, 2000, 2001, and Eggert et al. 2012).

During the litter addition years, we added fast-decomposing leaves for two years and slow-decomposing leaves for two years, followed by a year of mixed (slow-, fast-, and medium-decomposing leaves). During each addition, a total of 81 kg dry mass (DM; 27 kg of each of three leaf species of various breakdown rates) were evenly distributed (230 g AFDM/m², equivalent to natural input levels) over the experimental stream bottom during October and November of each year. FLA received 27 kg DM each of flowering dogwood (*Cornus florida*), tulip poplar (*Liriodendron tulipifera*), and American sweetgum (*Liquidambar styraciflua*), SLA received 27 kg DM each of rhododendron (*Rhododendron maximum*), white pine, (*Pinus strobus*), and red oak, (*Quercus rubra*), and MLA received 27 kg DM each of leaf species with fast (tulip poplar), slow (rhododendron), and medium (red maple; *Acer rubrum*) breakdown rates. Funding constraints prevented a second year of mixed-leaf addition. The LE canopy was maintained throughout all treatment periods.

Invertebrate and organic matter sampling monthly over the 37 stream-years was conducted using a standard protocol throughout (see Lughart and Wallace [1992] and Wallace et al. [1999] for complete description of the

protocol). Mixed substrate (MS) habitats were sampled using a 400-cm² corer ($n = 4$ cores), where invertebrates and organic matter were collected to a uniform depth of 10 cm. Rockface (RF) habitat was sampled by scraping a 15 × 15 cm area ($n = 3$ scrapings) of moss and associated particles into a plastic bag held to the bedrock surface. Invertebrates were separated from organic matter using stereomicroscopes, identified to genus level (all insects except Chironomidae, which were identified as Tanypodinae or non-Tanypodinae) or to family or ordinal level (most non-insect taxa), and measured to the nearest millimeter. Biomass was obtained using published length–mass regressions developed from streams in the region (Benke et al. 1999). Annual production was estimated using either the size-frequency method (Hamilton 1969) with corrections for cohort production interval (Benke 1979), the production:biomass ratios and standing-stock biomass method, or the community-level method of Huryn and Wallace (1986) for non-Tanypodinae chironomids. Production was estimated separately for MS and RF habitats and habitat-weighted for the whole stream using proportions of each habitat type per stream. Abundance, biomass, and production for each taxon were combined by functional feeding group (shredder, scraper, collector [filterer or gatherer], or predator) according to Merritt et al. (2008) or our knowledge of diets. CPOM and FPOM from each sample was separated, weighed, ashed, and re-weighed to obtain ash-free dry mass (AFDM) by category and used to determine organic matter standing crop (see Lughart and Wallace [1992] for detailed protocol).

Differences in invertebrate abundance, biomass, and production between MS and RF habitats were examined during reference, LE, wood removal (WR), and leaf addition years using paired *t* tests or Mann-Whitney rank sum tests for data not meeting assumptions of

equal variance and normality. We used regression analysis to determine long-term relationships between (1) organic matter standing crop and invertebrate production and (2) predator production and total secondary production using monthly and annual data for C53 (reference years only), C54 (reference years only), and C55 (reference and treatment years) from 1984 to 2006. Data were $\log(x + 1)$ -transformed where necessary to meet assumptions of normality.

We used randomized intervention analysis (RIA; Carpenter et al. 1989) to test the null hypotheses of no change in monthly invertebrate abundance and biomass by functional feeding group in the treatment stream (C55) relative to the reference stream (C53) following the LE, WR, PVC, and leaf addition periods. The pretreatment period included data from 1 September 1992 to 31 August 1993, when no manipulations occurred in either stream. RIA uses paired observations within reference and treatment sites before and after a manipulation, along with random permutations of the sequence of intersite differences (1000 permutations) to determine whether a nonrandom change in the intersite difference occurred following the manipulation. We could not run RIA analyses on annual production data since it is an annual measurement that resulted in very small before and after sample sizes. Rejection of the null hypothesis of no change in the relationship between sites following a manipulation plus visual inspections of divergent trends in the data set implies a manipulation effect. Effects were considered significant at $P = 0.05$.

RESULTS

Functional group classification

More than 80 benthic invertebrate taxa were encountered in the treatment and reference streams. Dominant taxa within each functional feeding group are given in Appendix A: Table A1. The list of genera is not complete as it does not individually list the Chironomidae (Diptera) genera, which included 24 genera of gatherers (non-Tanypodinae) and four genera of Tanypodinae (e.g., Entrekin et al. 2007).

Benthic organic matter

Leaf standing crops in mixed substrates (MS) of the LE stream declined with each successive year of litter exclusion, approached zero during the third year of exclusion (RIA, $P < 0.0001$), and remained near zero for 85 months until the first year of fast-leaf addition (Fig. 1A; RIA, $P < 0.001$). Monthly leaf standing crops fluctuated greatly within each year as leaves were added and processed during the leaf addition periods (RIA; FLA, $P < 0.0001$; SLA, $P < 0.01$; MLA, $P > 0.05$). The decline in total particulate organic matter (POM) was not as rapid as that of leaf detritus over the 168-month period (Fig. 1B). Total POM decreased during the initial 3-yr exclusion period (RIA, $P < 0.05$), as did leaf detritus, and subsequently increased during certain months following SWR (RIA, $P < 0.01$) as storms

uncovered additional organic matter buried in the stream bed. Ongoing litter exclusion combined with small- and large-wood removal resulted in continuing reductions in total POM until leaf addition during the last 60 months of the study (RIA; FLA, $P < 0.0001$; SLA, $P < 0.0001$; MLA, $P > 0.05$; see Eggert et al. 2012).

Benthic invertebrate abundances

Mean annual abundances in MS of the reference streams were ~ 4.4 times higher than in RF habitats (Table 2). All functional groups displayed significant differences in abundance between MS and RF habitats during reference years; however, the pattern differed among functional groups (Table 2). Abundances of scrapers and filterers were greater in RF habitats than in MS. Conversely, shredders, collectors, and predators were more abundant in MS (Table 2). Abundance patterns between habitats during LE and WR periods in the treatment stream were reversed from reference years; abundances in RF habitats exceeded those in MS by 1.6 times during LE and WR periods (Table 2). Significant differences in functional group abundances between substrate types observed during reference years became insignificant during the LE and WR periods in the treatment stream, with the exception of filterers, which maintained significantly greater abundances in the RF substrates (Table 2). For the treatment stream, scrapers were the only functional group that increased in abundance during the LE and WR years compared to reference years in both substrates (Table 2). During leaf addition, total abundance in MS was 1.8 times greater than that in RF habitats. Furthermore, differences in functional group abundances between substrates during the leaf addition periods were similar to those observed in reference conditions (Table 2).

There were no significant intersite differences in monthly abundances between the treatment and reference streams for any functional feeding group on RF habitats during the LE and WR or leaf addition periods based on RIA (Appendix B: Table B1). In contrast, abundance of three functional groups (shredders, gatherers, and predators) as well as total abundance was significantly lower than reference conditions in MS during LE and WR (Appendix B: Table B1). During the leaf addition period, shredder and filterer abundance in MS habitats of the treatment stream was statistically similar to reference years (Appendix B: Table B1).

Benthic invertebrate biomass

Mean annual biomass during reference years was 3.3 times higher in MS than RF habitats, where biomasses of shredders, gatherers, and predators were all significantly greater, whereas those of filterers and scrapers were higher in the RF habitat (Table 2). In contrast, during LE and WR, shredder, gatherer, and predator biomass in MS of the treatment stream had become more similar to the RF habitats than during reference

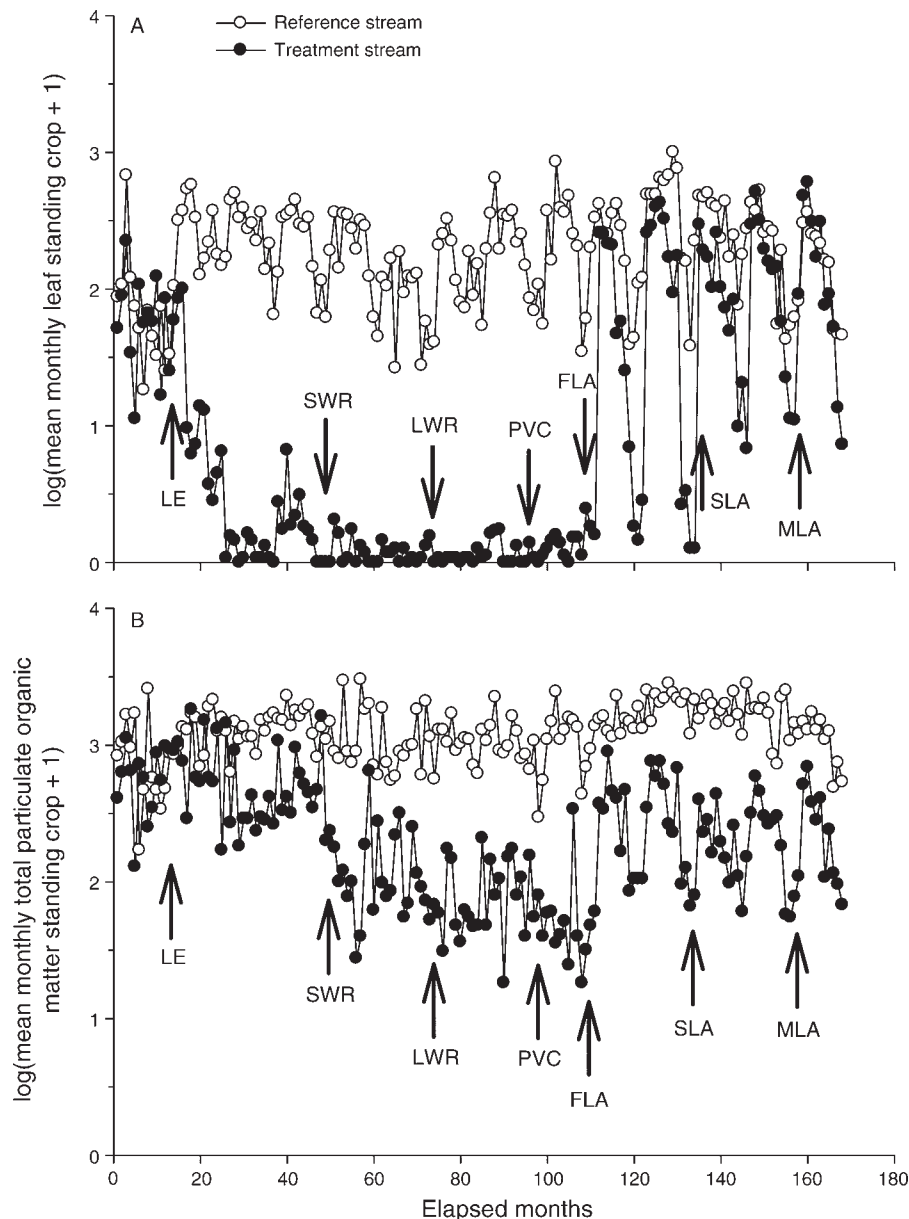


FIG. 1. (A) Monthly leaf litter standing crop and (B) monthly total particulate organic matter (POM) in mixed substrates in the reference and treatment stream from September 1992 to September 2006. The $\log(x + 1)$ -transformed data were originally measured as g ash-free dry mass (AFDM)/m². The first 12 months are untreated periods for both streams, followed by (for treatment stream only) litter exclusion (LE; 36 months), small (<10 cm diameter) wood removal (SWR; 24 months), large (>10 cm diameter) wood removal (LWR; 24 months), PVC pipe addition (PVC; 12 months), fast-leaf (one-third-each mixture of tulip poplar (*Liriodendron tulipifera*), dogwood (*Cornus florida*), and sweet gum (*Liquidambar styraciflua*) addition (FLA; 24 months), slow-leaf (one-third-each mixture of rhododendron (*Rhododendron maximum*), white pine (*Pinus strobus*), and northern red oak (*Quercus rubra*)) addition (SLA; 24 months), and mixed-leaf (one-third-each mixture of tulip poplar, rhododendron, and red maple (*Acer rubrum*)) addition (MLA; 12 months).

conditions (Table 2). Shredders in MS actually showed a lower initial response to litter exclusion than total invertebrates (Table 2, Figs. 2 and 3). Shredder biomass decline coincided with small-wood removal (Fig. 3). With leaf addition, total invertebrate biomass reverted toward reference conditions with greater increases in biomass in MS than in RF habitats (Table 2, Fig. 2).

Mean annual biomass of invertebrates in MS during leaf addition increased by >2.9 times from the LE and WR periods, but remained less than half of the reference streams (Table 2). During leaf addition, all functional groups in the treatment stream displayed a significant difference in distribution between MS and RF habitats (Table 2).

TABLE 2. Annual abundance (no./m²), biomass (mg AFDM/m²), and secondary production (mg AFDM·m⁻²·yr⁻¹) by functional feeding group (standard error) in reference streams and treatment stream.

Parameter, by functional group	Reference (<i>n</i> = 24 years)			LE + WR + PVC (<i>n</i> = 8 years)		
	Mixed	Rockface	<i>P</i>	Mixed	Rockface	<i>P</i>
Abundance (no./m ²)						
Shredders	2 691 (231)*	743 (71)	<0.001	342 (71)	495 (84)	ns
Scrapers	103 (12)	264 (20)*	<0.001	386 (24)	530 (117)	ns
Gatherers	73 028 (5 592)*	14 689 (1 348)	<0.001	11 805 (2 063)	19 234 (6 092)	ns
Filterers	418 (37)	1 030 (108)*	<0.001	222 (41)	830 (129)*	<0.001
Predators	9 235 (55)*	2 548 (183)	<0.001	2 021 (371)	2 048 (183)	ns
Total	85 475 (5 592)*	19 312 (1 449)	<0.001	14 776 (2 487)	23 137 (6 474)	ns
Biomass						
Shredders	743 (56)*	117 (15)	<0.001	110 (38)	43 (9)	ns
Scrapers	8 (3)	31 (3)*	<0.001	8 (1)	43 (11)*	<0.001
Gatherers	348 (24)*	130 (11)	<0.001	48 (8)	68 (8)	ns
Filterers	52 (5)	236 (25)*	<0.001	21 (3)	110 (17)*	<0.001
Predators	847 (55)*	98 (12)	<0.001	106 (30)	46 (6)	0.083
Total	1 998 (108)*	612 (40)	<0.001	292 (73)	310 (26)	ns
Secondary production						
Shredders	3 843 (313)*	641 (70)	<0.001	502 (206)	312 (55)	ns
Scrapers	36 (12)	153 (22)*	<0.001	42 (4)	154 (35)*	0.015
Gatherers	3 174 (254)*	1 261 (99)	<0.001	497 (76)	857 (130)*	0.032
Filterers	323 (35)	1 735 (217)*	<0.001	125 (14)	846 (147)*	<0.001
Predators	3 265 (218)*	482 (45)	<0.001	458 (121)	252 (37)	0.105
Total	10 641 (623)*	4 272 (275)	<0.001	1 623 (377)	2 420 (217)	0.088

Notes: LE + WR stands for litter exclusion and wood removal, and PVC indicates PVC addition. Values are given for both mixed substrates and rock face substrates. An asterisk indicates that one substrate had significantly higher levels than the other during the period (according to a paired *t* test when data passed an equal variance test, or a Mann-Whitney rank sum test when data failed an equal variance test). *P* values for differences between substrates are provided except where *P* > 0.10 (ns, not significant).

Based on RIA analyses, mean monthly biomasses of shredders, filterers, gatherers, predators, and total invertebrate biomass in MS of the treatment stream during LE and WR were significantly lower than during reference conditions (Appendix B: Table B1). Total biomass in MS habitats during the leaf addition period remained significantly lower, as did that of shredders, filterers, and predators in MS habitats. Total biomass in RF habitats in the treatment stream during leaf addition did not differ significantly from that of reference conditions (Appendix B: Table B1).

Invertebrate production

Production of scrapers and filterers followed a pattern similar to that observed for abundance and biomass. Only scraper and filterer production in RF habitats exceeded that in MS, whereas production of shredders, collectors, and predators, as well as total production, were greater in MS than RF habitats (Fig. 4A, Table 2). Overall production in MS was 2.5 times greater than RF under reference conditions (Table 2). In contrast, production during the LE and WR periods was 1.5 times greater for RF than MS. Shredders showed a strong tendency toward much higher production in MS than RF habitats in reference streams; however, there was no significant difference between substrate types for shredder production during LE/WR (Table 2). Scraper production in RF habitats in the treatment stream remained greater than that in MS habitats during the LE and WR periods (Fig. 4B and Table 2). Gatherers and

filterers had significantly higher production in RF than MS habitats during litter exclusion. Total secondary production was greater, but not significantly so, in RF than MS habitats during the LE and WR periods (Fig. 4B, Table 2). Shredder, gatherer, predator, and total production was significantly greater in MS than RF habitats during the leaf addition periods (Fig. 4C, Table 2). The distribution of production among functional groups in the treatment stream during leaf addition was similar to that of reference conditions, although total production remained only one-half of that observed in reference conditions on MS and two-thirds that of reference for RF habitats.

Invertebrate predator-prey relationships

We previously found significant relationships between annual predator production and annual prey production in reference and treatment streams during the first four years of litter exclusion (Wallace et al. 1999). Using data from all treatment years (LE, SWR, LWR, PVC, and leaf additions) as well as data from 20 additional years for reference streams, the relationship between predator and prey production is remarkably similar across streams (Fig. 5). Slopes of the regression lines for both the reference and leaf addition periods (~0.287) and the LE, SWR, LWR, and PVC periods (~0.292) are virtually identical (Fig. 5). These slopes are well within the range of gross production efficiencies (production/ingestion) of most predators and indicate a tight

TABLE 2. Extended.

Leaf addition ($n = 5$ years)		
Mixed	Rockface	P
1 713 (337)*	307 (61)	<0.003
233 (60)	419 (17)*	<0.018
29 154 (3 748)*	15 417 (1 132)	<0.008
382 (116)	811 (149)*	0.05
2 520 (358)*	1 414 (245)	0.034
34 003 (4 182)*	18 367 (1 486)	<0.008
407 (99)*	74 (23)	<0.008
7 (2)	34 (4)*	<0.001
136 (18)*	72 (7)	0.011
26 (2)	144 (39)*	<0.008
284 (36)*	69 (28)	<0.001
860 (135)*	392 (60)	0.013
2 513 (618)*	653 (284)	<0.016
29 (7)	98 (11)*	<0.001
1 380 (180)*	903 (108)	0.05
162 (21)	997 (298)*	<0.008
1 188 (53)*	283 (42)	<0.001
5 272 (785)*	2 933 (478)	0.034

coupling of predators with their prey within these headwater streams.

Invertebrate–organic matter relationships

Invertebrate abundance was clearly related to organic matter manipulations, especially in MS habitats. Plots of organic matter standing crop vs. invertebrate biomass and production provide further evidence for this relationship. The 24 years of reference stream data incorporated 70-yr extremes of wet and dry years at Coweeta; this long-term record revealed a significant relationship between monthly standing stock biomass of invertebrates and POM standing crop in MS habitats (Fig. 6A). As standing crop of organic matter increased, so did that of invertebrates in reference streams (Fig. 6A; $r^2 = 0.18$, $P < 0.001$). The relationship was considerably stronger during litter exclusion ($r^2 = 0.36$, $P < 0.001$). The leaf addition period produced an even stronger fit for monthly organic matter standing crop vs. invertebrate biomass ($r^2 = 0.43$, $P < 0.001$; Fig. 6A).

Total habitat-weighted invertebrate production was also strongly related to organic matter standing crop (Fig. 6B). Under reference conditions, habitat-weighted production was strongly skewed toward MS habitats, which had a much greater proportion of stream area, higher organic matter standing crops, and higher secondary production. Habitat-weighted secondary production declined during LE, remained extremely low in response to SWR, LWR, and PVC addition, and increased following leaf addition (FLA, SLA, and MLA in Fig. 6B). Higher levels of production occurred at lower levels of organic matter standing crop during leaf addition (Fig. 6B). During leaf addition, a greater

proportion of organic matter standing crop was leaves, and a lower proportion was older, more refractory organic matter such as wood (Eggert et al. 2012).

Annual habitat-weighted secondary production (g AFDM)/habitat-weighted total organic matter standing crop (g AFDM) differed among streams and time periods. Reference streams had an average (standard deviation) of 0.00583 g (0.00251 g) secondary production per g organic matter standing crop vs. only 0.00268 g (0.000620 g) during LE in the experimental stream; however, this increased to 0.00772 g (0.00144 g) during the leaf addition period. The ratio of production to organic matter standing crop in reference streams was significantly different from the treatment stream during LE (Mann-Whitney rank sum test, $P < 0.001$), and the ratio was also significantly different between the LE and leaf addition periods ($P < 0.002$). The ratio during the leaf addition period vs. reference streams was marginally significant ($P = 0.065$). Thus, secondary production per unit organic matter standing crop was greatest for leaf addition \geq reference streams $>$ LE.

Conceptual overview

Several patterns emerge from a summary of 37 stream-years of data from our comparative and experimental data sets (Fig. 7). First, invertebrate production is strongly related to riparian organic matter inputs in forested headwater streams; second, variability in physical habitat in these streams can affect ecosystem responses to resource availability; and third, ecosystem responses to changes in riparian inputs may not happen instantly. Twenty-four stream-years of data collected under reference conditions demonstrated the strong effects of habitat on ecosystem function, where MS production averaged 10.6 g AFDM·m⁻²·yr⁻¹ vs. 4.2 g AFDM·m⁻²·yr⁻¹ for RF substrates. Initial litter exclusion had a much greater impact on MS invertebrate production than that of the RF habitats, as MS production decreased by 80% from reference conditions. During initial litter exclusion, total OM standing crop was reduced by only 46%; however, leaf litter standing crop was reduced by >99%. MS production decreased another >60% following WR and PVC addition. In contrast to MS, production of invertebrates on RF habitats decreased by only ~25% during initial LE and another ~29% following WR and PVC addition (Fig. 7). Wood was the only OM category showing significant reduction in the RF substrates of the treatment stream and this was following WR. In the MS, invertebrate production subsequently increased 6.6 times by the fifth year of leaf addition.

DISCUSSION

Importance of scale for ecosystem-level manipulations

Differences among various habitats embedded within an ecosystem provide important comparisons about spatial variation in ecological processes among physical

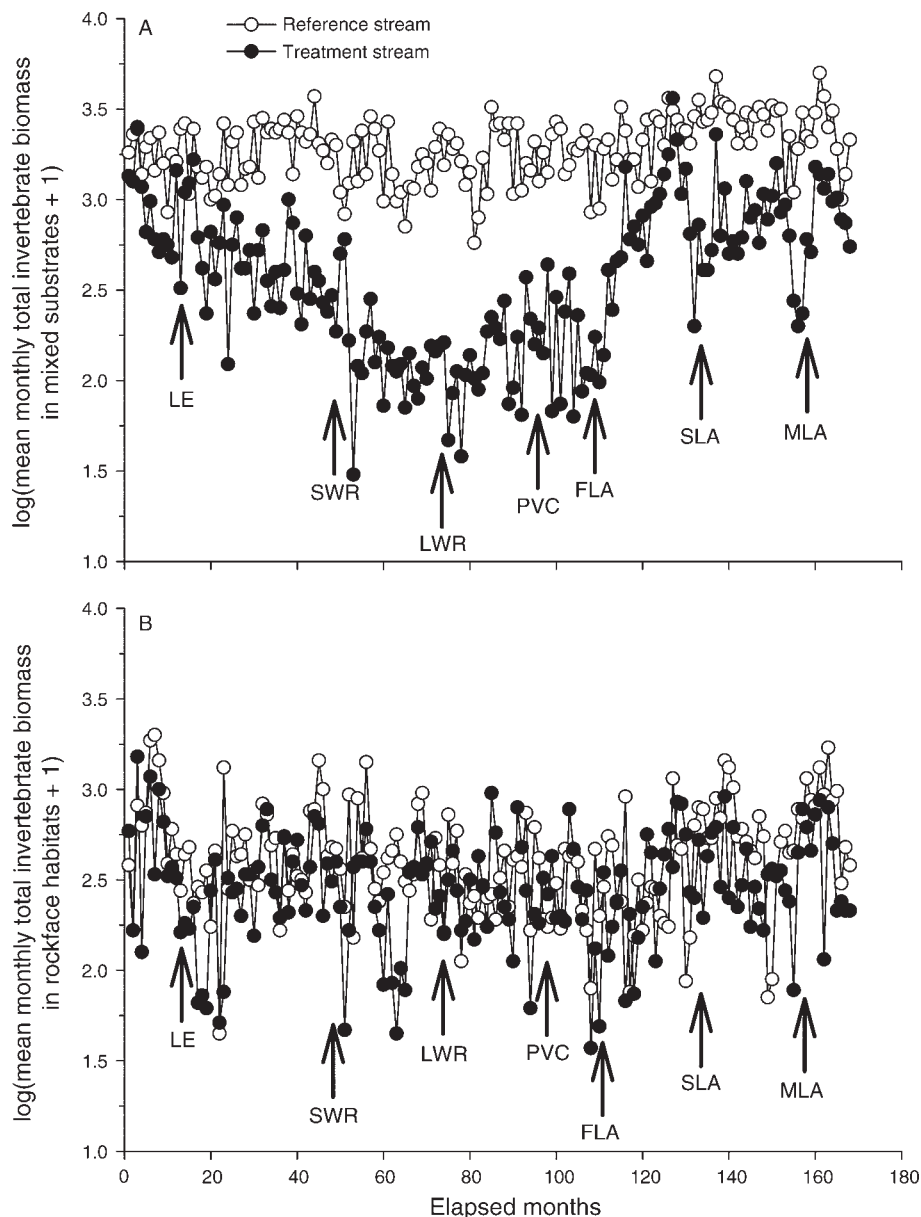


FIG. 2. Monthly invertebrate biomass (originally measured as g AFDM/m²) for (A) mixed substrate (MS) and (B) rockface habitats (RF) in the reference and treatment streams from September 1992 to September 2006. All abbreviations are as in Fig. 1.

habitats (Carpenter 1998, Peterson et al. 1998). Peterson et al. (1998) proposed that species interact with scale-dependent sets of ecological structures that influence functional structure of the taxa, and therefore field experiments should be designed to test the response of species to resource availability at different scales. The response to reduced resources differed among MS and RF habitats in our study. Clearly, invertebrates in the MS habitat are at least partially resilient in that their production increased following leaf addition, but certainly production levels did not increase to reference stream conditions (Fig. 7). Despite canopy removal at the termination of the experiment, it is highly question-

able whether secondary production in this stream can reach a pretreatment state without significant long-term woody inputs. Wood provides retention for other organic matter and sediments and the surface biofilms on wood provide a food resource for some invertebrates as well as a long-term source of organic matter to the stream. The input of wood is event related and variable through time (S. L. Eggert and J. B. Wallace, *unpublished data*). Wood has been shown to persist in the study stream for many decades (Wallace et al. 2001). Thus, complete recovery of secondary production may not occur for many decades until wood standing crops are restored in the experimental stream.

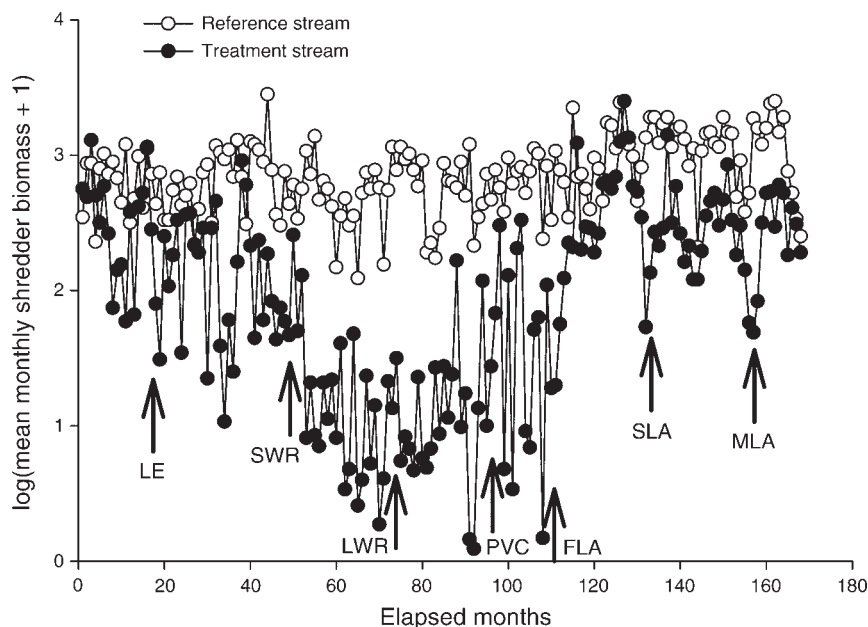


FIG. 3. Monthly biomass of invertebrate shredders (originally measured as g AFDM/m²) in mixed substrates in the reference and treatment streams from September 1992 to September 2006. All abbreviations are as in Fig. 1.

In contrast to invertebrates in the MS habitats, those in the RF habitats appear to be resistant to change, as the treatments had less impact on species in the RF habitat. However, we caution that RF habitats are characterized by steeper gradients, higher current velocities, less organic matter retention (other than FPOM trapped in moss), and higher particle transport velocities than MS habitats. With the exception of gradient, these physical and retention attributes are more similar to larger downstream reaches of streams. Likewise, the dominant functional groups comprising RF habitats in these headwater streams (filterers, scrapers, and gatherers) reach greatest abundance downstream, where their feeding modes exploit the physical conditions. Therefore, it is not surprising that litter exclusion had less impact on

RF habitats. Although the RF assemblages may appear to be more resistant to litter exclusion than the MS assemblages, this may be due in part to the nature of the disturbance (litter exclusion). In fact, during record drought, Lughart and Wallace (1992) noted assemblages on RF habitats in the study stream changed the most as prolonged low flows resulted in accumulation of leaf litter on the RF. These were readily exploited by shredders, while filterers were limited by low-flow conditions on the outcrops. Thus, the nature of the disturbance may influence one's view of resistance.

Differences in functional group abundance, biomass, and production between RF and MS habitats have been noted previously for Coweeta headwater streams (e.g., Hurny and Wallace 1987). In MS habitats, the substrate

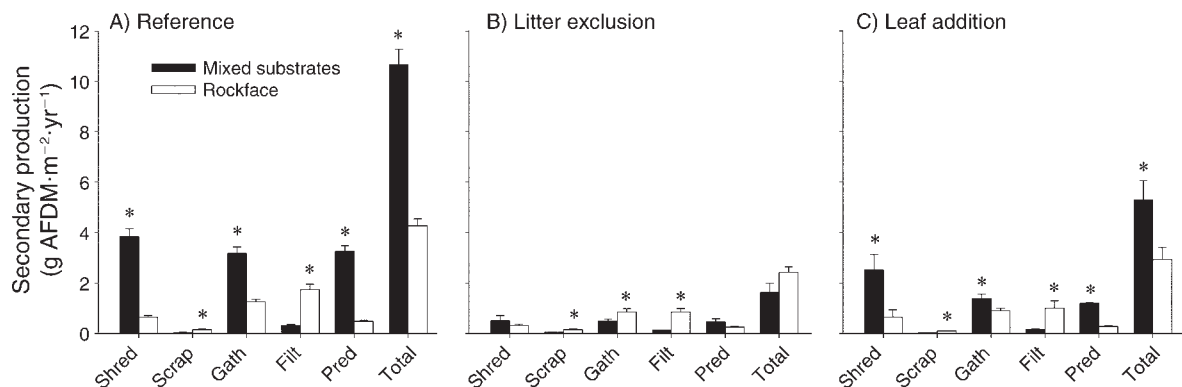


FIG. 4. Annual secondary production by functional feeding groups for MS and RF habitats for shredders (Shred), scrapers (Scrap), gatherers (Gath), filterers (Filt), predators (Pred), and total habitat-weighted production for (A) reference years, (B) LE years, and (C) leaf addition years. Means are shown with standard error. Asterisks indicate significant ($P < 0.05$) differences between MS and RF habitats.

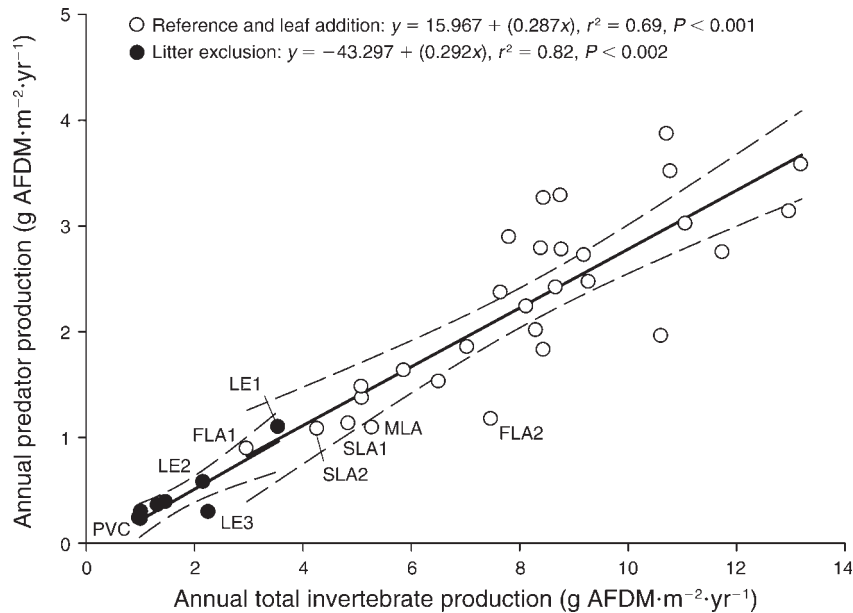


FIG. 5. Relationships between annual habitat-weighted invertebrate production and annual habitat-weighted predator production for reference and litter addition years and for LE and wood removal (WR) years. Numbers refer to years since beginning of treatment, i.e., LE1 denotes first year of LE, LE2 denotes second year of LE, etc. All abbreviations are as in Fig. 1.

is characterized by a broad range of substrate particle sizes, and both lower gradients and current velocities than the RF habitats. MS habitats are sites of the greatest organic matter retention including wood, CPOM, and FPOM. In contrast, the physical characteristics of RF habitats are generally high gradient, large substrate-particle size, high current velocity, shallow depth, and partial cover by dense short moss with FPOM but little CPOM retention within the moss (Eggert et al. 2012). Under reference conditions, the RF habitat generally supports lower abundances and biomass of some functional groups. This habitat is often dominated by filterers that can take advantage of the higher current velocities for their food delivery or scrapers that can graze on the rock substrate or, to a lesser extent, grazers within the moss habitat (Huryn and Wallace 1987). Mixed substrates tend to have greater abundances and biomass of invertebrates, especially gatherers and shredders and their predators.

We did not anticipate that LE and WR would have such a dominant effect on the pattern of invertebrate production among habitats in these streams. In Coweeta headwater streams, reduced retention of CPOM on high-gradient RF habitats and increased retention in MS habitats play a key role in the structure, function, and distribution of invertebrates within habitats of these headwater streams. We have not previously observed examples at Coweeta or other forested streams in the southern Appalachians where shredder production in MS and RF habitats were the same (e.g., Huryn and Wallace 1987, Lughart and Wallace 1992, Whiles and Wallace 1995, Wallace et al. 1997, 1999), yet those differences were eliminated during LE and WR primar-

ily because of reduced populations in MS habitats. Nor have we found elsewhere (1) significantly higher gatherer production in RF than MS habitats, (2) streams where predator abundance, biomass, and production in RF habitats significantly exceeds that of MS habitats, and (3) equal or greater levels of total abundance, biomass, and secondary production in RF than in MS habitats (Table 2). Some increases in certain functional groups are primarily the result of early instars of a number of insects using the stable RF substrate as habitat. Survivorship curves are clearly truncated long before immature instars have sufficient time to develop, indicating that the increases in some shredders and predators in the RF habitats are probably temporary (J. B. Wallace et al. *unpublished data*). Thus, the LE and WR manipulations drastically altered not only functional group absolute and relative abundance and biomass, but their previously reported within-stream habitat distributions as well. The inclusion of diverse physical and biotic functions within this ecosystem-level experiment underscores the need for including diverse habitats that may respond differently to manipulations (Carpenter 1998, Peterson et al. 1998).

The importance of organic matter standing crop in different physical habitats is evident in our results. Organic matter storage in RF habitats changed very little during treatments, and the invertebrate community on RF habitats responded much less than that on MS habitats. In contrast to MS habitats, standing crops of FPOM on the moss-covered RF substrates did not differ between the reference and treatment streams (Eggert et al. 2012). The absence of significant differences in functional group production in RF habitats during the

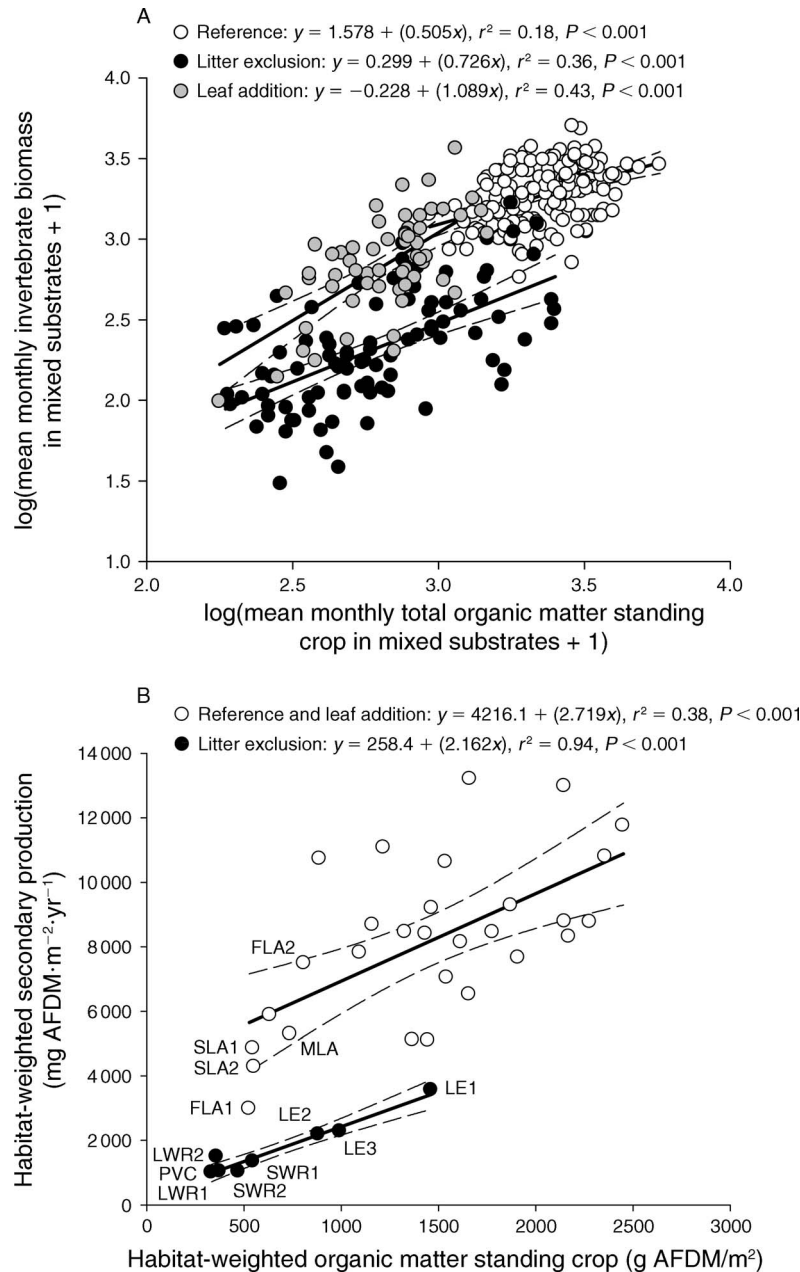


FIG. 6. Relationships between (A) monthly organic matter standing crop (originally measured as g AFDM/m²) and monthly invertebrate biomass (originally measured as mg AFDM/m²) in mixed substrates in reference streams; LE, WR, and PVC addition years in the treatment stream, and leaf addition years in the treatment stream, and, (B) habitat-weighted production and habitat-weighted total POM for treatment stream during treatment years and reference stream during reference years and leaf addition years of treatment stream. Numbers refer to years since beginning of treatment, as in Fig. 5.

treatment period vs. reference conditions is due largely to the continued availability of FPOM in the RF habitat, as seston concentrations never dropped below 2 mg AFDM/L of stream water, and total annual FPOM export remained >50 kg/yr, which are both within the ranges seen in reference streams (Eggert et al. 2012). Despite never dropping below an annual average of 0.3 kg AFDM/m² in MS habitats during LE and WR,

stored FPOM was greatly reduced in the treatment stream compared to reference conditions. Clearly, an adequate supply of organic matter could be trapped within the moss-covered substrate and replenish RF detrital resources during treatment. This was sufficient to support detritivores and eliminate any differences among functional feeding groups on RF habitats. The perfect ecosystem-level experiment has never been

devised, and the same can be said of our study, where the manipulated site, the stream, is physically downhill from the donor forest in the landscape. In such cases, it is virtually impossible to exclude all inputs to the system as FPOM and DOC, which continued to enter via the canopy, throughfall, groundwater, and soil particles.

Significance of long-term studies

Carpenter (1998) emphasized the importance of long-term studies in teasing out random variations within ecosystems among years, and that the scale of such studies should be large enough to detect physical variability within habitats. This latter point was driven home by the different responses we found between RF and MS substrates, but also by the ability of certain shredder taxa to persist on enhanced biofilms associated with wood in the treatment stream. In fact, this ability was the impetus for removing small wood from the system (Tank and Webster 1998, Eggert and Wallace 2007). WR resulted in further reduction of carbon, both as wood and FPOM. There is also evidence that biofilms were enhanced in the treatment stream during the LE period, as lower amounts of detritus decreased organic matter surface areas but enhanced nutrient availability to the remaining organic surfaces (wood; Tank and Webster 1998) as well to algae on the inorganic surfaces (rocks; S. L. Eggert et al. *unpublished data*). However, higher levels of primary production did not occur in the LE stream, even when deciduous trees were bare, because heavy shading by dense growths of riparian rhododendron limited primary production.

We are unaware of any other study with as many years of secondary productivity measurements as we report here. Such long-term studies can detect trends and patterns in responses to interannual variability in resource subsidies that may otherwise go undetected. Secondary production measurements during the reference years of this study, which included the years 1984–2006 in three different streams, reflect large annual variations in biomass and productivity of invertebrates as well as standing crops of detritus. In addition to the obvious exclusion of terrestrial litter and wood removal, factors influencing detrital standing crops include discharge and the frequency, seasonality, and intensity of storms. The study period incorporated extremes in precipitation observed over the preceding 70-year history of the Coweeta Hydrologic Laboratory (Laseter et al. 2012). Storms have previously been shown to strongly influence the annual variation in export and standing crop of organic detritus in these streams (Eggert et al. 2012). The strong relationships between invertebrate biomass and production and particulate organic matter shown here for both long-term reference and organic matter manipulative studies support the idea that the timing, frequency, and magnitude of storms that influence annual detrital standing crops also have significant effects on the secondary productivity of these headwater streams.

Tight coupling of predators with total production

The tight coupling between predator production and total invertebrate production was one of the surprising results of our initial study (Wallace et al. 1999), and this relationship remained through eight additional years of treatment and 20 additional reference years (Fig. 5). Although predators are included in total invertebrate production, predators eat other predators in these streams (Hall et al. 2000). These headwater streams are fishless, but include salamanders, whose larvae prey on all functional groups in these streams. The dominant salamander present, *Eurycea wilderae* (Blue Ridge two-lined salamander), had low annual productivity, i.e., ~8 mg AFDM/m² in the reference stream vs. ~2 mg in the LE stream (Johnson and Wallace 2005). Thus, inclusion of salamander production would not significantly alter the invertebrate predator–prey relationships seen in this study.

Previously, we calculated the slope for total predator production vs. total invertebrate production as ~0.35 for mixed substrates and ~0.23 for bedrock outcrop substrates (Wallace et al. 1999) and found that these slopes were within the range reported for bioenergetic efficiencies reported for invertebrate predators (gross production efficiency [GPE] ≈ 33–39%; Slansky and Scriber 1982). However, our previous calculations included only a few data points from two catchments (Wallace et al. 1999). Our current results incorporating data from 37 stream production years, including reference data from two additional streams and representing habitat-weighted results for each stream and year, yielded a slope of ~0.29 for all streams and treatments (Fig. 5). This is only slightly lower than GPEs of invertebrate predators given by Slansky and Scriber (1982); however, GPEs can be quite variable. For example, two ladybug species (Coleoptera: Coccinellidae) had conversion efficiencies ranging from 0.43 to 0.65 (mean ≈ 0.50) for one species and a range of 0.17–0.47 (mean ≈ 0.22) for another species. Furthermore, the conversion efficiencies of these two predators varied with larval instar, temperature, and larval and terminal body size (Isikber and Copland 2001). Our results show a rather consistent predator–total invertebrate production relationship, which is remarkable considering all the associated variables, including (1) multiple invertebrate predator taxa in various stages of development that display varying degrees of cannibalism, (2) multiple streams differing in amounts of RF and MS habitats, (3) multiple individuals doing the field sampling, and (4) a range of precipitation extremes over 23 years. Our results indicate a much tighter association between predators and prey than we previously suspected in these headwater streams. The tighter confidence intervals during litter exclusion years (lower left of Fig. 5) suggest tighter predator–prey coupling as basal detrital resources became more limiting and prey refuges are eliminated by reductions in organic matter standing crop.

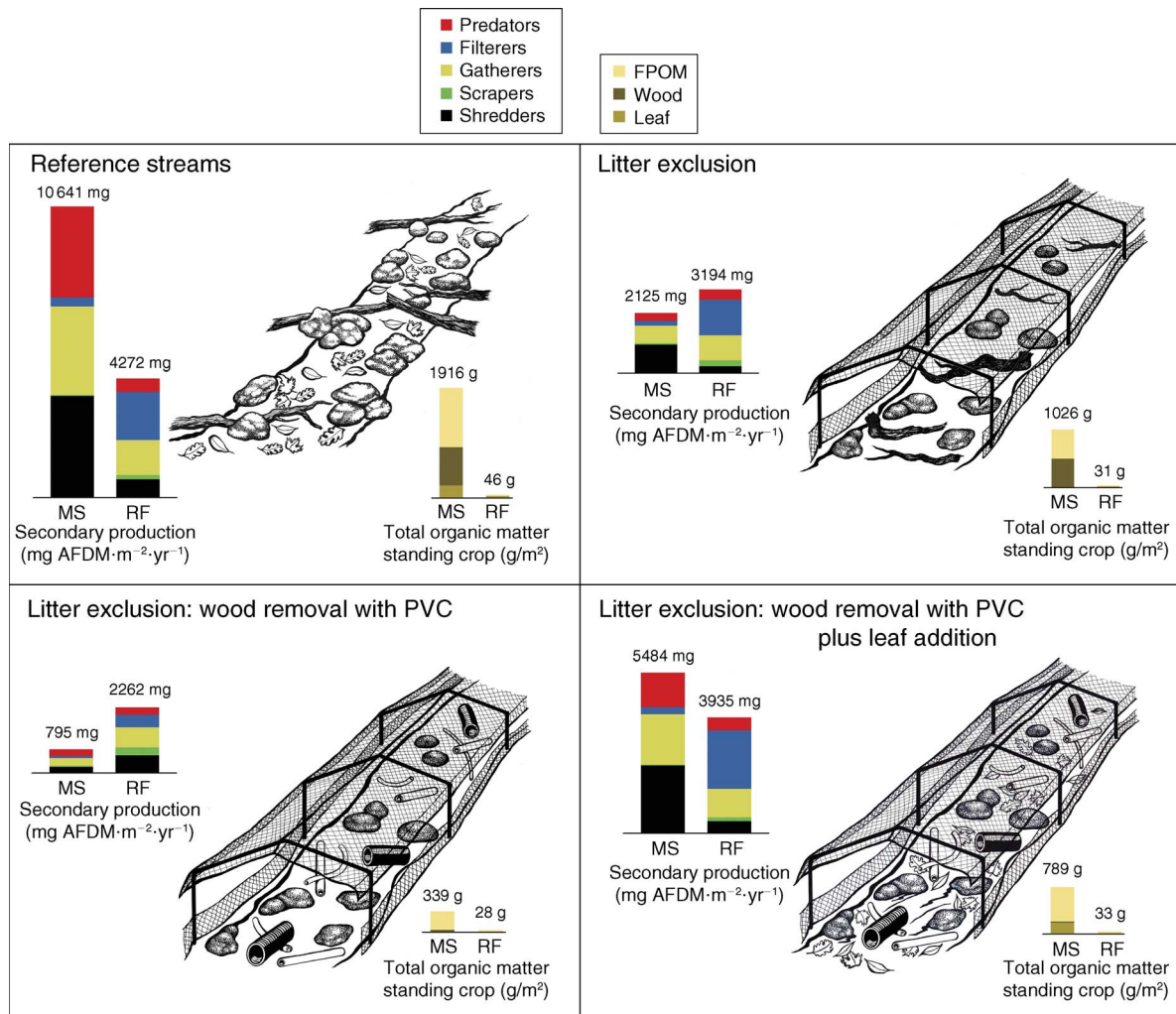


FIG. 7. Conceptual overview of comparison and experimental studies encompassing 37 stream-years showing secondary production (mg AFDM·m⁻²·yr⁻¹) and organic matter standing crops (g/m²) in both mixed substrate (MS) and rockface (RF) habitats (includes wood, leaf, and fine particulate organic matter [FPOM]); upper left, reference streams ($n = 24$ years); upper right, end of third year of LE period; lower left, end of small- and large-wood removal ($n = 4$ years) and first year of PVC addition period; and lower right, end of fifth year of leaf addition. LE canopy over treatment stream was maintained over the 13-year experimental period. Values represent total secondary production and organic matter standing crops for reference streams, and totals at the end of each experimental period for the LE stream. RF organic matter standing crops were extremely low and are drawn at a larger scale than MS organic matter standing crops. Secondary production values in both habitats are drawn at the same scale and are directly comparable.

The tight coupling of predators and their prey probably plays a much more important role in these headwater streams than is commonly recognized. Previously, two headwater streams were treated with an insecticide, C53 for one year in 1980 and C54 for three years from 1986 to 1988 (Cuffney et al. 1985). These treatments greatly reduced all invertebrate populations as well as the rates of leaf litter breakdown and seston export to downstream areas in both streams (Cuffney et al. 1990). During first year of recovery for both C53 (Wallace et al. 1986) and C54 (Chung et al. 1993), production/biomass of some primary consumers increased, predator biomass and/or production was

reduced to 23–27% of that in reference streams, and leaf litter decomposition rates exceeded reference conditions (Wallace et al. 1986, Whiles and Wallace 1992, 1995, Chung et al. 1993). With subsequent restoration of populations of predators, leaf litter processing rates were reduced to reference or pretreatment range (Wallace et al. 1986, Chung et al. 1993). Others have also observed a decrease in leaf processing rates in the presence of predaceous stoneflies (Malmqvist 1993), stoneflies and caddisflies (Oberndorfer et al. 1984), and fish (Ruetz et al. 2002). Macroinvertebrate predators generally have longer life cycles than those of prey taxa, which undoubtedly contributes to their slower

recovery following disturbance. Processing rates for leaf detritus by detritivores increase with lower predator abundance and may lead to early elimination of stream detrital resources. Predators thus play a role in mediating the rate at which detritus is processed and facilitate a dampening of oscillations in detritus standing crop and detritivore populations.

Significance for stream restoration

Prior to reconstructing the ecosystem by adding leaves of varying quality and complexity, we added PVC pipe and plastic branches to the treatment stream equivalent to the number of pieces and surface area of small and large wood removed from the stream during SWR and LWR (Eggert et al. 2012). The failure of this physical structure to produce any noticeable changes in production, abundance, or biomass of invertebrates indicates that the addition of structures without concomitant changes in the energy base, i.e., addition of leaf inputs, does not influence benthic assemblages. This result is very important for stream restoration. The restoration of physical habitat has been a major objective of stream restoration (see Palmer et al. 1997, Bond and Lake 2003), and structural restoration has been referred to as the Field of Dreams hypothesis: "if you build it, they will come" (Palmer et al. 1997). Palmer et al. (2010) reviewed numerous studies on stream restoration and found little evidence that enhancing physical structure alone had a positive effect on benthic assemblages. Likewise, without a source of available particulate organic carbon due to earlier treatments, there was no evidence that adding "wood" or physical structure in the form of PVC enhanced benthic invertebrate abundance, biomass, or production in our experiment. In fact, it was only after the addition of leaves that any significant changes in invertebrate abundance, biomass, or production occurred in MS habitats.

After excluding leaf litter, removing all wood, and PVC addition, secondary production in the exclusion stream ranked among the lowest reported for all temperate streams worldwide (Huryn and Wallace 2000), but increased severalfold during leaf addition (Table 2, Fig. 6B). However, invertebrate production during the leaf addition period remained at the lower range of reference streams (Fig. 6B). With the exception of the first year of fast-leaf addition and litter exclusion, leaf addition resulted in greater levels of invertebrate production at similar or lower levels of organic matter standing crop when compared with all other treatment periods. This level of production, $3\text{--}7\text{ g AFDM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, was higher than in previous treatment years, largely due to newly added leaf litter serving as the source of CPOM and FPOM. In fact, leaves alone had greater production per unit standing crop of organic matter than reference streams. Fresh leaf litter likely enhanced food quality, which was expressed as higher levels of production and production/unit organic matter standing crop during the five leaf addition years (see *Results: Invertebrate-organic*

matter relationships). Organic matter remaining in the litter exclusion stream during the pre-leaf-addition period was refractory and consisted primarily of material buried in the stream bed or soil organic matter from the surrounding forest, which was of lower nutritional value than that found in the same stream during leaf addition (Meyer et al. 2000).

Implications for long-term ecosystem changes

Our results have important implications for projected changes in climate and in forests as a result of diseases, drought, or pests. In addition to altering stream temperature and hydrologic regimes, global warming is likely to influence multiple stressors and cause changes that alter hydrological, nutrient, and carbon export patterns (e.g., Groffman et al. 2012). A changing climate may result in significant changes in suitable habitat for tree species (Iverson et al. 2008), as well as altered susceptibility to pests, drought, and disease (Elliott and Vose 2011). Such forest changes do not require centuries, but may occur within decades. Species composition of wood removed from the treatment stream during our study (1990s) was more similar to the terrestrial vegetation plots on this catchment in 1934 than recent vegetation plots (Wallace et al. 2001). In the late 1930s and 1940s, the chestnut blight devastated the Appalachians. As a result, much of the wood removed from the treatment stream in the late 1990s was American chestnut. Thus, large-scale changes in forests can occur within decades, and changes in adjacent forests possess the potential to impact both the amounts and types of terrestrial subsidies to forested streams. Furthermore, the diverse array of leaves from different riparian tree species with different breakdown rates, i.e., fast to slow, confers a more continual supply of organic matter over the annual cycle (Fisher and Likens 1973). Thus, diverse riparian forests provide a more continuous supply of resources to aquatic food webs than riparian forests with few species. This is critical for stream restoration and conservation.

Unfortunately, in addition to climate change, pests, and disease, headwater streams are under assault by additional anthropogenic practices including improper riparian forestry and agricultural practices, piping, urbanization, mining, road building, etc. This study clearly demonstrates the importance of maintaining sufficient quantities of allochthonous detritus to headwater streams draining forested catchments. Recovery of functional group abundance, biomass, and production in disturbed streams will require sustained inputs of leaf, wood, and other organic matter from adjacent riparian habitats to sustain and maintain invertebrate assemblages and productivity. Recovery and restoration of streams in forested regions require much more than the restoration of physical attributes such as habitat and flow regimes; efforts must also restore the energy base of the stream by reconnecting lost aquatic/terrestrial linkages.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-1589.1.sm>