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PRIMARY RESEARCH PAPER

Macroinvertebrate and organic matter export from headwater tributaries of a Central Appalachian stream

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Abstract Headwater streams export organisms and other materials to receiving streams, and macroinvertebrate drift can shape colonization dynamics in downstream reaches while providing food for downstream consumers. Spring-time drift and organic matter export was measured once monthly (February–May) over a 24-h period near the outlets of 12 eastern Kentucky (USA) streams to document and explore factors governing downstream transport. We compared drift measures as loads (day^{-1}) and concentrations ($volume^{-1}$) including drift density, biomass, richness, composition, and particulate organic matter across catchment area, month, reach scale factors, and network proximity. Aquatic invertebrate drift densities were roughly 10 times greater than terrestrial invertebrate densities; aquatic richness ranged from 18 to 45 taxa with Ephemeroptera, Plecoptera, Trichoptera, and Diptera genera dominating drift sample richness and abundance. Ordination revealed that assemblages clustered by month and catchment area; organic matter exports (loads or concentrations) also varied by month and catchment area factors. While drift measures were correlated with catchment area and sample date, local factors (e.g., substrate composition, riffle length, channel slope, and network proximity) were generally non-influential. The findings can be used to inform preservation and restoration strategies where headwater streams serve as sources of colonizers and provide food subsidies to receiving streams.

Keywords Drift · Headwater streams · Central Appalachian Mountains · Aquatic insects · Dispersal

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Introduction

Invertebrate drift (water column entry of benthic invertebrates) is ubiquitous, playing a large role in the colonization dynamics of many species in streams (Brittain & Eikeland, 1988). Drift occurs both behaviorally (e.g., seeking food and avoiding predators) and accidentally (e.g., detached from substrate in swift current) and can vary with abiotic and biotic factors. A rich literature exists where drift studies have been

conducted in multiple biomes and encompassing diel and seasonal patterns (Elliott, 1970; Hansen & Closs, 2007; Neale et al., 2008), drift distance (Elliott, 1973; Lancaster et al., 1996), abiotic and biotic controls (O'Hop & Wallace, 1983; Poff & Ward, 1991), and as food subsidies for drift-feeding fishes (Wipfli & Gregovich, 2002; Romaniszyn et al., 2007). Importantly, drift forms a critical biological connection linking upstream–downstream reaches in river networks (Waters, 1964; Townsend & Hildrew, 1976; Altermatt, 2013).

Knowledge of invertebrate transport and dispersal within and between streams is lacking in the Central Appalachians but could be a key controlling factor in determining rates of recovery after disturbance and restoration (e.g., Sundermann et al., 2011; Merovich et al., 2013; Tonkin et al., 2014). In this region, headwater streams harbor diverse and sensitive macroinvertebrates that are vulnerable to extirpation from regional land uses such as large-scale surface mining and streamside residential development (Pond et al., 2008; Pond, 2010; Bernhardt et al., 2012; Cormier et al., 2013; Merriam et al., 2013). In bioassessment, some evidence suggests that intact tributary streams likely contribute sensitive drifting larval colonists to impaired downstream reaches thereby increasing biodiversity and potentially lessening the perceived severity of impairment in receiving streams (Pond et al., 2014; Orlinskiy et al., 2015); others suggest that knowledge of dispersal constraints (e.g., fragmentation and lack of source populations) are critical in understanding appropriate stream restoration designs and predicting subsequent success (Parkyn & Smith, 2011; Sundermann et al., 2011; Tonkin et al., 2014). Support for these dispersal-based linkages was shown by Campbell Grant (2011) who simulated pruned (e.g., loss of headwaters through burial) versus fractal networks; when dispersal was downstream biased (drift), time to metapopulation extinction was shorter for the pruned stream network (conditions often found in upland areas of urbanized and mined landscapes) compared to a more branched, fractal network. This simulation suggests that leaving few or no headwater tributaries would have downstream consequences on the persistence of stream populations. Thus, intact headwaters are needed to counteract downstream extinction rates by providing constant supplies of drifting sensitive colonizers; however when present, these drifters could also affect bioassessment results by masking the detection of unabated stressors to a resident downstream assemblage especially since the fate of these sensitive colonizers is unknown (Pond et al., 2014). These tributaries are also important sites for organic matter inputs and transformation, where these products are ultimately exported to downstream consumers (Gomi et al., 2002; Wipfli & Gregovich, 2002; Meyer et al., 2007).

Because drift can potentially counteract local extinctions and aid in recovery following stream remediation (Parkyn & Smith, 2011), our study documents the quantity of invertebrates (and organic matter) exported from tributary outlets within a Central Appalachian stream network. Our aim was to assess the role of various spatial and temporal factors governing downstream transport from tributaries by analyzing patterns of multiple drift measures between tributary size, sample month, reach scale habitat factors, and network position. We used catchment area as a general proxy for stream size, flow duration and overall stream energy, whereas sample month was used to track phenological shifts in taxon distributions. We hypothesized that drift quantities (abundance, richness, and biomass) and drift community structure are mainly shaped by catchment area and sample month, but these relationships are likely moderated by local habitat and inter-site proximity differences. Therefore, we quantified and compared monthly invertebrate and organic matter exports (as total daily loadings and concentrations), focusing efforts during the spring bioassessment index period (February–May; Kentucky Department for Environmental Protection, KYDEP, 2011), a time when these headwaters have higher baseflows and occupancy rates by a diverse benthic assemblage but tend to lose surface flow in summer and autumn. Purposely, February–May represents a regulatory timeframe in context for headwater bioassessment in the region, and for measuring stream restoration (e.g., natural channel design) success where macroinvertebrates are used as biological indicators.

Methods

Study area

The 12 study streams were headwater tributaries of Clemons Fork (catchment area 15 km^2), a state
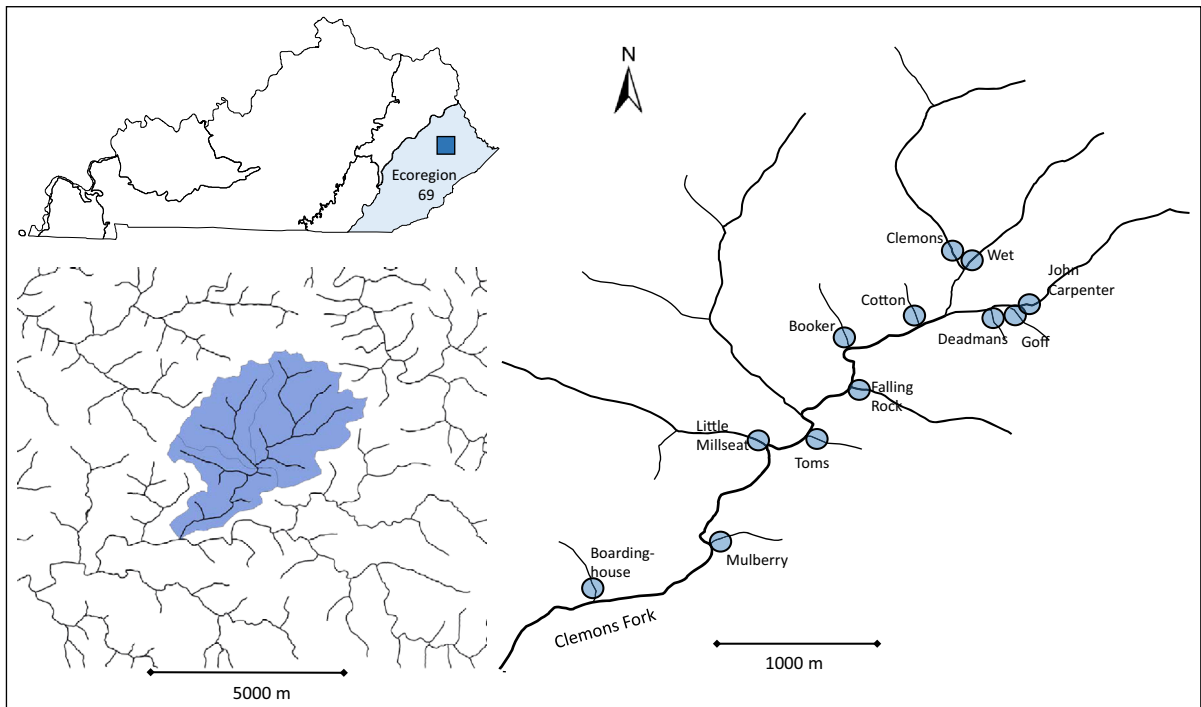
Fig. 1 *Maps* showing location of Clemons Fork catchment (*square*) in eastern Kentucky and the 12 tributary sites (*circles*) within the study catchment. The Level III Ecoregions (after Woods et al., 2002) are delineated on the Kentucky map, including the location of the Central Appalachians Ecoregion (*69*)

reference condition catchment within the University of Kentucky's Robinson Research Forest (37°27′N, 83°08′W) in eastern Kentucky, USA. The catchment lies within the Dissected Appalachian Plateau of the Central Appalachian Mountain ecoregion (ecoregion 69d; Woods et al., 2002). Annual precipitation ranges from 100 to 125 cm, and mean annual air temperature is 12°C (Owenby et al., 2001). Prior studies (Pond & McMurray, 2002; Grubbs, 2011; Pond & North, 2013) confirmed that benthic macroinvertebrate assemblages within Robinson Research Forest are similar to other intact headwater streams throughout this ecoregion. Mainstem Clemons Fork is a third order, moderately high-gradient stream draining intact second-growth upland hardwood and mixed-mesophytic forest (Phillippi & Boebinger, 1986) and has relatively low land-use pressures (the catchment has unimproved roads with areas of past and recent silviculture). The network position of the study tributaries (first and second order) were evenly distributed along the length of the Clemons Fork mainstem (Fig. 1). Tributary catchments ranged from 15 to 190 ha and drained 90–100% forested land cover. Study reaches (~50 m)

near the mouths of each tributary had relatively high gradients (~2–21% slope) and were fully canopied with extensive riparian forest (Table 1).

Sampling and processing

We collected monthly 24-h drift samples from the 12 tributaries in February, March, April, and May 2014 (approximate baseflow, each ~30 days apart). Low, interstitial flow conditions in May precluded sampling with drift nets at four of the smallest sites. Table 1 lists mean and range of physical variables across study sites. Depending on stream width, we secured one or two driftnets (0.45-m wide by 1-m long, 250-μm mesh; Aquatic Research Instruments, Hope, ID) with rebar on the channel bottom across the wetted width. Each net was fitted with PVC collection buckets with 250-μm mesh. Our aim was to capture >90% of wetted width (and thus flow) at the base of riffles near the tributary mouths under non-storm flow conditions (approximate seasonal baseflows); in wider tributaries, this was accomplished by setting two nets side-by-side in riffles with naturally narrowed channel

Table 1 General physical characteristics among study sites

Sites	Catchment area (ha)	Elevation (masl)	Valley aspect	Channel slope (%)	Riffle length (m)	Mean riffle width (m)	Mean riffle depth (m)	Mean net velocity (m s^{-1})	Mean net discharge (l s^{-1})	Mean pH	Mean SC (μS cm^{-1})
Boardinghouse	27.6	284	S	7.8	4	1.1	0.05	0.21	3.0	6.1	35
Mullberry*	32	280	W	20.9	6.5	1.1	0.03	0.29	2.2	6.3	37
Little Millseat	147.5	285	SE	6.9	7	1.6	0.08	0.19	11.2	6.2	38
Toms*	28.4	292	NW	21	17	1.1	0.04	0.28	2.7	6.3	37
Falling Rock	102.2	297	NW	5	4	3.1	0.04	0.58	8.7	6.4	41
Booker	56.8	298	S	11.1	6.5	1.2	0.06	0.33	4.7	6.6	35
Cotton*	17.9	312	S	18.6	1.6	0.6	0.07	0.08	2.0	6.4	23
Deadmans*	14.6	329	N	7.7	11	0.8	0.03	0.15	1.4	5.8	33
Goff	35.1	334	N	8.2	2	1.7	0.05	0.25	3.3	5.8	37
John Carpenter	103.2	336	SW	16	3.1	1.9	0.08	0.23	10.2	6.1	35
Wet	109.2	331	SW	6.7	15	3.2	0.09	0.14	9.8	6.3	38
Clemons	189.4	319	S	1.7	2	2.5	0.11	0.23	14.5	6.5	79

Means based on $n = 4$ unless marked with asterisk (*), where $n = 3$

* Could not be sampled in May (interstitial flow only)

dimensions (see Online Resource 1 for examples). Net discharge was measured using depth and velocity readings at four equidistant locations across each net opening. On retrieval, nets were removed and the contents washed into a 250-μm sieve; all material was preserved in containers containing 90% ethyl alcohol. We observed little or no clogging of nets throughout the study duration.

On each occasion, we measured pH, temperature, specific conductance, dissolved oxygen concentration (DO), and % DO saturation with a multi-probe sonde (YSI, Yellow Springs Instruments, OH). Local habitat was recorded on the first and last occasions (February and May), and included mean length of the immediate upstream riffle (below pool), mean riffle width, mean water depth, and mean substrate composition (%). For each site, we used ArcGIS® 10.1 (ESRI, Redlands, CA) and ArcHydro® tools to calculate catchment area, land cover types (deciduous, coniferous, or mixed forest; from 2011 National Land Cover Dataset, US Geological Survey), mean valley slope, reach slope (lower 50 m above mouth), valley aspect, and fluvial distance between sites.

In the laboratory, high volume samples were split with a Folsom plankton splitter to obtain subsamples of 1/2 to 1/8 of the entire amount (by volume). Lower volume samples were processed in their entirety. All aquatic and terrestrial organisms were sorted from debris under a microscope. Our target number of subsampled organisms ranged from 200 to 300 to help reduce time and effort, but mainly to standardize richness and composition measures across samples (Vinson & Hawkins, 1996); in some cases, we sorted additional subsampled material to reach this target. Additionally, the remaining portion of the sample was scanned for 15 min to search for large/rare taxa; these taxa were only used for richness metrics and not included in density or biomass estimates. Organisms were identified to the lowest possible taxon (usually genus for aquatic; order or family for terrestrial), counted, and body lengths were measured to the nearest 1 mm. Length measurements were used to estimate the ash-free dry mass (AFDM) of drifting organisms using length–weight equations found in the literature (e.g., Sample et al., 1993; Benke et al., 1999; Sabo et al., 2002). Adults of aquatic taxa (e.g., Diptera, Plecoptera) were treated as terrestrial drift. The total number of organisms was extrapolated based on proportion of subsample and discharge measures were used to calculate drift density (individuals m^{-3} day^{-1}), richness concentrations (no. of taxa m^{-3} day^{-1}), and animal biomass (mg AFDM m^{-3} day^{-1}). After sorting organisms from subsamples all debris (particulate detritus, inorganic sediments and remaining organisms) was dried at 50° C for 48 h, weighed, and then ashed at 550°C and re-weighed to determine the transported organic matter (AFDM). The proportion of invertebrate biomass not sorted and identified from subsampling was calculated and subtracted to determine the total particulate organic matter (POM >250 μm).

Data analysis

Tributary catchment area and sample month were the key factors we used in our sampling design to characterize the export of invertebrates and organic matter. We contrasted monthly metric values as loads (totals per day) and concentrations (total m^{-3} day^{-1}) using general linear models (GLMs; Systat v. 13) to detect differences ($\alpha = 0.05$) in slope equality among month classes across a gradient of catchment area. In addition to drift density and total abundance, we focused on invertebrate metrics commonly used in bioassessments in the Central Appalachian region and these metrics included: total aquatic richness, Ephemeroptera + Plecoptera + Trichoptera (EPT) richness, Ephemeroptera and Plecoptera richness and relative abundance (%). Further, we compared monthly exported biomass (invertebrate and POM). Data were checked for normality (Shapiro–Wilks test) and transformed (log, arcsin sqrt) where necessary to meet the assumptions of the GLM. To explore relationships between abiotic factors and community structure, monthly drift assemblages (aquatic taxa) were ordinated using non-metric multidimensional scaling (NMDS; PC-ORD v. 6, Gleneden Beach, OR). NMDS used Bray–Curtis (BC) distances and log-transformed abundances, omitting rare taxa (observed in <5% of samples) (McCune et al., 2002). We investigated the relationship between drift metrics (concentrations and relative abundance) and reach scale habitat variables using Spearman correlation on mean values (averaged over month classes). To evaluate the role of spatial proximity on community structure and turnover, we evaluated community drift data using both BC dissimilarity (for quantitative data) and Jaccard's dissimilarity indices (J; for binary data)

(Anderson et al., 2011). BC was calculated from averaged relative abundances among February–April samples (May was excluded because four of the smallest tributaries had no surface flow) whereas *J* was calculated similarly but using presence/absence. Here, we tested whether community similarity (based on composition and abundance) was related with how close sites were located in network space. We used channel-connected network distance because it is likely more appropriate given that our sites were located near tributary mouths, and since many aquatic invertebrates disperse within stream corridors, rather than overland (Griffith et al., 1998). For all pairwise BC and *J* calculations, we used the upper Clemons Fork site as an anchor site (it was the most physically distant site along the channel network; see Fig. 1) so that all dissimilarity values were relative to this site. We used linear regression to determine the relationship between both BC and *J* (as response variables) with spatial distance (i.e., distance–decay relationship), and with catchment area for comparison.

Results

Invertebrate drift composition

A total of 12,508 subsampled invertebrates were processed from 44 driftnet samples (only 8 samples in May). Aquatic invertebrates made up 89% of all drifting invertebrates collected over the duration of the study and ranged in numbers of individuals between 180 and 2,661 per day (corrected for any subsampling). A total of 208 distinct taxa were identified (167 aquatic, 41 terrestrial). Among the aquatic taxa, Diptera had the most genera (70; 40 were Chironomidae) followed by Plecoptera (23), Ephemeroptera (21), and Trichoptera (15). Combined, these four insect orders contributed most (>95%) of the total relative abundance of aquatic invertebrates exported: Diptera (37%), Ephemeroptera (36.6%), Plecoptera (18.3%), and Trichoptera (3.4%). Collembola (4 families) comprised the majority of all terrestrial drift (55%) followed by the hemlock woolly adelgids (*Adelges tsugae* Annand, 1924, 23%) and adult Diptera (14.7%). Monthly proportions of aquatic and terrestrial individuals and biomass are shown in Fig. 2. A list of common aquatic taxa and their frequency of
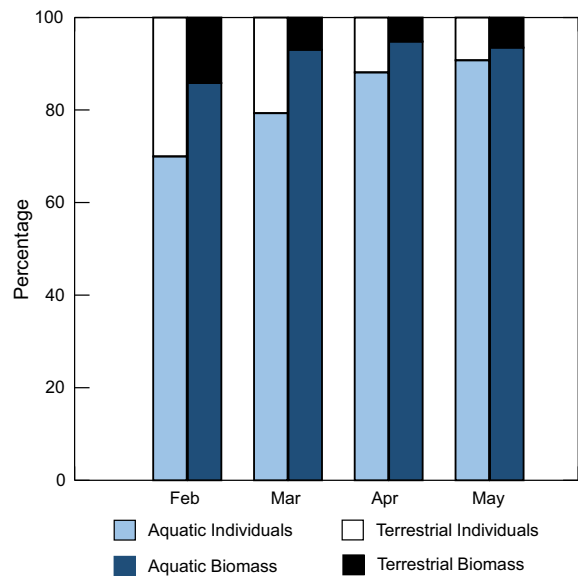

Fig. 2 Percent composition of aquatic and terrestrial individuals and biomass by sample months

occurrence (>10%) across all study sites is presented in Online Resource 2.

Comparing invertebrate and organic matter export with catchment area and month

Across all tributaries, aquatic and terrestrial invertebrate drift density and biomass varied by catchment area and sample month (Table 2). Given the much greater dominance by aquatic invertebrates and our study objectives, we focused the remaining analysis on these organisms. Relationships between monthly richness loadings (A; per day) and concentrations (B; per volume) versus catchment area are shown in Fig. 3. Richness loadings increased significantly with catchment area except for Plecoptera. Ephemeroptera richness showed the strongest response across month and catchment area based on GLMs (Table 3). An interaction between month and catchment area was found with all richness metrics (except Plecoptera) indicating that monthly differences in richness loadings were reliant on catchment area. For concentrations (richness m^{-3} day^{-1}), opposite trends were found and indicated that smaller streams tended to have more drifting taxa per volume, but this was dependent on sample month. The number of individuals, biomass, and POM increased significantly with

Table 2 Mean (range) daily drift densities (individuals m^{-3} day^{-1}) and biomass (mg AFDM m^{-3} day^{-1}) for aquatic and terrestrial invertebrates by month across all sites

	February	March	April	May	F	P
Aquatic density	0.96	1.00	4.77	13.80	18.4	<0.001
	(0.26–1.71)	(0.43–1.79)	(1.94–11.52)	(4.93–26.04)		
Terrestrial density	0.41	0.26	0.64	1.40	11.9	<0.001
	(0.06–1.36)	(0.08–0.52)	(0.19–11.52)	(0.13–2.82)		
Aquatic biomass	0.28	0.46	1.65	4.13	11.0	<0.001
	(0.07–0.79)	(0.24–1.14)	(0.49–4.45)	(0.13–2.82)		
Terrestrial biomass	0.05	0.04	0.09	0.29	11.8	<0.001
	(0.01–0.13)	(0.01–0.07)	(0.02–0.21)	(0.05–0.68)		

F-statistic based on one-way analysis of variance depicting the influence of month on drift densities and biomass

increasing catchment area (Fig. 4A) though when standardized by discharge (Fig. 4B), the catchment area effect was reduced (Table 3); however differences between monthly concentrations were significant. Monthly POM concentrations differed markedly among smaller tributaries but not the larger tributaries (i.e., >100 ha, Fig. 4B).

Community structure also varied significantly by month and catchment area. A two dimensional NMDS ordination for the aquatic invertebrate composition was produced (stress = 0.13) with axis 1 and 2 representing 62 and 14% of the explained variance, respectively (Fig. 5). Sites exhibited relatively distinct clustering among month classes, but the invertebrate composition from smaller sites appeared to vary more among streams and across months than that of larger sites (as indicated by position in relation to catchment area vector). Tighter clustering was observed for larger sites. Sample date (and corresponding stream temperature and DO) appeared to drive the ordering of sites in space along axis 1 ($|r| > 0.54$), whereas axis 2 was negatively correlated with measures related to catchment area, net velocity, and export of POM ($|r| > 0.50$). Genera contributing to the spread of sites along axes 1 and 2 (highest correlations) included the mayflies *Ephemerella* Walsh, 1862, *Baetis* Leach, 1815, and *Paraleptophlebia* Lestage, 1917 and blackflies *Prosimulium* Roubaud, 1906 (all $|r| > 0.70$). Notably, ephemerellid mayflies decreased with increasing sample month, while baetid mayflies increased, peaking in May (Online Resource 3). Similarly, the drift densities of simuliid blackflies was highest in February and March but declined in April and May. Although individual genera of

Chironomidae exhibited monthly patterns, the family as a whole did not vary in monthly relative abundances. A list of the top 20 taxa (expressed as drift densities) among sample month is provided in Online Resource 3.

Correlation of drift metrics with reach scale factors

We found few significant correlations ($P < 0.05$) between the means of select drift concentrations or % composition measures and reach scale variable means (Table 4). While physical and chemical measures were correlated with drift, most covaried with sample month (e.g., temperature and DO) or catchment area (e.g., specific conductance) and were excluded from the correlation analysis. Channel slope (ranged from 1.7 to 20.9), the length of the immediate upstream riffle (ranged from 0.6 to 15 m) and substrate composition (i.e., % boulder, cobble, gravel, etc.) were not significantly correlated ($P > 0.05$) with any drift measures except % Ephemeroptera was negatively correlated with slope ($r = -0.60$). Net velocity and pH were weakly but positively associated with % Ephemeroptera and negatively for % Plecoptera. By comparison, all mean measures were significantly correlated with catchment area except biomass (m^{-3} day^{-1}); notably, % Ephemeroptera strongly increased ($r = 0.85$) with catchment area while mean Plecoptera richness (m^{-3} day^{-1}) and relative abundance decreased ($r = -0.92$, -0.75, respectively).

Site proximity and ecological distance

Invertebrate assemblages did not display a distance–decay relationship along the network (spatial distance

Fig. 3 Relationship between richness measures and catchment area by sample months for **A** daily loadings (no. day^{-1}), and **B** concentrations (no. m^{-3} day^{-1})
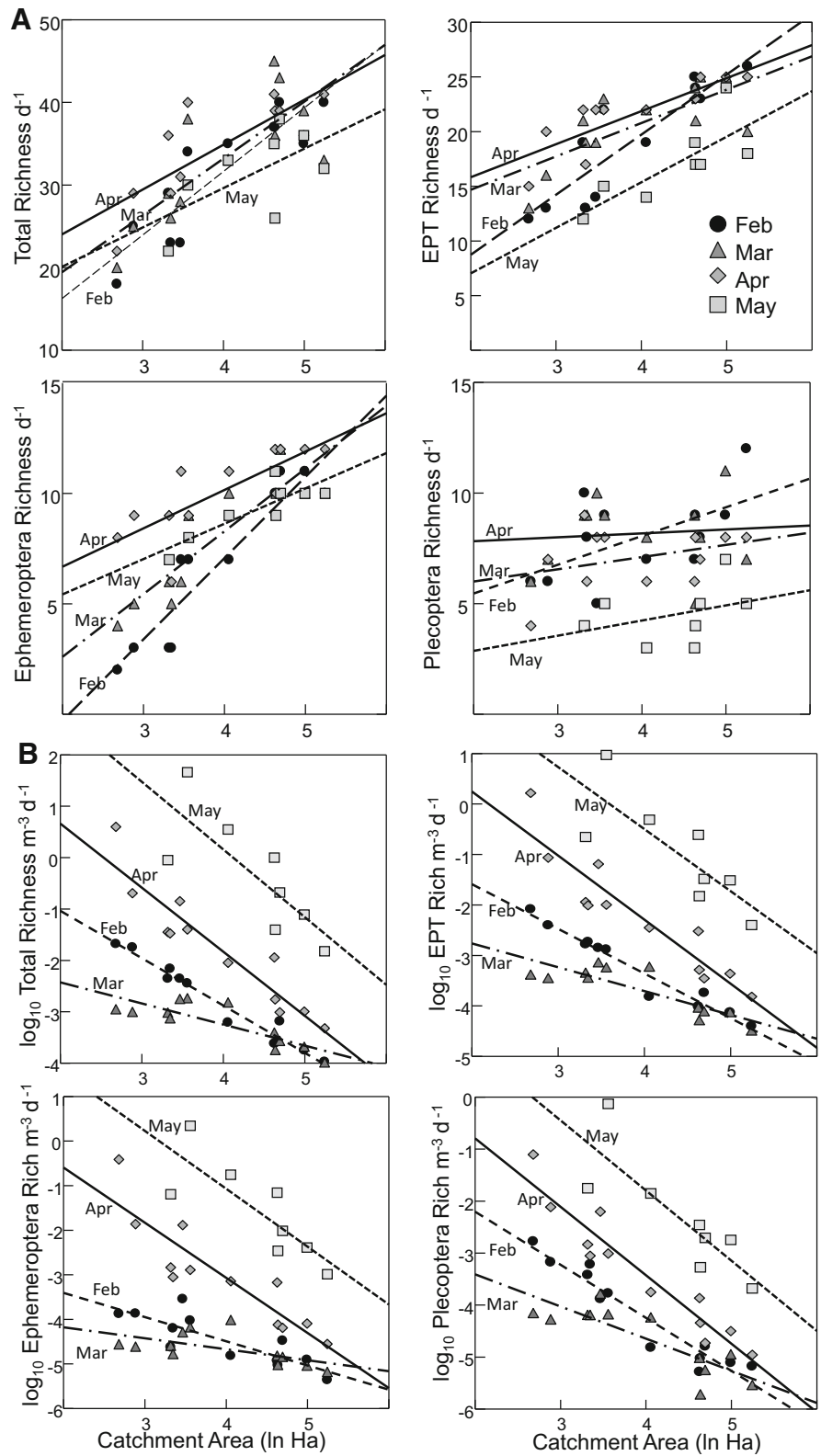
Table 3 General linear model results for drift metrics and particulate organic matter (POM >250 μm) for export loadings (total per day) and concentrations (per volume) analyzed by sample month and catchment area (CA); bolded values are $P < 0.05$

Metrics	Loadings		Concentrations	
	F	P	F	P
Total richness				
Month	4.1	**0.049**	3.7	0.060
CA	17.4	**<0.001**	1.8	0.182
Month * CA	4.3	**0.044**	0.1	0.714
EPT richness				
Month	3.2	0.080	4.2	**0.048**
CA	14.7	**<0.001**	2.0	0.170
Month * CA	4.5	**0.039**	0.2	0.645
Ephemeroptera richness				
Month	35.9	**<0.001**	10.1	**0.003**
CA	59.2	**<0.001**	0.0	0.985
Month * CA	28.2	**<0.001**	2.0	0.157
Plecoptera richness				
Month	0.0	0.928	3.0	0.089
CA	2.3	0.138	3.4	0.072
Month * CA	1.0	0.327	0.1	0.728
Aquatic individuals				
Month	4.1	**0.049**	5.1	**0.030**
CA	22.0	**<0.001**	0.7	0.399
Month * CA	4.5	**0.041**	3.6	0.065
Aquatic biomass				
Month	1.0	0.325	6.0	**0.019**
CA	7.3	**0.010**	1.1	0.307
Month * CA	1.0	0.320	2.2	0.144
POM				
Month	1.3	0.269	5.0	**0.032**
CA	16.5	**<0.001**	2.0	0.170
Month * CA	2.8	0.056	2.5	0.120
% Ephemeroptera				
Month	10.4	**0.002**	6.0	**0.019**
CA	12.4	**0.001**	7.3	**0.010**
Month * CA	4.6	**0.038**	1.9	0.175
% Plecoptera				
Month	0.1	0.733	0.1	0.730
CA	17.1	**<0.001**	1.3	0.270
Month * CA	0.0	0.838	0.0	0.851

gradient) nor display any resemblance based on proximity to one another within this network (Fig. 6). Spatial distance of sites and their faunal distance (BC and J dissimilarity) were not related ($r^2 = 0.03$, $P = 0.62$ for BC, $r^2 = 0.01$, $P = 0.95$ for J). In contrast, a stronger and significant relationship between catchment area and BC ($r^2 = 0.58$, $P = 0.003$) and J ($r^2 = 0.64$, $P = 0.006$) was observed (Fig. 6).

Discussion

Invertebrate drift is common and widespread in lotic systems and has been considered to be the prevalent mode of dispersal by most stream invertebrates (Waters, 1965). While the pattern of drift and downstream transport of other materials is complex, it is understood that delivery of taxa and materials from upstream sources can contribute to the character of the receiving streams (Gomi et al., 2002). Our hypotheses that drift quantities (abundance, richness, and biomass) and drift community structure would vary mainly by catchment area and sample month were confirmed, but drift metrics or community structure was not strongly related with local habitat or inter-site proximity differences. For most of our drift metrics, we rejected general null hypotheses concerning the roles of tributary catchment area and sample month and rejected the premise that local habitat and network proximity strongly moderated exports or community structure. However, the relationships with catchment area and month varied among drift measures (including data as load or concentration). Whereas larger tributaries individually exported more invertebrates and POM per day, the concentration of invertebrates and POM transported each day from smaller tributaries was often higher (especially April and May).

From the perspective of downstream contributions from headwater streams, our results document that during spring-time baseflow conditions (non-storm), small first–second order tributaries can deliver dozens of genera and hundreds to thousands of organisms on a daily basis to receiving waters. As suspected, the relationship between catchment area, stream width, net discharge, total organism drift and biomass, and organic matter transport were strongly interrelated. When standardizing data by discharge (m^{-3} day^{-1}), the correlations between some biological endpoints and catchment area were reduced (however, our main interest was to document both total daily loads and concentrations). When standardized by discharge,

Fig. 4 Relationship between individuals, biomass, and particulate organic matter (POM) and catchment area by sample month for **A** daily loadings (total day^{-1}), and **B** concentrations (m^{-3} day^{-1})
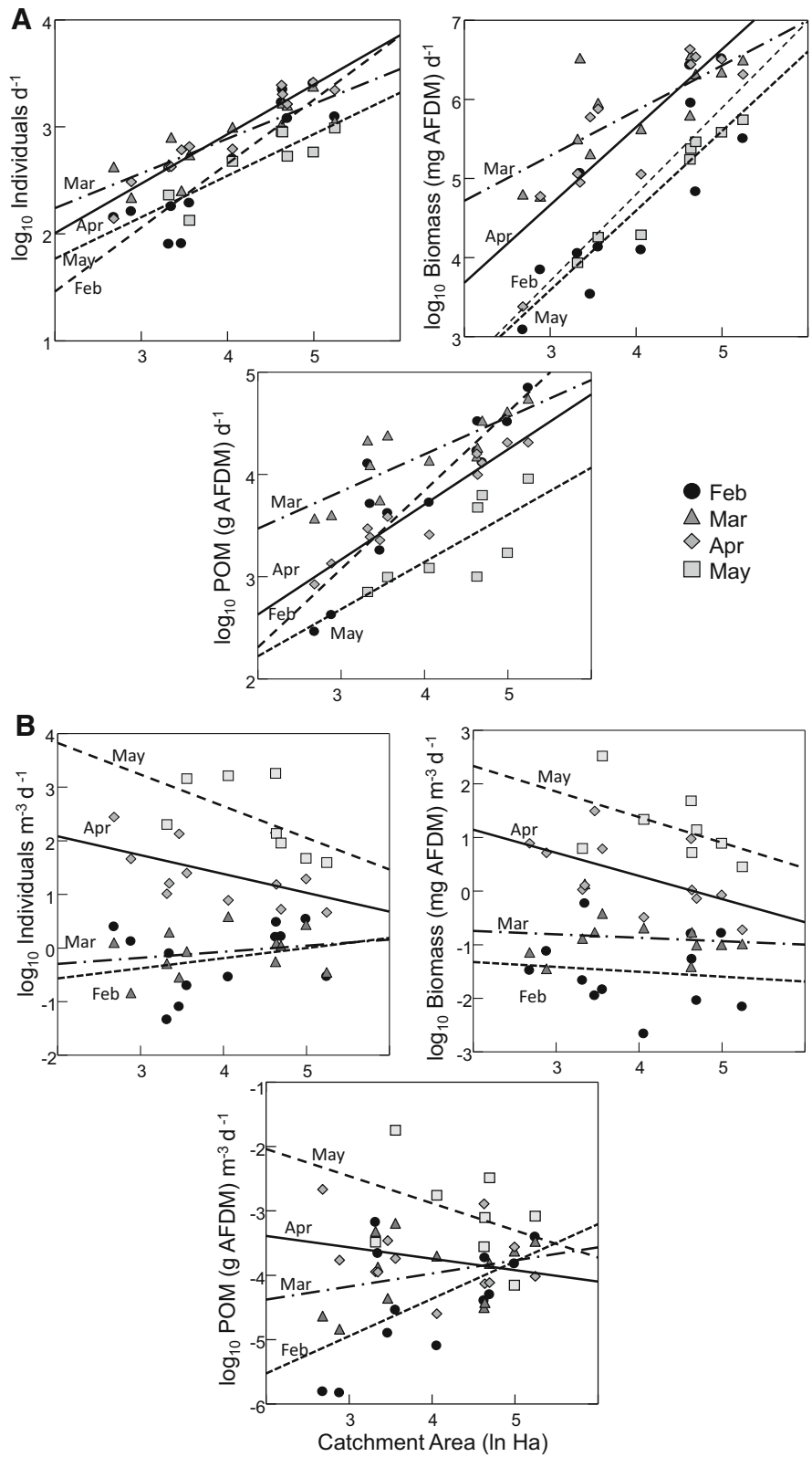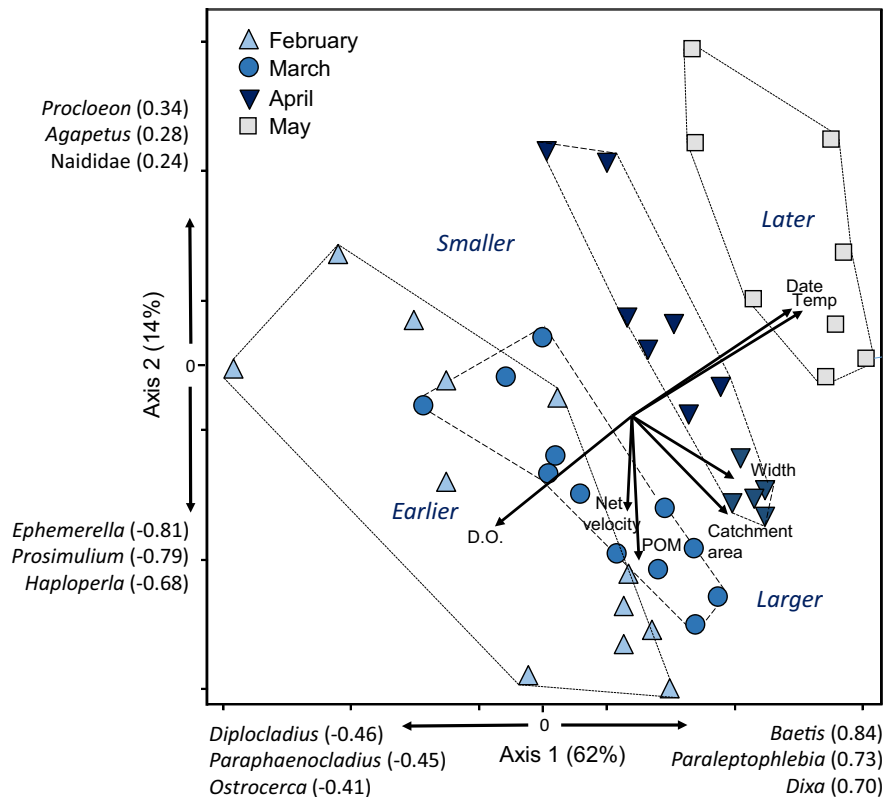
Fig. 5 NMDS ordination of driftnet samples grouped by sample month (enclosed by *convex hulls*). Percent variance for each *axis*, environmental vectors ($r > 0.3$), and top three taxa correlated with each *axis* are provided

greater aquatic drift densities and organism biomass tended to occur during lower flows in April and May and might indicate increased behavioral drift in response to declining habitat and food resources as found by others (Minshall & Winger, 1968; Poff & Ward, 1991), or be otherwise related to life history cues. Our daily export values are conservative since typical storm events would lead to export of far more invertebrates than our estimates (O'Hop & Wallace, 1983). In an Oregon headwater stream, Anderson & Lehmkuhl (1968) reported 4-fold increases in drift loads after 1–2 in. storm events (common events for Central Appalachia) that corresponded to a 5-fold increase in discharge. In experimental stream channels, Imbert & Perry (2000) observed 10–33-fold increases in drift abundance in what they deemed both stepwise and abrupt (respectively) non-scouring flows (both incurring ~ 0.01–0.03 m^3 s^{-1} increases). Our estimates of invertebrate biomass and drift density were roughly similar to other non-storm studies of forested, headwater Appalachian streams (O'Hop & Wallace, 1983; Romaniszyn et al., 2007). Although not studied here, we expect that drift in summer or fall

is far less than spring drift (O'Hop & Wallace, 1983) in our streams mainly because of reduced overall daily discharge (Williamson et al., 2015) and occurrence of interstitial flow and non-flowing conditions (personal observation) along many of the headwater tributaries in the catchment. However, summer storm events that increase stream discharge could certainly provide punctuated exports of organisms and organic material to downstream habitats (O'Hop & Wallace, 1983; Corti & Datry, 2012).

Taxonomically, we observed a rich assemblage of aquatic drifters that greatly resembled assemblages present in routine benthic sampling from similar headwater streams in the area (Pond & McMurray, 2002; Grubbs, 2011; Pond & North, 2013). Moreover, many of the common taxa collected in our drift samples (see Online Resources 2 and 3) represent taxa that are frequently lost from coal mining impacts in the region (Pond et al., 2008; Pond, 2010; Bernhardt et al., 2012; Cormier et al., 2013). Overall, EPT dominated the drift, with Ephemeroptera comprising the most richness and abundance in larger tributaries, and Plecoptera often dominating richness and abundance

Table 4 Spearman correlation coefficients for monthly mean drift metrics (standardized as concentrations m^{-3} day^{-1}) and reach scale variables (bolded values are $P < 0.05$)

|	Total richness	EPT richness	Ephemeroptera richness	Plecoptera richness	% Ephemeroptera individual	% Plecoptera individual	Total individual	Total biomass
Channel slope	0.08	0.15	0.01	0.36	**−0.60**	0.38	−0.17	0.01
Riffle length	−0.04	−0.04	−0.07	−0.07	−0.09	−0.05	−0.13	0.26
Net velocity	−0.24	−0.15	−0.31	−0.41	**0.53**	**−0.57**	**0.55**	0.36
pH	0.01	0.02	−0.02	−0.13	**0.48**	**−0.48**	0.32	0.29
% Boulder	−0.32	−0.35	−0.25	−0.37	0.09	−0.40	0.09	−0.02
% Cobble	−0.01	−0.05	0.01	−0.01	−0.32	−0.01	0.04	−0.42
% Coarse gravel	−0.30	−0.23	−0.35	−0.30	0.33	−0.18	−0.22	0.12
% Fine gravel	0.21	0.17	0.27	0.18	0.16	0.05	0.08	0.31
% Sand	0.14	0.18	0.07	0.04	0.23	0.00	0.15	0.37
% Wood	−0.07	−0.07	0.00	0.00	0.19	0.26	−0.07	−0.13
Catchment area	**−0.63**	**−0.67**	**−0.52**	**−0.92**	**0.85**	**−0.75**	−0.09	0.05

Catchment area coefficients provided for comparison

in the smaller tributaries (but this varied by sample month). Since EPT (particularly mayfly richness and abundance) are typically reduced in mining-impacted streams throughout the region (e.g., Pond et al., 2008; Timpano et al., 2015), our finding has potential implications on the importance of intact tributaries to biodiversity and conservation of receiving streams (Pond et al., 2014). Daily export of EPT taxa was strongly related to catchment area and month while the opposite was found for EPT taxon concentrations where smaller steams produced higher monthly richness per volume of water. This was also supported by negative Spearman coefficients for all richness metrics (standardized by daily discharge) confirming that on average, taxa were more concentrated in the water column of smaller tributaries. We also found that catchment area was highly correlated with the relative abundance of drifting Ephemeroptera (positively) and Plecoptera (negatively) indicating unique patterns in the presence (and transport) of these orders based on catchment area.

The shift in dominance (by abundance) over the months studied was related to phenology (e.g., responding to water temperature and increasing photoperiod) as some taxa were either emerging as adults, or were new to the site as early instar hatchlings. Dominance among Ephemeroptera shifted from Ephemerellidae (*Ephemerella*, *Drunella* Needham, 1905, *Eurylophella* Tiensuu, 1935) in February–March, to Baetidae (mostly *Baetis*, *Acentrella* Bengtsson 1912, *Procloeon* Bengtsson 1915) in April–May suggesting shifts in emergence, egg hatch, or larval activity. Another phenological observation was the large numbers of drifting blackflies (Simuliidae, mostly *Prosimulium* and *Stegopterna* Enderlein, 1930) found in February and March samples, but significantly declined by April and May. These compositional changes were illustrated in the NMDS ordination where distinctive clusters of site assemblages were arranged by month. Assemblage composition at smaller sites was more variable than at large sites, suggesting that stream size (even at this fine scale) was a key controlling factor on invertebrate drift. Overall, this catchment area influence overrode detection of other factors (i.e., local habitat variables weakly affected drift measures within the range of natural stream types in our study). In a separate study, seasonal and stream size factors in other headwater

Fig. 6 Distance–decay relationship between average Bray–Curtis (BC) dissimilarity and Jaccard's dissimilarity (February, March, and April drift samples) with network distance and catchment area (for comparison). Dissimilarities are based on comparisons of each site with upper Clemons Fork site (the largest and most distant site in the network used here as a gradient anchor site). All *trend lines* based on linear regressions
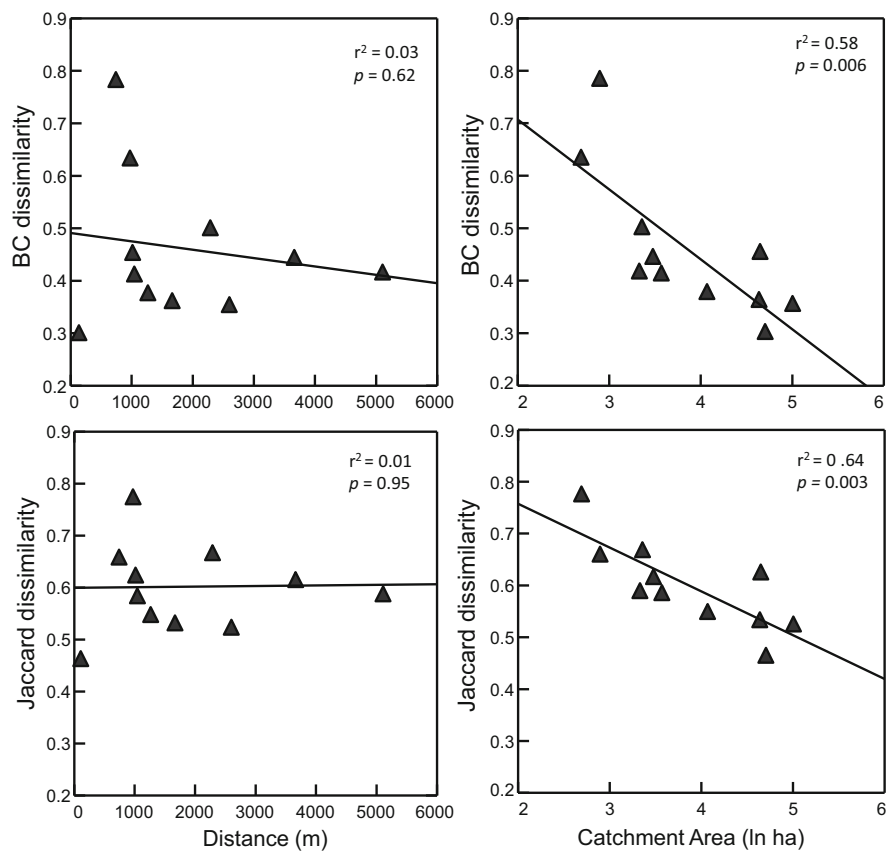
tributaries of Clemons Fork were found to be important indicators of benthic assemblages (Grubbs, 2011), particularly between the months of February and May.

Spatial proximity of tributaries did not influence overall assemblage structure as commonly found in some distance–decay studies (e.g., Thompson & Townsend, 2006; Rouquette et al., 2013; Cañedo-Argüelles et al., 2015). In Appalachian streams of Maryland, Brown & Swan (2010) compared invertebrate communities from headwater tributary and mainstem sites and found that within the headwater sites, community similarity was mostly driven by local environmental factors, not spatial distance. In contrast, mainstem site similarities exhibited both environmental and distance-related responses, indicating that dispersal (from upstream and downstream sources) also drives community structure in mainstems. Although our study did not compare assemblages in tributaries with those in the mainstem Clemons Fork, but we acknowledge that Brown & Swan (2010) describes a phenomenon that likely occurs in our study

area but requires further testing. In large-scale assessments (i.e., across wide geographic distances), proximity is often a strong driver of community structure with high taxa turnover rates over wide spatial gradients (Cañedo-Argüelles et al., 2015). Our study was confined to a relatively small stream network and this may have limited our ability to detect a distance–decay relationship. Further research should be done to integrate drift and benthic datasets to understand metacommunity dynamics.

Implications of drift contributions to receiving streams

Certainly, tributaries (whether polluted or unpolluted) contribute to the structure and function of their receiving waters (Benda et al., 2004; Meyer et al., 2007; Altermatt, 2013). From a vertebrate food resource perspective, the tributaries in the present study provided invertebrate biomass estimates roughly similar to headwater streams in the Southern

Appalachians (O'Hop & Wallace, 1983; Siler et al., 2001), Alaska (Wipfli & Gregovich, 2002), and British Columbia (Leung et al., 2009). From a bioassessment perspective, constant localized drift supplies from intervening unimpaired streams at baseflow (and with punctuated increases during storm events) could also confound detection and identification of stressors using invertebrate indicators observed in receiving streams (e.g., where chemically or physically impacted segments temporarily harbor sensitive colonizers that would otherwise be extirpated). These source populations might be transient, where impacted receiving streams exist as sinks supported only by immigrations from unimpacted tributaries (e.g., Pulliam, 1988). Pond et al. (2014) detected improved bioassessment scores when upstream forested tributaries were present, despite ongoing mainstem water quality problems (from coal mining); the authors called for studies to examine the longitudinal influence of intact tributaries on recruitment in degraded receiving streams. From a downstream recruitment perspective, the design of restoration projects should consider connectivity to sources of colonists. In the Appalachian coal mining region where headwater streams are directly damaged, compensatory mitigation is legally required to offset ecological losses of impacted reaches, but little attention has been given to recruitment sources. Parkyn & Smith (2011), Merovich et al. (2013), and Tonkin et al. (2014) each alluded to the importance of spatial proximity and accounting for dispersal constraints in restoration and recovery scenarios.

While our results demonstrate that sensitive invertebrate colonizers are readily exported from unimpaired tributaries, previous studies on the direct influence that tributaries have on receiving streams reported mixed results. In Pennsylvania, the influence by a tributary on large river assemblages was attributed to direct (drift) and indirect (habitat) mass effects (Wilson & McTammany, 2014). In Germany, forested tributaries supplied sensitive taxa to agricultural reaches (although pesticide exposures were high enough to extirpate those taxa downstream) and that the length of forested streams (e.g., catchment area) was a key factor (Orlinskiy et al., 2015). In contrast, assumed inputs from tributaries did not always affect composition of receiving streams in Brazil, although this was highly dependent on the tributary to mainstem size ratio (Milesi & Melo, 2014). Similarly, MacNally

et al. (2011) did not find substantial biological difference between tributaries and mainstems in Australia. A limitation of these two no-effect comparisons is that the studies were done in relatively undisturbed catchments (and with a potentially larger species pool); further studies are necessary to determine the influence of dispersing invertebrates from intact tributaries on downstream assemblages versus more degraded tributaries, or where tributaries supply streams of highly different character with novel taxa (e.g., as seen with glacial streams in Knispel & Castella, 2003; limestone streams in Hellmann et al., 2015). While these scenarios suggest inconsistencies on the direct influence of tributary exports, we believe methodological improvements that combine drift, benthic sampling, block-netting, and stable isotope labeling techniques would be insightful.

It is critical to understand network–dispersal relationships particularly in the Central Appalachians where large-scale upland land disturbance routinely impacts the biological integrity of downstream waters. Failing restoration attempts (e.g., Palmer & Hondula, 2014) could be tied to a lack of direct sources of drifting colonists from undisturbed tributaries (Parkyn & Smith, 2011), given that adult flight-based dispersal between catchments might not be effective for recolonization (Griffith et al., 1998; Frieden et al., 2014). In a review of stream mitigation/restoration data sets from the mountaintop mining region (KY, VA, WV), Palmer & Hondula (2014) documented poor recovery of macroinvertebrate assemblages tied mostly to lingering poor water quality. A network based meta-analysis on those mitigation projects might be fruitful in discerning whether lack of upstream sources of drifting colonists were partially responsible.

Conclusions

Results presented here provide evidence that small Appalachian tributaries can supply a relatively diverse and abundant suite of taxa to receiving streams during spring-time baseflow conditions. From a regulatory perspective where water quality compliance, biological integrity, and stream restoration are required under environmental laws, we believe that the spatial and temporal contribution of organisms and other materials from intervening tributary streams must be considered. Since catchment area and month

structured invertebrate and organic matter exports, these filters should be used as guides to predict tributary influences on exports as they relate to energy subsidies, recolonization of restored areas, maintaining local biodiversity, and explaining bioassessment results in receiving streams. Additional drift and dispersal datasets (in conjunction with benthic data) from the region are necessary to also assist in explaining taxon extirpation risks and to be used in designing successful restoration projects where recruitment is a key limiting factor.

Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

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