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SPATIAL DRIVERS OF ECOSYSTEM STRUCTURE AND FUNCTION
IN A FLOODPLAIN RIVERSCAPE: SPRINGBROOK NUTRIENT DYNAMICS

By

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Bachelor of Science, Environmental Biology & Ecology,
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Thesis

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

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ABSTRACT

On riverine floodplains, reorganization by fluvial processes creates and maintains a mosaic of aquatic and riparian landscape elements across a biophysical gradient of disturbance and succession. I hypothesized that ecosystem processes in spring brooks would differ spatially across biophysical zones because landscape position dictates severity of flood disturbance and allochthonous inputs from contiguous terrestrial and groundwater systems. Between July and October 2011, I quantified aspects of ecosystem structure and function among six streams (i.e., spring brooks) originating on the Nyack floodplain, Flathead River, Montana. Among sites large wood standing stocks differed over 300-fold ($0.04 - 13.5 \text{ kg m}^{-2}$), dominant particle size class varied by an order of magnitude ($< 2 - 64 \text{ mm}$), and measures of vertical hydraulic gradient (-0.14 to $+0.20 \text{ cm cm}^{-1}$) reflected landscape position (i.e., parafluvial and orthofluvial zones). I found fine sediment accumulation, stronger groundwater inputs, and greater benthic and large wood standing stocks in orthofluvial compared to parafluvial spring brooks. Algal biomass was negatively correlated with insolation and positively related to vertical hydraulic gradient. Solute injections were used to address biogeochemical cycling of nitrogen at the reach scale. Limited uptake of nitrate in spring brooks suggested abiotic interference or strong co-limitation by nitrogen and phosphorus. However, results from microcosm experiments showed increasing nitrogen uptake across the gradient from parafluvial to orthofluvial spring brooks. Functional response to landscape-scale organization of springbrook structure underscores the need for a spatially-explicit model of floodplain ecology.

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TABLE OF CONTENTS

Abstract.....	ii
Acknowledgements.....	iii
Table of Contents.....	iv
List of Tables.....	v
List of Figures.....	vi
Introduction.....	1
Study Site.....	9
Methods.....	10
Results.....	21
Discussion.....	30
Literature Cited.....	45
Appendix.....	75

LIST OF TABLES

Table 1: Summary of methods used to assess the structural and functional character of spring brooks on the Nyack flood plain.....	56
Table 2: Chemical properties of ground water at the upwelling point of spring brook streams occupying different landscape positions on the Nyack flood plain.....	57
Table 3: Stream characteristics, insolation, and canopy cover in spring brooks occupying different landscape positions on the Nyack flood plain.....	58
Table 4: Benthic standing stocks in spring brooks occupying different landscape positions on the Nyack flood plain.....	59
Table 5: Physiochemical properties of surface and ground water at the upwelling point and along study reaches of spring brooks occupying different landscape positions on the Nyack flood plain.....	60
Table 6: Chemical properties of surface and ground water at the upwelling point and along study reaches of spring brooks occupying different landscape positions on the Nyack flood plain.....	61
Table 7: Comparison of ground and surface water chemical environments within spring brooks occupying different landscape positions on the Nyack flood plain.....	62
Table 8: Ambient and peak NO ₃ -N concentrations and nutrient spiraling metrics associated with solute releases in spring brooks of parafluvial, active orthofluvial, and passive orthofluvial floodplain zones.....	63
Appendix 1: Summary of data transformations, statistical procedures, and test results.....	75

LIST OF FIGURES

Figure 1: Conceptual diagram illustrating interactions between aquatic and terrestrial ecosystems within floodplain landscapes.....	64
Figure 2: Flow diagram illustrating proposed drivers of springbrook structure and function across landscape, biophysical zone, and ecosystem scales.....	65
Figure 3. Map of the Nyack flood plain study site on the Middle Fork Flathead River in northwest Montana, USA.....	66
Figure 4: Relationship between percent vegetative canopy cover and photosynthetically active radiation in spring brooks on the Nyack flood plain.....	67
Figure 5: Relative abundance of sediment size classes in spring brooks of parafluvial, active orthofluvial, and passive orthofluvial floodplain biophysical zones.....	68
Figure 6: Relationship between chlorophyll <i>a</i> standing stocks and photosynthetically active radiation in spring brooks on the Nyack flood plain.....	69
Figure 7: Mean vertical hydraulic gradient measured in parafluvial, active orthofluvial, and passive orthofluvial spring brooks on the Nyack flood plain.....	70
Figure 8: Mean isotopic radon activity in ground water sampled from parafluvial, active orthofluvial, and passive orthofluvial spring brooks on the Nyack flood plain.....	71
Figure 9: Observed and predicted nitrate-nitrogen breakthrough curves at the base of parafluvial, active orthofluvial, and passive orthofluvial springbrook reaches.....	72
Figure 10: Mass-specific and areal uptake rates of nitrate by springbrook substrates in response to ambient and high nitrate-nitrogen treatment levels.....	73
Figure 11: Conceptual model illustrating multi-scale organization and proposed drivers of nutrient processing domains on a floodplain landscape.....	74

INTRODUCTION

Ecosystem structure and function across heterogeneous landscapes

Ecologists have long suggested that ecosystem functioning is organized by the biotic and abiotic structure of the environment, a paradigm in which pattern dictates process (Hutchinson 1953, Vannote et al. 1980, Frissell et al. 1986, Montgomery 1999, Sponseller and Fisher 2006), and functional response to variability in environmental patterns can be considered from a number of spatial scales. 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 and differences in structure 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 1989, 2005, Fisher et al. 2007).

Disturbances maintain the spatial heterogeneity of landscapes (Paine and Levin 1981) by periodically restructuring ecosystems (Connell and Slatyer 1977, 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, Poole 2002). 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 degree of exposure to disturbance and seral stage is frequently reset, patches will exist in a range of successional 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, Ward et al. 2002, Lorang et al. 2005, Stanford et al. 2005) characterized by longitudinal (upstream to downstream), lateral (transition from river channel to terrestrial environment), and vertical (subsurface exchange and interstitial flow) dimensions (Stanford 2006). Extensive restructuring and regeneration of floodplain habitats occurs during years with large magnitude floods and greater frequencies of moderate floods (Whited et al. 2007). As a result, change over time represents a fourth dimension that is characteristic of these systems (Ward 1989). Regular hydrologic disturbance, fluvial reorganization, and ecosystem processes maintain the overall abundance of aquatic, semi-aquatic, and riparian landscape elements driving the ‘shifting habitat mosaic’ (Ward et al. 2002, Stanford et al. 2005, Whited et al. 2007). Cut-and-fill alluviation, channel avulsion, driftwood deposition, and woody vegetation succession create characteristic features including lateral point bar and braid channel accretions, bars, islands, shelves, and meander scrolls. Abandoned channels and paleochannels remain after the main channel shifts to alternate flow paths (Ward et al. 2002, Stanford et al. 2005).

Parafluvial environments are floodplain zones experiencing frequent scour during near bankfull discharge and characterized by cut-and-fill alluviation processes including erosion, sediment transport, and bedload deposition (Lorang and Hauer 2006). Sediment accumulation occurs on gravel bars and around fallen trees which obstruct flow. Gradual accumulation leads to the formation of depositional shelves and allows pioneer species to

establish. Early successional species such as cottonwood (*Populus trichocarpa*) and willow (*Salix spp.*) that are able to establish recruits then develop into pole stands which become traps for sediments and organic matter by decreasing flow competence. Since floods initiate the formation of new geomorphic surfaces on which pioneering stages of succession are initiated, all landscape features found on a flood plain were originally formed in the parafluvial zone (Lorang and Hauer 2006, Stanford 2006).

Transition to later successional stages occurs in the orthofluvial zone, a depositional area lacking widespread scouring flows and characterized by advanced-stage regeneration and mature-stage plant succession (Lorang and Hauer 2006). This zone 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 inundated by annual flood waters with primarily thin, organic-poor, well-drained soils associated with ridge and swale microtopography. The active orthofluvial zone is typically dominated by mid- to late-stage successional riparian forests or wet meadows (Lorang and Hauer 2006, Stanford 2006). Eventual establishment of mature gallery forests consisting of 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 ground water and various surface entities contributes to floodplain heterogeneity (Grapes et al. 2006, Acuña and Tockner 2009, Mouw et al. 2009) and sustains aquatic systems which are not connected to the river via surface channels. Aquatic habitat types distributed across flood plains include main and

side channels, backwaters, ponds, scour holes, wetlands, and spring brooks. Spring brooks are running water systems formed by points of upwelling ground water in flood channels often blocked at the upstream end by deposition of alluvium and woody debris, and may be seasonally intermittent or persist throughout the baseflow period as a result of groundwater inputs (Stanford and Ward 1993, Stanford et al. 2005). Spring brooks in the parafluvial zone are frequently reworked by floods and fed by shallow ground water with short flow paths during periods of lower flow. Spring brooks emerging in paleochannels of the orthofluvial zone are infrequently reworked by large floods but regularly inundated by annual flood waters (Stanford et al. 2005, Stanford 2006).

Frequency and magnitude of disturbance vary with location on flood plains (Whited et al. 2007) and position on the landscape has been found to influence susceptibility to further disturbance and reorganization (Turner 1989, Lorang et al. 2005). Bornette et al. (1994) investigated the influence of spatial position on riverine landscape succession in six former braided channels isolated during the same time period by submersible embankments and subsequent formation of alluvial plugs at the upstream ends. The channels existed in various stages of succession, from early to advanced, based on degree of protection from flood scour and rates of groundwater input (Bornette et al. 1994). Spatial drivers of structural differences and exchange may give rise to heterogeneity in rates of biogeochemical and metabolic processes among these types of systems.

Material and energy exchange across aquatic-terrestrial boundaries

Aquatic and terrestrial systems are linked by landscape processes, and factors

influencing the strength of connectedness across land-water interfaces change over time (Milner et al. 2007) and vary with position on the landscape (Gregory et al. 1991, Webster et al. 1996). The ‘flood pulse concept’ describes the pulse in river discharge as an agent of connectivity and exchange of matter across river-floodplain gradients. Processing of organic matter and nutrients consequently varies within aquatic and terrestrial patches as strength of connectedness changes spatially and temporally (Junk et al. 1989). Within floodplain landscapes where assemblages of contrasting ecological subsystems are linked laterally and longitudinally, flowing water systems encounter a diversity of patches and should therefore experience variation in types and magnitudes of exchanges (Naiman et al. 1988).

In terrestrial floodplain soils, total nitrogen (TN) and dissolved inorganic nitrogen (DIN) increase across a gradient of successional development from gravel bar to mature cottonwood environments. TN in hyporheic sediments increases across the same successional gradient, but standing stocks are lower relative to corresponding soil developmental stages (Morris et al. 2010). Aerial loading of leaves to terrestrial environments increases across the vegetation chronosequence of young *Populus* (10-15 years), pole *Populus* (15-20 years), and mature *Populus* (20-50 years) stands, reaching a maximum in old growth mixed conifer-*Populus* stands (50-100 years). In contrast, aerial loading decreases dramatically in old growth conifer stands (>100-175 years) (Harner and Stanford 2003, Anderson 2008). Aerial loading of carbon, nitrogen, and phosphorus associated with leaf litter follows this same trend (Anderson 2008). Rates of leaf decomposition (Langhans et al. 2008) and soil and sediment respiration (Döring et al. 2011) are heterogeneous across aquatic and terrestrial habitat types on a montane flood

plain in northeast Italy.

Interaction with the surrounding terrestrial environment is known to be an important driver of the character of aquatic systems (Gregory et al. 1991, Nakano and Murakami 2001, Hanson et al. 2003). Allochthonous inputs of terrestrial organic matter provide the primary energy source to heavily-shaded forested streams (Fisher and Likens 1973, Webster and Benfield 1986, Meyer et al. 1998). Exclusion of leaf litter and removal of woody debris from forested headwater streams has been shown to significantly decrease productivity and bring about strong bottom-up changes to food webs (Wallace et al. 1997, 1999). Terrestrial inputs also influence the physical structure of fluvial systems and control water and material residence times. Obstruction of flow by debris dams leads to increased organic matter (Bilby 1981, Smock et al. 1989) and dissolved solute (Valett et al. 2002, Gucker and Boechat 2004) residence times and extends the duration of contact with surface and subsurface substrates (Valett et al. 1996). These terrestrial inputs may vary both seasonally and over stages of forest development and influence stream functioning (Valett et al. 2002, Warren et al. 2007).

Surface-groundwater linkages are important in regulating aspects of stream organization and processes in both surface (Pepin and Hauer 2002, Wyatt et al. 2008) and subsurface systems (Ellis et al. 1998, Boulton et al. 2010). Mixing of surface water and ground water occurs in the saturated interstitial (i.e., hyporheic) zone below the stream bed and adjacent banks (White 1993, Dahm et al. 2006). Groundwater residence time related to length of flow (Ford and Naiman 1989, Holmes et al. 1994, Ellis et al. 1998) and abiotic and metabolic processes taking place in the aquifer (Ellis et al. 1998, Craft et al. 2002) and hyporheic zone (Grimm and Fisher 1984, Poole 2002) alter physical and

chemical properties of waters that upwell into aquatic habitats. Ground water with shorter flow paths typically has characteristics more similar to surface channels (Diehl 2004, Stanford et al. 2005). Transport of nutrients from the hyporheic zone into surface water occurs variably along stream reaches via upwelling (Mulholland et al. 1997, Dent et al. 2001) and may enhance resilience and stability following disturbance (Valett et al. 1994) suggesting that different types and magnitudes of linkages may have strong influence over ecosystem structure and function.

Exchange of energy and materials among patches within streams is facilitated by the advective nature of lotic systems (Vannote et al. 1980). Connection between main and side channels occurs during floods (Junk et al. 1989, Hamilton et al. 2002), and the hydrologic regime is known to control benthic organic matter accumulation and standing stocks, thereby affecting rates of ecosystem respiration (Acuña et al. 2004). Fusion of the flood pulse and shifting habitat mosaic concepts has led to the development of a framework of floodplain ecosystem formation and maintenance which integrates the physical and biotic processes of lateral overland flood inundation, hydrogeomorphic energy, surface-groundwater exchange, physical habitat turnover, and plant succession (Tockner et al. 2010).

Depending upon the nature of exchange between aquatic and terrestrial systems, ecosystem function may be organized by intrinsic or extrinsic drivers (Valett et al. 2008). Similar to the model established for hardwood forest succession (Vitousek and Reiners 1975), Grimm (1987) found that diminished net biomass increment and reduced nitrogen retention were characteristic of the late stages of desert stream succession. However, Valett et al. (2002) found that streams draining old-growth forested catchments remain

more retentive of organic matter and nutrients in late stages of forest succession. Their study suggests that during the transitional stage of terrestrial development where cohort biomass declines due to patch senescence, streams draining old-growth forests accumulate organic matter and are characterized by high levels of nutrient retention during late successional stages.

Floodplain position, complexity, and ecosystem function

While 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), this relationship remains largely unexplored among dynamic, heterogeneous components of floodplain landscapes. Because floodplain streams are embedded in terrestrial systems of various seral stages and disturbance frequency, exchange with the alluvial aquifer is maintained and terrestrial inputs to spring brooks increase as floodplain regeneration proceeds (Fig. 1). I focused on spring brooks distributed along a biophysical gradient of disturbance on the Nyack flood plain to investigate how floodplain succession and exchanges with adjacent systems organize ecosystem structure and function.

Spatial position within floodplain landscapes ultimately drives the structural patterns which influence biogeochemical functioning in spring brooks (Fig. 2). With this conceptual model, nutrient dynamics in spring brooks differ spatially across parafluvial and orthofluvial zones because landscape position dictates intensity of flood disturbance and allochthonous inputs from contiguous terrestrial and groundwater systems. In this way, transition from parafluvial to orthofluvial should modulate the availability of light, organic matter, and nutrients in spring brooks. Spatial variation in floodplain structure

should then contribute to differences in sediment composition, nutrient concentration, organic matter standing stocks, and biogeochemical functioning. Greater retention of organic matter and dissolved solutes in spring brooks of passive orthofluvial zones should generate the highest rates of nutrient uptake. Less retention in spring brooks of parafluvial zones should result in reduced demand and lower rates of nutrient uptake. Further, I argue that the drivers of ecosystem structure and function are scale-dependent, and that local controls become more important in determining orthofluvial springbrook ecosystem character than landscape-scale geomorphic processes that dominate earlier stages of springbrook succession. To address this conceptual model of ecosystem behavior in floodplain riverscapes, I relate structural measures and proxies of exchange and disturbance to measures of nutrient uptake in spring brooks of parafluvial, active orthofluvial, and passive orthofluvial biophysical zones.

STUDY SITE

The Nyack flood plain is a long-term research site on the Middle Fork Flathead River in northwest Montana (Fig. 3). This fifth-order river forms the southern boundary of Glacier National Park in northwest Montana, USA, and drains 3,000 km² of mostly forested catchment including portions of the Bob Marshall and Great Bear Wilderness areas (United States Forest Service). Peak annual discharge occurs in spring (May – June) and averages 541 m³ s⁻¹. Baseflow conditions average 17 m³ s⁻¹ and occur during winter (December – January; Whited et al. 2007). The flood plain is approximately 10 km long and 1 – 2 km wide bounded by bedrock canyon walls at each end forming knickpoints. The anastomosed river is highly connected to an alluvial aquifer which extends from

valley wall to valley wall (Stanford and Ward 1993). A heterogeneous mixture of alluvial cobble, gravel, and sand fill exist atop layers of sand and clay which generates variability in aquifer hydraulic conductivity ($1 - 1000 \text{ m day}^{-1}$; mean of 400 m day^{-1}) and diversification of groundwater flow paths through porous bed materials (Diehl 2004).

METHODS

Study sites were selected using a qualitative assessment of spring brook proximity to the main channel, stream bed sediment size, riparian vegetation, and soil development as indicators of seral stage and landscape position. A combination of structural and functional measures was used to deduce landscape position (i.e., parafluvial or orthofluvial), disturbance history, exchange, and nutrient uptake (Table 1). Springbrook ecosystem structure was evaluated by mapping stream channels, characterizing ground water inputs, and quantifying standing stocks of benthic materials. Nutrient and conservative tracer additions were used to characterize nutrient uptake in spring brooks using a spiraling approach (Webster and Valett 2006). A laboratory microcosm experiment was conducted as a supplemental measure of nutrient uptake. These rates were tied to measures of structure and disturbance intensity to understand their influence on ecosystem function in these classes of floodplain streams.

Broad-scale survey: springbrook ground water

In September 2010, I conducted a preliminary survey of the chemical conditions in ground water at the upwelling head of spring brooks in parafluvial ($n = 3$), active orthofluvial ($n = 5$), and passive orthofluvial ($n = 3$) floodplain biophysical zones. Points

of upwelling were determined by installing clear polyethylene mini-piezometers to a sampling depth of 50 cm below the stream bed surface and visually confirming a positive hydraulic head inside the mini-piezometer. Duplicate groundwater samples were obtained using a peristaltic pump and filtered in the field through pre-ashed glass fiber filters (Whatman GF/F, 0.70 μm pore size). Samples were transported on ice to the Freshwater Research Laboratory at Flathead Lake Biological Station for chemical analysis.

Spring brook channel structure: geomorphology, insolation, and riparian canopy cover

From July – October 2011, I gathered morphometric, structural, and hydraulic data from six spring brooks distributed across parafluvial (PF; $n = 2$), active orthofluvial (AO; $n = 2$), and passive orthofluvial (PO; $n = 2$) floodplain biophysical zones. I selected study reaches (75 – 100 m) and established a series of in-stream transects. Transects oriented perpendicular to direction of flow ($n = 7 - 10$ m per study site) were used to measure basic morphometric features including average depths and widths of the wetted channel during near-baseflow conditions. I measured photosynthetically active radiation (PAR, photon flux density, $\mu\text{mol m}^{-2} \text{sec}^{-1}$) at three points and canopy density facing upstream, downstream, towards stream, and away from stream from the center point along each in-stream transect. Overstory percent riparian canopy cover was estimated by holding a concave spherical canopy densitometer waste-level and counting the number of points of intersection (out of 17) overlapping with reflected overhead vegetation (Lemmon, 1956).

Stream bed composition was assessed using a modified Wolmann pebble count (Bevenger and King 1995) to estimate the distribution of sediment size classes. A single

longitudinal transect was established along the length of the study reach in a zigzag pattern and calipers were used to measure the diameter of inorganic substrates sampled at 0.5- to 1-m intervals. The proportion of observations belonging to Wentworth size classifications was calculated based on a minimum of 200 data points for each spring brook and used to determine particle size distributions and relative abundances (Bevenger and King 1995, Valett et al. 2002).

Springbrook channel structure: benthic standing stocks

Standing stocks of large woody debris were quantified using the line-transect method (Wallace and Benke 1984). The diameter (at point of transect intersection) was measured and used to calculate total volume of woody debris, and these values were multiplied by mean wood density for the dominant tree species on the Nyack flood plain (Brown et al. 1977) to calculate wood mass per unit area. Because of patchy distribution at one passive orthofluvial site, a random number generator was used to establish 20 transects rather than evenly spaced transects every 10 m.

To sample epixylon, I selected the largest (≥ 1 cm in diameter) piece of submerged wood crossing the transect that could be removed from the stream and placed a template (4 cm²) on a homogeneous section. I used a spatula to gently scrape the epixylic layer and then slurried and filtered the scrapings on to a pre-ashed and pre-weighed glass fiber filter (Whatman GF/F). This procedure was repeated for two separate samples from the same piece of wood. Half of the samples were stored in tinfoil and frozen in the lab at -20 °C for chlorophyll *a* determination, and the other half were dried (60 °C, ≥ 48 hours), weighed, combusted (500 °C, ≥ 5 hours), and re-weighed for

calculation of ash-free dry mass (AFDM; g m^{-2}) and percent organic matter.

Photosynthetic pigments were extracted in methanol and analyzed on a Perkin-Elmer 559 UV-VIS spectrophotometer at 666 and 750 nm pre- and post-acidification (Tett et al. 1975, 1977). Chlorophyll *a* standing crop (mg m^{-2}) was calculated using an acidification ratio of 18.8 (J.B. Jones, University of Alaska Fairbanks, personal communication). Chlorophyll *a*:AFDM was computed as a measure of the photoautotrophic component of benthic biomass within each spring brook.

Benthic standing stocks of coarse (CPOM; particle size > 1 mm) and fine particulate (FPOM; particle size < 1 mm) organic matter were sampled at randomly selected points along each transect using an open-bottomed cylindrical bucket to isolate an area of stream bottom (Mulholland et al. 2000). Organic particulates > 1 mm were collected from the cylinder and stored in paper bags. Particulate organic matter < 1 mm was then collected by agitating the benthos, mixing the suspended particulate in the water column, sampling the suspended materials, and filtering a known volume through pre-combusted and pre-weighed glass fiber filters (Whatman GF/F) that were used to obtain AFDM (g L^{-1}). A minimum of 10 depth measurements were collected inside the open-bottomed cylinder to calculate total volume and convert AFDM to FPOM standing stock (g m^{-2}). Another well-mixed sample was collected and filtered through a pre-combusted glass fiber filter for chlorophyll *a* determination as per epixylic samples.

Macroautotrophic above-ground biomass was collected from within a randomly placed 0.25 m^2 frame and stored in separate paper bags. Large samples (e.g., CPOM and macrophytes) were ground after drying at $60 \text{ }^\circ\text{C}$, and ($n = 3$) subsamples were combusted and re-weighed to determine whole-sample AFDM and percent organic matter.

To measure epilithic standing stocks, I randomly selected cobbles ($n = 3 - 5$) along each in-stream transect, scrubbed the surface of each cobble using a wire brush, and collected the slurry of loosened material in a container (Mulholland et al. 2000). The approximate planar area of each surface sampled was determined by tracing on tinfoil, cutting the tracings, and weighing them to calculate total sampling area. The total volume of each pooled slurry container was measured and two separate well-mixed sub-samples were collected and filtered through a pre-ashed glass fiber filter (Whatman GF/F) for chlorophyll *a* determination and calculation of AFDM as per epilithic and FPOM samples.

Physical and chemical properties of surface water and ground water

Ground and surface water were sampled at the upwelling head of the spring brook channel and every 25 m along each study reach. At each sampling point, I installed transects of mini-piezometers ($n = 3$) to a sampling depth of 50 cm below the stream bed surface. Mini-piezometers consisted of 1.59-cm-diameter chlorinated polyvinyl chloride (CPVC) pipe (inner diameter, 1.11 cm) that was perforated with 30 evenly spaced holes (hole diameter, 0.238 cm) over the bottom 15 cm of length and plugged with epoxy putty at the bottom (Baxter et al. 2003, Dahm et al. 2006). In order to quantify potential for surface-groundwater exchange, I used a manometer to measure difference in hydraulic head pressure between ground water in the mini-piezometer and surface water at the benthic interface. The difference in hydraulic head pressures (cm) was divided by piezometer depth (i.e., depth to perforations, cm) to calculate vertical hydraulic gradient (VHG, a unitless measure that is positive under upwelling conditions and negative under

downwelling conditions). A peristaltic pump was used to clear mini-piezometers and collect water samples and physical measures in ground water. I measured temperature (°C), specific conductivity ($\mu\text{S cm}^{-1}$), pH, dissolved oxygen concentration (mg L^{-1} , % saturation) at time of sampling.

The radioactivity of naturally occurring radon (^{222}Rn) isotope (an inert gas product in the radioactive decay series of $^{238}\text{Uranium}$) was determined as a proxy for ground water residence time in the alluvial aquifer (Hoehn and von Gunten 1989). Samples were collected from each mini-piezometer and sealed in gas-tight vials (time of collection was noted), transported on ice, and transferred to scintillation vials in a 1:1 ratio with Beckman Coulter Ready GelTM liquid scintillation cocktail and stored at 4 °C at the Freshwater Research Laboratory at Flathead Lake Biological Station until analyzed. Radioactive decay of ^{222}Rn was determined by liquid scintillation counting on a Beckman LS6500 Multi-Purpose Scintillation Counter (Beckman Coulter, Fullerton, California, USA). Samples were background-corrected using surface water collected from the main stem Middle Fork Flathead River at the upstream knickpoint of the flood plain.

Upon infiltration of surface water with negligible ^{222}Rn concentration to the shallow aquifer, exchange with the atmosphere is eliminated, and ^{222}Rn concentration increases over residence time in the aquifer. Activity measured in becquerels (1 Bq = 1 decay per second) corresponds to the ingrowth of a radioactive nuclide from its parent. Activity changes with time and is proportional to number of radioactive nuclei. ^{222}Rn activity per unit volume (Bq L^{-1}) at time of sample collection (A_s) was calculated using Eq.1:

$$A_s = A_t / e^{-\lambda t} \quad (1)$$

where A_t is activity per unit volume at time of scintillation counting relative to ^{226}Ra standards, λ is the radioactive decay constant (-0.18 day^{-1} for ^{222}Rn), and t is time elapsed between sampling and counting (Hoehn and von Gunten 1989).

To characterize the chemical environments of ground and surface water in spring brooks, samples were collected for analysis of dissolved inorganic nutrient (ammonium ($\text{NH}_4\text{-N}$), nitrate-nitrogen ($\text{NO}_3\text{-N}$), and soluble reactive phosphorus (SRP)) and organic carbon (DOC). Water samples were filtered in the field through pre-ashed glass fiber filters (Whatman GF/F), transported on ice, and stored at $-20 \text{ }^\circ\text{C}$ at the Freshwater Research Laboratory at Flathead Lake Biological Station until analyzed. DOC samples were preserved with phosphoric acid (H_3PO_4) and stored at $4 \text{ }^\circ\text{C}$ until analyzed.

Concentrations of $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, SRP, and chloride (Cl) were determined using continuous flow injection analysis on a Technicon Autoanalyzer II (Technicon, Emeryville, California, USA). The phenolhypochlorite (Solorzano 1969) and cadmium-copper reduction (Wood et al. 1967) methods were used to determine $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$, respectively. The molybdate-antimony method (Murphy and Riley 1962) was used to determine SRP. Cl was analyzed with the mercuric thiocyanate-ferric nitrate method (Zall et al. 1956). DOC concentrations were determined by high-temperature catalytic oxidation (Sugimura and Suzuki 1988) on a Tekmar-Dohrman Apollo 9000HS Total Organic Carbon Analyzer (Teledyne Tekmar, Mason, Ohio, USA).

Nitrate uptake: solute releases

Co-releases of conservative (Cl) and biologically-active solute (nitrate, NO_3^-) tracers were conducted in order to assess nutrient uptake in spring brooks (Triska et al.

1989, Webster and Valett 2006). Tracers were added to stream flow as an instantaneous release (i.e., slug) of concentrated Cl (as sodium chloride, NaCl) and NO₃-N (as sodium nitrate, NaNO₃) dissolved in stream water at a point of natural constriction at the top of each study reach. When necessary, stream flow was constricted at the release point to facilitate mixing before tracer arrival at the downstream sampling location.

Change in tracer concentration over time (i.e., the breakthrough curve, BTC) was monitored in real time as specific conductance ($\mu\text{S cm}^{-1}$) using hand-held conductivity probes and logged at set intervals (5 – 30 sec) using automated sondes (Hyrdolab Model MS5, Austin, Texas, USA) placed at the downstream sampling point. I used the change in conductivity as a guide for sample collection across the slug profile and samples were collected before tracer arrival (i.e., background) and as the slug passed the downstream sampling points ($n = 19 - 25$ samples per BTC). Samples were placed on ice until returned to the lab where they were filtered (Whatman GF/F) within 8 hours of collection and stored at -20 °C until analyzed for NO₃-N and Cl. A series of pre-prepared Cl standards was used to calibrate the conductivity probes and develop a standard curve relating specific conductance to Cl concentrations (Webster and Valett 2006) for use in discharge calculations. BTC integration was used to calculate discharge (L s^{-1} ; Q) using dilution gauging methods (Payn et al. 2009).

For each solute release, concentrations of background-corrected conservative Cl and nonconservative NO₃-N in grab samples were plotted against time. Tracer mass recovered at the base of the reach was calculated as the product of Q and the time-integrated tracer concentration (Tank et al. 2008). Any reduction in N mass relative to the conservative tracer (i.e., area under the BTC) was assumed to result from biological use

over the injection reach. The natural log of N:Cl ratios in the release solution and BTC-integrated masses were plotted against distance downstream and the first-order decay coefficient (longitudinal uptake rate, k_W) was derived from the slope of these data pairs. The negative inverse of k_W is the uptake length (S_W ; m), defined as the average distance traveled by NO_3^- in dissolved inorganic form before it is removed from solution.

Areal uptake (U ; $\mu\text{g m}^{-2} \text{s}^{-1}$) was used to determine flux of $\text{NO}_3\text{-N}$ using Eq. 2:

$$U = Q \times [\text{NO}_3\text{-N}] / S_W \times w \quad (2)$$

where w is stream average reach wetted width, and $[\text{NO}_3\text{-N}]$ is the geometric mean of observed and conservative $\text{NO}_3\text{-N}$ concentration determined from measured Cl and N:Cl ratios in the release solution, calculated as Eq. 3 (following Covino et al. 2010):

$$[\text{NO}_3\text{-N}] = \sqrt{\frac{\int_0^t [\text{NO}_3\text{-N}_{obs}](t) dt}{\int_0^t Q(t) dt} \times \frac{\int_0^t [\text{NO}_3\text{-N}_{cons}](t) dt}{\int_0^t Q(t) dt}} \quad (3)$$

where $[\text{NO}_3\text{-N}_{obs}]$ is the background corrected $\text{NO}_3\text{-N}$ concentration observed in a sample, and $[\text{NO}_3\text{-N}_{cons}]$ is the background-corrected $\text{NO}_3\text{-N}$ concentration predicted in the sample if added $\text{NO}_3\text{-N}$ traveled conservatively. Uptake velocity (v_f) describes nutrient uptake efficiency relative to availability and was calculated from values of U to correct for hydrologic influence on uptake length using Eq. 4:

$$v_f = U / [\text{NO}_3\text{-N}] \quad (4)$$

Uptake velocities calculated using slug enrichment techniques (Tank et al. 2008) were also applied to ambient stream concentrations using Eq. 4 to determine rates of areal uptake (U_{amb}) under ambient conditions in spring brooks.

Nitrate uptake: microcosm experiment

Replicate samples ($n = 16$ per stream) of the dominant sediment size class determined within 3 spring brooks (i.e., one each in parafluvial, active orthofluvial, and passive orthofluvial zones) were collected using sediment cores (core diameter: 65 mm) or by selecting cobbles from a 10-25 m representative reach. Sediment cores were driven 20 – 40 mm in to the benthos and sealed to transfer contents in to plastic 520 mL beakers. Cobbles were randomly selected from the center of the spring brook channel. Samples were stored on ice and transported to the Freshwater Research Laboratory at Flathead Lake Biological Station within 3 hours of collection.

In the laboratory, ambient spring brook water was drained from each sample container and replaced with 250 mL of filtered (Whatman GF/F) water collected from the main stem of the Middle Fork Flathead River. A three-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) $\text{NO}_3\text{-N}$ concentration (levels = ambient or high), and (3) DOC (levels = ambient or high). High concentrations were targeted to be ten-fold springbrook background concentrations (0.10 and 0.35 mg L^{-1} $\text{NO}_3\text{-N}$ and DOC, respectively) and achieved by spiking samples with 250 and 800 μL of 1000 mg L^{-1} $\text{NO}_3\text{-N}$ and DOC, respectively.

An incubator was used to keep samples at constant temperature ($15 \text{ }^\circ\text{C}$) and photoperiod (12 h light) for the duration of the experiment. Samples of water within each microcosm were collected and filtered (Whatman GF/F) for analysis of DOC concentration at time 0 and 12 h, and $\text{NO}_3\text{-N}$ concentration at time 0, 3, 6, 9 and 12 h.

Handheld meters were used to collect pH and DO (mg L^{-1} , % sat.) at time 0, 6, and 12. Following the 12-h experimental period, samples were processed for organic matter content (AFDM) as per benthic compartments.

To quantify uptake during the microcosm experiment, I plotted $\text{NO}_3\text{-N}$ concentration against time and fit a linear regression to the data collected from each microcosm. Uptake rates (U ; $\mu\text{g m}^{-2} \text{h}^{-1}$) were calculated for each replicate using Eq. 5:

$$U = m \times [\text{NO}_3\text{-N}] \times V / A \quad (5)$$

where m is the slope derived from linear regressions ($\mu\text{g L}^{-1} \text{h}^{-1}$), $[\text{NO}_3\text{-N}]$ is the initial $\text{NO}_3\text{-N}$ concentration ($\mu\text{g L}^{-1}$), V is sample volume (L), and A is substrate area (m^2).

Values of U were also calculated per unit of organic matter (i.e., mass-specific uptake, $\mu\text{g AFDM}^{-1} \text{h}^{-1}$) for each microcosm. Replicate means were natural log-transformed and compared using a three-way analysis of variance (ANOVA) test. Because the DOC treatment factor had no significant effect on NO_3^- uptake, replicates across experimental units were combined ($n = 8$ per treatment), and a two-way ANOVA was used to test main and interaction effects for landscape position and NO_3^- enrichment.

Data Analysis

Spatial replication at the ecosystem scale is often difficult and results in constrained statistical analysis (Carpenter 1989). However, comparative approaches have revealed important features of ecosystem structure and function (Schindler 1974, Valett et al. 1996). Duplicate spring brooks were chosen to represent spatial organization on the flood plain, but small sample size prevented direct statistical tests for effects of landscape position. Descriptive summary statistics (i.e., measures of central tendency and

variability) were calculated and assumptions of normality and equal variances tested for structural and functional measures across sites. Appropriate sampling distributions were determined and a combination of parametric and nonparametric tests ($\alpha = 0.05$) was used to assess differences among physical, chemical, structural, and functional variables.

One-way ANOVA and Tukey's HSD pair-wise comparisons ($P < 0.05$) were applied to test for differences in water chemistry among biophysical zones ($n = 3 - 5$ streams per zone) and structural measures (e.g., benthic standing stocks, physical, and chemical parameters) among individual sites. When assumptions of normality and/or homogeneity of variance were violated, non-normally distributed data were transformed. Otherwise, nonparametric Wilcoxon signed-ranks and Kruskal-Wallis ANOVA tests were used to compare non-normally distributed data sets. Within sites, a Wilcoxon two-sample test was applied to test differences between ground and surface water chemistry, and paired t-tests were used to compare predicted and observed tracer concentrations of samples collected during solute releases. For a detailed account of all statistical analyses, see Appendix 1. All statistical analyses were performed on SAS Version 9.3.

RESULTS

Broad-scale survey: springbrook ground water

In 2010, mean nutrient and radon concentrations of springbrook upwelling points differed with landscape position (Table 2). Mean radon concentration increased over parafluvial to orthofluvial zones. However, only $\text{NO}_3\text{-N}$ differed significantly among landscape positions and was three-times higher ($34.3\text{--}109.4 \mu\text{g L}^{-1}$) in parafluvial than in active or passive orthofluvial sites ($P = 0.0333$).

Springbrook channel and benthic structure

Discharge and mean stream velocity differed across spring brooks and ranged from 4.44 – 43.41 L s⁻¹ and 1.64 – 8.36 cm s⁻¹, respectively (Table 3). Channel width (1.71 – 10.59 m) and depth (6.1 – 30.8 cm) ranged over five-fold among spring brooks ($P < 0.0001$), but distinct patterns across landscape position were not evident. PAR declined across biophysical zones (Table 3) from highest in parafluvial (1290.6 – 1316.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$), to intermediate in active orthofluvial (547.6 – 805.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$), and lowest in passive orthofluvial spring brooks (102.4 – 411.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Percent vegetative canopy cover followed the opposite pattern among sites and was negatively related to PAR ($r^2 = 0.49$, $P = 0.1239$, $n = 6$, Fig. 4). Mean insolation in passive orthofluvial zones was 8 – 30% of incident light in parafluvial zones where there was no vegetative canopy cover.

Size of the dominant sediment size class decreased across the floodplain biophysical gradient from parafluvial to orthofluvial zones (Fig. 5). Passive orthofluvial spring brooks were characterized by a right-skewed distribution and high relative abundance (45 – 95%) of fine-grain sediments (< 2 mm). In contrast, relative abundance of particle size classes showed that parafluvial spring brooks were dominated (64 – 74%) by large-grained sediments (8 – 64 mm). Active orthofluvial sites were of character comparable to passive orthofluvial or parafluvial spring brooks. AO1 was dominated by fine-grain sediments (< 2 mm, 66%), while the stream bed of AO2 was primarily composed of large-grained sediments (8 – 64 mm, 70%). Among parafluvial and AO2 springbrook sites, sediments of the smallest size class (< 2 mm) represented only 10 –

18% of sampled particles. Mean rank scores for particle size distributions were significantly different across sites ($H = 546.27$, $df = 5$, $P < 0.0001$).

Large wood standing stocks differed over 300-fold ($0.04 - 13.51 \text{ kg m}^{-2}$) among sites ($P < 0.0001$), with greatest stocks in PO1 and lowest in PF1, but with variation among zones (Table 4). Standing stocks in PO1 were more than four-times the next greatest value (e.g., 3.9 kg m^{-2} in AO1, Table 3). Total wood volume in passive orthofluvial spring brooks was one to two orders of magnitude greater than parafluvial spring brooks, and varied significantly among sites ($P < 0.0001$). Epixylic standing stocks were greater in both passive orthofluvial and AO2 spring brooks compared to parafluvial and AO1, corresponding to greater availability of substrate (Table 4). This pattern was evident for measures of epixylic algal standing stocks as well ($P < 0.0001$), while mean percent organic matter varied from 1 – 28.2% (Table 3) with a mean value of 11.8% across all spring brooks.

Epilithic organic matter and chlorophyll *a* standing stocks generally increased from parafluvial to orthofluvial zones (Table 4). Epilithic organic matter (57.2 g m^{-2}) and algal (47.9 mg m^{-2}) standing stocks were 10 to 50 times greater in PO1 than in parafluvial spring brooks ($P < 0.0001$). Active orthofluvial spring brooks had epilithic standing stocks intermediate to PO1 and parafluvial sites (Table 4). Very low epilithic organic matter and chlorophyll *a* standing stocks were detected in PO2 as a result of stream bed composition and lack of substrate availability (95% of bed particles $< 2 \text{ mm}$). Epilithic organic matter content was generally similar among sites (16 – 25%), except for PO2 where infrequent substrates of appropriate size supported epilithon of low organic composition (1.4%, Table 4).

Fine particulate organic matter differed over an order of magnitude among sites, increasing from parafluvial to orthofluvial zones ($P < 0.0001$). Mean FPOM standing stock was significantly greater in PO2 (781.6 g AFDM m⁻²) compared to all other sites (10.4 – 221.3 g AFDM m⁻²). Algal standing stocks associated with FPOM were also an order of magnitude greater in PO1 (373.8 mg m⁻²) compared to other sites (3.2 – 48.9 mg m⁻²). Among spring brooks, the greatest chlorophyll *a* standing stocks were associated with fine particulate organic matter (Table 4). Percent organic matter in FPOM was low (3.8 – 12.4%) compared to other benthic compartments.

Course particulate organic matter standing stocks varied three orders of magnitude over the gradient of parafluvial to orthofluvial zones (Table 4). Greatest CPOM standing stocks occurred in passive orthofluvial spring brooks (272.2 and 1204.7 g AFDM m⁻²) and one active orthofluvial site (AO2, 150.0 g AFDM m⁻²), and were significantly lower in parafluvial spring brooks (47.0 and 51.5 g AFDM m⁻²; $P < 0.0001$). Aquatic macrophytes were uncommon in spring brook study reaches, but occurred in AO2 and PO2. Estimates of mean above ground biomass were low (0.3 – 4.6 g m⁻²), but significantly greater in PO2 ($P < 0.0001$) compared to other sites (Table 4).

Overall, organic matter standing stocks (kg m⁻²) increased over parafluvial to orthofluvial zones, but individual compartments contributed differentially to the magnitude of total standing stocks (Table 4). Autotrophic biomass made up a small proportion of total organic matter and chlorophyll *a*:AFDM ratios were low (0.0010 – 0.0027), but significantly greater in PO1 (Table 4). Mean chlorophyll *a* standing crops (combined epilithic, epixylic, and FPOM) were negatively related to mean PAR ($r^2 = 0.92$, $P = 0.0024$, $n = 6$; Fig. 6), and positively related to mean VHG, but this relationship

was not significant ($r^2 = 0.30$, $P = 0.3079$, $n = 6$) primarily reflecting low sample size.

Physical and chemical characteristics of spring brooks

Springbrook channels were characterized by variable patterns of vertical hydraulic exchange. VHG was positive at the head of each spring brook channel. Along study reaches, VHG was positive for all sites except PF1, and significantly greater in passive and active orthofluvial spring brooks compared to parafluvial spring brooks ($P < 0.0001$; Fig. 7). PO1 and AO2 were upwelling (+VHG) while PF1 was downwelling (-VHG) at every mini-piezometer sampling point ($n = 18 - 21$). Otherwise, spring brooks were characterized by points of upwelling and downwelling ground water along channel reaches. VHG was positively related to springbrook discharge but this relationship was not statistically significant ($r^2 = 0.61$, $P = 0.0677$, $n = 6$). Mean radon concentrations varied over five-fold among spring brook sites (Fig. 8), were lowest in parafluvial sites ($2.0 - 2.4 \text{ Bq L}^{-1}$), and highest in active ($6.8 - 10.9 \text{ Bq L}^{-1}$) and passive ($5.3 - 10.3 \text{ Bq L}^{-1}$) orthofluvial sites ($P < 0.0001$).

Mean electrical conductivity of ground water was higher in passive (225.3 and $299.2 \mu\text{S cm}^{-1}$) and active (228.4 and $247.2 \mu\text{S cm}^{-1}$) orthofluvial than in parafluvial (192.8 and $212.9 \mu\text{S cm}^{-1}$) spring brooks (Table 5). However, surface- and ground-water conductivity was variable within sites, and ranged over tens to hundreds of μS (Table 5). As a result, significant differences occurred across sites ($P < 0.0001$), but did not group predictably by landscape position (Tukey's HSD, $P < 0.05$). Surface- and ground-water temperatures were highest in parafluvial (surface = $12.5^\circ - 15.3^\circ \text{C}$), intermediate in active orthofluvial ($8.6^\circ - 12.5^\circ \text{C}$), and lowest in passive orthofluvial ($7.8^\circ - 10.4^\circ \text{C}$) spring

brooks ($P < 0.0001$, Table 5).

Mean pH in surface (6.9 – 8.2) and ground (7.0 – 8.1) water differed by ten-fold across sites ($P < 0.0001$), but did not group predictably by landscape position (Table 5, Tukey's HSD, $P < 0.05$). DO in both ground and surface water varied from 0.2 – 8.2 mg L⁻¹ among spring brooks and was surprisingly low in percent saturation (1.9 – 66.7%, Table 5). Surface waters had similar mean DO concentration ($P = 0.0853$) and percent of saturation ($P = 0.0738$) among spring brooks (Table 5). In ground water, DO differed significantly across sites (1.6 – 5.6 mg L⁻¹, 15.4–47.5% of saturation, $P < 0.0001$), but did not group predictably by landscape position (Tukey's HSD, $P < 0.05$).

DOC and inorganic nutrient concentrations were consistently low across sites and water types, but varied among springbrook channels (Table 6). Highest mean concentrations of DOC were found in ground (1.64 mg L⁻¹, $P < 0.0001$) and surface (0.81 mg L⁻¹, $P = 0.0002$) water of PO2. NH₄-N concentrations in surface and ground water were below or slightly higher than method detection limits (5 µg L⁻¹), but higher in ground water of PO2 ($P < 0.0001$). NO₃-N concentrations differed among sites, but were less than 25 µg L⁻¹ in surface water ($P = 0.0468$) and less than 68 µg L⁻¹ in ground water ($P = < 0.0001$). SRP concentrations in surface and ground water were below or slightly higher than method detection limits (1 µg L⁻¹), but higher in ground water of PF2, AO1, and PO2 ($P = 0.0003$). Mean atomic N:P ratios primarily reflected variation in NO₃-N concentration and ranged from 5.9 – 13.3 in surface water and 7.6 – 35.6 in ground water. Highest atomic N:P ratios were found in passive and active orthofluvial springbrook ground ($P < 0.0001$) and surface ($P = 0.0358$) water, however significant differences were not detected by pair-wise comparisons among surface waters (Tukey's HSD, $P >$

0.05, Table 6).

Chemical environments in surface and ground water were different within spring brooks, but those differences were not consistent across all sites or landscape positions (Table 7). DOC concentrations differed significantly between ground and surface water in PO1 ($P = 0.0102$), AO2 ($P = 0.0492$), and PO2 ($P = 0.0118$), but were not consistently higher in one water type. $\text{NH}_4\text{-N}$ concentrations were eight-fold greater ($P = 0.0029$) in ground water ($41.7 \mu\text{g L}^{-1}$) than in surface water ($5.6 \mu\text{g L}^{-1}$) for PO2, but no other significant differences were detected between water types among sites. $\text{NO}_3\text{-N}$ concentrations were greater in ground water than in surface water for PF2 ($P = 0.0005$), AO2 ($P = 0.0282$), and PO1 ($P = 0.0027$), but greater in surface water than in ground water for AO1 ($P = 0.0373$). SRP concentrations were low ($< 3 \mu\text{g L}^{-1}$) and not different among water types (Table 7). However, atomic N:P ratios in ground water increased across parafluvial to orthofluvial zones and were significantly greater than those calculated from corresponding surface-water samples for sites PF2 ($P = 0.0027$), AO2 ($P = 0.0282$), and PO1 ($P = 0.0005$). Due to consistently low SRP concentrations, this trend was primarily a result of variability in $\text{NO}_3\text{-N}$ concentrations among sites.

Nitrate uptake: solute releases

At peak concentrations, solutes released increased $\text{NO}_3\text{-N}$ approximately 50- to 60-fold above background for five of six spring brook sites, and over 200-fold in PF1 (Table 8). In general, differences between actual and predicted $\text{NO}_3\text{-N}$ concentrations observed at downstream sampling stations were small (Fig. 9). The mean difference between predicted (conservative) and observed $\text{NO}_3\text{-N}$ concentrations calculated across

the BTC was not significantly greater than zero ($P > 0.05$) in five of six spring brooks, suggesting no uptake of NO_3^- (Table 8).

Despite lack of significant differences in mean values among individual observations, longitudinal uptake rates (k_w) calculated from comparative N loads during enrichment were negative for PF1, PF2, and PO2, suggesting uptake of NO_3^- occurred during solute releases at these sites (Table 7). For these sites, uptake lengths (S_w) ranged from 0.25 – 1.25 km while corresponding uptake velocities (v_f) ranged from 0.005 – 0.017 mm s^{-1} and were highest in parafluvial spring brooks. Areal uptake rates (U) reflecting enrichment differed by an order of magnitude (0.411 – 11.521 $\mu\text{g m}^{-2} \text{s}^{-1}$) among these same sites. In contrast, increases in observed N load in AO1, AO2, and PO1 led to negative values for spiraling metrics (Table 8), suggesting no uptake and potential production of $\text{NO}_3\text{-N}$ along study reaches. In addition, the mean difference between predicted and observed $\text{NO}_3\text{-N}$ for AO2 was significantly greater than zero ($P = 0.0066$, Table 8), supporting the notion of $\text{NO}_3\text{-N}$ production, rather than uptake, over the course of the solute release.

Nitrate uptake: microcosm experiment

Sediments of the size class sampled for the microcosm study comprised 37% , 66%, and 45%, respectively of the parafluvial, active orthofluvial, and passive orthofluvial springbrook stream beds from which they were sampled. Carbon treatment levels had no main effects ($P = 0.6606$) on response variables or significant interaction ($P > 0.05$) with other factors. As a result, replicates were combined across carbon treatment levels ($n = 8$). $\text{NO}_3\text{-N}$ concentration decreased linearly in all microcosms over the

duration of the experiment. Regressions were significant for all microcosms with coefficients of determination differing among parafluvial ($r^2 = 0.74 - 0.78$), active orthofluvial ($r^2 = 0.44 - 0.45$), and passive orthofluvial ($r^2 = 0.73 - 0.80$) sediments. Regression slopes (m) were not different among parafluvial (-1.78), active orthofluvial (-1.30), and passive orthofluvial (-1.42) microcosms under ambient $\text{NO}_3\text{-N}$ availability, but were more negative in parafluvial (-32.8), active orthofluvial (-8.21), and passive orthofluvial (-32.8) microcosms under high $\text{NO}_3\text{-N}$ amendment ($P < 0.0001$).

Mean values (\pm SE) of uptake normalized to organic matter standing stocks ($\mu\text{g g AFDM}^{-1} \text{ h}^{-1}$) varied over three orders of magnitude across treatment groups (0.5 – 516.1), and differed significantly as a result of landscape position ($P < 0.0001$), $\text{NO}_3\text{-N}$ amendment ($P < 0.0001$), and between factors ($P = 0.0041$). Overall, mass-specific uptake was greatest for parafluvial sediments under high (516.1 ± 89.1) and ambient (24.1 ± 2.9) $\text{NO}_3\text{-N}$ availability. Mass-specific uptake rates did not differ in response to high- $\text{NO}_3\text{-N}$ amendment among sediments from active (10.4 ± 1.9) and passive (7.9 ± 2.4) orthofluvial landscape positions, but were over three-times greater for active (1.7 ± 0.2) than for passive (0.5 ± 0.04) orthofluvial sediments under ambient- $\text{NO}_3\text{-N}$ supply (Fig. 10, top panel).

In contrast to mass-specific rates (Fig. 10, top panel), areal rates indicated greatest uptake by passive orthofluvial sediments (Fig. 10, bottom panel). Mean values (\pm SE) of areal uptake ($\mu\text{g h}^{-1} \text{ m}^{-2}$) ranged over two orders of magnitude across treatment groups, and differed as a result of landscape position ($P < 0.0001$) and $\text{NO}_3\text{-N}$ ($P < 0.0001$) main effects indicating that the influence of $\text{NO}_3\text{-N}$ -amendment depended upon landscape position. At the same time, there was a significant interaction between landscape position

and $\text{NO}_3\text{-N}$ level ($P < 0.0001$). Areal uptake rates in the high $\text{NO}_3\text{-N}$ treatment groups containing passive orthofluvial substrates (2476.4 ± 399.7) were significantly greater than those with parafluvial (722.1 ± 83.8) or active orthofluvial (618.6 ± 71.8) substrates (Fig. 10, bottom panel). Rates of areal uptake were significantly lower under ambient $\text{NO}_3\text{-N}$ treatment regardless of landscape position, but greater for passive (140.1 ± 3.8) and active (98.1 ± 12.0) orthofluvial than for parafluvial (38.4 ± 3.3) sediments (Fig. 10).

DISCUSSION

The floodplain landscape was a model setting for investigating spatial drivers of ecosystem structure and function. Spring brook structure varied across the flood plain reflecting routing (i.e., continuum-driven) and local (i.e., patch-driven) controls depending on landscape position. Fine sediment accumulation, strong groundwater inputs, and large benthic standing stocks were associated with spring brooks in passive orthofluvial zones. Parafluvial spring brooks were characterized by gravel-bottom stream beds, less ground water input, little canopy cover, and sparse benthic standing stocks. Generally, structural characteristics of active orthofluvial spring brooks were intermediate in character to spring brooks in parafluvial and passive orthofluvial zones, reflecting the balance of concurrent processes that create and maintain floodplain heterogeneity. Assays of nutrient uptake illustrated a predictable functional response to this structural heterogeneity at the landscape scale. Together these relationships suggest a multi-scale organization of form and process that reflects interaction among landscape and local exogenous drivers that together impart springbrook structure and function.

Springbrook channel and benthic structure

Spring brooks in parafluvial zones had little to no overhead canopy cover leading to relatively greater insolation, whereas dense riparian canopy cover and understory vegetation surrounding passive orthofluvial spring brooks intercepted up to 92% of incident light. Differences in canopy cover may be attributed to differences in structure of riparian vegetation and stream width. Over stages of successional development, the relationship between riparian canopy cover and light availability may be an important determinate of ecosystem structure and process rates. In streams with open canopies, rates of primary production often exceed respiration rates (McTammany et al. 2003). However, decreasing light intensity has been shown to drive an increase in the chlorophyll content of algal biomass and influence metabolic rates (Hill and Boston 1991). In floodplain spring brooks, light availability reflected landscape position but was negatively correlated with chlorophyll abundance indicating lowest algal biomass in well-lit parafluvial streams and much greater standing crops in dimly-lit streams of the orthofluvial zones.

In passive orthofluvial zones, the abundance of fine sediments suggests deposition during inundation and progressive accumulation as a result of low stream power during low magnitude flood-disturbance events. In contrast, parafluvial spring brooks were dominated by larger particles, suggesting organization by scour and high magnitude flood disturbance. The structural character of active orthofluvial stream beds, however, was intermediate of parafluvial and passive orthofluvial zones. Low relative abundance of fine sediments in AO1 and lack of large-grain particles in AO2 is indicative of concurrent geomorphic processes which create and sustain the active orthofluvial zone (Lorang and

Hauer 2006). Channel avulsion and recruitment of vegetation initiate floodplain development and succession, while lateral erosion and reclamation of abandoned channels can reverse this process (Ward et al. 2002, Stanford et al. 2005, Whited et al. 2007, Bertoldi et al. 2011). Spring channels emerging in these transitional zones should therefore be exposed to variable frequencies and magnitudes of disturbance based on patch size and proximity to the river channel.

The quantity and distribution of organic matter in streams depends on the input rate, abiotic and biotic processing, hydraulic transport capacity, channel geomorphology, and retention structures (Naiman and Sedell 1979). Patterns of wood accumulation observed among spring brooks distributed along the lateral gradient of floodplain succession provide evidence for both landscape- and patch-scale drivers of structural character in lotic floodplain habitats. In AO1, a large log jam spanned the width of the wetted channel. The concomitance of large wood accumulation and large-grained particle distribution at this site provides evidence for a strong linkage to floodplain-scale geomorphic processes. Lateral erosion of floodplain surfaces or valley walls during bank-full flows uproot and disperse large trees across the floodplain landscape, leading to further accumulation and formation of large debris dams that contribute to habitat complexity (Ward et al. 2002, Collins et al. 2012).

Large wood accumulation was one to two orders of magnitude greater in passive orthofluvial than in parafluvial spring brooks, and similar to standing stocks determined in streams of old-growth coniferous ($9 - 30 \text{ kg m}^{-2}$, calculated from Lienkamper 1987) and deciduous (8 kg m^{-2} , Valett et al. 2002) forests. In contrast, large wood standing stocks in parafluvial spring brooks were comparable to those in second-growth deciduous

streams (0.05 kg m^{-2} , Valett et al. 2002). Spring brooks in passive orthofluvial zones are bordered by late-stage successional forests and receive inputs from the adjacent riparian zone. Seral stage and composition of the terrestrial environment has been shown to influence allochthonous loading to floodplain patches (Chauvet and Jean-Louis 1988, Cuffney 1988, Anderson 2008). Early in succession, forests accumulate biomass and inputs to streams are low. As trees mature and senesce, wood inputs to streams increase (Hedin et al. 1988). As a result, streams become more retentive of organic and inorganic particles (Bilby 1981, Smock et al. 1989). Large benthic standing stocks and lower stream power during flooding of the passive orthofluvial zones provide evidence for allochthonous loading from adjacent terrestrial environments rather than delivery from upstream during flooding. These findings are consistent with a previous assessment of CPOM and FPOM isotopic composition (^{13}C and ^{15}N) from spring brooks of the Nyack floodplain that reflected terrestrial plant signatures (Anderson 2008).

Greater standing stocks of benthic biomass and presence of macrophytes in orthofluvial zones were consistent with greater allochthonous loading and lack of export as a result of reduced stream power, physical retention, and relatively stable substrate. Correspondingly, epilithic and epixylic standing stocks were substantially greater in orthofluvial spring brooks and little accumulation of fine or coarse particulate organic matter was found in parafluvial systems. Benthic characteristics of spring brooks were consistent with results of a 2005 survey of floodplain habitats on the Nyack flood plain in which algal biomass, biofilm standing stock, and periphyton C:N ratio were greater in orthofluvial spring brooks than in parafluvial spring brooks or main channel sites (Anderson 2008).

Following the annual spring flood event in 2005, periphyton biomass in Nyack spring brooks recovered to or exceeded pre-flood standing crop within 2-4 months across floodplain habitat types, but was more susceptible to loss as a result of flood scour in parafluvial spring brooks compared to orthofluvial spring brooks. This same study provided evidence for the annual flood pulse disturbance as the primary driver of periphyton biomass distribution and species composition, and secondary control by surface- and groundwater mediated fluctuations in water chemistry during periods of low flow (Anderson 2008). The negative relationship I observed between algal biomass (as chlorophyll *a*) and light availability further suggests that the relative stability of springbrook ecosystems is an important driver of benthic character at the patch scale. Despite greater light availability for primary production in spring brooks of the parafluvial zone, algal biomass was much lower than observed in heavily shaded orthofluvial spring brooks.

At the same time, the positive relationship between VHG and algal biomass provides evidence for additional drivers of benthic character. Bansak (1998) identified hotspots of productivity with higher algal biomass and chlorophyll accumulation rates in upwelling zones of spring brooks. Vertical exchange with the alluvial aquifer has been shown to influence periphyton accrual and biomass at reach (Valett et al. 1994) and floodplain (Stanford and Ward 1993, Pepin and Hauer 2002) scales, suggesting a potential role for local groundwater subsidies in alleviating nutrient limitation to periphyton accrual. Greater N availability in ground water of most spring brooks and predominantly gaining character, especially in passive orthofluvial zones, further supports this potential.

Physical and chemical properties of spring brooks

When river water flowing through confined valley segments enters an unconfined flood plain segment, surface water penetrates and recharges the alluvial aquifer (Creuze des Chatellier et al. 1994). In the upper 2 km of the Nyack flood plain's 10-km length, approximately 30% of the river volume enters the alluvial aquifer at baseflow discharge and returns to the river primarily over the lower half of the flood plain (Stanford et al. 1994, 2005). Hyporheic water travels along interstitial pathways and emerges at points along lateral floodplain surfaces (Stanford and Ward 1993, Baxter and Hauer 2000). These subsurface flow paths expose river water to interstitial substrate surface areas on which biogeochemical processes take place (Ellis et al. 1998). Physical and chemical properties of ground water may vary greatly depending on flowpath residence time and the magnitude of exposure to biotic and abiotic processes (Brunke and Gonsler 1997).

Interstitial zones of preferential flow exist through well-sorted alluvium in the aquifer, leading to discharge of groundwater (i.e., positive VHG) at the head of each springbrook channel. Downstream, localized patterns of surface-groundwater exchange along spring channels result from differences in stream bed topography and sediment heterogeneity (Woessner 2000). In PF1, VHG was negative at every point along the section of channel downstream of the upwelling head. Along this losing reach, stream stage was greater than the underlying and adjacent groundwater head, and streambed sediments with high porosity were bordered by zones of low hydraulic conductivity (Woessner 2000). All other spring brook 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.

While not a direct measure of groundwater residence time (due to unknown extent of mixing by source ground water), relative measures of radon activity in hyporheic water sampled along springbrook channels suggest that these systems are fed by ground water that has spent considerably different amounts of time in the alluvial aquifer. Higher radon activity in ground water feeding orthofluvial spring brooks indicates travel along longer flow paths and greater residence time in the alluvial aquifer. The physiochemical character (e.g., gradients of DO and ionic strength) of groundwater has been shown to change predictably with distance along subsurface flow paths in the Nyack flood plain (Reid 2007, Valett et al. in review), and may generate variability in composition of upwelling water. In my study, DO content and ionic strength in springbrook hyporheic zones were not predicted by landscape position. Heterogeneous physical conditions along flow paths in the hyporheic zone influence rates and types of chemical transformations (Triska et al. 1993, Brunke and Gonser 1997), and may contribute to differences in chemical composition observed among spring brooks as a result of groundwater residence time.

The pristine Middle Fork Flathead River is nutrient poor (Stanford et al. 1994), and despite seasonal fluctuations (Anderson 2008), overall C and N concentrations are low in main channel and springbrook habitats. Relatively higher concentrations of DOC observed in PO1 may be attributed to a greater abundance of sources in the stream

channel including leachate from allochthonous particulate carbon and exudates from autochthonous biofilms (Meyer et al. 1998). N and P concentrations observed in spring brooks were typical of undisturbed streams draining heavily forested watersheds (Omernick 1977) including long-term study sites such as Walker Branch, Tennessee and Hugh White Creek, North Carolina (Mulholland et al. 1997). Previous surveys of spring brooks on the Nyack floodplain have also found consistently low N and P concentrations, and high N:P ratios (Bansak 1998, Anderson 2008), without evident differences among springbrook types.

Nitrate uptake: whole-stream assessments

Limited nutrient uptake was observed in spring brooks during reach-scale solute releases despite characteristically low ambient N concentrations, the presence of well-developed biofilms, and large standing stocks of organic matter and woody debris. Ambient uptake rates were orders of magnitude lower than those observed in streams of comparably forested environments in Tennessee and North Carolina (Valett et al. 2008). In northern temperate regions, NO_3^- is not typically affected by physical-chemical processes of removal (i.e., abiotic sorption to sediments), and when nutrient demand is high, streams tend to be biogeochemically responsive to additions of dissolved inorganic nitrogen (Peterson et al. 2001). Many of the compartments shown to actively cycle nutrients, including coarse (Mulholland et al. 1985) and fine particulate organic matter (Hoellein et al. 2009), attached algae (Sebetich et al. 1984, Grimm 1987), and large wood (Munn and Meyer 1990, Tank and Webster 1998) were present and abundant in many of the study streams. Lack of uptake in some spring brooks and comparatively low uptake

rates in others suggests that other influences, in addition to N availability alone, were responsible for observed N-cycling response to enrichment at the reach scale.

Although spring brooks represent points of discharging ground water from the alluvial aquifer, most sites exhibited localized downwelling (-VHG) at several or all points along the study reach, suggesting effective infiltration of surface water into the sediments. At this interstitial interface, contact between added NO_3^- and sediment surface area should have occurred and provided opportunity for biotic assimilation. Uptake of NO_3^- was observed in PF1, PF2, and PO1 where the lowest mean values of VHG were calculated among sites. In spring brooks where no uptake was observed during slug releases, physical prevention of biotic uptake may have occurred as a result of insufficient mixing of solutes in the stream channel reflecting intense upwelling across the benthic interface. Additionally, stratification in the water column due to thermal differences in density (between release-solution and surface-water ionic strength) may have prevented contact between added solutes and benthic substrata.

In addition to potential limitation of nutrient uptake by abiotic forces, biological constraints may have influenced uptake rates. The elemental composition of the benthic community relative to supply in the water column determines the degree of nutrient demand and biotic assimilatory rates (Sturner et al. 1992, Cross et al. 2005). High atomic N:P ratios observed in spring brooks point to potential limitation of uptake by P availability. In 2005, evidence from nutrient diffusion experiments indicated co-limitation by N and P on periphyton biomass in spring brooks (Anderson 2008). Lack of response to NO_3^- enrichment despite potentially high demand suggests that low P availability limits N uptake and retention in spring brooks. Alternatively, well-developed

biofilms may be proficient at internal cycling of nutrients and less dependent upon supply of inorganic nutrients in the water column (Riber and Wetzel 1987, Mulholland et al. 1991).

Nitrate uptake: microcosms

Microcosm experiments were critical for describing the functional character of spring brooks by allowing sufficient replication and control of abiotic conditions that were not feasible at the scale of whole systems. Carpenter (1999) argued limited relevance for microcosm studies in ecosystem ecology, citing several studies in which results of microcosm assessments were inappropriately extrapolated to whole-system scales. He also describes microcosm studies as being important supportive and heuristic tools that may be applied to appropriately-scaled studies (e.g., for estimating rates under controlled conditions). Spivak et al. (2011) conducted an experiment using mesocosms spanning five orders of magnitude in volumetric scale (from 4 L to whole ponds) to determine the suitability of extrapolation of process rates determined in mesocosms to whole ecosystems. They found that mesocosm shape and volume had little influence on the response of algae to nutrient enrichment, and that results from small-scale enrichment experiments may be applied to larger aquatic systems (Spivak et al. 2011). Rates of NO_3^- uptake I observed in microcosms provide opportunity for comparative assessment of benthic function across springbrook types.

DOC concentration in the surface and subsurface waters of the Nyack-reach of the Flathead River and its floodplain are very low, approaching detection level for most instrumentation. Nevertheless, NO_3^- uptake rates were unresponsive to amendment with

labile DOC. Stoichiometric demand has been shown to link C and N cycles in streams (Dodds et al. 2004, Brookshire et al. 2005, Goodale et al. 2005), but the absence of altered NO_3^- uptake in response to DOC enhancement suggests that C is not limiting to microbial processing in spring brooks. Instead, the overall strong increase in N uptake rates during NO_3^- -N augmentation suggests nitrogen limitation among spring brooks regardless of landscape position, and is an observation consistent with low ambient concentrations of dissolved inorganic N observed in spring brooks.

Areal uptake rates in microcosms were comparable to those observed in 24 reference streams distributed across eight regions and several biomes in the continental United States and Puerto Rico (Mulholland et al. 2008). In my study, uptake per unit organic matter was greatest in parafluvial microcosms regardless of N treatment, but substantially greater organic matter standing stocks occur per unit area in orthofluvial microcosms and led to higher uptake rates per unit area. These patterns of organic matter abundance were also observed as greater standing stocks in springbrook study reaches. These results provide support for the contention that greater NO_3^- 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. This proposal is consistent with findings from Anderson (2008) who reported higher C:N ratios in periphyton of orthofluvial vs. parafluvial zones, potentially reflecting greater demand for N (Dodds et al. 2004).

Interestingly, uptake rates in microcosms containing material from passive and active orthofluvial spring brooks differed despite the fact that the same size class of sediments (< 2 mm) was present in each. Under high NO_3^- -N treatment, uptake rates per

unit organic matter were not significantly different between active and passive orthofluvial zones despite greater organic matter standing stocks in passive orthofluvial spring brooks. This suggests that N uptake per unit organic matter is similar despite increased organic matter availability. Accordingly, areal uptake rates would be greatest in passive orthofluvial spring brooks and lowest in active orthofluvial and parafluvial sites if biomass-specific rates are extended to field standing stocks. Areal uptake rates were significantly greater in passive orthofluvial sediments than in active orthofluvial and parafluvial sediments in response to $\text{NO}_3\text{-N}$ augmentation.

Indeed, N-enrichment led to areal uptake of comparable magnitude in microcosms ($0.17 - 0.69 \mu\text{g m}^{-2} \text{s}^{-1}$) and whole-reach assays at sites PO1 and PF2 ($0.41 - 0.88 \mu\text{g m}^{-2} \text{s}^{-1}$), whereas PF1 responded more strongly to reach-scale enrichment ($11.52 \mu\text{g m}^{-2} \text{s}^{-1}$). Rates of N-uptake under ambient N conditions were higher in microcosms ($0.01 - 0.04 \mu\text{g m}^{-2} \text{s}^{-1}$) than in whole-stream releases ($0.0006 - 0.002 \mu\text{g m}^{-2} \text{s}^{-1}$). Microcosm experiments may have allowed greater contact between sediments and nutrients than would occur during slug solute releases. Additionally, abiotic conditions in the microcosms may have caused liberation of adsorbed phosphorus from sediments and accumulation in the overlying water, alleviating phosphorus demand and enhancing uptake of NO_3^- . Further, uptake rates were low in parafluvial zones when derived from microcosm experiments and high when derived from whole-stream tracer studies. This discrepancy may result from selection of a particular size class for microcosm experiments, whereas whole-stream studies encompassed all available substrate types.

Towards 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 1989, 2005). For studies at the ecosystem scale, homogeneous sites are generally chosen as templates to explore pools, fluxes, and regulating factors in order to minimize complications associated with spatial heterogeneity. However, ecosystem boundaries are porous, and disregard of the spatial configuration of ecosystems may lead investigators to overlook important drivers of point processes when rates are measured at a particular location (Turner and Chapin III 2005). Landscape studies have traditionally 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 in to how whole systems respond to landscape-scale heterogeneity.

Montgomery (1999) described the multi-scale 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 geomorphic process domains respond to routing (i.e., continuum-like) processes or local (i.e., patch-scale) controls depending on position in the landscape. Although the PDC primarily makes predictions regarding community structure within process domains, these ideas may be extended to generate predictions for ecosystem function.

High biophysical complexity and biodiversity on floodplains of large gravel-bed rivers result from a combination of routing and local controls (Montgomery 1999, Stanford et al. 2005). At the landscape-scale, three-dimensional routing processes such as fluvial transport of energy and materials, lateral erosion, and large-scale vertical hydrologic exchange between ground and surface water entities generate a mosaic of biophysical zones (Fig. 11). Depending on spatial array and relative strength of routing controls at specific locations on the landscape, patches exist in various stages of seral development. Exchange processes (e.g., allochthonous inputs) and regulation of physical conditions (e.g., incident light, temperature) influence the character of adjacent patches. Both routing and local controls at the biophysical scale drive structural patterns and point processes at the ecosystem scale. Lotic systems such as spring brooks should therefore be viewed as hierarchically nested and interactive elements (Frissell et al. 1986, Poole 2002). Overlap of spatially explicit layers forms unique ‘nutrient processing domains’ in landscape space that may be scaled to predict rates of nitrogen uptake and retention at the floodplain scale (Fig. 11).

Large-river floodplains provide the necessary spatial heterogeneity and replication of landscape elements to generate a multi-scale predictive model of the drivers of ecosystem function in mosaic landscapes (Poole 2002, Tockner et al. 2010). Future studies should attempt to increase sample size and sufficiently replicate spring brooks by landscape position in order to improve statistical inference and accurately characterize model parameters on the ground. Further investigation should consider organization of spring brooks along the entire length of the flood plain in order to account for variability over lateral and longitudinal gradients. The conceptual model proposed here could be

expanded beyond springbrook nutrient processing domains to incorporate structural measures and predict rates of functional processes in the abundance of terrestrial and aquatic systems that occur on floodplain landscapes. This research highlights the variable structural and functional response of lotic systems to configuration on heterogeneous landscapes and I emphasize a need for further development of a spatially explicit framework for ecosystem ecology.

Literature Cited

- Acuña, V., A. Giorgi, I. Munoz, U. Uehlinger, and S. Sabater. 2004. Flow extremes and benthic organic matter shape the metabolism of a headwater mediterranean stream. *Freshwater Biology* **49**:960-971.
- Acuña, V. and K. Tockner. 2009. Surface-subsurface water exchange rates along alluvial river reaches control the thermal patterns in an alpine river network. *Freshwater Biology* **54**:306-320.
- Anderson, M. L. 2008. Lateral habitat ecology of an alluvial river floodplain. Dissertation. The University of Montana, Missoula, Montana, USA.
- Arcott, D. B., K. Tockner, D. van der Nat, and J. V. Ward. 2002. Aquatic habitat dynamics along a braided alpine river ecosystem (tagliamento river, northeast italy). *Ecosystems* **5**:802-814.
- Bansak, T. 1998. The influence of vertical hydraulic exchange on habitat heterogeneity and surficial primary production on a large alluvial floodplain. Thesis. The University of Montana, Missoula, Montana, USA.
- Baxter, C. V. and F. R. Hauer. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*salvelinus confluentus*). *Canadian Journal of Fisheries and Aquatic Sciences* **57**:1470-1481.
- Baxter, C. V., F. R. Hauer, and W. W. Woessner. 2003. Measuring groundwater-stream water exchange: New techniques for installing minipiezometers and estimating hydraulic conductivity. *Transactions of the American Fisheries Society* **132**:493-502.
- Bertoldi, W., N. A. Drake, and A. M. Gurnell. 2011. Interactions between river flows and colonizing vegetation on a braided river: Exploring spatial and temporal dynamics in riparian vegetation cover using satellite data. *Earth Surface Processes and Landforms* **36**:1474-1486.
- Bevenger, G. and R. King. 1995. A pebble count procedure for assessing watershed cumulative effects. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station Research Paper RM-RP-319.
- Bilby, R. E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. *Ecology* **62**:1234-1243.
- Bornette, G., C. Amoros, and D. Chessel. 1994. Effect of allogenic processes on successional rates in former river channels. *Journal of Vegetation Science* **5**:237-246.

- Boulton, A. J., T. Datry, T. Kasahara, M. Mutz, and J. A. Stanford. 2010. Ecology and management of the hyporheic zone: Stream-groundwater interactions of running waters and their floodplains. *Journal of the North American Benthological Society* **29**:26-40.
- Brookshire, E. N. J., H. M. Valett, S. A. Thomas, and J. R. Webster. 2005. Coupled cycling of dissolved organic nitrogen and carbon in a forest stream. *Ecology* **86**:2487-2496.
- Brown, J. K., J. A. Kendall Snell, and D. L. Bunnell. 1977. Handbook for predicting slash weight of western conifers. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station Research Paper.
- Brunke, M. and T. Gonser. 1997. The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* **37**:1-33.
- Carpenter, S. R. 1989. Replication and treatment strength in whole-lake experiments. *Ecology* **70**:453-463.
- Carpenter, S. R. 1999. Microcosm experiments have limited relevance for community and ecosystem ecology: Reply. *Ecology* **80**:1085-1088.
- Chauvet, E. and A.M. Jean-Louis. 1988. Litter production in the Garonne riparian forest and allochthonous input to the river. *Acta Oecol. Oecol. Gen.* **9**:265-279.
- Collins, B. D., D. R. Montgomery, K. L. Fetherston, and T. B. Abbe. 2012. The floodplain large-wood cycle hypothesis: A mechanism for the physical and biotic structuring of temperate forested alluvial valleys in the north pacific coastal ecoregion. *Geomorphology* **139**:460-470.
- Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**:1119-1144.
- Covino, T. P., B. L. McGlynn, and R. A. McNamara. 2010. Tracer additions for spiraling curve characterization (TASCC): Quantifying stream nutrient uptake kinetics from ambient to saturation. *Limnology and Oceanography-Methods* **8**:484-498.
- Craft, J. A., J. A. Stanford, and M. Pusch. 2002. Microbial respiration within a floodplain aquifer of a large gravel-bed river. *Freshwater Biology* **47**:251-261.
- Cross, W. F., J. P. Benstead, P. C. Frost, and S. A. Thomas. 2005. Ecological stoichiometry in freshwater benthic systems: Recent progress and perspectives. *Freshwater Biology* **50**:1895-1912.

- Creuze des Chatellier, M., Poinsart, D., and J.P. Bravard. 1994. Geomorphology of alluvial groundwater ecosystems. Pages 157-185 in J. Gilbert, D. L. Danielopol, and J. A. Stanford, editors. *Groundwater Ecology*. Academic Press, San Diego, California.
- Cuffney, T.F. 1988. Input, movement, and exchange of organic matter within a subtropical coastal blackwater river-floodplain system. *Freshwater Biology* **19**:305-320.
- Dahm, C. N., H. M. Valett, C. V. Baxter, and W. W. Woessner. 2006. Hyporheic zones. Pages 119-142 in F. R. Hauer and G. A. Lamberti, editors. *Methods in Stream Ecology*, San Diego, California.
- Dent, C. L., N. B. Grimm, and S. G. Fisher. 2001. Multiscale effects of surface-subsurface exchange on stream water nutrient concentrations. *Journal of the North American Benthological Society* **20**:162-181.
- Diehl, J. C. 2004. Hydrogeological characteristics and groundwater/river exchange in a gravel-dominated floodplain, middle fork of the flathead river, northwestern montana. Thesis. The University of Montana, Missoula, Montana, USA.
- Dodds, W. K., E. Marti, J. L. Tank, J. Pontius, S. K. Hamilton, N. B. Grimm, W. B. Bowden, W. H. McDowell, B. J. Peterson, H. M. Valett, J. R. Webster, and S. Gregory. 2004. Carbon and nitrogen stoichiometry and nitrogen cycling rates in streams. *Oecologia* **140**:458-467.
- Döring, M., U. Uehlinger, T. Ackermann, M. Woodtli, and K. Tockner. 2011. Spatiotemporal heterogeneity of soil and sediment respiration in a river-floodplain mosaic (tagliamento, ne italy). *Freshwater Biology* **56**:1-15.
- Ellis, B. K., J. A. Stanford, and J. V. Ward. 1998. Microbial assemblages and production in alluvial aquifers of the flathead river, montana, USA. *Journal of the North American Benthological Society* **17**:382-402.
- Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* **52**:93-110.
- Fisher, S. G., J. B. Heffernan, R. A. Sponseller, and J. R. Welter. 2007. Functional ecomorphology: Feedbacks between form and function in fluvial landscape ecosystems. *Geomorphology* **89**:84-96.
- Fisher, S. G. and G. E. Likens. 1973. Energy flow in bear brook, new hampshire - integrative approach to stream ecosystem metabolism. *Ecological Monographs* **43**:421-439.

- Ford, T. E. and R. J. Naiman. 1989. Groundwater surface-water relationships in boreal forest watersheds - dissolved organic-carbon and inorganic nutrient dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* **46**:41-49.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification - viewing streams in a watershed context. *Environmental Management* **10**:199-214.
- Goodale, C. L., J. D. Aber, P. M. Vitousek, and W. H. McDowell. 2005. Long-term decreases in stream nitrate: Successional causes unlikely; possible links to doc? *Ecosystems* **8**:334-337.
- Grapes, T. R., C. Bradley, and G. E. Petts. 2006. Hydrodynamics of floodplain wetlands in a chalk catchment: The river lambourn, uk. *Journal of Hydrology* **320**:324-341.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *Bioscience* **41**:540-551.
- Grimm, N. B. 1987. Nitrogen dynamics during succession in a desert stream. *Ecology* **68**:1157-1170.
- Grimm, N. B. and S. G. Fisher. 1984. Exchange between interstitial and surface-water - implications for stream metabolism and nutrient cycling. *Hydrobiologia* **111**:219-228.
- Gucker, B. and I. G. Boechat. 2004. Stream morphology controls ammonium retention in tropical headwaters. *Ecology* **85**:2818-2827.
- Hamilton, S. K., S. J. Sippel, and J. M. Melack. 2002. Comparison of inundation patterns among major south american floodplains. *Journal of Geophysical Research-Atmospheres* **107**.
- Hanson, P. C., D. L. Bade, S. R. Carpenter, and T. K. Kratz. 2003. Lake metabolism: Relationships with dissolved organic carbon and phosphorus. *Limnology and Oceanography* **48**:1112-1119.
- Harner, M.J. and J.A. Stanford. 2003. Differences in cottonwood growth between a losing and gaining reach of an alluvial flood plain. *Ecology* **84**:1453-1458.
- Hedin, L. O., M. S. Mayer, and G. E. Likens. 1988. The effect of deforestation on organic debris dams. *Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie* **23**:1135-1141.
- Hill, W. R. and H. L. Boston. 1991. Community-development alters photosynthesis irradiance relations in stream periphyton. *Limnology and Oceanography* **36**:1375-1389.

- Hoehn, E. and H. R. von Gunten. 1989. Radon in groundwater - a tool to assess infiltration from surface waters to aquifers. *Water Resources Research* **25**:1795-1803.
- Hoellein, T. J., J. L. Tank, E. J. Rosi-Marshall, and S. A. Entekin. 2009. Temporal variation in substratum-specific rates of n uptake and metabolism and their contribution at the stream-reach scale. *Journal of the North American Benthological Society* **28**:305-318.
- Holmes, R. M., S. G. Fisher, and N. B. Grimm. 1994. Parafluvial nitrogen dynamics in a desert stream ecosystem. *Journal of the North American Benthological Society* **13**:468-478.
- Huff, M. H. 1995. Forest age structure and development following wildfires in the western olympic mountains, washington. *Ecological Applications* **5**:471-483.
- Hutchinson, G. E. 1953. The concept of pattern in ecology. *Proceedings of the Academy of Natural Sciences of Philadelphia* **95**:137-145.
- Junk, W. J., P. B. Baylet, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publications of Fisheries and Aquatic Sciences* **106**:110-127.
- Langhans, S. D., S. D. Tiegs, M. O. Gessner, and K. Tockner. 2008. Leaf-decomposition heterogeneity across a riverine floodplain mosaic. *Aquatic Sciences* **70**:337-346.
- Lemmon, P.E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science* **2**:314-320.
- Lienkaemper, G. W. and F. J. Swanson. 1987. Dynamics of large woody debris in streams in old-growth douglas-fir forests. *Canadian Journal of Forest Research- Revue Canadienne De Recherche Forestiere* **17**:150-156.
- Lorang, M. S. and F. R. Hauer. 2006. Fluvial geomorphic processes. Pages 145-168 *in* F. R. Hauer and G. A. Lamberti, editors. *Methods in Stream Ecology*, San Diego, California.
- Lorang, M. S., D. C. Whited, F. R. Hauer, J. S. Kimball, and J. A. Stanford. 2005. Using airborne multispectral imagery to evaluate geomorphic work across floodplains of gravel-bed rivers. *Ecological Applications* **15**:1209-1222.
- McTammany, M. E., J. R. Webster, E. F. Benfield, and M. A. Neatrour. 2003. Longitudinal patterns of metabolism in a southern appalachian river. *Journal of the North American Benthological Society* **22**:359-370.

- Meyer, J. L., J. B. Wallace, and S. L. Eggert. 1998. Leaf litter as a source of dissolved organic carbon in streams. *Ecosystems* **1**:240-249.
- Milner, A. M., C. L. Fastie, F. S. Chapin, D. R. Engstrom, and L. C. Sharman. 2007. Interactions and linkages among ecosystems during landscape evolution. *Bioscience* **57**:237-247.
- Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs* **53**:1-25.
- Montgomery, D. R. 1999. Process domains and the river continuum. *Journal of the American Water Resources Association* **35**:397-410.
- Morris, M. R., B. O. Brouwer, J. K. Caves, M. J. Harner, and J. A. Stanford. 2010. Successional changes in soil and hyporheic nitrogen fertility on an alluvial flood plain: Implications for riparian vegetation. *Aquatic Sciences* **72**:519-532.
- Mouw, J. E. B., J. A. Stanford, and P. B. Alaback. 2009. Influences of flooding and hyporheic exchange on floodplain plant richness and productivity. *River Research and Applications* **25**:929-945.
- Mulholland, P. J., A. M. Helton, G. C. Poole, R. O. Hall, S. K. Hamilton, B. J. Peterson, J. L. Tank, L. R. Ashkenas, L. W. Cooper, C. N. Dahm, W. K. Dodds, S. E. G. Findlay, S. V. Gregory, N. B. Grimm, S. L. Johnson, W. H. McDowell, J. L. Meyer, H. M. Valett, J. R. Webster, C. P. Arango, J. J. Beaulieu, M. J. Bernot, A. J. Burgin, C. L. Crenshaw, L. T. Johnson, B. R. Niederlehner, J. M. O'Brien, J. D. Potter, R. W. Sheibley, D. J. Sobota, and S. M. Thomas. 2008. Stream denitrification across biomes and its response to anthropogenic nitrate loading. *Nature* **452**:202-U246.
- Mulholland, P. J., E. R. Marzolf, J. R. Webster, D. R. Hart, and S. P. Hendricks. 1997. Evidence that hyporheic zones increase heterotrophic metabolism and phosphorus uptake in forest streams. *Limnology and Oceanography* **42**:443-451.
- Mulholland, P. J., J. D. Newbold, J. W. Elwood, L. A. Ferren, and J. R. Webster. 1985. Phosphorus spiraling in a woodland stream - seasonal-variations. *Ecology* **66**:1012-1023.
- Mulholland, P. J., A. D. Steinman, A. V. Palumbo, J. W. Elwood, and D. B. Kirschtel. 1991. Role of nutrient cycling and herbivory in regulating periphyton communities in laboratory streams. *Ecology* **72**:966-982.
- Mulholland, P. J., J. L. Tank, D. M. Sanzone, W. M. Wollheim, B. J. Peterson, J. R. Webster, and J. L. Meyer. 2000. Nitrogen cycling in a forest stream determined by a N-15 tracer addition. *Ecological Monographs* **70**:471-493.

- Munn, N. L. and J. L. Meyer. 1990. Habitat-specific solute retention in 2 small streams - an intersite comparison. *Ecology* **71**:2069-2082.
- Murphy, J. and J. P. Riley. 1962. A modified single solution method for determination of phosphate in natural waters. *Analytica Chimica Acta* **26**:31-&.
- Naiman, R. J., H. Decamps, J. Pastor, and C. A. Johnston. 1988. The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society* **7**:289-306.
- Naiman, R. J. and J. R. Sedell. 1979. Benthic organic-matter as a function of stream order in oregon. *Archiv Fur Hydrobiologie* **87**:404-422.
- Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America* **98**:166-170.
- Newbold, J.D. 1992. Cycles of spirals and nutrients. Pages 379-399 *in* P. Calow and G.E. Petts, editors. *The Rivers Handbook*. Blackwell Scientific Publications, Oxford.
- Omernick, J. M. 1977. Non-point source-stream nutrient level relationships: A nationwide study., US Environmental Protection Agency, Corvallis, OR, USA.
- Paine, R. T. and S. A. Levin. 1981. Inter-tidal landscapes - disturbance and the dynamics of pattern. *Ecological Monographs* **51**:145-178.
- Payn, R. A., M. N. Gooseff, B. L. McGlynn, K. E. Bencala, and S. M. Wondzell. 2009. Channel water balance and exchange with subsurface flow along a mountain headwater stream in montana, united states. *Water Resources Research* **45**.
- Pepin, D. M. and F. R. Hauer. 2002. Benthic responses to groundwater-surface water exchange in 2 alluvial rivers in northwestern montana. *Journal of the North American Benthological Society* **21**:370-383.
- Peterson, B. J., W. M. Wollheim, P. J. Mulholland, J. R. Webster, J. L. Meyer, J. L. Tank, E. Marti, W. B. Bowden, H. M. Valett, A. E. Hershey, W. H. McDowell, W. K. Dodds, S. K. Hamilton, S. Gregory, and D. D. Morrall. 2001. Control of nitrogen export from watersheds by headwater streams. *Science* **292**:86-90.
- Pickett, S. T. A., J. Kolasa, J. J. Armesto, and S. L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* **54**:129-136.
- Pickett, S. T. A. and P. S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida.

- Poole, G. C. 2002. Fluvial landscape ecology: Addressing uniqueness within the river discontinuum. *Freshwater Biology* **47**:641-660.
- Reid, B.L. 2007. Energy flow in a floodplain aquifer system. Dissertation. The University of Montana, Missoula, Montana, USA.
- Riber, H. H. and R. G. Wetzel. 1987. Boundary-layer and internal diffusion effects on phosphorus fluxes in lake periphyton. *Limnology and Oceanography* **32**:1181-1194.
- Schindler, D. W. 1974. Eutrophication and recovery in experimental lakes - implications for lake management. *Science* **184**:897-899.
- Sebetich, M. J., V. C. Kennedy, S. M. Zand, R. J. Avanzino, and G. W. Zellweger. 1984. Dynamics of added nitrate and phosphate compared in a northern California woodland stream. *Water Resources Bulletin* **20**:93-101.
- Smock, L. A., G. M. Metzler, and J. E. Gladden. 1989. Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology* **70**:764-775.
- Spasojevic, M. J., R. J. Aicher, G. R. Koch, E. S. Marquardt, N. Mirotchnick, T. G. Troxler, and S. L. Collins. 2010. Fire and grazing in a mesic tallgrass prairie: Impacts on plant species and functional traits. *Ecology* **91**:1651-1659.
- Spivak, A. C., M. J. Vanni, and E. M. Mette. 2011. Moving on up: Can results from simple aquatic mesocosm experiments be applied across broad spatial scales? *Freshwater Biology* **56**:279-291.
- Sponseller, R. A. and S. G. Fisher. 2006. Drainage size, stream intermittency, and ecosystem function in a sonoran desert landscape. *Ecosystems* **9**:344-356.
- Solorzano, L. 1969. Determination of ammonia in natural waters by phenolhypochlorite method. *Limnology and Oceanography* **14**:799-801.
- Stanford, J. A. 2006. Landscapes and riverscapes. Pages 3-21 *in* F. R. Hauer and G. A. Lamberti, editors. *Methods in Stream Ecology*. Academic Press, San Diego, California.
- Stanford, J. A., M. S. Lorang, and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **29**:123-136.
- Stanford, J. A. and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers - connectivity and the hyporheic corridor. *Journal of the North American Benthological Society* **12**:48-60.

- Stanford, J. A., J. V. Ward, and B. K. Ellis. 1994. Ecology of the alluvial aquifers of the flathead river, montana (USA). Pages 367-390 in J. Gilbert, D. L. Danielopol, and J. A. Stanford, editors. *Groundwater Ecology*. Academic Press, San Diego, California.
- Sterner, R. W., J. J. Elser, and D. O. Hessen. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. *Biogeochemistry* **17**:49-67.
- Sugimura, Y. and Y. Suzuki. 1988. A high-temperature catalytic-oxidation method for the determination of non-volatile dissolved organic-carbon in seawater by direct injection of a liquid sample. *Marine Chemistry* **24**:105-131.
- Tank, J. L., E. J. Rosi-Marshall, M. A. Baker, and R. O. Hall. 2008. Are rivers just big streams? A pulse method to quantify nitrogen demand in a large river. *Ecology* **89**:2935-2945.
- Tank, J. L. and J. R. Webster. 1998. Interaction of substrate and nutrient availability on wood biofilm processes in streams. *Ecology* **79**:2168-2179.
- Tett, P., M. G. Kelly, and G. M. Hornberger. 1975. Method for spectrophotometric measurement of chlorophyll-a and pheophytin-a in benthic microalgae. *Limnology and Oceanography* **20**:887-896.
- Tett, P., M. G. Kelly, and G. M. Hornberger. 1977. Estimation of chlorophyll-a and pheophytin-a in methanol. *Limnology and Oceanography* **22**:579-580.
- Triska, F. J., J. H. Duff, and R. J. Avanzino. 1993. Patterns of hydrological exchange and nutrient transformation in the hyporheic zone of a gravel-bottom stream - examining terrestrial aquatic linkages. *Freshwater Biology* **29**:259-274.
- Triska, F. J., V. C. Kennedy, R. J. Avanzino, G. W. Zellweger, and K. E. Bencala. 1989. Retention and transport of nutrients in a 3rd-order stream - channel processes. *Ecology* **70**:1877-1892.
- Turner, M. G. 1989. Landscape ecology - the effect of pattern on process. *Annual Review of Ecology and Systematics* **20**:171-197.
- Turner, M. G. 2005. Landscape ecology: What is the state of the science? *Annual Review of Ecology Evolution and Systematics* **36**:319-344.
- Turner, M. G. and F. S. Chapin III. 2005. Causes and consequences of spatial heterogeneity in ecosystem function. Pages 9-30 in G. M. Lovett, C. G. Jones, M. G. Turner, and K. C. Weathers, editors. *Ecosystem Function in Heterogeneous Landscapes*. Springer, New York, NY.

- Turner, M. G., D. B. Tinker, W. H. Romme, D. M. Kashian, and C. M. Litton. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, yellowstone national park (USA). *Ecosystems* **7**:751-775.
- Valett, H. M., C. L. Crenshaw, and P. F. Wagner. 2002. Stream nutrient uptake, forest succession, and biogeochemical theory. *Ecology* **83**:2888-2901.
- Valett, H. M., S. G. Fisher, N. B. Grimm, and P. Camill. 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. *Ecology* **75**:548-560.
- Valett, H. M., J. A. Morrice, C. N. Dahm, and M. E. Campana. 1996. Parent lithology, surface-groundwater exchange, and nitrate retention in headwater streams. *Limnology and Oceanography* **41**:333-345.
- Valett, H.M., B.L. Reid, F.R. Hauer, and J.A. Stanford. In review. Local and routing control of oxygen dynamics in the alluvial aquifer of a gravel-bed river. *Ecological Monographs*.
- Valett, H. M., S. A. Thomas, P. J. Mulholland, J. R. Webster, C. N. Dahm, C. S. Fellows, C. L. Crenshaw, and C. G. Peterson. 2008. Endogenous and exogenous control of ecosystem function: N cycling in headwater streams. *Ecology* **89**:3515-3527.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. River continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:130-137.
- Vitousek, P. M. and W. A. Reiners. 1975. Ecosystem succession and nutrient retention - hypothesis. *Bioscience* **25**:376-381.
- Wallace, J. B. and A. C. Benke. 1984. Quantification of wood habitat in sub-tropical coastal-plain streams. *Canadian Journal of Fisheries and Aquatic Sciences* **41**:1643-1652.
- Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* **277**:102-104.
- Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* **69**:409-442.
- Ward, J. V. 1989. The 4-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* **8**:2-8.
- Ward, J. V., K. Tockner, D. B. Arscott, and C. Claret. 2002. Riverine landscape diversity. *Freshwater Biology* **47**:517-539.

- Warren, D. R., E. S. Bernhardt, R. O. Hall, and G. E. Likens. 2007. Forest age, wood and nutrient dynamics in headwater streams of the Hubbard Brook experimental forest, NH. *Earth Surface Processes and Landforms* **32**:1154-1163.
- Webster, J. R. and E. F. Benfield. 1986. Vascular plant breakdown in fresh-water ecosystems. *Annual Review of Ecology and Systematics* **17**:567-594.
- Webster, J. R. and H. M. Valett. 2006. Solute dynamics. Pages 169-185 in F. R. Hauer and G. A. Lamberti, editors. *Methods in stream ecology*. Academic Press, San Diego, California.
- Webster, K. E., T. K. Kratz, C. J. Bowser, J. J. Magnuson, and W. J. Rose. 1996. The influence of landscape position on lake chemical responses to drought in northern Wisconsin. *Limnology and Oceanography* **41**:977-984.
- White, D. S. 1993. Perspectives on defining and delineating hyporheic zones. *Journal of the North American Benthological Society* **12**:61-69.
- Whited, D. C., M. S. Lorang, M. J. Harner, F. R. Hauer, J. S. Kimball, and J. A. Stanford. 2007. Climate, hydrologic disturbance, and succession: Drivers of floodplain pattern. *Ecology* **88**:940-953.
- Winemiller, K. O., A. S. Flecker, and D. J. Hoeinghaus. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. *Journal of the North American Benthological Society* **29**:84-99.
- Woessner, W. W. 2000. Stream and fluvial plain ground water interactions: Rescaling hydrogeologic thought. *Ground Water* **38**:423-429.
- Wood, E. D., Armstrong, F. A., and F. A. Richards. 1967. Determination of nitrate in sea water by cadmium-copper reduction to nitrite. *Journal of the Marine Biological Association of the United Kingdom* **47**:23-&.
- Wyatt, K. H., F. R. Hauer, and G. F. Pessoney. 2008. Benthic algal response to hyporheic-surface water exchange in an alluvial river. *Hydrobiologia* **607**:151-161.
- Zall, D. M., D. Fisher, and M. Q. Garner. 1956. Photometric determination of chlorides in water. *Analytical Chemistry* **28**:1665-1668.
- Zimov, S. A., Y. V. Voropaev, I. P. Semiletov, S. P. Davidov, S. F. Prosiannikov, F. S. Chapin, M. C. Chapin, S. Trumbore, and S. Tyler. 1997. North Siberian lakes: A methane source fueled by Pleistocene carbon. *Science* **277**:800-802.

Table 1. Summary of methods used to assess the structural and functional character of spring brooks occupying different landscape positions on the Nyack flood plain.

Measure	Method	Deduction
Structure	Stream bed particle size distribution	Disturbance gradient & stream power
	Photosynthetically active radiation	Channel structure & landscape position
	Canopy density	Channel structure & landscape position
	Benthic organic matter standing stocks	Allochthonous inputs
	Groundwater chemistry & hydraulics	Allochthonous inputs
	Surface water chemistry	Channel structure & background conditions
Function	Reach-scale solute releases	Nutrient uptake
	Microcosm experiment	Nutrient uptake

Table 2. Chemical properties of ground water at the upwelling point of spring brooks occupying different landscape positions on the Nyack flood plain. Data are means \pm 1 SE. *P*-values represent ANOVA results among landscape positions. Means with unique superscripts within a row are statistically different (Tukey's HSD, *P* < 0.05).

Analyte	Landscape Position			<i>P</i>
	Parafluvial	Active Orthofluvial	Passive Orthofluvial	
Dissolved organic carbon (mg L ⁻¹)	< 0.05	< 0.05	< 0.05	0.571
NO ₃ -N (μg L ⁻¹)	109.4 \pm 35.9 ^A	32.3 \pm 9.0 ^B	34.3 \pm 4.8 ^B	0.033
NH ₄ -N (μg L ⁻¹)	< 5.0	< 5.0	< 5.0	-
SRP (μg L ⁻¹)	1.8 \pm 0.1	1.5 \pm 0.5	< 1.0	0.521
Atomic N:P	63.0 \pm 16.6	34.1 \pm 12.9	47.6 \pm 13.3	0.396
²²² Rn (Bq L ⁻¹)	6.0 \pm 2.8	7.8 \pm 1.2	10.1 \pm 3.7	0.554

Notes: Sample size (*n*) used to determine mean values: parafluvial (*n* = 3), active orthofluvial (*n* = 5), passive orthofluvial (*n* = 3).

Table 3. 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. Data are means \pm 1 SE. *P*-values represent Kruskal-Wallis or ANOVA test results among sites. Means with unique superscripts within a row are statistically different (Tukey's HSD, *P* < 0.05).

Reach Characteristics	Landscape Position and Site Number						<i>P</i>
	PF1	PF2	AO1	AO2	PO1	PO2	
Stream characteristics							
Discharge (L s ⁻¹)	4.44	43.41	28.21	17.84	30.14	23.92	
Mean velocity (cm s ⁻¹)	2.55	7.94	1.64	8.36	2.02	1.88	
Wetted Width (m)	3.59 \pm 0.51 ^B	1.71 \pm 0.18 ^C	5.98 \pm 1.1 ^B	4.44 \pm 0.5 ^B	10.95 \pm 0.79 ^A	3.85 \pm 0.29 ^B	<0.0001
Depth (cm)	6.1 \pm 0.4 ^D	15.8 \pm 0.7 ^C	23.2 \pm 2.2 ^B	8.3 \pm 0.5 ^D	18.5 \pm 0.8 ^{BC}	30.8 \pm 1.3 ^A	<0.0001
Insolation and canopy cover							
PAR photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1290.6 \pm 20.2 ^A	1316.9 \pm 46.0 ^A	805.3 \pm 82.1 ^B	547.6 \pm 82.6 ^{BC}	102.4 \pm 10.5 ^D	411.1 \pm 90.8 ^C	<0.0001
Vegetative canopy cover/shading (%)	0.0 ^E	2.4 \pm 1.0 ^{DE}	10.0 \pm 3.2 ^{CD}	12.4 \pm 1.5 ^{BC}	21.5 \pm 2.1 ^B	49.7 \pm 4.1 ^A	<0.0001

Notes: Sample size (*n*) used to determine mean values: wetted width (11–20), depth (149–428), PAR (33), and canopy cover (44). Wetted width data were log-transformed for statistical analysis; data shown are actual mean values for all variables.

Table 4. Benthic standing stocks in spring brooks of parafluvial (PF), active orthofluvial (AO), and passive orthofluvial (PO) zones on the Nyack flood plain. Data are means \pm 1 SE ($n = 10-11$). P -values represent ANOVA test results among sites. Means with unique superscripts within a row are statistically different (Tukey's HSD, $P < 0.05$).

Benthic Characteristics	Landscape Position and Site Number						P
	PF1	PF2	AO1	AO2	PO1	PO2	
Large woody debris							
Wood mass (kg m ⁻²)	0.041 \pm 0.029 ^C	0.340 \pm 0.320 ^{BC}	3.985 \pm 1.956 ^B	0.101 \pm 0.063 ^{BC}	1.330 \pm 0.508 ^{BC}	13.508 \pm 2.156 ^A	<0.0001
Wood volume (m ³ m ⁻²)	0.0001 \pm 0.0001 ^B	0.0009 \pm 0.0008 ^B	0.0106 \pm 0.0052 ^B	0.0002 \pm 0.0001 ^B	0.0035 \pm 0.0014 ^B	0.0360 \pm 0.0057 ^A	<0.0001
Epixylon							
AFDM (g m ⁻²)	1.3 \pm 1.0 ^C	3.4 \pm 1.8 ^C	4.4 \pm 1.9 ^{BC}	1.2 \pm 0.7 ^C	8.8 \pm 1.6 ^{AB}	49.7 \pm 31.6 ^A	<0.0001
Organic matter (%)	12.9 \pm 9.5 ^{AB}	10.4 \pm 6.1 ^{AB}	1.0 \pm 0.4 ^B	7.2 \pm 4.4 ^B	28.2 \pm 5.9 ^A	11.3 \pm 3.3 ^{AB}	0.0047
Chlorophyll a (mg m ⁻²)	0.2 \pm 0.2 ^C	3.8 \pm 3.1 ^{BC}	1.4 \pm 0.76 ^{BC}	0.4 \pm 0.2 ^C	7.1 \pm 1.8 ^A	7.6 \pm 3.4 ^{AB}	<0.0001
Epilithon							
AFDM (g m ⁻²)	1.5 \pm 0.1 ^C	4.2 \pm 1.0 ^C	5.8 \pm 3.0 ^B	5.9 \pm 1.1 ^B	57.2 \pm 14.2 ^A	0.4 \pm 0.4 ^D	<0.0001
Organic matter (%)	25.0 \pm 2.8 ^A	23.0 \pm 3.6 ^A	15.4 \pm 1.9 ^A	23.4 \pm 2.5 ^A	16.1 \pm 1.8 ^A	1.4 \pm 1.4 ^B	<0.0001
Chlorophyll a (mg m ⁻²)	0.9 \pm 0.2 ^{CD}	3.5 \pm 1.4 ^{BC}	2.5 \pm 0.4 ^{BC}	5.6 \pm 1.2 ^B	47.9 \pm 10.5 ^A	0.5 \pm 0.5 ^D	<0.0001
FPOM							
AFDM (g m ⁻²)	10.4 \pm 9.4 ^C	15.7 \pm 2.0 ^C	13.5 \pm 4.2 ^C	221.3 \pm 71.2 ^B	781.6 \pm 139.3 ^A	127.7 \pm 92.9 ^B	<0.0001
Organic matter (%)	4.7 \pm 0.7 ^{BC}	4.7 \pm 0.3 ^{BC}	6.2 \pm 0.4 ^B	3.8 \pm 0.3 ^C	12.4 \pm 1.3 ^A	5.7 \pm 0.3 ^{BC}	<0.0001
Chlorophyll a (mg m ⁻²)	3.2 \pm 0.9 ^C	4.1 \pm 1.0 ^C	3.4 \pm 1.1 ^C	18.5 \pm 8.3 ^{BC}	373.8 \pm 83.5 ^{AB}	48.9 \pm 14.9 ^A	<0.0001
CPOM							
AFDM (g m ⁻²)	2.1 \pm 1.6 ^C	12.6 \pm 9.8 ^C	3.0 \pm 1.7 ^C	150.0 \pm 74.2 ^B	272.2 \pm 102.1 ^B	1204.7 \pm 395.8 ^A	<0.0001
Organic matter (%)	47.0 \pm 13.0	51.5 \pm 10.1	50.8 \pm 11.3	56.8 \pm 7.3	59.7 \pm 5.6	59.0 \pm 4.2	0.903
Macrophytes (g m ⁻²)	0 ^B	0 ^B	0 ^B	0.3 \pm 0.3 ^B	0 ^B	4.6 \pm 2.2 ^A	<0.0001
Total organic matter (kg m ⁻²)	0.056	0.376	4.012	0.480	2.450	14.895	
Chlorophyll a : AFDM	0.0011 \pm 0.0002 ^B	0.0011 \pm 0.0002 ^B	0.0011 \pm 0.0002 ^B	0.00012 \pm 0.0001 ^B	0.0027 \pm 0.0003 ^A	0.0010 \pm 0.0002 ^B	<0.0001

Notes: Benthic standing stocks were log-transformed and proportions were arcsine square root-transformed for statistical analysis; data shown are untransformed mean values.

Table 5. Physiochemical properties of surface and ground water at the upwelling point and along study reaches in spring brooks of parafluvial (PO), active orthofluvial (AO), and passive orthofluvial (PO) zones on the Niyack flood plain. *P*-values represent ANOVA results among sites. Means with unique superscripts within a row are statistically different (Tukey's HSD, *P* < 0.05).

Water Type & Measure	Landscape Position & Site Number						<i>P</i>
	PF1	PF2	AO1	AO2	PO1	PO2	
Surface water							
Temperature (°C)	13.9 ± 0.5 ^{AB}	15.3 ± 1.6 ^A	12.2 ± 0.3 ^{BC}	8.9 ± 0.5 ^D	8.7 ± 0.6 ^D	9.6 ± 0.4 ^{CD}	< 0.0001
Conductivity (µS cm ⁻¹)	218.0 ± 4.4 ^B	202.5 ± 0.6 ^C	223.1 ± 3.0 ^B	249.1 ± 4.2 ^A	241.0 ± 4.5 ^A	183.1 ± 1.9 ^D	< 0.0001
pH	8.10 ± 0.04 ^A	6.96 ± 0.04 ^B	8.01 ± 0.02 ^A	7.97 ± 0.04 ^A	8.10 ± 0.04 ^A	7.2 ± 0.2 ^B	< 0.0001
Dissolved Oxygen (mg L ⁻¹)	4.7 ± 0.9	4.3 ± 0.3	4.3 ± 0.4	3.5 ± 0.6	5.9 ± 0.6	4.6 ± 0.2	0.0853
Dissolved Oxygen (% saturation)	43.1 ± 6.8	41.2 ± 2.9	39.4 ± 4.9	30.1 ± 4.9	50.6 ± 4.5	40.1 ± 1.5	0.0738
Ground water							
Temperature (°C)	14.7 ± 0.4 ^A	12.4 ± 0.5 ^B	12.5 ± 0.2 ^B	8.6 ± 0.4 ^D	7.8 ± 0.01 ^D	10.4 ± 0.3 ^C	< 0.0001
Conductivity (µS cm ⁻¹)	212.9 ± 2.0 ^{BC}	192.8 ± 3.2 ^C	247.2 ± 6.5 ^B	227.9 ± 3.1 ^{BC}	225.3 ± 3.3 ^{BC}	299.2 ± 39.2 ^A	< 0.0001
pH	8.1 ± 0.02 ^A	6.97 ± 0.01 ^C	7.91 ± 0.02 ^B	8.06 ± 0.03 ^{AB}	8.15 ± 0.04 ^A	6.95 ± 0.10 ^C	< 0.0001
Dissolved Oxygen (mg L ⁻¹)	4.5 ± 0.4 ^{AB}	4.2 ± 0.2 ^{AB}	1.63 ± 0.26 ^D	3.9 ± 0.3 ^{BC}	5.6 ± 0.4 ^A	2.6 ± 0.4 ^{CD}	< 0.0001
Dissolved Oxygen (% saturation)	42.1 ± 3.6 ^{AB}	41.7 ± 1.8 ^{AB}	15.4 ± 2.5 ^D	33.9 ± 2.7 ^{BC}	47.5 ± 3.8 ^A	23.5 ± 3.8 ^{CD}	< 0.0001

Notes: Data for temperature, conductivity, pH, and dissolved oxygen data are calculated from *n* = 8 – 11 (surface water) and *n* = 15 – 21 (ground water) sampling points.

Table 6. Chemical properties of surface and ground water at the upwelling point and along study reaches in spring brooks of parafluvial (PF), active orthofluvial (AO), and passive orthofluvial (PO) zones on the Nyack flood plain. Data are means \pm 1 SE. *P*-values represent Kruskal-Wallis ANOVA results among sites. Means with unique superscripts within a row are statistically different (Tukey's HSD, *P* < 0.05).

Water Type & Analyte	Landscape Position & Site Number						<i>P</i>
	PF1	PF2	AO1	AO2	PO1	PO2	
Surface water							
Dissolved organic carbon (mg L ⁻¹)	0.44 \pm 0.05 ^B	0.53 \pm 0.03 ^B	0.47 \pm 0.02 ^B	0.37 \pm 0.04 ^B	0.42 \pm 0.04 ^B	0.81 \pm 0.06 ^A	0.0002
NH ₄ -N (μ g L ⁻¹)	< 5.0	< 5.0	< 5.0	< 5.0	< 5.0	5.6 \pm 2.5	0.0521
NO ₃ -N (μ g L ⁻¹)	10.5 \pm 1.3	9.2 \pm 0.2	22.4 \pm 5.9	25.0 \pm 5.3	21.2 \pm 4.2	21.0 \pm 1.3	0.0468
SRP (μ g L ⁻¹)	1.4 \pm 0.2	1.3 \pm 0.3	< 1.0	1.4 \pm 0.6	< 1.0	1.3 \pm 0.2	0.0754
Atomic N:P	6.5 \pm 0.7	5.9 \pm 0.1	12.4 \pm 2.9	13.8 \pm 2.6	11.9 \pm 2.1	13.3 \pm 1.8	0.0358
Ground water							
Dissolved organic carbon (mg L ⁻¹)	0.37 \pm 0.02 ^B	0.53 \pm 0.02 ^B	0.58 \pm 0.06 ^B	0.27 \pm 0.03 ^B	0.27 \pm 0.04 ^B	1.64 \pm 0.30 ^A	< 0.0001
NH ₄ -N (μ g L ⁻¹)	< 5.0 ^B	< 5.0 ^B	23.9 \pm 12.3 ^B	< 5.0 ^B	< 5.0 ^B	41.7 \pm 14.7 ^A	< 0.0001
NO ₃ -N (μ g L ⁻¹)	12.7 \pm 0.7 ^B	22.9 \pm 3.0 ^B	9.2 \pm 2.8 ^B	52.6 \pm 7.5 ^A	68.5 \pm 7.2 ^A	14.3 \pm 4.5 ^B	< 0.0001
SRP (μ g L ⁻¹)	1.4 \pm 0.4 ^{ABC}	2.3 \pm 0.5 ^{AB}	1.3 \pm 0.2 ^{ABC}	1.1 \pm 0.1 ^{BC}	< 1.0 ^C	2.7 \pm 0.7 ^A	0.0003
Atomic N:P	7.6 \pm 0.3 ^C	12.7 \pm 1.5 ^{BC}	17.2 \pm 6.2 ^{BC}	27.6 \pm 3.8 ^{AB}	35.6 \pm 3.6 ^A	29.1 \pm 7.3 ^{AB}	< 0.0001

Notes: Mean values calculated from *n* = 8 – 11 (surface water) and *n* = 15 – 21 (ground water) background samples. N:P ratios were calculated as the mean of sample TIN (NO₃-N + NH₄-N):SRP concentration.

Table 7. Comparison of ground and surface water chemical environments within spring brooks of parafluvial (PF), active orthofluvial (AO), and passive orthofluvial (PO) zones on the Nyack flood plain. Values represent results (*P*) of Wilcoxon two-sample tests ($\alpha = 0.05$) for differences within sites.

Analyte	Landscape Position & Site Number					
	PF1	PF2	AO1	AO2	PO1	PO2
Dissolved organic carbon	0.1457	0.9778	0.3305	0.0492	0.0102	0.0118
NH ₄ -N	-	-	0.128	-	0.5597	0.0029
NO ₃ -N	0.1374	0.0005	0.0373	0.0282	0.0027	0.0704
SRP	0.3492	0.155	0.1404	0.1896	0.4466	0.1444
Atomic N:P	0.1374	0.0005	0.7931	0.0282	0.0027	0.0945

Table 8. Ambient and peak nitrate-nitrogen ($\text{NO}_3\text{-N}$, mg L^{-1}) concentrations and nutrient spiraling metrics (S_{sp} , v_f , U , U_{amb}) associated with solute releases in spring brooks of parafluvial (PF), active orthofluvial (AO), and passive orthofluvial (PO) floodplain zones. P -values represent paired t-test ($\alpha = 0.05$) results for the mean difference between observed and predicted (i.e., conservative) $\text{NO}_3\text{-N}$ among sites.

Landscape Position	Site	Reach Length (m)	$\text{NO}_3\text{-N}$ (mg L^{-1})		P	k_{sp} (m^{-1})	S_{sp} (km)	v_f (mm s^{-1})	U ($\mu\text{g m}^{-2}\text{s}^{-1}$)	U_{amb} ($\mu\text{g m}^{-2}\text{s}^{-1}$)
			Ambient	Peak						
Parafluvial	PF1	50	0.013	2.792	-0.041 \pm 0.029	0.1798	0.25	0.017	11.521	0.0008
	PF2	100	0.010	0.577	0.002 \pm 0.004	0.5520	0.85	0.014	0.887	0.0023
Active Orthofluvial	AO1	105	0.006	0.370	0.003 \pm 0.002	0.1080	-10.06	-0.0005	-0.065	-0.00001
	AO2	79	0.036	2.037	0.103 \pm 0.034	0.0066	-0.87	-0.005	-2.087	-0.004
Passive Orthofluvial	PO1	59	0.021	1.058	0.016 \pm 0.008	0.0754	-0.81	-0.0004	-0.416	-0.0001
	PO2	100	0.012	0.613	0.017 \pm 0.020	0.4209	1.25	0.005	0.411	0.0006

Notes: Predicted values were calculated as the product of conservative tracer (Cl) concentration and the ratio of $\text{NO}_3\text{-N:Cl}$ in the slug injectate. Mean (\pm 1 SE) predicted – observed values determined from $n = 19\text{-}25$ grab samples per solute release.

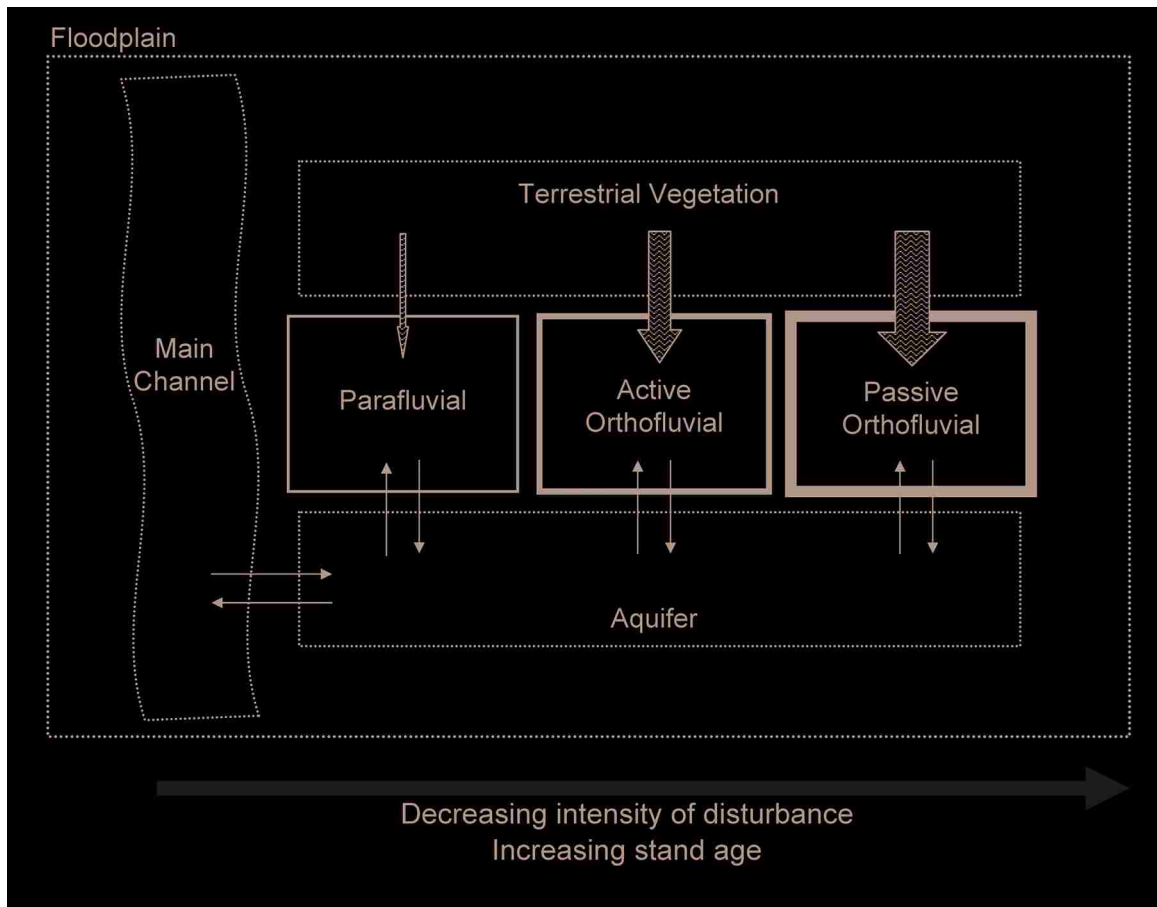


Figure 1. Conceptual diagram illustrating interactions between aquatic and terrestrial ecosystems within floodplain landscapes. Spring brooks are represented as solid boxes and classified by position on the floodplain. The thickness of the border indicates relative physical stability increasing as intensity of flood disturbance is reduced. Within the floodplain, solid arrows represent the exchange of water due to upwelling and downwelling between the main channel, alluvial aquifer, and spring brooks. Patterned arrows correspond to inputs of terrestrial organic matter.

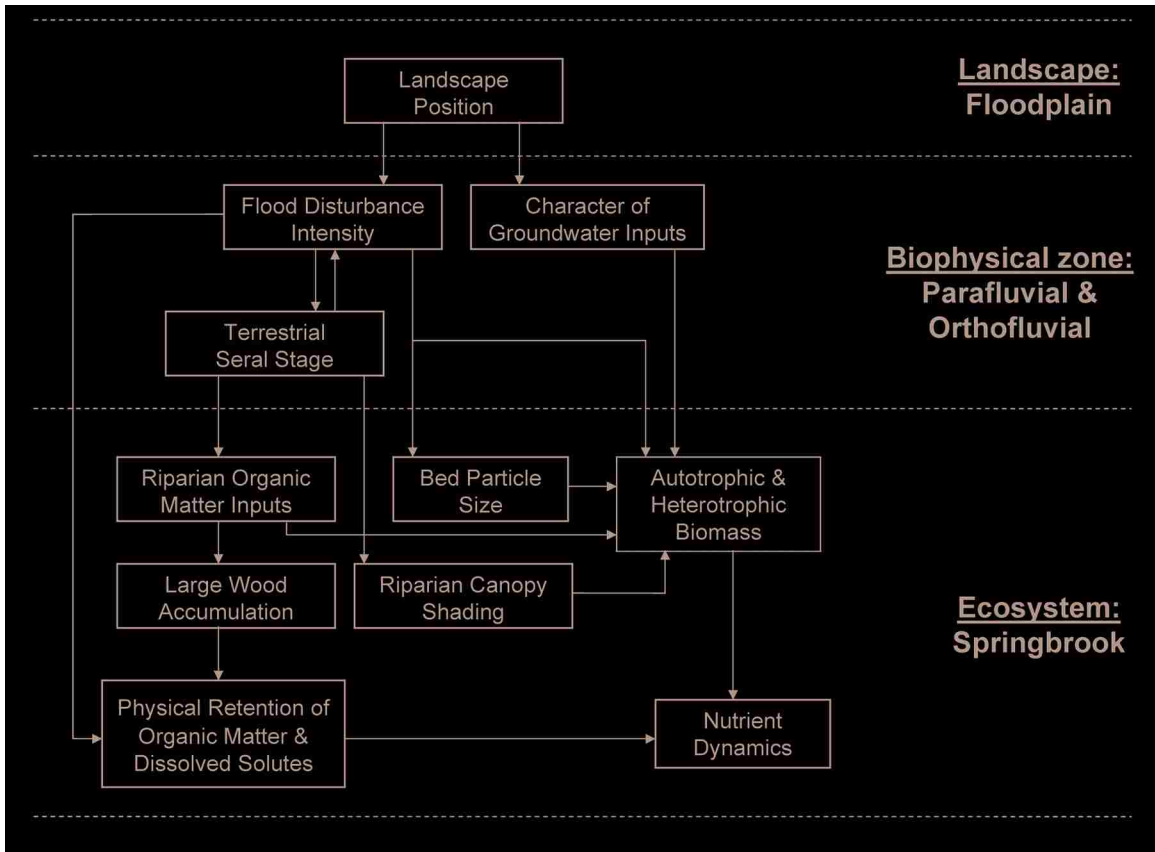


Figure 2. Flow diagram illustrating proposed drivers of springbrook structure and function across landscape, biophysical zone, and ecosystem scales.

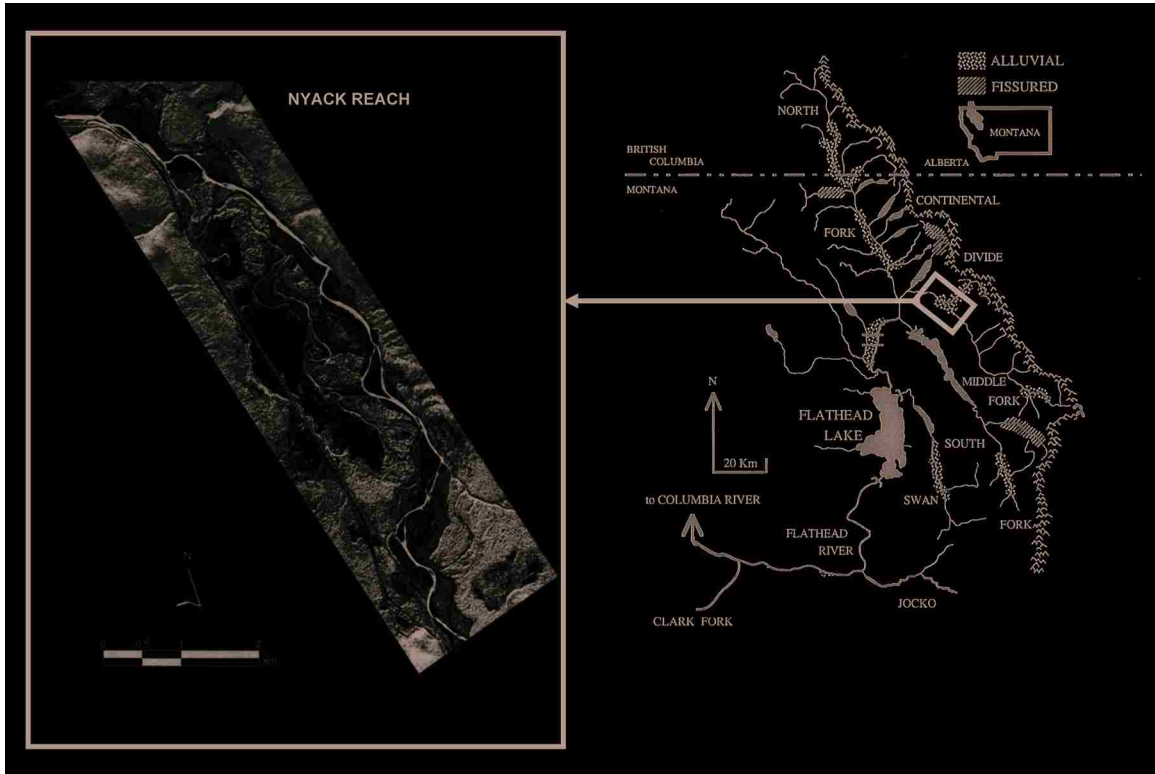


Figure 3. Map of the Nyack flood plain study site on the Middle Fork Flathead River in northwest Montana, USA. Adapted from Whited et. al 2007 and Anderson (2008).

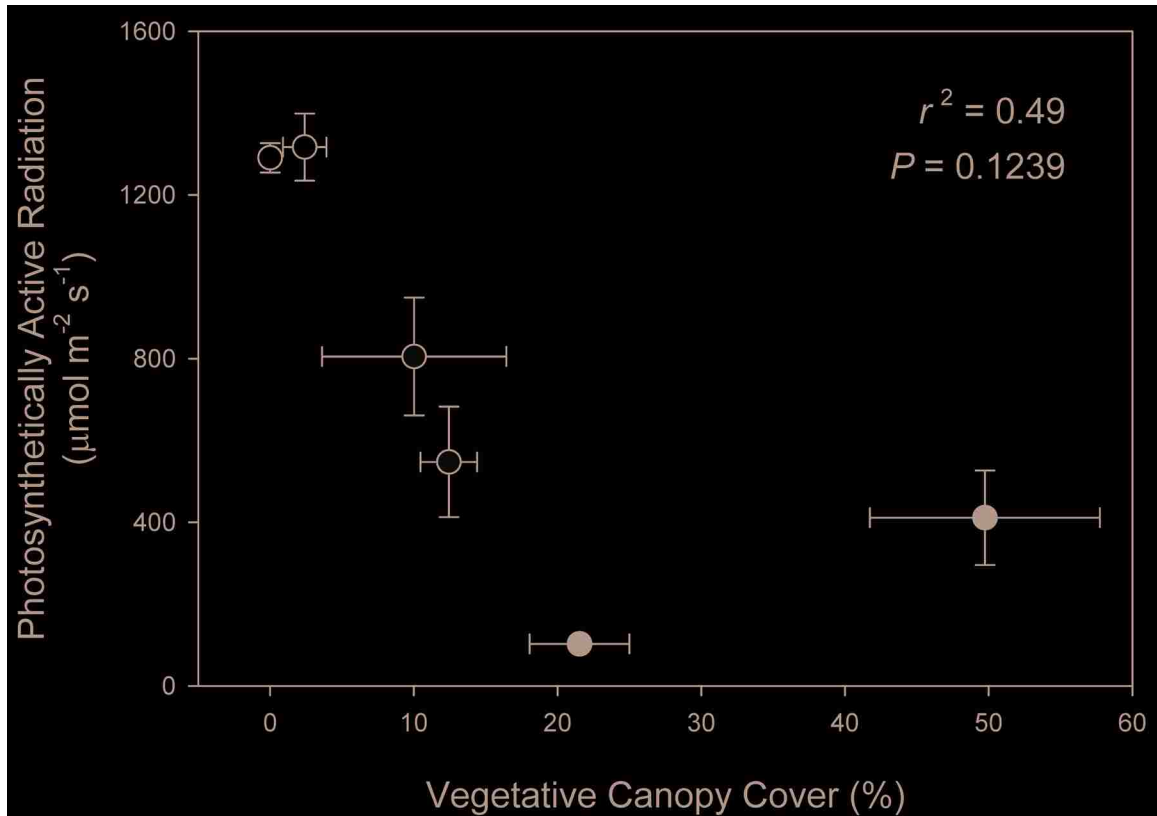


Figure 4. Relationship between percent vegetative canopy cover and photosynthetically active radiation (PAR) in spring brooks on the Nyack flood plain. Symbols are means (± 1 SE) of percent canopy cover ($n = 44$) and PAR ($n = 33$) measurements collected along parafluvial (white), active orthofluvial (grey), and passive orthofluvial (black) spring brooks on the Nyack flood plain. The coefficient of determination (r^2) and P -value were derived from simple linear regression.

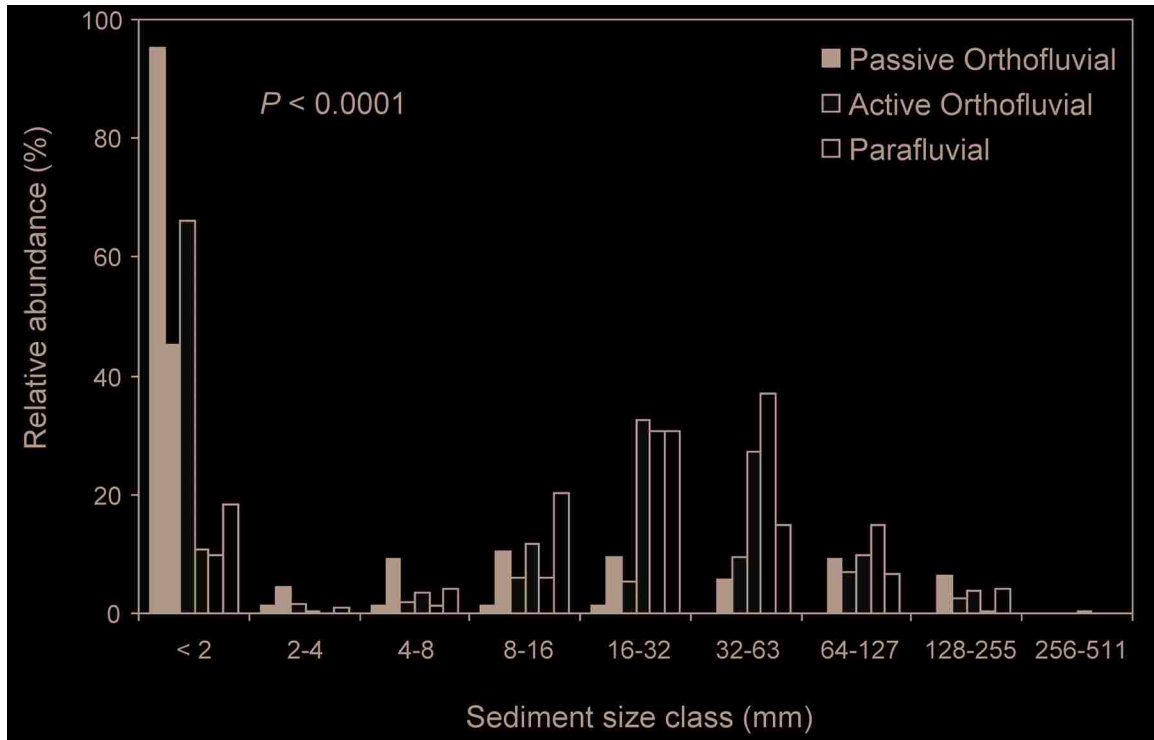


Figure 5. Relative abundance (%) of sediment size classes in spring brooks of parafluvial (white), active orthofluvial (grey), and passive orthofluvial (black) floodplain biophysical zones. The P -value represents Kruskal-Wallis ANOVA test results ($\alpha = 0.05$) among sites.

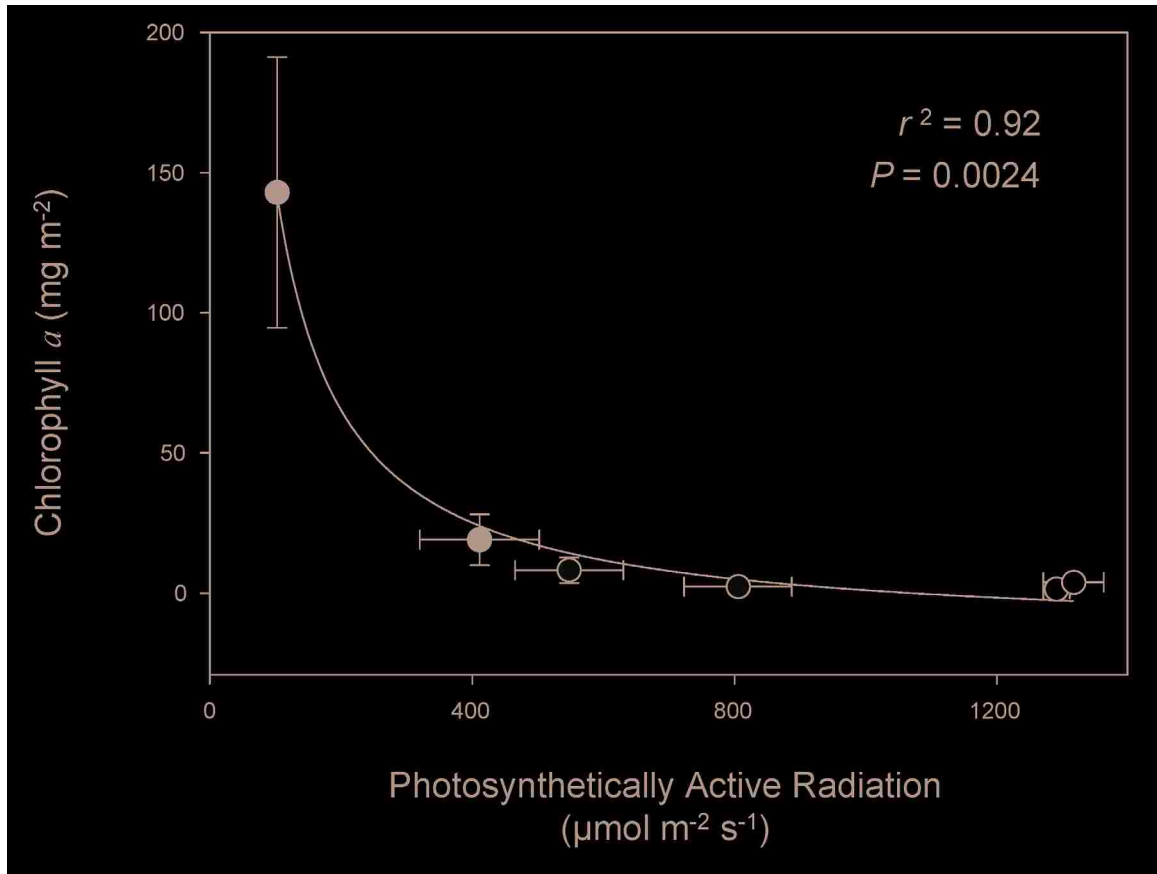


Figure 6. Relationship between chlorophyll *a* standing stock (mg m⁻²) and photosynthetically active radiation (μmol m⁻² s⁻¹). Symbols are means (± 1 SE) of chlorophyll *a* ($n = 32 - 33$) and photosynthetically active radiation ($n = 33$) measures collected from parafluvial (white), active orthofluvial (grey), and passive orthofluvial (black) spring brooks on the Nyack flood plain. Coefficients of determination (r^2) and P -values were derived from simple linear regression of natural-log transformed data.

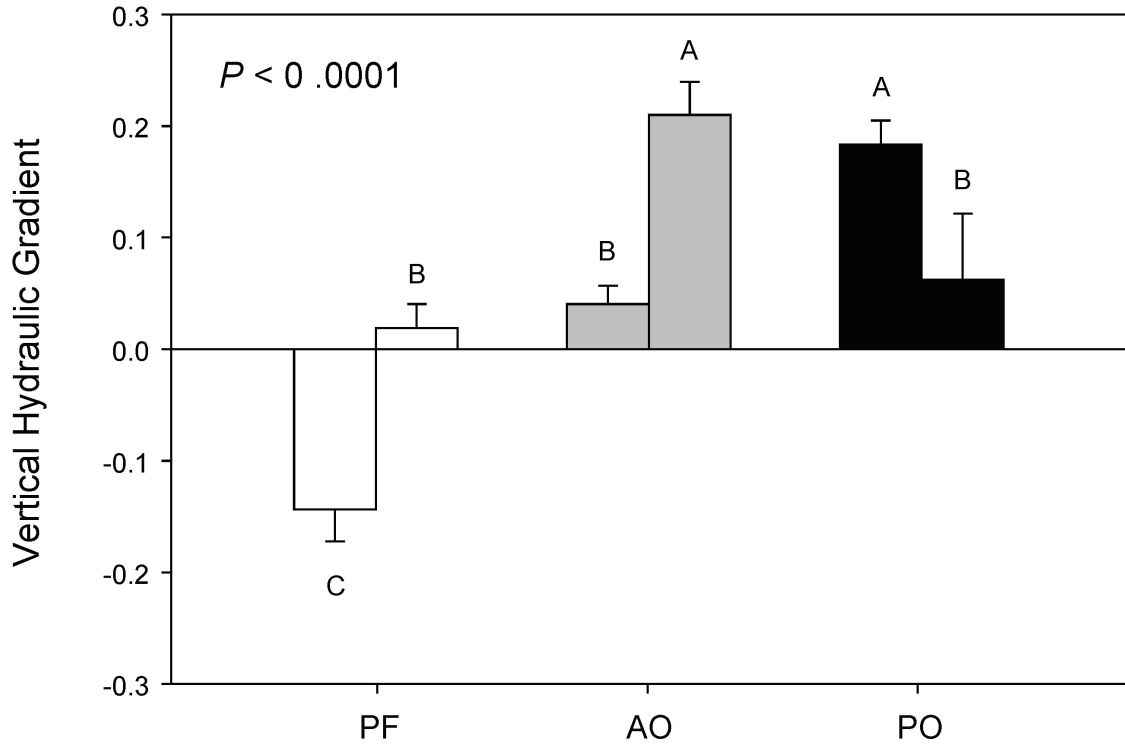


Figure 7. Mean (± 1 SE) vertical hydraulic gradient measured in parafluvial (PF, white), active orthofluvial (AO, grey), and passive orthofluvial (PO, black) spring brooks on the Nyack flood plain. Mini-piezometers were installed to 0.5 m below the streambed surface at the channel origin (i.e., ‘upwelling point’) and along an 75 – 100 m study reach. Positive values are upwelling, negative values are downwelling. The P -value represents overall ANOVA test results among sites. Bars with unique subscripts are statistically different (Tukey’s HSD, $P < 0.05$).

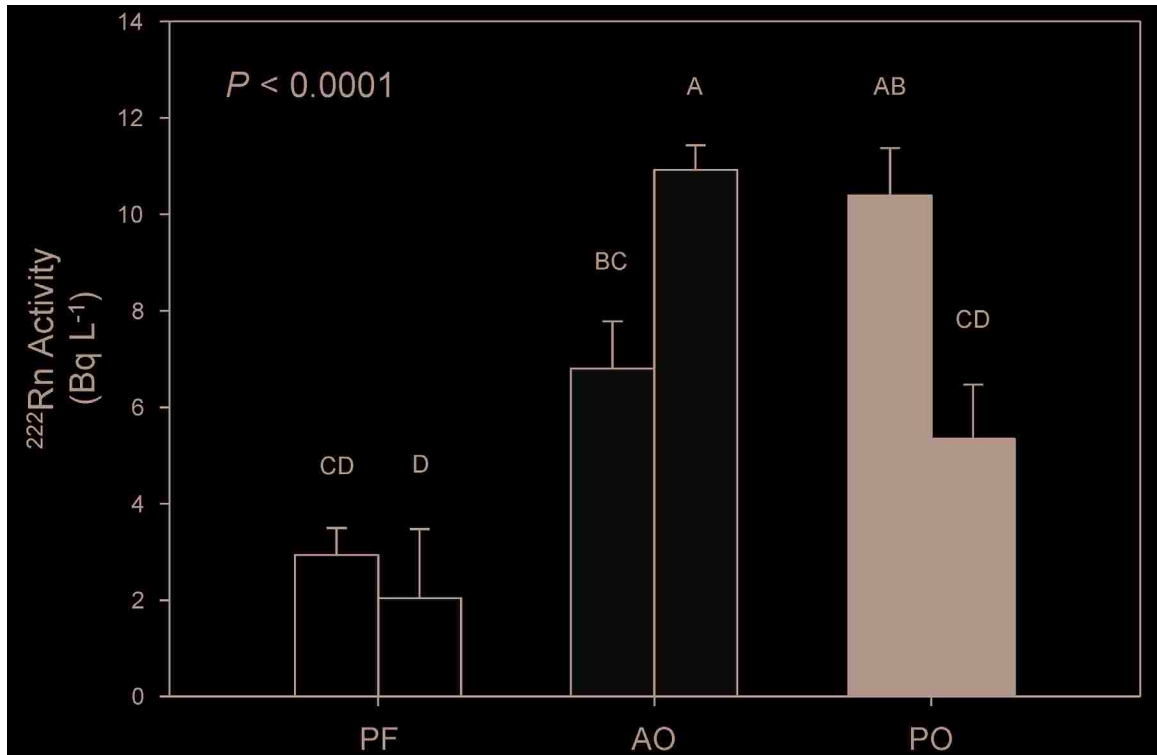


Figure 8. Mean (± 1 SE) isotopic radon activity (Bq L^{-1}) in ground water sampled from parafluvial (PF, white), active orthofluvial (AO, grey), and passive orthofluvial (PO, black) spring brooks on the Nyack flood plain. Samples were collected from the channel origin (i.e., ‘upwelling point’) and along an 80 – 100 m study reach. The P -value represents overall ANOVA test results among sites. Bars with unique subscripts are statistically different (Tukey’s HSD, $P < 0.05$).

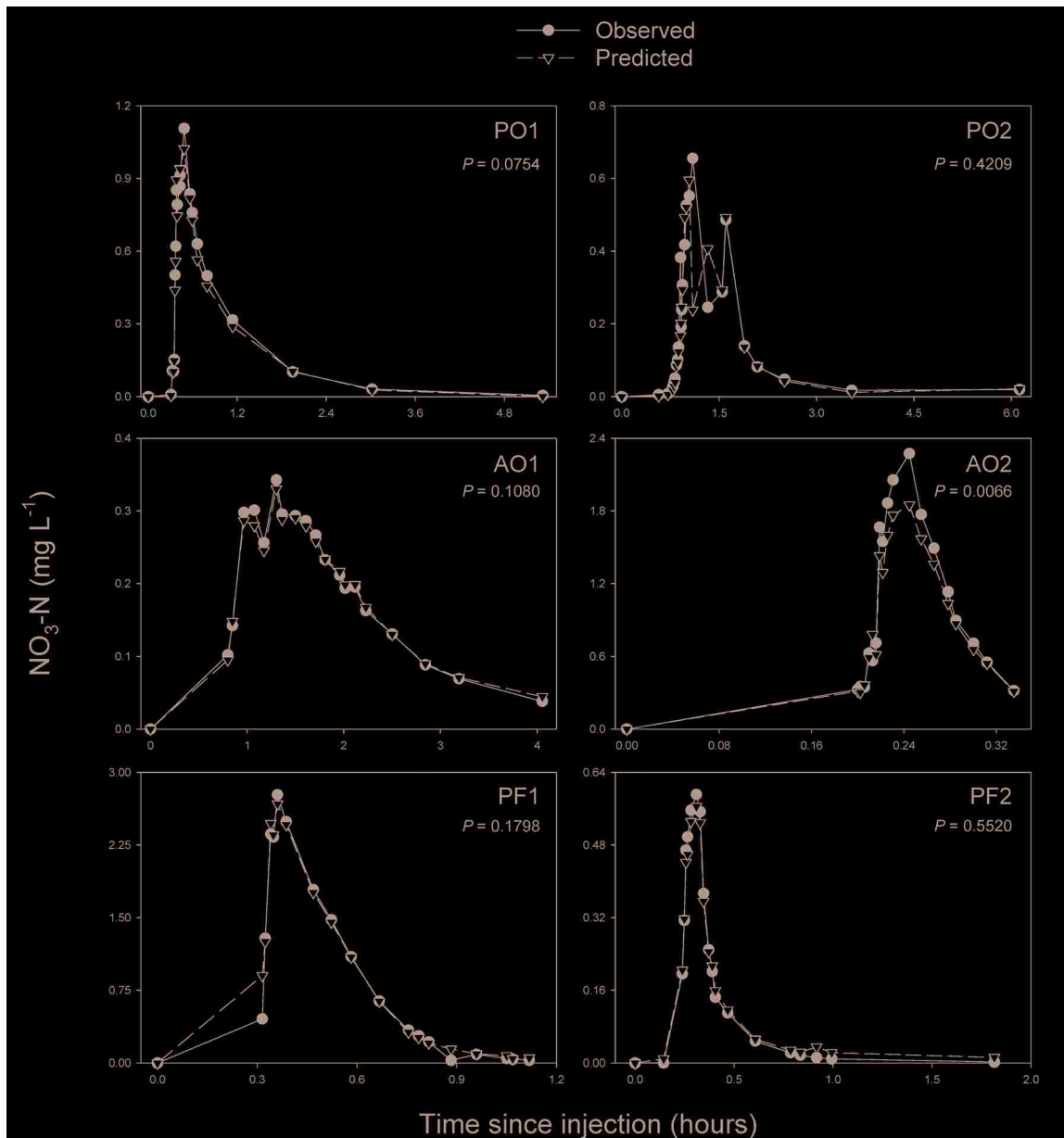


Figure 9. Observed (black circles) and predicted (white triangles) nitrate-nitrogen ($\text{NO}_3\text{-N}$, mg L^{-1}) breakthrough curves at the base of parafluvial (PO), active orthofluvial (AO), and passive orthofluvial (PO) springbrook injection reaches. The release solution was added instantaneously to the head of the reach at time 0. Predicted values were calculated as the product of conservative tracer (Cl) concentration and the ratio of N:Cl in the release solution. P -values represent paired t-test ($\alpha = 0.05$) results for the mean difference between observed and predicted $\text{NO}_3\text{-N}$.

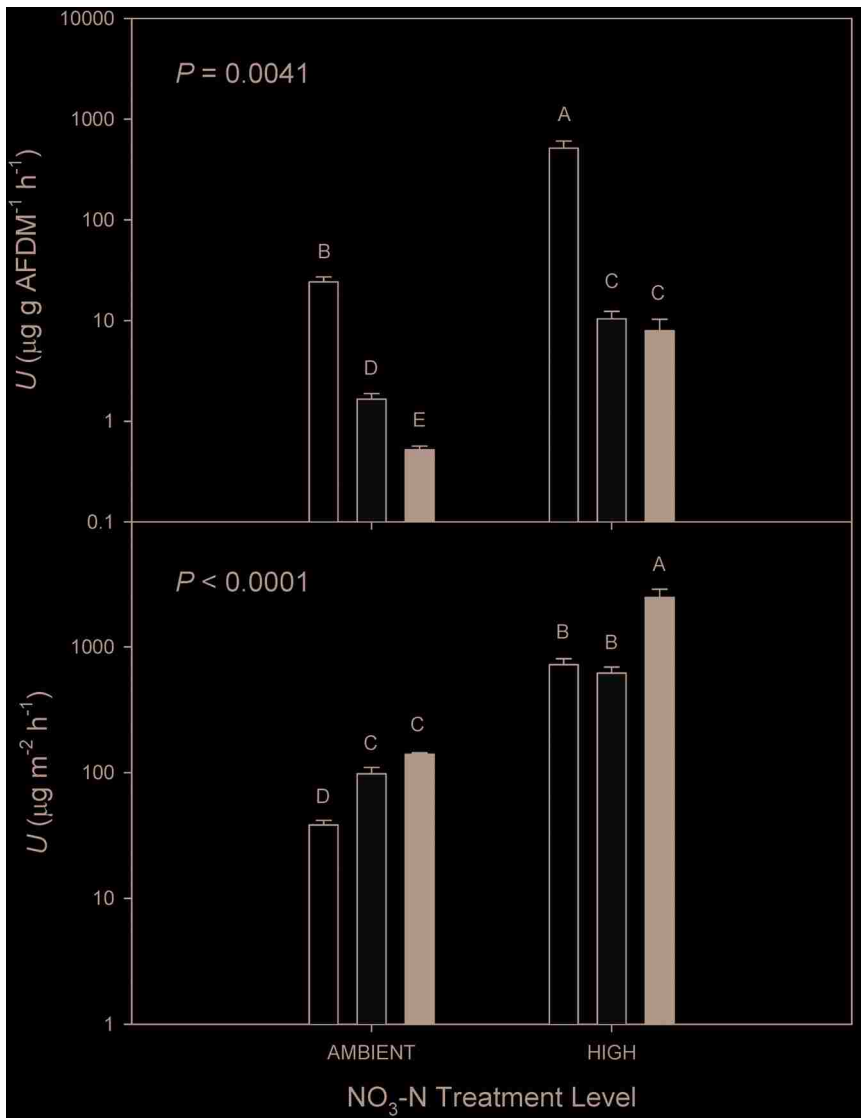


Figure 10. Mass-specific ($\mu\text{g g AFDM}^{-1} \text{h}^{-1}$; top panel) and areal ($\mu\text{g m}^{-2} \text{h}^{-1}$; lower panel) uptake rates of NO_3^- by substrates in response to ambient and high $\text{NO}_3\text{-N}$ treatment levels. Substrates were collected from parafluvial (PF, white), active orthofluvial (AO, grey), and passive orthofluvial (PO, black) spring brooks on the Nyack flood plain. Vertical bars are means (± 1 SE) and unique subscripts indicate statistically significant differences (Tukey's HSD, $P < 0.05$). P -values represent results of two-way ANOVA test on $\text{NO}_3\text{-N}$ and landscape position interaction effects on response variables.

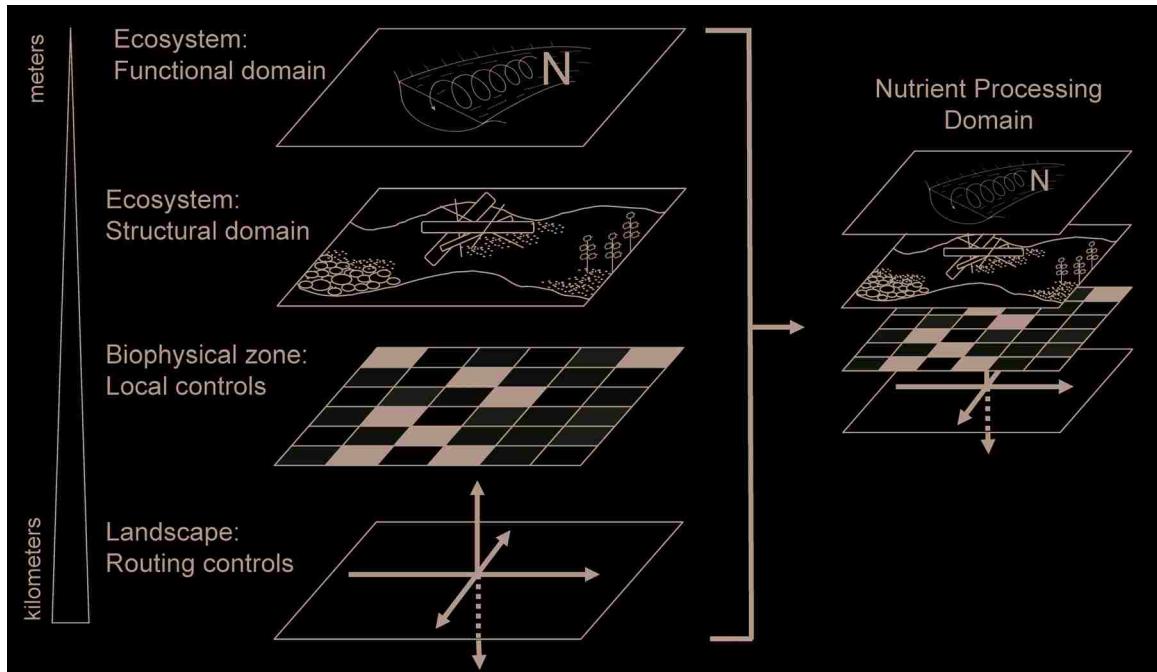


Figure 11. Conceptual model illustrating multi-scale organization and proposed drivers of nutrient processing domains on a floodplain landscape. Geomorphic, fluvial, and vertical exchange processes (i.e., routing controls) generate a mosaic of biophysical zones wherein exchange and internal processes (i.e., local controls) drive structural patterns of component ecosystems. Overlap of these spatially explicit layers can be used to model unique 'nutrient processing domains' based on landscape position. N-spiraling cartoon adapted from Newbold et al. 1992.

Appendix 1. Summary of data transformations, statistical procedures, and test results for each variable measured in spring brooks on the Nyack flood plain. *P*-values represent overall test results ($\alpha = 0.05$).

Variable	Transformation	Statistical Test	Class	Test Statistic	†Degrees of freedom	<i>P</i>	
Reach Characteristics							
Wetted width (m)	common log	ANOVA	site	$F = 23.03$	5	< 0.0001	
Depth (m)		Kruskal-Wallis	site	$H = 267.741$	5	< 0.0001	
PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		Kruskal-Wallis	site	$F = 48.58$	5	< 0.0001	
Canopy cover (%)		Kruskal-Wallis	site	$H = 150.845$	5	< 0.0001	
PAR vs. percent canopy cover		Simple linear regression			$F = 3.78$	1,4	0.1239
Particle size distributions		Kruskal-Wallis	site	$H = 546.271$	5	< 0.0001	
2011 surface water							
Dissolved oxygen (mg L^{-1})		ANOVA	site	$F = 2.09$	5	0.0853	
Dissolved oxygen (% sat.)		ANOVA	site	$F = 2.19$	5	0.0722	
Conductivity ($\mu\text{S cm}^{-1}$)		ANOVA	site	$F = 55.63$	5	< 0.0001	
Temperature ($^{\circ}\text{C}$)		ANOVA	site	$F = 13.82$	5	< 0.0001	
pH		ANOVA	site	$F = 31.98$	5	< 0.0001	
DOC (mg L^{-1})		Kruskal-Wallis	site	$H = 24.707$	5	0.0002	
$\text{NO}_3\text{-N}$ ($\mu\text{g L}^{-1}$)		Kruskal-Wallis	site	$H = 11.243$	5	0.0521	
$\text{NH}_4\text{-N}$ ($\mu\text{g L}^{-1}$)		Kruskal-Wallis	site	$H = 10.965$	5	0.0468	
SRP ($\mu\text{g L}^{-1}$)		Kruskal-Wallis	site	$H = 9.994$	5	0.0754	
Atomic N:P		Kruskal-Wallis	site	$H = 11.927$	5	0.0358	
2011 ground water							
Dissolved oxygen (mg L^{-1})		ANOVA	site	$F = 15.77$	5	< 0.0001	
Dissolved oxygen (% sat.)		ANOVA	site	$F = 16.04$	5	< 0.0001	
Conductivity ($\mu\text{S cm}^{-1}$)		ANOVA	site	$F = 6.25$	5	< 0.0001	
Temperature ($^{\circ}\text{C}$)		ANOVA	site	$F = 51.39$	5	< 0.0001	
pH		ANOVA	site	$F = 169.73$	5	< 0.0001	
DOC (mg L^{-1})		Kruskal-Wallis	site	$H = 70.925$	5	< 0.0001	
$\text{NO}_3\text{-N}$ ($\mu\text{g L}^{-1}$)		Kruskal-Wallis	site	$H = 45.763$	5	< 0.0001	
$\text{NH}_4\text{-N}$ ($\mu\text{g L}^{-1}$)		Kruskal-Wallis	site	$H = 68.478$	5	< 0.0001	
SRP ($\mu\text{g L}^{-1}$)		Kruskal-Wallis	site	$H = 23.268$	5	0.0003	
Atomic N:P		Kruskal-Wallis	site	$H = 34.371$	5	< 0.0001	
^{222}Rn Radon (Bq L^{-1})		ANOVA	site	$F = 16.44$	5	< 0.0001	

VHG	ANOVA	site	F = 22.43	5	< 0.0001
Mean VHG vs. discharge (Q)	Simple linear regression		F = 6.18	1,4	0.0677
2011 surface- vs. groundwater					
DOC					
PF1	Wilcoxon two-sample	water type	Z = 1.454	18,8	0.1457
PF2	Wilcoxon two-sample	water type	Z = 0.027	18,8	0.9778
AO1	Wilcoxon two-sample	water type	Z = -0.973	18,8	0.3305
AO2	Wilcoxon two-sample	water type	Z = 1.967	20,11	0.0492
PO1	Wilcoxon two-sample	water type	Z = 2.568	18,8	0.0102
PO2	Wilcoxon two-sample	water type	Z = -2.519	15,8	0.0118
NO ₃ -N					
PF1	Wilcoxon two-sample	water type	Z = -1.485	17,7	0.1374
PF2	Wilcoxon two-sample	water type	Z = -3.466	17,7	0.0005
AO1	Wilcoxon two-sample	water type	Z = 2.082	17,7	0.0373
AO2	Wilcoxon two-sample	water type	Z = -2.194	19,10	0.0282
PO1	Wilcoxon two-sample	water type	Z = -3.000	17,7	0.0027
PO2	Wilcoxon two-sample	water type	Z = -1.459	14,7	0.0704
NH ₄ -N					
PF1	Wilcoxon two-sample	water type	-	18,8	-
PF2	Wilcoxon two-sample	water type	-	18,8	-
AO1	Wilcoxon two-sample	water type	Z = -1.574	18,8	0.128
AO2	Wilcoxon two-sample	water type	-	20,11	-
PO1	Wilcoxon two-sample	water type	Z = -0.583	18,8	0.5597
PO2	Wilcoxon two-sample	water type	Z = -2.978	15,8	0.0029
SRP					
PF1	Wilcoxon two-sample	water type	Z = 0.936	18,8	0.3492
PF2	Wilcoxon two-sample	water type	Z = -1.42	18,8	0.155
AO1	Wilcoxon two-sample	water type	Z = -1.474	18,8	0.1404
AO2	Wilcoxon two-sample	water type	Z = -0.879	20,11	0.1896
PO1	Wilcoxon two-sample	water type	Z = -0.761	18,8	0.4466
PO2	Wilcoxon two-sample	water type	Z = -1.459	15,8	0.1444
Atomic N:P					
PF1	Wilcoxon two-sample	water type	Z = -1.485	18,8	0.1374
PF2	Wilcoxon two-sample	water type	Z = -3.466	18,8	0.0005
AO1	Wilcoxon two-sample	water type	Z = 0.262	18,8	0.7931
AO2	Wilcoxon two-sample	water type	Z = -2.194	20,11	0.0282

PO1		Wilcoxon two-sample	water type	Z = -3.000	18,8	0.0027			
PO2		Wilcoxon two-sample	water type	Z = -1.672	15,8	0.0945			
2010 groundwater									
DOC (mg L ⁻¹)		ANOVA	landscape position	F = 0.60	5	0.5716			
NO ₃ -N (µg L ⁻¹)		ANOVA	landscape position	F = 5.36	5	0.0333			
NH ₄ -N (µg L ⁻¹)		ANOVA	landscape position	-	-	-			
SRP (µg L ⁻¹)		ANOVA	landscape position	F = 0.71	5	0.5218			
Atomic N:P		ANOVA	landscape position	F = 1.04	5	0.3964			
²²² Radon (Bq L ⁻¹)		ANOVA	landscape position	F = 0.64	5	0.5541			
Benthic Characteristics									
Large woody debris									
mass (kg m ⁻²)		ANOVA	site	F = 27.12	5	< 0.0001			
volume (m ³ m ⁻²)		ANOVA	site	F = 14.87	5	< 0.0001			
Epilithon									
mass (g m ⁻²)		ANOVA	site	F = 57.27	5	< 0.0001			
OM (%)		ANOVA	site	F = 30.48	5	< 0.0001			
chlorophyll <i>a</i> (mg m ⁻²)		ANOVA	site						
Epixylon									
mass (g m ⁻²)		ANOVA	site	F = 8.91	5	< 0.0001			
OM (%)		ANOVA	site	F = 3.80	5	0.0047			
chlorophyll <i>a</i> (mg m ⁻²)		ANOVA	site						
FPOM									
mass (g m ⁻²)		ANOVA	site	F = 27.57	5	< 0.0001			
OM (%)		ANOVA	site	F = 26.46	5	< 0.0001			
chlorophyll <i>a</i> (mg m ⁻²)		ANOVA	site						
CPOM									
mass (g m ⁻²)		ANOVA	site	F = 26.83	5	< 0.0001			
OM (%)		ANOVA	site	F = 0.58	5	0.7121			
Macrophytes (g m ⁻²)		ANOVA	site	F = 8.16	5	< 0.0001			
Chlorophyll <i>a</i> : AFDM		ANOVA	site	F = 9.01	5	< 0.0001			
PAR vs. chlorophyll <i>a</i>		Simple linear regression	site	F = 46.79	1,64	0.0024			
VHG vs. chlorophyll <i>a</i>		Simple linear regression	site	F = 4.33	1,4	0.1058			
NO ₃ ⁻ uptake: solute releases									
Predicted – observed NO ₃ -N									
PF1		Paired t-test		t = -1.39	19	0.1798			

PF2	Paired t-test	$t = 0.61$	19	0.552
AO1	Paired t-test	$t = 1.69$	19	0.108
AO2	Paired t-test	$t = 2.14$	19	0.0456
PO1	Paired t-test	$t = 1.88$	19	0.0754
PO2	Paired t-test	$t = 0.82$	24	0.4209
NO ₃ ⁻ uptake: microcosms				
Ambient NO ₃ -N				
Parafluvial	Simple linear regression	F = 93.98	1,33	< 0.0001
Active orthofluvial	Simple linear regression	F = 31.71	1,38	< 0.0001
Passive orthofluvial	Simple linear regression	F = 95.10	1,36	< 0.0001
High NO ₃ -N				
Parafluvial	Simple linear regression	F = 131.50	1,38	< 0.0001
Active orthofluvial	Simple linear regression	F = 29.69	1,38	< 0.0001
Passive orthofluvial	Simple linear regression	F = 108.73	1,28	< 0.0001
Mass-specific uptake ($\mu\text{g AFDM}^{-1} \text{h}^{-1}$)	natural log			
	Two-way ANOVA	$F = 316.27$	5	< 0.0001
Areal uptake ($\mu\text{g m}^{-2} \text{h}^{-1}$)	natural log			
	Two-way ANOVA	$F = 583.79$	5	< 0.0001

Notes: All pair-wise comparisons carried out using Tukey's HSD post-hoc test.

†Degrees of freedom for Wilcoxon two-sample test and simple linear regressions given as df1,df2.