Spatial drivers of ecosystem structure and function in a floodplain riverscape: springbrook nutrient dynamics

Samantha K. Caldwell[1,4], Marc Peipoch[2,5], and H. Maurice Valett[3,6]

[1]University of Montana, Flathead Lake Biological Station, 32125 Bio Station Lane, Polson, Montana 59860 USA
[2]Centre d'Estudis Avançats de Blanes (CSIC), Accés a la Cala Sant Francesc 14, Blanes E-17300, Girona, Spain
[3]University of Montana, Flathead Lake Biological Station, 32125 Bio Station Lane, Polson, Montana 59860 USA

Abstract: On riverine flood plains, reorganization by fluvial processes creates and maintains a mosaic of aquatic and riparian landscape elements across a biophysical gradient of disturbance and succession. Across flood plains of gravel-bottom rivers, spring brooks emerge from points of groundwater discharge that may occur in distinct landscape positions. We investigated how ecosystem processes in spring brooks differ spatially across biophysical zones, reflecting how landscape position dictates severity of flood disturbance, allochthonous loading from riparian forests, and inputs from groundwater systems. Between July and October 2011, we quantified aspects of ecosystem structure and function among 6 spring brooks of the Nyack flood plain, Flathead River, Montana. Structural features varied predictably across near-channel (i.e., parafluvial) and late successional (i.e., orthofluvial) biophysical zones. Large wood standing stocks increased >40× (0.19–9.19 kg/m^2), dominant particle size class differed by an order of magnitude (median particle size [D_{50}] = 2–27), and measures of vertical hydraulic gradient (−0.06 to +0.12 cm/cm) reflected differences in landscape position. We found fine sediment accumulation, stronger groundwater inputs, and greater benthic and large wood standing stocks in orthofluvial than in parafluvial spring brooks. Algal biomass was negatively correlated with insolation and positively related to vertical hydraulic gradient. Results from microcosm experiments showed increasing N uptake across the gradient from parafluvial to orthofluvial spring brooks. Functional response to landscape-scale organization of spring-brook structure underscores the need for a spatially explicit model of floodplain ecology.
Key words: riverscape, landscape mosaic, flood plain, streams, nitrogen uptake

Ecologists have long suggested that ecosystem functioning is organized by environmental structure, a paradigm in which pattern dictates process (Hutchinson 1953, Vannote et al. 1980, Montgomery 1999, Sponseller and Fisher 2006). At the landscape scale, organisms and processes respond to patterns of spatiotemporal heterogeneity in dynamic habitat templates (Winemiller et al. 2010). Research relating landscape patterns to variation in ecosystem processes is emerging as a fusion of landscape and ecosystem ecology and is critical to elucidating spatial fluxes of materials and energy among integrated systems (Turner 2005, Fisher et al. 2007).

Disturbances maintain the spatial heterogeneity of landscapes (Paine and Levin 1981) by periodically restructuring ecosystems (Whited et al. 2007) and altering function at different hierarchical scales (Fisher et al. 1982, Pickett et al. 1989). Large-scale geomorphic processes generate mosaics of distinct spatial units (i.e., patches) that are dynamically related to one another and the surrounding matrix (Naiman et al. 1988, Pickett et al. 1989, Montgomery 1999). Local controls and exchanges across patch boundaries may fundamentally influence processes taking place in adjacent ecological systems (Naiman et al. 1988) and dictate patch dynamics (Pickett and White 1985). On landscapes where location influences exposure to disturbance, patches will exist in a range of seral stages, and exchanges across boundaries may be important during different phases of development.

Floodplain landscapes and the shifting habitat mosaic

Riverine flood plains are spatially and temporally dynamic landscapes (Arscott et al. 2002, Stanford et al. 2005)

characterized by variation along longitudinal (fluvial transport), lateral (erosion, sedimentation, and seral development), and vertical (subsurface exchange and interstitial flow) dimensions. Extensive restructuring and regeneration of floodplain habitats occur during years with large-magnitude floods and greater frequencies of moderate floods (Whited et al. 2007). Regular hydrologic disturbance, fluvial reorganization, and ecosystem processes maintain the overall abundance of aquatic, semiaquatic, and riparian landscape elements and create a 'shifting habitat mosaic' (Stanford et al. 2005), but at larger scales, organization emerges as distinct biophysical zones that differ in fundamental ways (Stanford et al. 2005, Whited et al. 2007, Fellman et al. 2013).

Parafluvial environments are floodplain biophysical zones near the river's channel that experience scour, cut-and-fill processes of erosion, sediment transport, and bedload deposition during annual floods (Lorang and Hauer 2006). Following sediment accumulation, pioneer species, such as cottonwood (*Populus* spp.) and willow (*Salix* spp.), become established in parafluvial zones and initiate pioneering stages of succession such that all successional features found on flood plains were originally formed in the parafluvial zone (Lorang and Hauer 2006).

Transition to later successional stages drives the emergence of the orthofluvial biophysical zone, a depositional area lacking widespread scouring flows where inundation may act as a resource subsidy (Megonigal et al. 1997) supporting advanced-stage regeneration and mature-stage plant succession (Lorang and Hauer 2006). Orthofluvial zones may be further classified as active or passive based on rate of accretion, frequency of inundation by annual floodwaters, depth of soils, and microtopography. Active orthofluvial zones are rapidly enlarging areas of accretion with primarily thin, organic-matter-poor, well-drained soils typically dominated by mid- to late-stage successional riparian forests or wet meadows (Stanford et al. 2005, Lorang and Hauer 2006). Eventual establishment of mature gallery forests that potentially include cottonwood (*Populus trichocarpa*), red alder (*Alnus incana*), Douglas fir (*Pseudotsuga menziesii*), and spruce (*Picea* spp.) occurs in passive orthofluvial zones where scour is infrequent, accretion is slower, and soils are deep and organically enriched.

Vertical hydraulic exchange between alluvial aquifers and surface water contributes to floodplain heterogeneity (Acuña and Tockner 2009) and sustains aquatic systems not connected to the river via surface channels. These spring brooks are flowing-water ecosystems formed by focused groundwater discharge within flood channels and may be seasonally intermittent or persist throughout the baseflow period (Stanford and Ward 1993). Spring brooks in the parafluvial zone are frequently reworked by floods, and during base flow, are fed by shallow groundwater return (e.g., Harvey and Bencala 1993) with short flow paths. Spring brooks emerging in paleochannels of the orthofluvial zone are reworked only by infrequent large floods, but are regularly inundated by annual flood waters (Stanford et al. 2005).

The influence of structural drivers on stream functioning has been investigated in the context of river continua (Vannote et al. 1980, Minshall et al. 1983), but this relationship remains largely unexplored among dynamic, heterogeneous components of floodplain landscapes. Across flood plains of montane gravel-bottom rivers, litterfall and annual loading of C, N, and P increase along the vegetation chronosequence, reach maxima in old-growth, mixed conifer–*Populus* stands (50–100 y), and decrease dramatically in old-growth (>100–175 y) conifer stands (Anderson 2008). Floodplain streams are embedded in terrestrial systems of various seral stages and disturbance frequency, so flowing-water systems encounter a diversity of patches and, therefore, should experience variation in types and magnitudes of exchanges (Naiman et al. 1988). To address how ecosystem structure and function are related to landscape position (i.e., biophysical zone), we focused on how floodplain succession and exchanges with adjacent systems organize spring brooks distributed along a biophysical gradient of disturbance on the Nyack flood plain, Middle Fork Flathead River, Montana, USA. We used a combination of whole-system and patch-level assessments (Carpenter 1989) relating structural measures, proxies of exchange and disturbance, and measures of nutrient uptake in spring brooks of parafluvial, active orthofluvial, and passive orthofluvial biophysical zones.

METHODS
Study site
The Nyack flood plain is a long-term research site on the Middle Fork Flathead River in northwestern Montana. This 5th-order river forms the southern boundary of Glacier National Park in northwestern Montana and drains 3000 km^2 of mostly forested catchment including portions of the Bob Marshall and Great Bear Wilderness areas. Peak annual discharge occurs in spring (May–June) and averages 541 m^3/s. Baseflow conditions average 17 m^3/s and occur during winter (December–January; Whited et al. 2007). The flood plain is ~10 km long, 1 to 2 km wide, and bounded by bedrock canyon walls at each end forming knickpoints. The anastomosed river is strongly connected to an alluvial aquifer that extends from valley wall to valley wall (Stanford and Ward 1993). A heterogeneous mixture of alluvial cobble, gravel, and sand fill exists atop layers of sand and clay and generates variability in aquifer hydraulic conductivity (1–1000 m/d; mean = 400 m/d) and diversification of groundwater flow paths through porous bed materials (Diehl 2004).

Springbrook channel structure and benthic biomass
From July to October 2011, we gathered structural and hydraulic data from 6 spring brooks distributed across parafluvial (PF1 and PF2), active orthofluvial (AO1 and AO2), and passive orthofluvial (PO1 and PO2) biophysical

zones. We selected sites based on a qualitative assessment of proximity to the main channel, riparian vegetation, and soil development.

We established transects (n = 7–10/site) along study reaches (75–100 m long) to measure morphometric features (e.g., water depth, wetted-channel widths). We measured photosynthetically active radiation (PAR; photon flux density, µmol m^{-2} s^{-1}, n = 3 points/transect) with a LI-190 quantum sensor (LI-COR Inc., Lincoln, Nebraska) and % riparian canopy cover (n = 4 measures/transect) with a concave spherical canopy densitometer (Lemmon 1956). To characterize streambed composition, we used a modified Wolman pebble count to calculate the proportion of inorganic particles (≥200/site) belonging to Wentworth size classifications and calculated the median, 16th, and 84th percentiles of particle diameter (D$_{50}$, D$_{16}$, D$_{84}$, respectively; Bevenger and King 1995).

We quantified standing stocks of large woody debris (kg/m^2) with the line-transect method (Wallace and Benke 1984) and included only wood that was entirely or partially submerged and ≥1 cm in diameter. Epixylic biomass and chlorophyll a (chl) standing crop were measured on selected pieces of submerged wood by scraping (4 cm^2, n = 2/piece) and filtering material onto precombusted glass-fiber filters (Whatman GF/F, Whatman International, Maidstone, UK). We split samples and measured epixylic biomass as ash-free dry mass (AFDM, g/m^2; Mulholland et al. 2000) and chl (Tett et al. 1975, 1977). We used hot methanol extraction and a Perkin–Elmer 559 UV-VIS spectrophotometer (Perkin Elmer, Waltham, Massachusetts) to measure chl. We calculated chl:AFDM as a measure of the photoautotrophic component of benthic biomass in each spring brook.

We used an open-ended cylinder (0.01 or 0.04 m^2) to isolate an area of stream bottom for collection of coarse (CPOM; particle size > 1 mm) and fine (FPOM; particle size < 1 mm) particulate organic matter following Mulholland et al. (2000). We collected 2 well mixed FPOM subsamples for AFDM and chl estimation as per epixylic samples. We collected aboveground macroautotrophic biomass from within a 0.25-m^2 frame. Large particulates (e.g., CPOM and macrophytes) were ground after drying, and 3 subsamples were combusted to estimate whole-sample AFDM. We scrubbed the surface of randomly selected cobbles (n = 3–5/transect), and collected 2 well mixed subsamples from the slurry of loosened material (Mulholland et al. 2000) for measurement of epilithic AFDM and chl as described above.

Physical and chemical properties of surface water and ground water

We sampled ground and surface water at the upwelling head of springbrook channels and every 25 m along study reaches. We installed minipiezometers (n = 3/transect) to 50 cm below the streambed surface and measured the vertical hydraulic gradient (VHG) as the difference in hydraulic head pressure (cm) between ground and surface waters divided by depth to perforations (cm; Dahm et al. 2006). At each sampling point, we also measured water temperature (°C), specific conductivity (µS/cm), pH, and dissolved O$_2$ (DO) concentration (mg/L, % saturation) with a YSI meter (model 85; Yellow Springs Instruments, Yellow Springs, Wisconsin).

We collected samples of surface and ground waters for analysis of NH$_4$-N, NO$_3$-N, soluble reactive P (SRP), and dissolved organic C (DOC). We measured concentrations of NH$_4$-N, NO$_3$-N, SRP, and Cl by flow-injection analysis on a Technicon Autoanalyzer II (Technicon, Emeryville, California) using the phenolhypochlorite (Solorzano 1969), Cd–Cu reduction (Wood et al. 1967), molybdate-Sb (Murphy and Riley 1962), and mercuric thiocyanate-ferric nitrate (Zall et al. 1956) methods, respectively. We measured DOC concentrations by high-temperature catalytic oxidation (Sugimura and Suzuki 1988) on a Tekmar-Dohrman Apollo 9000HS Total Organic Carbon Analyzer (Teledyne Tekmar, Mason, Ohio).

NO$_3^-$ uptake: microcosm experiments

We collected replicate samples (n = 16/site) of the dominant sediment size class from one study system of each springbrook type (PF2, AO1, and PO1) with sediment corers driven 20–40 mm into the stream bottom or by randomly selecting cobbles from a representative reach (10–25 m). We transported samples directly to the laboratory, where we drained and replaced springbrook water with filtered water collected from the main stem of the Middle Fork Flathead River. A 3-way factorial design was implemented with the following treatment factors applied to each substrate sample (n = 4 per treatment): 1) landscape position (levels = parafluvial, active orthofluvial, or passive orthofluvial), 2) NO$_3$-N concentration (levels = ambient or high), and 3) DOC (levels = ambient or high). We achieved target high concentrations by spiking samples with sodium nitrate and acetate. We kept samples in an experimental chamber with constant temperature (15°C) and photoperiod (12 h light) for the duration of the experiment. We collected and filtered water samples from each microcosm for analysis of DOC concentration at time 0 and 12 h, and NO$_3$-N concentrations at time 0, 3, 6, 9, and 12 h. Following the experimental period, we processed samples for AFDM as per benthic compartments.

Data analysis

We chose duplicate spring brooks within each landscape position to represent spatial organization on the flood plain. We accommodated limited replication within landscape position with a mixed-model nested analysis of variance (ANOVA) with landscape position as the fixed main factor, and patch as the random nested factor to test for differences in structural measures (e.g., benthic standing stocks, physical, and chemical variables) in spring

brooks among biophysical zones. Patches correspond to transects distributed along study reaches. Results for the patch factor indicate whether response variables differ among transects across the 6 reaches regardless of landscape position. We do not present these results because they are not relevant to our research objectives (sensu Sonoda et al. 2009). If an ANOVA was significant ($p < 0.05$), we used Tukey's Honestly Significant Difference pairwise comparisons of means among landscape positions ($\alpha = 0.05$). When assumptions of normality or homogeneity of variance were violated, we transformed data. To assess differences in sediment particle-size distributions among biophysical zones, we used the Kruskal–Wallis nonparametric test followed by Bonferroni-corrected Mann–Whitney U-tests.

For the microcosm experiment, we calculated uptake rates (U; $\mu g\, m^{-2}\, h^{-1}$) for each replicate as:

$$U = \frac{mV}{A} \qquad \text{(Eq. 1)}$$

where m is the slope ($\mu g\, L^{-1}\, h^{-1}$) derived from linear regressions of NO_3-N concentration vs time, V is sample volume (L), and A is substrate area (m^2). We also calculated U per unit of organic matter (OM) (i.e., mass-specific uptake, $\mu g\, g^{-1}$ AFDM h^{-1}) for each microcosm. We ln(x)-transformed replicate means and compared them with a 3-way ANOVA. After finding that the C-enrichment factor (ambient vs high DOC treatments) had no significant effect on NO_3^- uptake ($p > 0.05$), we combined replicates across experimental units ($n = 8$/treatment) and used a 2-way ANOVA. We used SAS (version 9.3; SAS Institute Inc., Cary, North Carolina) for all analyses.

RESULTS
Springbrook channel and benthic structure

Discharge (23.03–27.03 L/s) and velocity (1.95–5.25 cm/s) differed across spring brooks, but distinct patterns across landscape position were not evident (Table 1). Channel depth and width were lowest in parafluvial zones and increased over active and passive orthofluvial zones. PAR declined by an order of magnitude across biophysical zones (Table 1). It was greatest in parafluvial, intermediate in active orthofluvial, and least in passive orthofluvial spring brooks. Percent vegetative canopy cover followed the opposite pattern and drove the decline in PAR among sites ($R^2 = 0.84$, $p = 0.009$, $n = 6$, PAR vs arcsin√[% canopy]). Mean insolation in passive orthofluvial zones was 20% of incident light recorded in portions of the parafluvial zone where vegetative canopy cover was absent.

D_{50} decreased from parafluvial to orthofluvial zones (Table 1), and mean rank scores for particle size distributions differed significantly across sites ($H = 276.14$, df = 2, $p < 0.0001$). Passive orthofluvial spring brooks were characterized by a right-skewed distribution with high relative abundance (45–95%) of fine-grained sediments (<2 mm). In contrast, parafluvial spring brooks were dominated (64–74%) by large-grained sediments (8–64 mm). Active orthofluvial sites were similar to either passive orthofluvial or parafluvial spring brooks. AO1 was dominated by fine-grained sediments (<2 mm, 66%), whereas the stream bed of AO2 was composed primarily of large-grained sediments (8–64 mm, 70%).

Large wood standing stocks differed ≥40-fold (0.19–9.19 kg/m^2) among sites, with greatest stocks in passive orthofluvial zones and lowest in parafluvial zones (Table 2). Standing stocks in PO2 (13.51 kg/m^2) were >3× the next greatest value (e.g., 3.9 kg/m^2 in AO2). Total wood volume in passive orthofluvial spring brooks was more than an order of magnitude greater than in parafluvial spring brooks and varied significantly among sites. Epixylic OM and chl standing stocks were greater in passive orthofluvial than in parafluvial and active orthofluvial zones, corresponding to greater availability of substrate (Table 2). Similarly, epilithic OM and chl standing stocks generally increased from parafluvial to orthofluvial zones (Table 2). OM and algal standing stocks were 5 to 10× greater in spring brooks of passive orthofluvial than of parafluvial zones. Active orthofluvial spring brooks had epilithic standing stocks intermediate to passive orthofluvial and parafluvial sites (Table 2). Very low epilithic OM and chl standing stocks were detected in PO2 where epilithic surfaces were found embedded among dominant substrate of very small size (95% of bed particles <2 mm).

Standing stocks of FPOM within spring brooks increased by more than an order of magnitude from parafluvial to orthofluvial zones ($p < 0.0001$; Table 2). In addition, greatest chl standing crops were associated with FPOM (Table 2). Specifically, mean FPOM standing stock was greatest in passive orthofluvial spring brooks, and algal standing stocks associated with FPOM were more than an order of magnitude greater than in other zones. An even larger gradient characterized distribution of CPOM across the biophysical zones where standing stocks differed by 2 orders of magnitude (Table 2). Greatest CPOM standing stocks occurred in spring brooks of passive orthofluvial zones where stocks were 1 to 2 orders of magnitude greater than in parafluvial and active orthofluvial zones (Table 2). Aquatic macrophytes were uncommon in spring brooks, but standing crop was greatest in passive orthofluvial, intermediate in active orthofluvial, and least in parafluvial zones (Table 2).

OM standing stocks generally increased from parafluvial to orthofluvial zones, but individual compartments contributed differentially to the magnitude of total standing stocks (Table 2). Autotrophic biomass made up a small proportion of total OM and chl:AFDM ratios were low (0.0011–0.0018). At the same time, chl standing crops (combined epixylic, epilithic, and FPOM) increased exponentially

Table 1. Mean (±1 SE) values of streambed and stream characteristics, insolation, and % canopy cover in spring brooks of parafluvial (PF), active orthofluvial (AO), and passive orthofluvial (PO) zones on the Nyack flood plain. D-values represent 16th, 50th, and 84th percentiles of sediment particle diameters. p-values are associated with Kruskal–Wallis or nested analysis of variance test results among zones. Means with the same superscripts within a row are not statistically different (Tukey's Honestly Significantly Difference, $\alpha = 0.05$). Nonnormally distributed data were transformed for statistical analysis, but data shown are actual values for all variables. PAR = photosynthetically active radiation.

| | Landscape position | | | |
Reach characteristics	PF	AO	PO	p
Stream characteristics				
Discharge (L/s)	23.93 ± 19.49	23.03 ± 5.19	27.03 ± 3.11	
Velocity (cm/s)	5.25 ± 2.70	5.00 ± 3.36	1.95 ± 0.07	
Wetted width (m)	0.53 ± 0.04[B]	0.76 ± 0.04[A]	0.81 ± 0.04[A]	<0.0001
Depth (cm)	10.8 ± 1.5[B]	15.3 ± 3.6[B]	26.6 ± 2.7[A]	0.0015
Insolation and canopy cover				
PAR photon flux density (μmol m^{-2} s^{-1})	1303.7 ± 43.7[A]	676.5 ± 100.3[B]	256.8 ± 66.1[C]	<0.0001
Vegetative canopy cover (%)	1.2 ± 0.8[C]	11.2 ± 3.3[B]	35.6 ± 5.3[A]	<0.0001
Streambed particle size distribution				
D_{16}	8	<2	<2	
D_{50}	27	19	<2	
D_{84}	60	50	25	

Table 2. Mean (±1 SE) benthic standing stocks in spring brooks of parafluvial (PF), active orthofluvial (AO), and passive orthofluvial (PO) zones on the Nyack flood plain. p-values are associated with nested analysis of variance test results among zones. Means with the same superscripts within a row are not statistically different (Tukey's Honestly Significant Difference, $\alpha = 0.05$). Nonnormally distributed data were transformed for statistical analysis, but data shown are actual values for all variables. AFDM = ash-free dry mass, FPOM = fine particulate organic matter, CPOM = coarse particulate organic matter.

| | Landscape position and site number | | | |
Benthic characteristics	PF	AO	PO	p
Large woody debris				
Wood mass (kg/m^2)	0.191 ± 0.160[B]	2.043 ± 1.046[B]	9.187 ± 1.750[A]	<0.0001
Wood volume (m^3/m^2)	0.0005 ± 0.0004[B]	0.0054 ± 0.0027[B]	0.0245 ± 0.0047[A]	<0.0001
Epixylon				
AFDM (g/m^2)	1.5 ± 0.7[B]	2.8 ± 1.0[B]	28.8 ± 15.3[A]	<0.0001
Chlorophyll a (mg/m^2)	2.0 ± 1.6[B]	0.9 ± 0.4[B]	7.3 ± 1.9[A]	<0.0001
Epilithon				
AFDM (g/m^2)	2.8 ± 0.6[B]	5.9 ± 0.7[B]	28.8 ± 9.3[A]	0.0002
Chlorophyll a (mg/m^2)	2.1 ± 0.7[B]	4.0 ± 0.7[B]	24.2 ± 7.3[A]	<0.0001
FPOM				
AFDM (g/m^2)	13.0 ± 1.7[B]	117.4 ± 41.5[B]	454.6 ± 99.5[A]	<0.0001
Chlorophyll a (mg/m^2)	3.7 ± 0.7[B]	11.2 ± 4.6[B]	211.4 ± 54.5[A]	<0.0001
CPOM				
AFDM (g/m^2)	7.4 ± 5.0[B]	76.5 ± 39.6[B]	738.5 ± 223.9[A]	<0.0001
Macrophytes (g/m^2)	0[B]	0.2 ± 0.1[AB]	2.7 ± 1.4[A]	0.0024
Chlorophyll a:AFDM	0.0011 ± 0.0002	0.0012 ± 0.0001	0.0018 ± 0.0003	0.089

with decreasing light availability (i.e., were negatively related to PAR, R^2 = 0.92, p = 0.0024, n = 6) from parafluvial to passive orthofluvial settings.

Physical and chemical characteristics of spring brooks

All spring brooks originated from points of groundwater discharge (i.e., VHG was positive at the head of each channel). In orthofluvial environments, spring brooks were predominantly gaining systems (i.e., with positive VHGs of high magnitude), whereas parafluvial systems were characterized either by reduced magnitude of upwelling or by broadly distributed downwelling (Fig. 1). Among spring brooks mean algal standing crop (as chl) averaged across substrate types was positively related to mean VHG, but this relationship was not significant (R^2 = 0.52, p = 0.1058, n = 6), primarily reflecting small sample size.

In general, physiochemical features of springbrook ground water and surface water (i.e., temperature, specific conductivity, pH, and DO) differed among sites (Table 3), but did not group predictably with landscape position. DO in ground and surface water varied from 2.6–5.6 mg/L in spring brooks among landscape positions and was of low % saturation (23.7–48.2%). Surface-water DO was similar among biophysical zones. In contrast, surface- and groundwater temperatures were highest in spring brooks of parafluvial, intermediate in active orthofluvial, and lowest in passive orthofluvial zones (Table 3).

DOC and inorganic nutrient concentrations were consistently low across sites and water types, and varied among biophysical zones (Table 4). DOC concentrations in ground
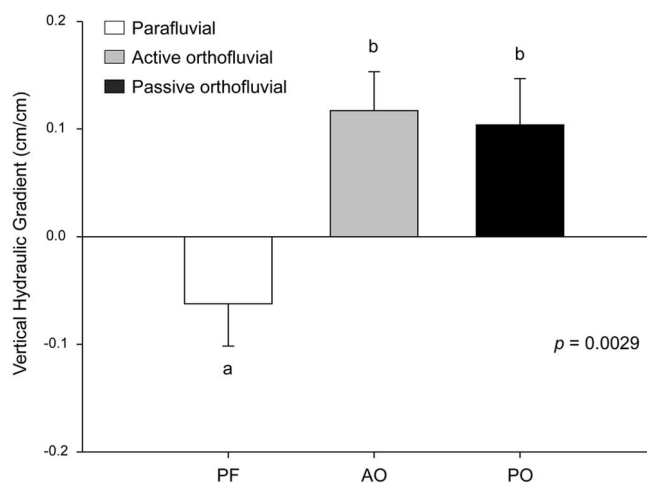

Figure 1. Mean (±1 SE) vertical hydraulic gradient (VHG) measured in parafluvial (PF), active orthofluvial (AO), and passive orthofluvial (PO) biophysical zones. Positive values are upwelling; negative values are downwelling. The p-value represents nested analysis of variance test results among zones. Bars with the same letter are not significantly different (Tukey's Honestly Significant Difference, α = 0.05).

water were greatest in passive orthofluvial spring brooks and similarly low among other zones (Table 4). Surface-water DOC concentrations were nearly 2× greater in passive than in active orthofluvial spring brooks. Surface water in parafluvial spring brooks had intermediate DOC concentrations (Table 4). NH_4-N concentrations in surface and ground water were near detection limits (2.5 µg/L), but were greater in ground water of passive orthofluvial spring brooks. NO_3-N concentrations in surface water were <25 µg/L across zones and <40 µg/L in ground water. Surface and subsurface waters were effectively void of SRP with concentrations only slightly higher than detection limits (1 µg/L). Mean atomic N : P ratios primarily reflected variation in NO_3-N concentration and ranged from 6.5–14.2 in surface water and 10.1–30.4 in ground water. Atomic N : P ratios in ground water were highest in passive orthofluvial, intermediate in active orthofluvial, and lowest in parafluvial spring brooks. A similar trend among landscape positions was detected for N : P ratios in surface waters, but significant differences were detected only by pairwise comparisons between passive orthofluvial and parafluvial spring brooks (Table 4).

NO_3^- uptake: microcosm experiment

Across all treatment combinations, C amendment had no influence (C main effect, p = 0.6606) on response variables or significant interaction (p > 0.05) with other factors. Accordingly, replicates were combined across C treatments (n = 8) to assess the influence of N enrichment. Mean values (±1 SE) of uptake normalized to OM standing stocks ($\mu g\ N\ g^{-1}\ AFDM\ h^{-1}$) varied 3 orders of magnitude across treatment groups and differed significantly as a result of landscape position (p < 0.0001) and NO_3-N amendment (p < 0.0001). With ambient N availability, mass-specific uptake differed significantly across landscape positions (Tukey's HSD, p < 0.0001; Fig. 2A). Rates declined from a maximum of 24.1 ± 2.9 $\mu g\ N\ g^{-1}\ AFDM\ h^{-1}$ for parafluvial sediments to 1.7 ± 0.2 $\mu g\ N\ g^{-1}\ AFDM\ h^{-1}$ for the active orthofluvial spring brook to even lower rates for passive orthofluvial sediments (0.5 ± 0.04 $\mu g^{-1}\ N\ g^{-1}\ AFDM\ h^{-1}$). NO_3-N enrichment increased mass-specific uptake rates robustly across all sites, but the magnitude of increase differed with landscape position (i.e., significant N × landscape position interaction, p = 0.0041). Under N enrichment, uptake was maximal in the parafluvial spring brook (516.1 ± 89.1 $\mu g\ N\ g^{-1}\ AFDM\ h^{-1}$) where rates increased >20× over ambient conditions. Enrichment increased uptake by sediments from active and passive orthofluvial spring brooks by 8 and 10×, respectively, compared to ambient rates, but mass-specific uptake did not differ significantly between types of orthofluvial streams (Fig. 2A).

In contrast to mass-specific rates, areal rates indicated greatest uptake by passive orthofluvial sediments (Fig. 2B). Mean values (±1 SE) of areal uptake ($\mu g\ N\ m^{-2}\ h^{-1}$) ranged

Table 3. Mean (±1 SE) physiochemical properties of surface and ground water in spring brooks of parafluvial (PO), active orthofluvial (AO), and passive orthofluvial (PO) zones on the Nyack flood plain. p-values are associated with nested analysis of variance test results among zones. Means with the same superscripts within a row are not statistically different (Tukey's Honestly Significant Difference, α = 0.05). Nonnormally distributed data were transformed for statistical analysis, but data shown are actual values for all variables.

	Landscape position			
Water type and variable	PF	AO	PO	p
Surface water				
Temperature (°C)	13.8 ± 0.8[A]	10.5 ± 0.6[B]	8.7 ± 0.3[B]	<0.0001
Specific conductivity (µS/cm)	208.5 ± 2.3[B]	234.1 ± 3.5[A]	208.6 ± 8.5[B]	<0.0001
pH	7.56 ± 0.17[B]	8.03 ± 0.02[A]	7.56 ± 0.19[B]	<0.0001
Dissolved O_2 (mg/L)	5.1 ± 0.4	4.5 ± 0.4	5.6 ± 0.4	0.2861
Dissolved O_2 (% saturation)	46.6 ± 2.9	39.5 ± 4.0	48.2 ± 3.0	0.3646
Ground water				
Temperature (°C)	13.6 ± 0.6[A]	10.8 ± 0.6[B]	9.0 ± 0.4[B]	<0.0001
Specific conductivity (µS/cm)	202.8 ± 4.3[B]	238.2 ± 6.5[A]	259.6 ± 23.8[A]	0.018
pH	7.56 ± 0.18[B]	7.99 ± 0.04[A]	7.54 ± 0.20[B]	<0.0001
Dissolved O_2 (mg/L)	4.4 ± 0.4[A]	2.6 ± 0.4[B]	4.1 ± 0.6[A]	0.025
Dissolved O_2 (% saturation)	41.9 ± 3.4[A]	23.7 ± 3.5[B]	35.8 ± 5.3[AB]	0.0067

over 2 orders of magnitude across treatment groups and differed as a result of landscape position ($p < 0.0001$) and NO_3-N amendment ($p < 0.0001$). Similar to results for mass-specific uptake, the influence of NO_3-N amendment on areal uptake depended upon landscape position (i.e., significant N × landscape position interaction, $p < 0.0001$). Rates of areal uptake under ambient NO_3-N treatment were greater for passive (140.1 ± 3.8 µg N m^{-2} h^{-1}) and active (98.1 ± 12.0 µg N m^{-2} h^{-1}) orthofluvial than for parafluvial (38.4 ± 3.3 µg N m^{-2} h^{-1}) sediments (Fig. 2B). Regardless of landscape position, N enrichment significantly increased areal uptake rates (i.e., N enrichment main effect, $p < 0.0001$), and areal uptake rates by passive orthofluvial substrates (2476.4 ± 399.7 µg N m^{-2} h^{-1}) were significantly

Table 4. Mean (±1 SE) chemical properties of surface and ground water in spring brooks of parafluvial (PF), active orthofluvial (AO), and passive orthofluvial (PO) zones on the Nyack flood plain. N:P ratios were calculated as the mean of sample total inorganic N (NO_3-N + NH_4-N):soluble reactive P (SRP) concentration. p-values are associated with nested analysis of variance test results among zones. Means with the same superscripts within a row are not statistically different (Tukey's Honestly Significant Difference, α = 0.05). Nonnormally distributed data were transformed for statistical analysis, but data shown are actual values for all variables.

|	Landscape position			
Water type and analyte	PF	AO	PO	p
Surface water				
Dissolved organic C (mg/L)	0.51 ± 0.04[AB]	0.38 ± 0.04[B]	0.63 ± 0.07[A]	0.0004
NH_4-N (µg/L)	<2.5	<2.5	4.6 ± 1.7	0.1422
NO_3-N (µg/L)	10.4 ± 0.6[B]	17.9 ± 3.3[AB]	23.9 ± 2.2[A]	0.0004
SRP (µg/L)	1.6 ± 0.2	1.2 ± 0.2	1.1 ± 0.2	0.1473
Atomic N:P	6.5 ± 0.3[B]	10.2 ± 1.6[AB]	14.2 ± 1.5[A]	0.0008
Ground water				
Dissolved organic C (mg/L)	0.45 ± 0.03[B]	0.42 ± 0.07[B]	0.97 ± 0.25[A]	<0.0001
NH_4-N (µg/L)	<2.5[B]	13.2 ± 7.2[A]	21.1 ± 8.3[A]	0.003
NO_3-N (µg/L)	17.7 ± 2.9	26.1 ± 8.0	39.7 ± 10.0	0.3189
SRP (µg/L)	1.9 ± 0.3	1.3 ± 0.2	1.9 ± 0.5	0.2879
Atomic N:P	10.1 ± 1.5[C]	19.7 ± 4.1[B]	30.4 ± 4.3[A]	0.0318
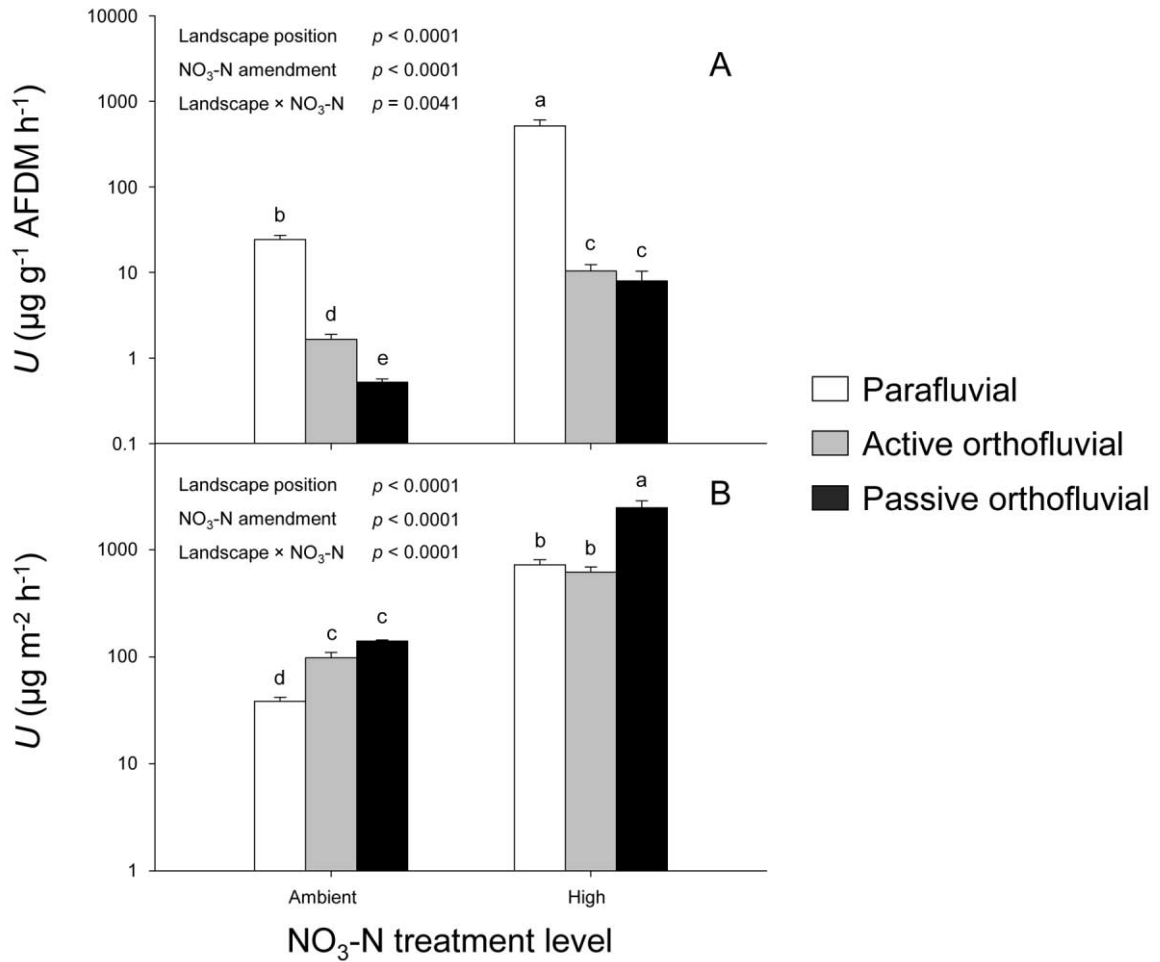
Figure 2. Mean (±1 SE) mass-specific (A) and areal (B) NO_3-N uptake rates (U) in response to ambient and high NO_3-N treatment levels. Substrates were collected from parafluvial, active orthofluvial, and passive orthofluvial spring brooks. The p-values represent 2-way analysis of variance test results for treatments and their interaction. Bars with the same letter are not significantly different (Tukey's Honestly Significant Difference, α = 0.05). AFDM = ash-free dry mass.

greater than those recorded for parafluvial (722.1 ± 83.8 µg N m^{-2} h^{-1}) or active orthofluvial (618.6 ± 71.8 µg N m^{-2} h^{-1}) substrates (Fig. 2B).

DISCUSSION

Springbrook structure varied across the flood plain reflecting large-scale organization (i.e., fluvial transport and material supply) and local (i.e., patch-driven) controls depending on landscape position. Spring brooks emerging in parafluvial zones were characterized by gravel-bottom stream beds, less groundwater input, little canopy cover, and sparse benthic standing stocks. Fine sediment accumulation, strong groundwater inputs, and large benthic standing stocks were associated with spring brooks in passive orthofluvial zones. Generally, structural characteristics of active orthofluvial spring brooks were intermediate in character to spring brooks in parafluvial and passive

orthofluvial zones, reflecting concurrent processes that create and develop floodplain heterogeneity. The microcosm assay of nutrient uptake illustrated a close association of functional response to this structural heterogeneity at the landscape scale. Together these patterns suggest a multiscale organization of form and process that reflects interaction among landscape-level and local exogenous drivers that together impart ecosystem structure and function.

Disturbance, landscape position, and linkage among floodplain systems

Driven by spring snowmelt, the annual flood pulse of the Middle Fork Flathead River is highly predictable, but variation in the frequency and magnitude of disturbance occurs at the floodplain scale along a lateral gradient based on seral stage and proximity to the river channel. Parafluvial environments are shaped by the scouring ef-

fects of extreme flows (Fisher et al. 1998). At the same time, pulses in river discharge act as agents of connectivity and exchange of matter across river–floodplain systems (Junk et al. 1989). In orthofluvial environments, pulse disturbances occur less frequently and are of lower magnitude, leading to greater physical stability and stronger connectivity to adjacent groundwater and terrestrial systems.

Spring brooks in the parafluvial zone were dominated by larger particles, suggesting organization by scour and high-magnitude-flood disturbance. In passive orthofluvial zones, the abundance of fine sediments suggests deposition during inundation and progressive accumulation as a result of low stream power during floods. The intermediate distribution of sediment particle sizes in active orthofluvial spring brooks reflects concurrent geomorphic processes that sustain the active orthofluvial zone (Lorang and Hauer 2006). Channel avulsion and recruitment of vegetation initiate floodplain development and succession, whereas lateral erosion and reclamation of abandoned channels can reverse this process (Stanford et al. 2005, Whited et al. 2007, Bertoldi et al. 2011).

Localized patterns of surface–groundwater exchange along spring channels result from differences in streambed topography and sediment heterogeneity (Woessner 2000). Orthofluvial springbrook reaches were gaining overall, characterized by mixed patterns of exchange (i.e., localized points of upwelling and downwelling), or positive VHG at every sampling point. Despite diminished interaction with the main channel as a result of channel migration and patch succession (Lorang and Hauer 2006), orthofluvial spring brooks appear to maintain strong interaction with the alluvial aquifer as reflected in widespread upwelling along their lengths. Vertical exchange with the alluvial aquifer can influence periphyton accrual and biomass at reach (Valett et al. 1994) and floodplain (Stanford and Ward 1993, Pepin and Hauer 2002, Wyatt et al. 2008) scales, suggesting a potential role for local groundwater subsidies in alleviating nutrient limitation. Upwelling in the stream channel and greater N availability in ground water of most spring brooks, especially in passive orthofluvial zones, further supports this potential.

Over stages of successional development, the relationship between riparian canopy cover and light availability may be an important determinant of ecosystem structure and process rates. In lotic systems with open canopies, rates of primary production often exceed respiration rates (McTammany et al. 2003). Spring brooks in parafluvial zones had little to no overhead canopy cover and relatively greater insolation, whereas dense riparian canopy cover and understory vegetation surrounding passive orthofluvial spring brooks intercepted up to 80% of incident light. In floodplain spring brooks, light availability reflected landscape position but was negatively correlated with chl abundance. Lowest algal biomass occurred in well lit para-

fluvial streams and much greater standing crops were found in dimly lit streams bordered by mid- to late-stage successional forests of the orthofluvial zones. This trend suggests that other biophysical factors promote springbrook algal abundance.

Seral stage and composition of the terrestrial environment can influence allochthonous loading to floodplain patches (Chauvet and Jean-Louis 1988, Cuffney 1988, Anderson 2008). Large wood accumulation in passive orthofluvial spring brooks was similar to streams of old-growth coniferous (9–30 kg/m^2; calculated from Lienkaemper and Swanson 1987) and deciduous (8 kg/m^2; Valett et al. 2002) forests, whereas parafluvial spring brooks were >2 orders of magnitude lower. Furthermore, greater standing stocks of benthic biomass in orthofluvial zones and little accumulation in parafluvial zones were consistent with greater allochthonous loading from adjacent terrestrial environments and lack of export as a result of reduced stream power, physical retention, and relatively stable substrate. Our findings are consistent with a previous assessment of spring brooks on the Nyack flood plain where algal biomass, biofilm standing stock, and periphyton C : N were greater in orthofluvial than in parafluvial spring brooks or main channel sites (Anderson 2008). These patterns reflect landscape-scale variability in OM storage over temporal and longitudinal succession and suggest that the relative physical stability of springbrook ecosystems is an important driver of benthic character at the patch scale.

Landscape position and ecosystem function

Microcosm experiments provided opportunity for comparative assessment of benthic function across springbrook types by allowing sufficient replication and control of abiotic conditions that were not feasible at the scale of whole systems. Despite very low DOC concentrations, NO$_3$-N uptake rates were unresponsive to amendment with labile DOC, suggesting that C is not limiting to microbial processing by springbrook sediments. However, strong increase in N uptake rates during NO$_3$-N augmentation suggests N limitation among spring brooks regardless of landscape position, an observation consistent with the widespread dearth of inorganic N in springbrook waters.

Springbrook uptake rates measured in microcosms were comparable to whole-stream NO$_3$-N uptake for 24 reference streams distributed across 8 regions and several biomes in the continental USA and Puerto Rico (Mulholland et al. 2008). In our study, uptake per unit OM was greatest in parafluvial microcosms regardless of N treatment, suggesting that parafluvial biofilms are strongly nutrient limited. Substantially greater OM standing stocks occurred per unit area in orthofluvial microcosms and led to higher uptake rates per unit area for streams occurring in that part of the flood plain. These results provide support for the contention that greater NO$_3$-N uptake occurs in passive

orthofluvial zones, where limited exposure to flood disturbance allows accumulation of greater benthic standing stocks (i.e., C sources) and development of more-extensive biofilms.

Functional response to spatial organization on complex flood plains has been documented across biomes. On a montane flood plain in northeastern Italy, rates of leaf decomposition (Langhans et al. 2008) and soil and sediment respiration (Doering et al. 2011) varied by up to an order of magnitude among aquatic and terrestrial habitat types in parafluvial and orthofluvial zones. On the tropical Orinoco river–floodplain system, rates of primary production and ecosystem respiration differed across habitat types and over spatial and temporal scales (Lewis et al. 2001). Despite the inherent complexity of this landscape, Lewis et al. (2000) suggested that spatial variability in ecosystem process rates may be predicted based on a suite of structural, hydrologic, and morphometric features characteristic of particular biophysical zones and habitat types. Such studies demonstrate the feasibility of developing a model linking ecosystem function to landscape-scale organization.

Toward a spatial framework of floodplain ecology

Ecosystem studies lack a spatially explicit framework despite recognition of variability in ecosystem process rates in response to heterogeneous patterns of abiotic and biotic factors (Turner 2005). In the ecosystem approach, homogeneous sites generally are chosen as templates to explore pools, fluxes, and regulating factors to minimize complications associated with spatial heterogeneity. Landscape studies, on the other hand, traditionally have related large-scale mosaic patterns to interactions among spatial elements in the context of disturbance (Huff 1995, Whited et al. 2007, Spasojevic et al. 2010), but tend to overlook ecosystem function (but see Zimov et al. 1997, Turner et al. 2004). A spatial theory of ecosystem function is needed to gain new insights into how whole systems respond to landscape-scale heterogeneity.

Montgomery (1999) described the multiscale Process Domains Concept (PDC) wherein spatial and temporal variability in disturbance and geomorphic processes establish the physical template upon which ecosystems develop. Distinct landscape units (i.e., process domains) are associated with a predictable suite of geomorphic processes and disturbance regimes that determine physical habitat type and structure. Ecosystem dynamics within process domains respond to routing processes or local controls depending on position in the landscape. Although the PDC primarily makes predictions regarding community structure, these ideas may be extended to generate predictions for ecosystem function.

High biophysical complexity and biodiversity on flood plains of large gravel-bed rivers result from a combination of routing and local controls (Montgomery 1999, Valett et al. 2014). At the landscape-scale, fluvial transport of energy and materials, lateral erosion, and large-scale vertical hydrologic exchange generate a mosaic of biophysical zones. Depending on spatial array and relative strength of routing controls at specific locations on the landscape, patches exist in various stages of seral development. Local exchange processes (e.g., allochthonous inputs) and regulation of physical conditions (e.g., incident light, temperature) influence the character of adjacent patches and drive processes at the ecosystem scale. Therefore, lotic systems, such as spring brooks, should be viewed as hierarchically nested and interactive elements (Frissell et al. 1986). Overlap of spatially explicit layers forms unique 'nutrient processing domains' in landscape space that may be used to address uptake and retention at the floodplain scale. Therefore, results from our work suggest that 'nutrient processing domains' exist across landscapes as a result of the combined influence of routing and local controls over biophysical structure and function.

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