

The Spatial Structure of Variability in a Semi-arid, Fluvial Ecosystem

David Bruce Lewis,^{1,2*} John D. Schade,¹ Anne K. Huth,³ and Nancy B. Grimm^{1,2}

¹*School of Life Sciences, Arizona State University, P.O. Box 873211, Tempe, Arizona 85287, USA;* ²*International Institute for Sustainability, Arizona State University, P.O. Box 873211, Tempe, Arizona 85287, USA;* ³*Department of Hydrology and Water Resources, University of Arizona, Tucson, Arizona 85721, USA*

ABSTRACT

The arrangement and composition of flowpath types within a given network are thought to govern its functioning. This concept assumes that different flowpath types are functionally distinct. We investigated this assumption in a fluvial ecosystem by comparing the riparian zone, parafluvial zone (in-channel gravel bars), and surface stream. We hypothesized that differences in advection, uptake, and sorption would render material cycles more (a) open and (b) mutable in the surface stream, whereas the converse would occur in the riparian zone, and an intermediate state would be seen in the intervening parafluvial zone. To test our first hypothesis, we predicted that spatial heterogeneity in solute concentrations would be least in the surface stream, greater in the parafluvial zone, and greatest in the riparian zone. Using a null model, we ascertained that this pattern was shown by all solute species we examined (nitrate, ammonium, total dissolved inorganic nitrogen [DIN], dissolved organic N, total dissolved N, soluble reactive phosphorus, dissolved organic carbon, and chloride). To test

our second hypothesis, we predicted that temporal change in spatial heterogeneity would be greatest in the surface stream, less in the parafluvial zone, and least in the riparian zone. Nitrate, DIN, and chloride showed this pattern. In particular, surface stream inorganic N was less spatially variable following months of high rainfall. According to an extant hypothesis, these results suggest that inorganic N processing may be a stable function in this ecosystem. Other solute species did not support our second prediction, perhaps because their retention and release dynamics are influenced principally by geochemistry. Generally, our findings indicate that a geomorphic template can generate spatial patterns in ecosystem function, warranting an expansion of the spiraling framework to a variety of flowpath types.

Key words: Arizona; ecosystem function; geomorphic template; null model; process; parafluvial zone; process; San Pedro River; riparian zone; stability.

INTRODUCTION

Ecosystems develop from a dynamic feedback between structure and function (Levin 1998) resulting in the generation of goods and services that may exceed the global gross national product

(Costanza and others 1997). Material transport networks, typically those of water, are structures hypothesized to influence ecosystem function (Fisher and others 2004; Sponseller and Fisher 2005). Along the ultimately downhill journey, water and entrained material flow overland, through upland and riparian soils, through coarse alluvium, and along stream channels. The spatial arrangement and relative abundance of these flowpath types within a catchment are thought to

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*Corresponding author; e-mail: db111@psu.edu

influence material retention by the entire catchment. Implicit in this hypothesis is the assumption that these flowpath types are biogeochemically distinct. There are, however, few direct comparisons of ecosystem processes among flowpath types (for example, see Pinay and others 2003).

We investigated the proposition that flowpath types in fluvial ecosystems are distinct. In riparian systems, alluvial sediments, and surface streams, materials cycle between biotic and abiotic pools, yet move inevitably downstream by advection. This interplay between cycling and longitudinal transport should leave a spatial pattern in the material (Dent and Grimm 1999). If flowpaths moving through different landscape elements process material differently owing to unique dynamics of cycling plus transport (that is, spiraling) (Newbold and others 1981), then they should show different spatial patterns in material distribution. We developed expectations for how flowpath types should differ vis-à-vis spatial pattern in solute concentrations and temporal change in this spatial pattern. These expectations derive from a theoretical framework describing relationships between the spatial complexity of fluvial ecosystems and the way they process materials (Fisher and others 1998; Grimm and others 2003; Groffman and others 2003).

Fisher and others (1998) conceptualize fluvial ecosystems (Figure 1) as nested, concentric cylinders, like telescopes. The surface stream runs through the core of the fluvial ecosystem. Beneath the stream lies the hyporheic zone (Grimm and Fisher 1984). Alongside, the parafluvial zone consists of sand and gravel bars with underlying saturated sediments within the annually flooded channel (Holmes and others 1994; Schade and others 2001). The riparian zone lies outside the annually flooded channel and often contains distinct soils and biota (Gregory and others 1991; Hill 1996).

We compared the surface stream, parafluvial zone, and riparian zone with respect to (a) spatial variability in solute concentrations and (b) degree of month-to-month change in spatial variability in solute concentrations. We expect subsystems to differ in terms of spatial variability in solute concentrations because they differ in terms of how spatially localized and temporally mutable their nutrient cycles are. Differences in cycles result from differences in community structure, soil texture, water residence time, and the turnover of these ecosystem components.

We expect that riparian zones will show greater, but less mutable, spatial variation in solute con-

centrations. In the riparian zone, advection is slow and opportunities for uptake and sorption abound, given the densities of soil sorption sites, microbes (enhanced by soil and root attachment sites), and plant roots. With little advection and ample uptake and sorption, we expect little advective displacement of an atom per cycle (Tank and others 2000; Mulholland and others 2002)—, that is, a short processing length (sensu Fisher and others 1998). If atoms do not move appreciably, they will be recycled locally many times over (Essington and Carpenter 2000), and any given volume of environmental space will contain relatively closed material cycles (Fisher and Likens 1973; DeAngelis 1980). If the riparian zone does contain many small, closed material cycles, then it should show spatial heterogeneity in groundwater solute concentrations.

Additionally, riparian material cycles should change slowly because hydrologic conditions, soils, and biota (relative to those of the surface stream) fluctuate little through time. Riparian hydrology does vary seasonally, with biogeochemical consequences (Baker and others 2000; Valett and others 2005). Nevertheless, riparian groundwater fluctuations are small relative to variability in surface stream hydrographs. Moreover, riparian flora (and presumably, the material processing it supports) native to the US Southwest withstands floods with up to 10-year recurrence intervals (Stromberg and others 1993). Primary producers are long-lived (relative to algae), and microbial populations have access to a steady supply of soil organic matter. Thus, we expect that the spatial mosaic in the riparian zone changes little through time. As a consequence, spatial variation in solute concentrations should be a relatively constant feature of the riparian landscape.

By contrast, we expect that surface streams will show less, but more mutable, spatial variation in solute concentrations. In the surface stream, advection is greater and opportunities for uptake and sorption fewer. The surface channel should show relatively greater displacement of an atom per cycle. We expect material cycling patches in the surface stream to be relatively longer and more open. However, material cycles of the surface stream may change rapidly. Surface channels of the arid Southwest are disturbance prone (Grimm 1987). Discharge — and thus advection of material — undergoes dynamic fluctuations. These fluctuations disturb the biota and sediments responsible for material processing (Fisher and others 1982; Stanley and others 1997; Lenzi 2004). Contributing to temporal variability, adaptive life history

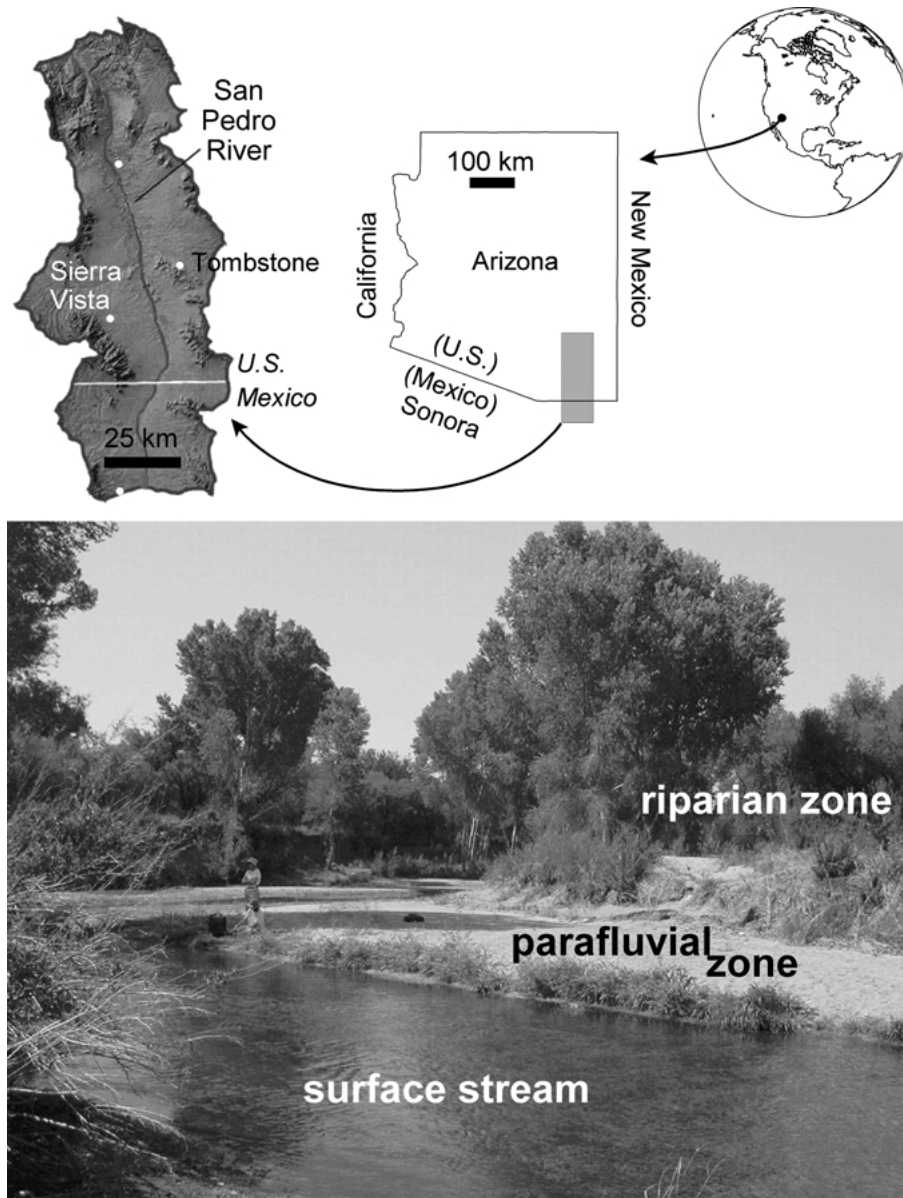


Figure 1. Study region. We studied the fluvial ecosystem of the middle San Pedro River approximately between the towns of Tombstone and Sierra Vista. The lower photograph (credit Jill Koehler, May 2001) depicts the three subsystem types that we investigated. The watershed map in the upper left was copied from <http://www.lastgreatplaces.org/sanpedro/geography/hydrology.html>.

characteristics permit these disturbed algal and invertebrate populations to recover quickly (Grimm 1987; Grimm and Fisher 1989). The spatial variation in solute concentrations should thus be low but inconstant. In the parafluvial zone, flow conditions, sediment–water interactions, populations, and temporal change in these features are intermediate relative to the neighboring subsystems. Solute concentrations in parafluvial groundwater should thus show intermediate spatial variation and month-to-month change in spatial variation.

To compare material cycles among flowpath types, we have two, nonexclusive hypotheses. First, cycles are small and most closed in the

riparian zone, less so in the parafluvial zone, and least so in the surface stream. Because these are advective systems, differences in cycles should leave different signatures in the spatial heterogeneity of solute concentrations. Thus, a prediction (P1) of this first hypothesis is that spatial heterogeneity in solute concentrations should decrease from riparian to parafluvial to surface. Second, cycles are least prone to change in the riparian zone, more so in the parafluvial zone, and even more so in the surface stream. We evaluated this hypothesis with the prediction (P2) that spatial variability in solute concentrations should show increasing temporal change from the riparian zone to the parafluvial zone to the surface.

METHODS

Study Site

We conducted this research on the San Pedro River, near Tombstone, Arizona, USA (Figure 1). Our research was set along approximately 1 km of river length within the San Pedro Riparian National Conservation Area, managed by the US Bureau of Land Management. The San Pedro River flows north from Sonora, Mexico, into southeastern Arizona. It is a tributary of the Gila River, itself a tributary of the Colorado River. The San Pedro drains arid grasslands and desert scrub. Water from shallow, rain-fed alluvial aquifers and deeper, permanent groundwater sources maintain perennial flow in our study area (Coes and others 1999), although the river is spatially intermittent in other areas by late summer following the months-long annual dry season. Rainfall and runoff undoubtedly influence advective transport of material, but the time lags between rainfall, discharge, and material transport are unclear. So, to provide context for this study, we gathered data on rainfall (Scott and others 2004) and discharge (from the US Geological Survey) for 1-, 3-, 10-, 32-, and 100-day windows (even spacing on log-10 scale) that end on the day of sampling.

We sampled surface stream, parafluvial groundwater, and riparian groundwater. Vertical, cut banks differentiate the surface stream and parafluvial zone in the annually flooded channel from the riparian floodplain. Primary producers in the surface stream comprise dynamic algal communities dominated by *Cladophora* and diatoms. *Cladophora* cover varied from 50 to 100% of the channel bottom from March through May to being visually absent following August floods and during winter (D. B. Lewis and others, personal observation). Relatively coarse, alluvial sediments of high hydrologic conductivity are deposited within the flooded channel, between the cut banks, as sand and gravel bars. Primary producers on the parafluvial sediments are the grasses and woody vegetation typical of the riparian zone, but they survive only a few months from germination in spring until monsoon floods scour the gravel bars.

The riparian zone differs from the flooded channel in several important aspects. Riparian soils are finer-grained, often compacted and clay-rich, forming aquitards in some places (D. B. Lewis and others, personal observation). Mature Frémont cottonwood (*Populus fremontii*)–Goodding willow (*Salix gooddingii*) forest galleries grow on the floodplain along the entire study area. The understory includes Johnson grass (*Sorghum halepense*),

Sacaton grass (*Sporobolus wrightii*), seepwillow (*Baccharis salicifolia*), side-oats grama (*Bouteloua curtipendula*), and tobosa (*Hilaria mutica*) [Krueper and others 2003]. This type of riparian forest typically occurs in unconstrained valleys of low-gradient, perennial rivers of the southwestern United States (Stromberg 1993).

Sampling and Analyses of Solutes

We collected water from sampling points (groundwater wells and surface stream locations) on seven occasions in 2001: February, March, May, June, August, October, and December. Total sample size for any one of the seven sampling events ranged from 59 to 94 individual points on the landscape; monthly variability in sample size resulted from the loss of wells owing to clogging and hydrological disruptions and from the occasional replacement of wells. For every sampling event, surface stream, parafluvial groundwater, and riparian groundwater categories were each represented by at least 10 sites and by similar longitudinal distributions.

Groundwater from the riparian and parafluvial zones was sampled from PVC wells, installed along 15 transects perpendicular to the channel. Transects were separated by 50–100 m of channel length. On each transect, wells were installed in the riparian zone on both banks unless precluded by near-surface bedrock or cobble beds. On each bank, between one and three wells were installed within 5 m of the bank edge. Scattered throughout the floodplain, an additional four riparian wells were installed 50–200 m from the channel. Each riparian well was installed to a depth of approximately 1 m below the water table as recorded during February 2001. Consequently, wells ranged from 1.5–4.5 m in length, and the bottom 1.5 m of each well was screened to permit the flowthrough of groundwater. Also along each transect, one or two wells were installed in the parafluvial zone if a sand or gravel bar was present. Parafluvial wells were also installed to about 1 m below the water table and were screened over the lower 0.5–1.5 m.

On each sampling event, triplicate samples were collected into acid-washed polyethylene bottles from each well and surface stream location. Samples were maintained on ice until analysis within 72 h at the Goldwater Environmental Laboratory of Arizona State University, in Tempe, Arizona. We analyzed all samples for concentrations of nitrite-nitrogen + nitrate-nitrogen (hereafter NO₃-N), ammonium-N (NH₄-N), total dissolved N (TDN), soluble reactive phosphorus (SRP), dis-

solved organic carbon (DOC), and chloride (Cl^-). Dissolved inorganic N (DIN) equaled $\text{NO}_3\text{-N} + \text{NH}_4\text{-N}$, whereas dissolved organic N (DON) equaled TDN-DIN . In our database, a solute concentration for a site on a sampling event is the mean of the triplicate samples. With the exception of DOC, all analyses were performed colorimetrically on a Lachat QC8000 autoanalyzer. Prior to analyses, water was centrifuged at 10^4 rpm for 10 min, which removes particulates as effectively as a $0.45\text{-}\mu\text{m}$ membrane filter (T. Colella unpublished) without risking NH_3 volatilization (N. B. Grimm, personal observation). Colorimetric methods were the phenol-hypochlorite method for $\text{NH}_4\text{-N}$ (Solorzano 1969); the cadmium-copper reduction method for $\text{NO}_3\text{-N}$ (Wood and others 1967); the UV/persulfate digestion and oxidation, followed by cadmium-copper reduction, method for TDN (D'Elia and others 1977); the ascorbic acid reduction method for SRP (Henriksen 1966); and the mercuric thiocyanate method for Cl^- (Zall and others 1956). DOC was analyzed using high-temperature combustion (Katz and others 1954) on a Shimadzu TOC5000 from water filtered through a Whatman GF/F glass-fiber filter (nominal pore size $0.7\mu\text{m}$).

Data Analyses

For P1, we compared among subsystems the spatial variation [measured as coefficient of variation (CV)] in solute concentrations. For each solute, each sampling point was assigned a single concentration value, the annual (across sampling events) mean. We then grouped points by subsystem. Finally, for each subsystem, we calculated spatial CV among the point-specific annual mean concentrations.

For P2, we compared among subsystems the month-to-month changes in spatial CV in solute concentrations. For each solute and each subsystem, we calculated spatial CV in concentration among sampling points for each of the seven sampling events. We then calculated the CV among the seven month-specific spatial CVs. We refer to this measure of temporal change in spatial heterogeneity as CV_{CV} .

We used a null model to determine whether the spatial CV and CV_{CV} values differed among subsystems. Null models produce a frequency distribution of values for the metric of interest expected at random; observed values are compared against this frequency distribution to determine if they are different than expected at random (Gotelli and Graves 1996). Because we compare spatial CV and

CV_{CV} among subsystems, our precise metrics of interest are differences among subsystems in these values. Thus, we compare observed Δ spatial CV against a frequency distribution of randomly generated Δ spatial CVs, where Δ spatial CV = spatial $\text{CV}_{\text{subsystem 1}} - \text{spatial CV}_{\text{subsystem 2}}$; similarly, $\Delta \text{CV}_{\text{CV}} = \text{CV}_{\text{CV subsystem 1}} - \text{CV}_{\text{CV subsystem 2}}$. There is a unique Δ spatial CV and a unique $\Delta \text{CV}_{\text{CV}}$ for each solute species and each pairwise comparison of subsystems. So, for each solute species and pair of subsystems, we compared Δ spatial CV and $\Delta \text{CV}_{\text{CV}}$ with values generated by randomly shuffling sampling points among subsystems.

In one iteration of the null model, all data (that is, all solute concentrations for all seven sampling events) associated with a given sampling point (that is, an individual well or surface stream location) were randomly assigned to any one of all the sampling points. We then calculated Δ spatial CV and $\Delta \text{CV}_{\text{CV}}$ values from this array of spatially relocated data exactly as we did from the observed data. For each comparison of interest (that is, spatial CV or CV_{CV} of a given solute compared between a pair of subsystem types), we generated a frequency distribution of Δ values expected at random by reshuffling the points 3.4×10^5 times (Figure 2). The variance of the data composing histograms like those of Figure 2 stabilized after between 10^4 and 10^5 iterations. The proportional area of a frequency distribution beyond an observed Δ value is the *P*-value.

RESULTS

P1 is that spatial variation in solute concentrations decreases from the distal to the core elements of the fluvial ecosystem. Differences among subsystems in spatial CV reflect differences in the ranges of the actual solute concentrations. For all solutes, the spread of the frequency distribution of concentration values increased from surface stream to parafluvial zone to riparian zone (Figure 3). The interquartile range (of site-specific, annually averaged concentration values) for [DIN] was $88\text{--}117 \mu\text{g L}^{-1}$ in the surface stream, $146\text{--}239 \mu\text{g L}^{-1}$ in the parafluvial zone, and $73\text{--}245 \mu\text{g L}^{-1}$ in the riparian zone; other solute species show a similar increase in range from surface to parafluvial to riparian. Consequently, spatial $\text{CV}_{\text{riparian}}$ was greater than spatial $\text{CV}_{\text{surface}}$. Spatial $\text{CV}_{\text{parafluvial}}$ was of intermediate value, although statistically similar to one or both of its neighboring subsystems (Table 1). In the riparian zone, standard deviation among observation points in solute concentration exceeded mean concentra-

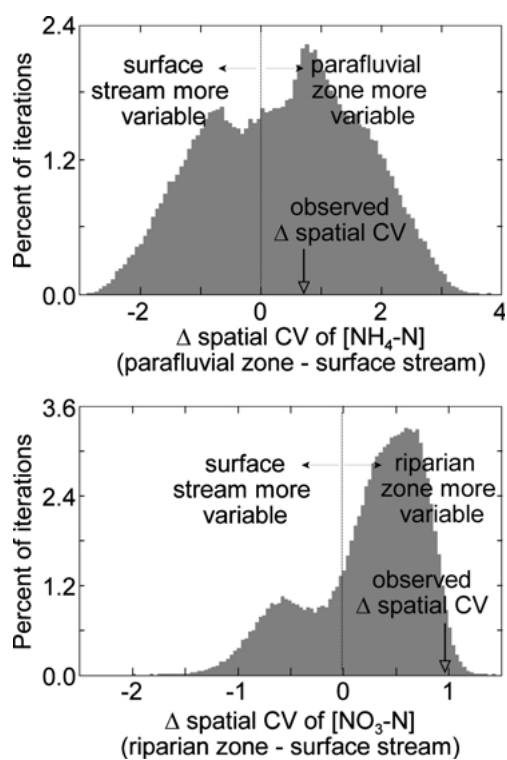


Figure 2. Example frequency distributions of Δ spatial CV values expected at random (*top*) Δ spatial CV = spatial CV of parafluvial zone $[\text{NH}_4\text{-N}]$ minus spatial CV of surface stream $[\text{NH}_4\text{-N}]$. In this example, the spatial heterogeneity of parafluvial $[\text{NH}_4\text{-N}]$ is deemed statistically indistinguishable from the spatial heterogeneity of surface stream $[\text{NH}_4\text{-N}]$ because the observed Δ spatial CV falls amidst the Δ spatial CV values expected at random. (*bottom*) Δ spatial CV = spatial CV of riparian zone $[\text{NO}_3\text{-N}]$ minus spatial CV of surface stream $[\text{NO}_3\text{-N}]$. In this example, riparian $[\text{NO}_3\text{-N}]$ is deemed more spatially heterogeneous than surface stream $[\text{NO}_3\text{-N}]$ because the observed Δ spatial CV is greater than that calculated from nearly all spatial randomizations of the data.

tion (that is, spatial $\text{CV}_{\text{riparian}}$ was greater than 1) for all N-based solute species. Spatial $\text{CV}_{\text{riparian}}$ was near unity for SRP and DOC, and was less than 1 for Cl^- . In the surface stream, the standard deviation was less than the mean (spatial $\text{CV}_{\text{surface}}$ was less than 1) for all solute species. Proportionally, spatial $\text{CV}_{\text{riparian}}$ zone exceeded spatial $\text{CV}_{\text{surface}}$ by the greatest degree for $\text{NH}_4\text{-N}$ (11.1-fold), DOC (6.6-fold), TON (5.8-fold), and Cl^- (5.7-fold). For other solute species, spatial $\text{CV}_{\text{riparian}}$ exceeded spatial $\text{CV}_{\text{surface}}$ by 2.8–4.7-fold. P1 was thus met by all solutes (Table 1).

P2 is that month-to-month changes in the spatial variation in solute concentrations would dampen from the core to the distal elements of the fluvial ecosystem. Proportionally, $\text{CV}_{\text{CV surface}}$ exceeded

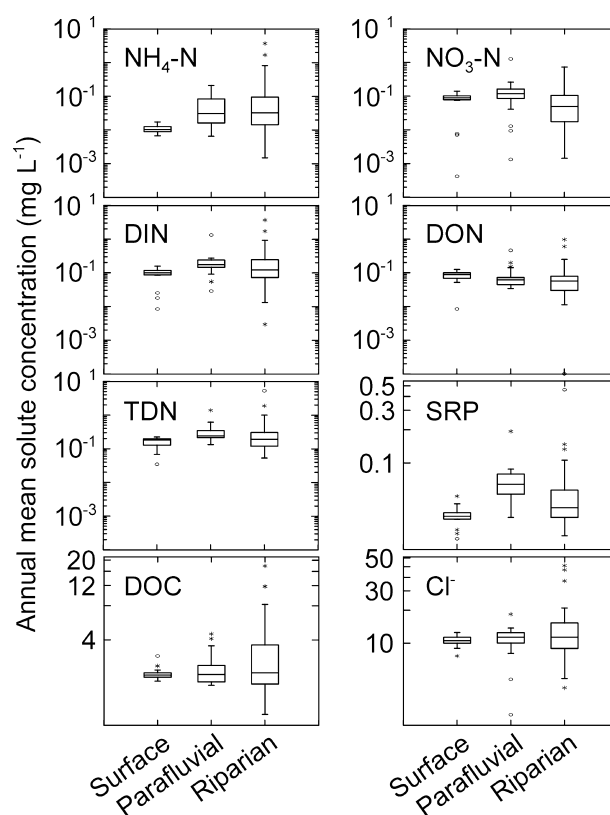


Figure 3. Box and whisker plots of solute concentrations in each subsystem type. Note log-10 transformation of the y axis. For each box and whisker set, the center line depicts the median, the *box* marks the midrange (the range of values between the 25th and 75th percentiles of the data), the *lower whisker* encapsulates values in the range [25th percentile – 1.5 times the span of the midrange), 25th percentile], the *upper whisker* encapsulates values in the range [75th percentile, (75th percentile + 1.5 times the span of the midrange)], and *asterisks* and *open circles* indicate far outlying values. The data used to generate any given box and whisker set were annual mean concentrations of the indicated solute in the indicated subsystem type, where a single annual mean concentration value (a single datum) is the average of multiple, sequential measurements from a single point on the landscape.

$\text{CV}_{\text{CV riparian}}$ by the greatest degree for Cl^- (6.2-fold) and DIN (2.3-fold) (Table 2). For other solute species, $\text{CV}_{\text{CV surface}}$ exceeded $\text{CV}_{\text{CV riparian}}$ by less than two fold; for SRP, $\text{CV}_{\text{CV surface}}$ did not exceed $\text{CV}_{\text{CV riparian}}$. With the exception of Cl^- observations from the riparian zone, the month-to-month standard deviation in spatial CV was always less than the temporally averaged spatial CV (CV_{CV} was less than 1).

Differences among subsystems in CV_{CV} reflect differences in the degree to which the range of solute concentrations changes from month to month. The

Table 1. Spatial CV by Solute and Subsystem Type

Solute	Riparian Zone	Parafluvial Zone	Surface
DIN	1.93 ^a	1.05 ^{a,b}	0.45 ^b
NO ₃ -N	1.44 ^a	1.44 ^a	0.51 ^b
NH ₄ -N	3.11 ^a	1.01 ^{a,b}	0.28 ^b
DON	1.59 ^a	1.05 ^{a,b}	0.35 ^b
TDN	1.98 ^a	0.80 ^{a,b}	0.34 ^b
SRP	1.04 ^a	0.45 ^{a,b}	0.22 ^b
DOC	0.92 ^a	0.34 ^b	0.14 ^b
Cl ⁻	0.63 ^a	0.27 ^b	0.11 ^b

For a given solute, similar letters denote subsystems with statistically similar spatial CVs. Subsystems are deemed to show different spatial CVs if the difference between them is greater than 95% of the Δ spatial CV values generated randomly by the null model.

DIN, dissolved inorganic nitrogen; NO₃-N, nitrite-nitrogen + nitrate-nitrogen; NH₄-N, ammonium-nitrogen; DON, dissolved organic nitrogen; TDN, total dissolved nitrogen; SRP, soluble reactive phosphorus; DOC, dissolved organic carbon; Cl⁻, chloride.

range of [NO₃-N] changes greatly from month to month in the surface stream but is relatively constant in the riparian zone (Figure 4). For NO₃-N, surface stream spatial CV ranged from 0.26 in August (when [NO₃-N] varied spatially from 186–354 $\mu\text{g L}^{-1}$) to 2.23 in March (when [NO₃-N] varied spatially from less than 1 to 31 $\mu\text{g L}^{-1}$; note that the detection limit for [NO₃-N] = 0.8 $\mu\text{g L}^{-1}$); this month-to-month variation in spatial CV (from 0.26 to 2.23) yields $CV_{CV \text{ surface}} = 0.80$ for NO₃-N. Conversely, riparian zone spatial CV ranged from 1.42 in February (when [NO₃-N] varied spatially from less than 1 to 997 $\mu\text{g L}^{-1}$) to 3.75 in August (when [NO₃-N] varied spatially from less than 1 to 4,904 $\mu\text{g L}^{-1}$); this month-to-month variation in spatial CV (from 1.42 to 3.75) yields $CV_{CV \text{ riparian}} = 0.42$. Thus, spatial variability in [NO₃-N] was more constant through time in the riparian zone than it was in the surface stream; namely, spatial CV was always high in the riparian zone and fluctuated between low and high in the surface stream. $CV_{CV \text{ parafluvial}}$ was intermediate (0.70) for NO₃-N, and was statistically similar to $CV_{CV \text{ riparian}}$. P2 was thus met by NO₃-N.

Other solute species differed in how well they met P2. NH₄-N and DIN showed a pattern similar to that of NO₃-N, wherein $CV_{CV \text{ riparian}}$ was roughly one-half $CV_{CV \text{ parafluvial}}$ and $CV_{CV \text{ surface}}$ (Table 2), although this riparian suppression of CV_{CV} of [NH₄-N] is not statistically significant ($P = 0.15$). CV_{CV} of DON and DOC show a continuous decline, from surface stream to parafluvial zone to riparian zone; this pattern is marginally significant for DOC ($P = 0.06$ for test of $CV_{CV \text{ surface}}$ greater than $CV_{CV \text{ riparian}}$) and not significant for DON. For TDN,

Table 2. CV_{CV} by Solute and Subsystem Type

Solute	Riparian Zone	Parafluvial Zone	Surface Stream
DIN	0.30 ^a	0.64 ^b	0.68 ^b
NO ₃ -N	0.42 ^a	0.71 ^b	0.80 ^b
NH ₄ -N	0.23 ^a	0.43 ^a	0.43 ^a
DON	0.35 ^a	0.42 ^a	0.53 ^a
TDN [†]	0.35 ^a	0.65 ^a	0.54 ^a
SRP	0.88 ^a	0.86 ^a	0.73 ^a
DOC [‡]	0.45 ^a	0.64 ^a	0.85 ^a
Cl ⁻	0.25 ^b	0.98 ^b	1.56 ^c

For a given solute, similar letters denote subsystems with statistically similar CV_{CV} values. Subsystems were deemed to show statistically different CV_{CV} values if the difference between them was greater than 95% of the Δ CV_{CV} values generated randomly by the null model.

DIN, dissolved inorganic nitrogen; NO₃-N, nitrite-nitrogen + nitrate-nitrogen; NH₄-N, ammonium-nitrogen; DON, dissolved organic nitrogen; TDN, total dissolved nitrogen; SRP, soluble reactive phosphorus; DOC, dissolved organic carbon; Cl⁻, chloride.

[†] Parafluvial $CV_{CV} >$ riparian CV_{CV} : $P = 0.07$.

[‡] Surface stream $CV_{CV} >$ riparian CV_{CV} : $P = 0.06$.

the month-to-month change in the among-point spatial heterogeneity was statistically similar in the surface stream ($CV_{CV \text{ surface}} = 0.54$) and the riparian zone ($CV_{CV \text{ riparian}} = 0.35$), contrary to P2. Spatial heterogeneity of [TDN] in the parafluvial zone changed more from month-to-month ($CV_{CV \text{ parafluvial}} = 0.65$); thus the parafluvial-riparian comparison is marginally ($P = 0.07$) consistent with P2. For SRP, there is no statistical difference among subsystems in CV_{CV} . Finally, Cl⁻ data were most strongly aligned with P2, because CV_{CV} increased nearly four-fold from riparian to parafluvial zone and by an additional 59% from parafluvial zone to surface stream (Table 2).

To put these results in the context of some determinants of advection, we investigated whether temporal fluctuation in spatial CV (which determines CV_{CV}) showed synchrony with rainfall and discharge. We restricted this analysis to solutes and subsystems with CV_{CV} substantially greater than $CV_{CV \text{ riparian}}$; these include DIN, NO₃-N, DOC, and Cl⁻ in the surface stream and TDN in the parafluvial zone. Figure 5 shows how the spatial CV for surface stream NO₃-N showed inverse synchronous variation with rainfall summed over 3-, 32-, and 100-day windows (month-specific spatial CV_{surface} versus 3-day total precipitation $r = -0.45$, 32-day $r = -0.48$, and 100-day $r = -0.40$). Similarly, DIN spatial CV_{surface} tended to go down when rainfall had been greater during the previous 32 and 100 days ($r = -0.45$ and -0.53 , respectively), and DOC spatial CV_{surface} declined when either rainfall or discharge had

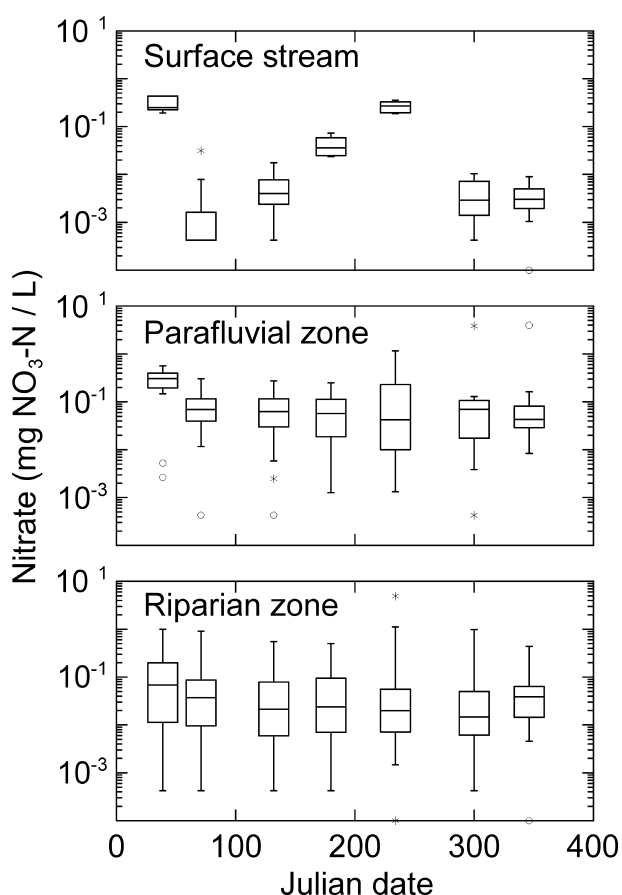


Figure 4. Box and whisker plots of $\text{NO}_3\text{-N}$ concentrations plotted through time in each subsystem type (see description of box and whisker sets in Figure 3). The data used to generate any single box and whisker set were $[\text{NO}_3\text{-N}]$ in the indicated subsystem on the indicated day of 2001 (Julian date 1 = 01 January). Thus, a single concentration value (a single datum) is the concentration measured at a point in time from a single point on the landscape. Note that spatial variability in $[\text{NO}_3\text{-N}]$ at a single point in time (the spread of a single box and whisker set) changes greatly from month to month in the surface stream (thus a high CV_{CV}) and is relatively constant among months in the riparian zone (thus a low CV_{CV}). We present this style of figure as a means of visualizing temporal change in spatial heterogeneity (that is, CV_{CV} values), but we do so for only $\text{NO}_3\text{-N}$, because this information is somewhat redundant of that shown in Table 2.

been greater during the previous 100 days ($r = -0.44$ and -0.55 , respectively; relation with discharge not shown in Figure 5). Finally, the spatial $\text{CV}_{\text{parafluvial}}$ of TDN showed inverse synchronous variation with mean discharge averaged over 32 days and with rainfall summed over 10-day windows prior to and including the day of solute sampling ($r = -0.42$ and -0.40 , respec-

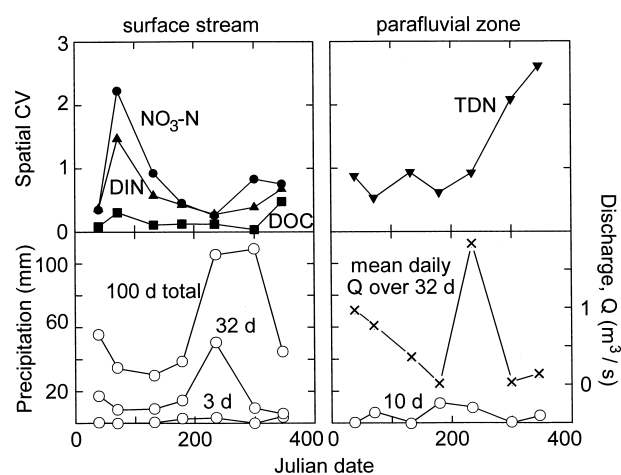


Figure 5. Synchrony plots of spatial CV in solute concentration versus rainfall and discharge. *Left-hand panels* show time series of the spatial CV of solute concentrations in the surface stream (*top*) and rainfall summed over 100-, 32-, and 3-day windows that terminate on the day solutes were sampled (*bottom*). *Right-hand panels* show time series of the spatial CV of [TDN] in the parafluvial zone (*top*) and rainfall summed over a 10-day window and discharge averaged over a 32-day window. Discharge data are from US Geological Survey gauge 9471550 on the San Pedro River near Tombstone, Arizona (<http://waterdata.usgs.gov/nwis/sw>).

tively; Figure 5). We did not conduct significance tests of these correlations.

DISCUSSION

This study supports the view that process has pattern. The spatial heterogeneity of solute concentrations match P1, supporting our first hypothesis that material cycles are smaller and more closed in the riparian zone, longer and more open in the surface stream, and intermediate in these regards in the parafluvial zone. Temporal change in the spatial heterogeneity of $\text{NO}_3\text{-N}$, DIN, and Cl^- match P2, supporting our hypothesis that for these solutes the length and openness of cycles are more subject to seasonal change in the surface stream and parafluvial zone than in the riparian zone. Other solutes do not support this second hypothesis. Generally, material processing appears to differ among subsystems of a fluvial ecosystem. This finding that different flowpath types are functionally different lends weight to another hypothesis (Fisher and others 2004) that the configuration and composition of flowpath types within an overall flow network governs the net functioning of that network. Our data also have implications for understanding pattern, process, and scale; future

directions for material spiraling research; and the stability of fluvial ecosystems.

Pattern, Process, and Scale

We observed two principal patterns. First, with data averaged annually, solute concentrations were most spatially variable in the riparian zone, less so in the parafluvial zone, and least spatially variable in the surface stream. This overall pattern comprises two subsidiary patterns, one at each of two spatial scales. The spatial heterogeneity *within* a subsystem type is one pattern in its own right, and the different magnitudes of spatial variability compared *among* subsystems form a second pattern. The second principal pattern we observed was that for inorganic N and Cl^- , snapshots (sampling events) of the spatial variability of solute concentrations changed most from month-to-month in the surface stream and least in the riparian zone. Again, there is a finer-scale pattern within the broader one: a temporal pattern of change in spatial variation within a subsystem and a spatial pattern of degrees of temporal change compared among subsystems.

We did not test any purported process–pattern relationship at the finer scale. We assumed one, and then tested whether that relationship shows variability at the broader (among subsystems) scale. We assumed that within a subsystem, the spatial heterogeneity in solute concentration and its temporal change result from the spatial extent and mutability, respectively, of material cycles within that subsystem type.

We are now interested in whether the subsystem-specific openness and mutability in material cycles show any spatial pattern among subsystems. Our data suggest that they do. Within-subsystem spatial heterogeneity in solute concentration is itself spatially variable among subsystems. And, temporal change in within-subsystem spatial heterogeneity of inorganic N and Cl^- is also spatially variable among subsystems. These results are consistent with our hypotheses that material cycles are more open and (for inorganic N and Cl^-) more mutable in the surface stream, whereas the converse occurs in the riparian zone. Given the association among communities, soils, and water residence time on the one hand, and uptake plus sorption opportunities and advection on the other (Fisher and others 1998), we argue that the among-subsystems spatial pattern in material cycle openness and mutability results from among-subsystem differences in these ecosystem structures. Namely, advection is slow and opportunities for

uptake and sorption are ample in the riparian zone. Furthermore, owing to the flood remediation properties of soils, the life history characteristics of riparian plants, and the steady supply of organic matter to riparian soil microbes, there is muted temporal change in riparian advection and biogeochemical processing. However, we do acknowledge that there are alternative explanations for our results. Low spatial variability in solute concentrations could accompany small, closed cycles if inputs to and outputs from each cycling “patch” were equal.

Our second hypothesis was supported only by inorganic N and Cl^- . This finding may reflect both an indiscriminate application of theory of material processing in advective systems (Newbold and others 1981; Fisher and others 1998) when formulating our hypotheses and an insufficiency of that theory for dealing with multiple elements (Fisher and others 2004). What are the principal uptake and release agents for each solute species, and how do they cause different solute species to exhibit different riparian zone–surface stream contrasts in the temporal variability of spatial heterogeneity?

For inorganic N, we suggest that temporal variation in material cycles is generated by temporal variation of the ecological community and advection, consistent with our second hypothesis. N limits channel (Grimm and Fisher 1986) and riparian (Adair and Binkley 2002) primary producers in the arid Southwest, and N demand and DIN uptake rates are tightly linked to biomass changes (Grimm 1987; Webster and others 2003). Thus, temporal variability in productivity generates temporal variability in DIN uptake rate and thus in the openness of DIN cycles. For such an assertion to hold, the surface stream community must be temporally more variable than the riparian community. Such a pattern can be inferred from the life history and turnover rates of the populations and communities inhabiting the various subsystems (Fisher and others 1982; Grimm 1987; Stromberg and others 1993; Lytle and Merritt 2004). In addition to these biotic drivers, variation in runoff may also influence whether inorganic N cycles shrink or elongate. This proposal is based on our observation that spatial variation in surface stream inorganic N tended to decline, presumably reflecting elongated cycles, after one to several months of high rainfall (Figure 4). For Cl^- , we suggest that mutability in the openness of the Cl^- cycle is generated by temporal variability in advection. Because Cl^- is biologically unreactive, its movements through space largely track water flow, which is more temporally

variable in the surface channel than in the riparian zone. But, it is puzzling that spatial CV_{surface} in Cl^- showed no synchrony with rainfall or discharge.

Uptake and release of other solutes, and thus temporal change in their cycles per unit longitudinal displacement, may be less influenced by turnover of the biotic community. Whereas the cycle of DIN is greatly influenced by biological processes (assimilation, mineralization, nitrification, dissimilatory reduction, and so on), the cycles of DON, DOC, and SRP are substantially influenced by geochemical processes, such as physical and chemical weathering, erosion, and chemical sorption/desorption. If such geochemical agents do not show increasing temporal variability from the riparian zone to the surface stream, then we would not observe a parallel increase in temporal fluctuations of spatial heterogeneity in DON, DOC, and SRP. In addition to geochemical processes, advection also seems to influence the openness of DON and DOC cycles, because concentrations of parafluvial TDN (= 25% organic N) and surface stream DOC were less spatially heterogeneous (presumably indicating elongated cycles) after weeks- to months-long periods of higher rainfall and discharge (Figure 5). Geochemical and advective influence over DON cycling is consistent with the "leaky N" hypothesis, which holds that because much N is contained in polyphenols and tanins, N is exported even from N-limited systems (Hedin and others 1995). Consequently, some amount of relatively low-quality DON leaches continuously from upland and riparian soils into surface streams and downstream recipient systems. Our results suggest that in-channel (surface stream and parafluvial zone) DON spatial heterogeneity was less temporally variable than in-channel DIN spatial heterogeneity. We see that for DON, $CV_{CV\text{parafluvial}} = 0.42$ and $CV_{CV\text{surface}} = 0.53$; whereas for DIN, these measures were greater, at 0.64 and 0.68, respectively (Table 2). We interpret this result as consistent with the leaky N hypothesis.

Hypothesis for Spiraling on a Geomorphic Template

Our findings bear on the material spiraling length framework (Newbold and others 1981). Spiraling length is the longitudinal displacement of an atom per cycle. Spiraling lengths are quantified along discrete flowpaths using tracers and permit comparative analyses of material budgets across a range of channel sizes and biomes (Webster and others 2003; Gücker and Boëchat 2004). Although the framework was developed for streams, its application to all ecosystems is evident (Wagener and

others 1998). Material in every ecosystem undergoes spatial displacement as it is transformed among physical and chemical states. Our data suggest that if spirals could be directly quantified along discrete flowpaths within a subsystem type, spiral length would be shortest in the riparian zone and longest in the surface stream. This would be a rigorous test of the hypothesis that ecosystem function is spatially variable. Spiraling lengths are typically measured in surface streams, but our data suggest a legitimate hypothesis that warrants measurements along subsurface flowpaths.

Geomorphological processes of river valley formation may partly underlie what we now purport is an among-subsystem spatial pattern in ecosystem function. Geomorphic processes sculpt surface morphology through construction (uplift and deposition) and degradation (weathering, glacial scouring, and hydrological downcutting). Associated with surface sculpting are sediment sorting processes that produce a distinct milieu of geology and soil deposits. These play a role in determining mineral and nutrient stores, habitat suitability, and hydrologic flowpaths (Gold and others 2001). Consequently, an array of patch types with different structural, and thus different functional, features assumes a nonrandom pattern that follows the action of the initiating geomorphic processes. Although the link between geomorphic template and community and ecosystem structure has been well investigated (for example, see Lewis and Magnuson 2000; Kratz and others 2005), this is one of the few studies to exemplify the link between template and function (see also Pinay and others 2000). This link is not the same for all functions. The identity of that function is also important. In our example, solute species identity was important, because the fluvial template did not similarly influence all solutes, particularly in terms of our second hypothesis. Landscape models of ecosystem functions should thus incorporate hypotheses about the interaction between the identity of the subsystem or patch type and the identity of the function.

Cross-linkages and Stability

Fluvial ecosystems are disturbed by floods, material loading, species invasions, and channel modification, which often occur interactively (Stanley and Doyle 2002). Fisher and others (1998) hypothesize that material processing capacity is more stable to such disturbances in fluvial ecosystems with more cross-linkages, which are fluxes between subsystems (Valett and others 1994). Cross-linkages

promote stability by interweaving resilient patches (surface streams) and resistant patches (riparian zone). This hypothesis begs the question: Is material processing resilient in surface streams and resistant in riparian zones? Our data suggest that the answer is yes with respect to inorganic N. We argued that the pronounced temporal change in inorganic N spatial heterogeneity in the surface stream reflects the greater mutability of advection and uptake in the surface stream. Mutability means that although advection and uptake are easily changed by disturbance, they also quickly return to pre-perturbation conditions. We speculate that our data showing a relatively constant spatial mosaic in riparian zone inorganic N indicate that advection and uptake in the riparian zone resist moderate disturbances; presumably, however, a large flood that uproots mature cottonwoods would alter uptake and preclude rapid return to pre-flood conditions. Given that the San Pedro contains cross-linkages connecting surface stream, parafluvial, and riparian patches (D.B. Lewis and others, unpublished tracer addition data), processing of inorganic N should, according to "Hypothesis 3" of Fisher and others (1998), be a generally stable feature of this ecosystem.

SUMMARY

We investigated spatial pattern in ecosystem function. We hypothesized (a) that material cycles are most open and elongated in the surface stream, intermediate in the parafluvial zone, and most closed and patchy in the riparian zone; and (b) that the openness of surface stream cycles was relatively mutable, whereas the closed nature of riparian cycles was not. The first hypothesis was supported by all solute species we examined. The second hypothesis was best supported by $\text{NO}_3\text{-N}$, DIN and Cl^- ; it was not supported by other solute species, perhaps because their uptake and release dynamics are principally influenced by geochemistry. Processing of inorganic N may be a stable function in this ecosystem. Generally, our findings indicate that a geomorphic template, interacting with sub-surface lithography and hydrology, can generate spatial patterns in ecosystem function, warranting an expansion of the spiraling framework to a variety of flowpath types.

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