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Evidence for self-organization in determining spatial patterns of stream nutrients, despite primacy of the geomorphic template

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Nutrients in freshwater ecosystems are highly variable in space and time. Nevertheless, the variety of processes contributing to nutrient patchiness, and the wide range of spatial and temporal scales at which these processes operate, obfuscate how this spatial heterogeneity is generated. Here, we describe the spatial structure of stream nutrient concentration, quantify the relative importance of the physical template and biological processes, and detect and evaluate the role of self-organization in driving such patterns. We examined nutrient spatial patterns in Sycamore Creek, an intermittent desert stream in Arizona that experienced an ecosystem regime shift (from a gravel/algae-dominated to a vascular plant-dominated hereafter, “wetland”) system in 2000 when cattle grazing ceased. We conducted high-resolution nutrient surveys in surface water along a 10-km stream reach over four visits spanning 18 y (1995–2013) that represent different successional stages and pre-wetland stage vs. post-wetland state. As expected, groundwater upwelling had a major influence on nutrient spatial patterns. However, self-organization realized by the mechanism of spatial feedbacks also was significant and intensified over ecosystem succession, as a resource (nitrogen) became increasingly limiting. By late succession, the effects of internal spatial feedbacks and groundwater upwelling were approximately equal in magnitude. Wetland establishment influenced nutrient spatial patterns only indirectly, by modifying the extent of surface water-groundwater exchange. This study illustrates that multiple mechanisms interact in a dynamic way to create spatial heterogeneity in riverine ecosystems, and provides a means to detect spatial self-organization against physical template heterogeneity as a dominant driver of spatial patterns.

The relationship between pattern and process is a long-standing topic of investigation in ecology (1–3). One of the fundamental questions underlying the study of pattern–process relationships is to what extent patterns are determined by local environmental conditions (e.g., soil and climate in terrestrial ecosystems, salinity and currents in oceans) and to what extent they are self-organized (4). A major challenge to understanding spatial heterogeneity is that multiple processes operating across a range of spatial scales contribute to it, and their relative contributions may themselves vary over time (5). Here, we used patterns of nutrient concentration in a desert stream as a model system to disentangle the relative influence of physical template and biological processes, evaluate the role of internal spatial feedbacks emerging from physical and/or biological processes, identify the spatial scales of underlying processes, and compare inferences over short-term succession and long-term ecosystem regime shifts.

The physical template can be defined as the relatively stable physical environment in which a pattern of interest develops (3), and is considered an overriding organizer of ecological patterns. At large spatial scales, spatial zonation of vegetation pattern is a classic example of the environmental template determining plant pattern formation in action (6). At smaller scales, microtopography significantly influences plant distribution (7). In streams, the physical template influences stream surface-water nutrient patterns (8). Longitudinally, tributary junctions bring water with distinct biogeochemical signatures into a stream. Laterally, streams are hydrologically connected to the riparian zone, the floodplain, and the upland portions of catchments (8), with riparian zones acting as “nutrient filters” that remove various chemical constituents as water moves from uplands to the stream (9). Vertically, subsurface water from the hyporheic zone can also alter the biogeochemical signature of surface water (10). At broader spatial scales, geomorphic features, such as slope breaks and canyons, determine the locations of upwelling and down-welling zones (11). Collectively, such connections among subsystems in the riverine landscape form the physical template that influences patterns of nutrient concentration in stream surface water.

Biological processes also contribute to spatial patterns in nutrient concentration. In many arid and semi-arid terrestrial ecosystems, canopy trees and shrubs produce organic litter and alter water flows, creating islands of fertility and spatial heterogeneity in soil moisture and nutrients across the landscape (12). Stream nutrient dynamics are influenced by similar in-stream biological processes (13). Many studies have documented longitudinal (i.e., downstream) declines in nutrient concentration (14), and others have shown that algal uptake represents a primary pathway of nitrogen (N) retention (15). Riverine wetland patches dominated by macrophytic vascular plants (“macrophytes”) have more complex relationships with stream nutrients. During the growing season, a

Significance

Rivers and streams are open, heterogeneous ecosystems. Stream water chemistry is influenced by organisms and the physical environment, resulting in longitudinal (upstream-downstream) heterogeneity that can be analyzed with time-series methods. Applying statistical techniques to longitudinal nutrient concentration data in a desert stream, we found evidence of substantial internal regulation of surface-water nutrient patterns, realized via spatial feedbacks. The strength of these feedbacks increased over succession. Although inputs from subsurface zones (a feature associated with the physical template) remained a major factor in explaining nutrient patterns, by late succession, the effect size of internal feedbacks was equal to the effect size of major upwelling zones. Our study demonstrates that multiple processes interact in a dynamic way to create ecosystem spatial heterogeneity.

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substantial amount of N and phosphorus (P) may be taken up by vascular plants (16). However, comparisons of stream reaches with different macrophyte covers showed that macrophytes have limited influence on water-column nutrient concentration (17). Riverine macrophytes accumulate fine sediments and reduce vertical hydrological exchange (18), which could dampen the biogeochemical signature of groundwater on surface water. N fixation (i.e., N2 to organic N) is another seasonally variable biological process that potentially contributes to variation in surface-water N concentration (19). Biological processes may be controlled, in turn, by factors that vary spatially, such as the physical template described above.

Last but not least, spatial heterogeneity can also emerge via self-organization. Broadly defined, self-organization is a process in which pattern at large scales emerges from local interactions (4). Self-organized, regular vegetation patterns have been studied extensively in the past decade in water-limited systems (e.g., refs. 20–22). Mathematical models (e.g., refs. 23, 24) and field observations (e.g., refs. 21, 22) show that terrestrial plants can form regular patterning driven by the local feedbacks between biomass and the limiting resource (water). In streams, nutrients (N and P) often represent limiting resources (25, 26), and thus could potentially induce local spatial feedbacks (i.e., self-organization). For example, elevated stream nitrate (NO\textsubscript{3}\textsuperscript{−}) concentration at upwelling zones induces the formation of algal patches that then may raise NO\textsubscript{3}\textsuperscript{−} concentrations further downstream, in turn, inducing the development of algal patches there (29). To what extent such internal spatial feedbacks, realized through biological and/or physical processes, inform nonregular spatial structure in heterogeneous systems remains unexplored to date.

The drivers described above have been studied relatively well in isolation. However, little is known about how they interact collectively to influence spatial heterogeneity, and even less is known about how their relative contributions may change over successional time in ecosystems. Here, we capitalized on two unique features of stream ecosystems: (i) unidirectional flow in streams simplifying the spatial pattern from 2D to 1D, which allows the use of time-series analyses to understand spatial patterns, and (ii) their rapid reorganization and regrowth (1–3 mo) after biomass-reducing floods, which allows investigation of multiple successional changes in spatial patterns within a short period (30). Regime shifts, another type of ecosystem change, occur abruptly as thresholds are crossed, and could result in dramatic changes that are difficult to reverse [e.g., a lake shifting from a clear-water state with abundant rooted aquatic plants to a turbid state, where shading by abundant algae suppresses rooted plants (31)]. Changes in the dominant species and altered biological processes may have significant biogeochemical consequences. Our study system (Sycamore Creek, a desert stream in Arizona) experienced a regime shift around 2000 when cattle were removed from the watershed, with dominant gravel- and benthic algae-dominated substrates transforming, over the course of several years, to a state dominated by riverine wetlands (32).

The removal of cattle is assumed to have favored the expansion of wetland cover over 20 y of prior research. Thus, the system provides an opportunity to evaluate short-term successional changes in stream nutrient patterns and longer term changes associated with an ecosystem regime shift.

We collected chemical concentration data [NO\textsubscript{3}\textsuperscript{−}-N, soluble reactive P (SRP), and conductivity (COND)] every 25 m along a 10-km stream segment in Sycamore Creek at four postflood successional stages (early-, mid-, mid- to late-, and late-successional stages), three of them before wetland establishment (1990s) and one afterward (2013). Comparing different successional stages before and after the ecosystem regime shift, we asked the following questions:

i) Are spatial patterns of nutrient concentration influenced by wetland establishment?

ii) What is the relative importance of physical and biological drivers, and what role do internal feedbacks play (if any) in influencing spatial patterns of nutrients?

iii) How do the underlying processes and the manifested patterns change over successional time?

These questions were answered by applying time-series models to evenly spaced, longitudinal (spatial) nutrient data. We used wavelet analysis to describe the scales at which the underlying processes operate. To quantify the relationships between the putative drivers and nutrient spatial heterogeneity, we used multivariate autoregressive state-space (MARSS) models, a time-series analysis method. The MARSS modeling framework is commonly used in population and community ecology to understand long-term trends in populations (e.g., refs. 34, 35) and the relative importance of internal regulation or species interactions vs. the effects of exogenous environmental variables on population dynamics (e.g., ref. 36). In this study, we applied MARSS models to one-dimensional chemical data to partition the relative importance of the physical template, biological processes, and internal concentration regulation over succession.

Two important findings emerge from our results. First, the physical template (here, groundwater upwelling) was a dominant factor influencing nutrient spatial patterns, about one order of magnitude higher than biological effects. The most visually obvious (biological) change in the system over the nearly two decades encompassed by the study, establishment of riverine wetlands, did not have a direct effect on nutrient spatial patterns. Second, internal spatial feedbacks, feedbacks that indicate self-organization but have not been considered in stream biogeochemical research, became stronger over succession as a resource becoming increasingly limiting, and were as important as the physical template by late succession. We conclude that research on stream nutrient spatial patterns requires an explicit consideration of the interplay between the physical template and the system’s internal self-organization, as well as how this interplay may change over successional or greater time scales.

Results

**Patterns of Nutrient Heterogeneity.** Nutrient concentrations were extremely variable in space (Fig. 1 and Table 1). Over 23 y (1976–1999) of approximately biweekly surface-water nutrient monitoring in Sycamore Creek at a single location yielded a coefficient of variation (CV) of NO\textsubscript{3}\textsuperscript{−} concentration that was only twice the NO\textsubscript{3}\textsuperscript{−} concentration over 10 km of space in midsuccession on a single day (CV over 23 y = 207% for 434 samples, CV over 10 km = 104% for 399 samples). The pattern of overall spatial variation in concentrations (CV) was highest for NO\textsubscript{3}\textsuperscript{−}, followed by SRP, and lowest for conductivity, regardless of successional stage.

A large sine-wave curve was observed across all four surveys for conductivity (Fig. 1). Mean SRP concentration was 60% higher after wetland establishment (same successional stage). In contrast, mean NO\textsubscript{3}\textsuperscript{−} concentration was similar before and after wetland establishment (Table 1). Spikes in NO\textsubscript{3}\textsuperscript{−} concentration were found in the same upwelling locations, regardless of timing of the survey (Fig. 1).

For NO\textsubscript{3}\textsuperscript{−}, net uptake length (a measure of tightness of nutrient cycling, with shorter lengths indicating tighter cycles) was shortest in late succession. Net NO\textsubscript{3}\textsuperscript{−} uptake length after wetland establishment was similar to NO\textsubscript{3}\textsuperscript{−} uptake length in early succession, much longer than in late succession (SI Appendix, Fig. S1). The net SRP uptake length with wetlands present was shortest during mid- to late succession after wetland establishment, even shorter than in late succession before wetland establishment.
Wavelet analysis revealed a strong influence of upwelling zones on NO$_3^-$ patterns (Fig. 2). The global wavelet spectrum (GWS) is the space-integrated version (i.e., across the entire stream length) of the wavelet power spectrum, and it identifies the dominant scales of spatial variation (by peaks in GWS). The GWS of NO$_3^-$ signals showed two distinct spectrum peaks at spatial scales of ∼1 km and 3 km, except during early succession, when the 1-km peak was absent (Fig. 3 and SI Appendix, Table S1). For SRP and conductivity, only one peak, between 1.5 and 1.8 km, was observed in the GWS over successive time (Fig. 3 and SI Appendix, Table S1). Wavelet analysis of wetland abundance distribution and its GWS showed that the spectrum peaks powered at spatial scales of ∼700 m and ∼2500 m at downstream distances of 5–7 km and 7–10 km, respectively (Figs. 2 and 3). Wavelet analysis for nutrient spatial heterogeneity and wetland distribution showed different patterns (Figs. 2 and 3 and SI Appendix, Fig. S2), suggesting different underlying contributing processes. By comparing the mean dissimilarities in the space–spatial scale plane (i.e., spatial locations on the x axis, spatial scale on the y axis) for different solutes, we found that SRP patterns varied most with successional stage, followed by NO$_3^-$ and then conductivity (SI Appendix, Fig. S3A). Differences in spatial patterns among solutes increased with successional stage (SI Appendix, Fig. S3B).

Relative Importance of Drivers over Successional Time. The explanatory variables in MARSS include three physical variables (water permanence, reach types, and presence/absence of upwelling zones), three biological variables (presence/absence of algae, presence/absence of cyanobacteria, and macrophyte abundance), and internal spatial feedbacks. We constructed two models. In the first one (model I), we compared the local effects of physical variables and biological drivers on nutrient concentration. In the second one (model II), we focused on partitioning internal spatial feedbacks and physical drivers (template) by leaving out processes (variables) that could potentially contribute to the internal spatial feedbacks to avoid double counting (Methods and SI Appendix, SI Materials and Methods).

Upstream wetland abundance was not a significant factor in explaining the SRP, NO$_3^-$, or conductivity [in 2013, we measured chloride (Cl$^-$), also a nonreactive metric] spatial patterns. We explored wetland abundance across a variety of upstream distances (scales: 25 m, 50 m, 75 m, 100 m, 125 m, and 150 m), but at none of these scales was a wetland effect statistically significant (only results at 100-m scales are shown in Fig. 4). Algal communities showed a significant negative effect on NO$_3^-$ in 2013 (Fig. 4). In late succession, the effect of cyanobacteria on NO$_3^-$ was positive and significant (Fig. 4).

The influence of upwelling (physical template) on NO$_3^-$ concentration was approximately one order of magnitude greater than the influence of upwelling of biological processes [i.e., the value of the coefficient for upwelling was at 10$^{-6}$ (Fig. 5), and it was at 10$^{-1}$ for biological processes (Fig. 4)]. The upwelling effect on NO$_3^-$ and SRP was significantly positive in three successional stages before wetland establishment, and its effect size increased from early to late succession (Fig. 5). For NO$_3^-$, before wetland establishment, the upwelling effect was negatively correlated with the amount of surface water in the stream (Fig. 6). However, following wetland establishment, this effect size decreased, showing significantly lower values than predicted by the amount of surface water at the time the survey was conducted (Fig. 6B). Similarly, for SRP patterns, after wetland establishment, the effect of upwelling zones became nonsignificant (Fig. 5). Other physical drivers, including water permanence and reach type, influenced nutrient spatial patterns in some surveys.

![Fig. 1](image)

Spatial patterns of nutrient concentration in Sycamore Creek over 10 km across four stages of postflood succession and two ecosystem states (early succession in March 1997, midsuccession in May 1995, late succession in December 1995, and mid- to late succession with wetlands present in May 2013). In 2013, we measured Cl$^-$ concentration instead of conductivity. Small and large red dots denote minor and major upwelling locations, respectively. Data from Dent et al. (10).

<table>
<thead>
<tr>
<th>Table 1. Water chemistry characteristics over the 10-km stretch of Sycamore Creek</th>
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<td>Characteristics</td>
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<td>Early succession (2 wk postflood/March 1997)</td>
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<td>NO$_3^-$-N</td>
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<td>SRP</td>
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<td>Conductivity</td>
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<td>N/P</td>
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<td>Midsuccession (2 mo postflood/May 1995)</td>
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<td>NO$_3^-$-N</td>
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<td>SRP</td>
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<tr>
<td>Conductivity</td>
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<td>N/P</td>
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<tr>
<td>Late succession (9 mo postflood/December 1995)</td>
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<tr>
<td>NO$_3^-$-N</td>
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<tr>
<td>SRP</td>
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<tr>
<td>Conductivity</td>
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<td>N/P</td>
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<tr>
<td>Mid- to late succession (2 mo postflood/May 2013)</td>
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<tr>
<td>NO$_3^-$-N</td>
</tr>
<tr>
<td>Cl$^-$</td>
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<td>N/P</td>
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All values are calculated across the n sample locations; values at each sample location are means of two analytical replicates. Data for 1995 and 1997 are from Dent and Grimm (54).
but none of these physical drivers had an explanatory power as strong as the explanatory power of upwelling (SI Appendix, Tables S2 and S3).

The effects of internal spatial feedbacks were quantified with the $b$ coefficient in univariate autoregressive state-space models (model II; Methods). When dealing with population time series data, this coefficient quantifies internal regulation of a population via density dependence [Ives et al. (37)]. Here, the $b$ coefficient quantified the strength of concentration-dependent effects: Values of 1 indicate no concentration-dependent effects, and values closer to 0 suggest strong concentration dependence, or processes causing downstream concentration to return to its mean level quickly. For all $b$ coefficients, the 95% confidence intervals did not include 1 (Fig. 7), indicating significant regulation of nutrient concentration via internal spatial feedbacks (self-organization) in the system. Values decreased from early to late successions for NO$_3^-$, indicating stronger concentration-dependent effects toward late successions (Fig. 7). The strength of internal regulation increased by a factor of eight from early to late succession for NO$_3^-$; meanwhile, the effect size of upwelling increased by a factor of four. The ratio between the effects of internal regulation and external geomorphic control increased from 0.5:1 in early succession, to 0.7:1 in mid-succession and mid- to late successions, and up to 1:1 in late succession (Figs. 7 and 8). Such successional trends did not exist for SRP or COND (Fig. 7 and SI Appendix, Table S4).

### Discussion

The central question of which processes generate spatial heterogeneity in terrestrial and aquatic ecosystems has received attention from ecologists for decades, but the challenge of disentangling the simultaneous effects of exogenous drivers and internal feedbacks on the spatial structure of elements or biota remains unmet (1–4). Here, using recent advances in time-series methods applied to a desert stream, we identified the spatial scales of drivers underlying observed patterns of solute concentrations, partitioned the relative influences of physical drivers and biological processes, quantified internal spatial feedbacks, and compared inferences over short-term succession and a long-term ecosystem regime shift. The observation that internal spatial feedbacks contribute to regulating biogeochemical patterns in rivers and streams is novel and could influence how stream ecosystems respond to environmental perturbations (38, 39). Our study also illustrates that data and methods capable of appraising this complexity and dynamism are essential for understanding pattern–process relationships in rivers, lending importance to long-term data coming online in the United States and elsewhere, such as the National Ecological Observatory Network’s stream monitoring program.

### Effects of Wetlands on Spatial Heterogeneity of Nutrients

Wetlands are considered biogeochemical hotspots (40), in the sense that riverine macrophyte patches exhibit significant nutrient retention (41). However, studies quantifying biogeochemical influences of wetlands typically integrate large downstream distances (or areas) to calculate total nutrient uptake; hence, the particular contribution of macrophytes to nutrient spatial patterns remains unresolved. In our study, although wetland plants covered ~40% of the stream in 2013, we found no evidence of wetland patches affecting spatial patterns of NO$_3^-$ or SRP concentrations directly. In contrast, algae had a significant negative effect on NO$_3^-$ (but not on SRP; Fig. 4), even though the amount of N stored in algae is only about a third of the amount of N stored in vascular plants (SI Appendix, SI Materials and Methods). Concentration of SRP is additionally affected by physical adsorption/desorption and solubility processes, which may explain why SRP concentration is not negatively associated with algae in this system. Vascular macrophytes do assimilate these nutrients and, in fact, represent a much greater nutrient storage pool than algae. We suggest that local
effects of wetlands on surface water nutrients are undetectable compared with local effects of algae because macrophytes obtain their nutrients via root uptake (42), which is not reflected in surface-water concentration.

We observed no direct effect of wetlands on surface-water spatial patterns of nutrients, but wetlands indirectly affected nutrient spatial patterns through their influence on surface-subsurface hydrological exchange. After wetland establishment, the effect size of upwelling on NO$_3^-$ in 2013 was significantly lower than predicted by the amount of fixation.

and SRP peaks occurred at (18). Reduced exchange and Rivers and streams are open ecosystems, highly influ- enced by their physical environment. This characterization is supported in our study: The effect size of upwelling on NO$_3^-$ concentration was about one order of magnitude higher than the direct effect of biological processes (Figs. 4 and 5), indicating a dominant role for the geomorphic template in shaping patterns of NO$_3^-$ in Sycamore Creek. However, patchiness in any landscape is likely to result from a mixture of both exogenous drivers and internal feedbacks (49). Variability in nutrient concentration induces internal spatial feedbacks, realized through interaction among wetlands and macrophytes.

Changes in the Spatial Scales of Underlying Drivers over Successional Time. The geomorphic template determines the spatial scales at which geomorphic drivers operate; it was relatively stable over the time scale of this study. The NO$_3^-$ and SRP peaks occurred at major upwelling zones, repeating approximately every 3 km (Fig. 1). This distance between major upwelling zones corresponded to a stable peak at the ~3-km spatial scale in the GWS over four successional stages (Fig. 3).

In contrast, the spatial scale of the influence of biological processes is determined by the process rates and by the propagation rate of the results of processes (43), both of which may change over successional time. The 0.75- to 1.5-km spatial scale (Fig. 3) could be attributed to the introduction of NO$_3^-$ due to N$_2$ fixation. According to Grimm and Petrone (28), N$_2$ fixation in late suc- cession in Sycamore Creek is about 2 mg m$^{-2}$ h$^{-1}$. This fixation rate translates to a distance of ~1.5 km for NO$_3^-$ to accumulate a peak of 50 μg L$^{-1}$ (SI Appendix, Table S1), about the size of the small peaks observed in late succession (Fig. 1). Cyanobacteria are usually absent in early spring (28), but over seasonal and successional time, rates of N$_2$ fixation, flow velocity, and areal coverage of N$_2$ fixers tend to increase (28). These changes explain why the spatial scales of N$_2$ fixation changed over successional time (Fig. 3).

Alternatively, the 0.75- to 1.5-km signal could also be generated by minor upwelling spots (not the major reach-scale upwelling zones used as the physical template in the model) caused by a decrease in channel slope that may cause subsurface water to upwell to the surface (44). This signal became stronger as surface water (dilution water) declined toward late succession (45).

For SRP, the first maximum GWS was reached at a spatial scale of 1.2–1.8 km (Fig. 3B). Adsorption/desorption equilibrium between sediments and the overlying water column often plays an important role in P dynamics (46). A desorption rate of 1.7–2.5 μg L$^{-1}$ d$^{-1}$ would increase SRP concentration by μg L$^{-1}$ within a 1.2- to 1.8-km downstream distance (SI Appendix, Table S1). This desorption rate is within the range observed in other streams and rivers (e.g., refs. 47, 48).

Relative Influences of Exogenous Factors and Internal Spatial Feedbacks. Rivers and streams are open ecosystems, highly influ- enced by their physical environment. This characterization is supported in our study: The effect size of upwelling on NO$_3^-$ concentration was about one order of magnitude higher than the direct effect of biological processes (Figs. 4 and 5), indicating a dominant role for the geomorphic template in shaping patterns of NO$_3^-$ in Sycamore Creek. However, patchiness in any landscape is likely to result from a mixture of both exogenous drivers and internal feedbacks (49). Variability in nutrient concentration induces internal spatial feedbacks, realized through interaction among wetlands and macrophytes.

**Fig. 4.** Maximum likelihood (ML) estimates of the MARSS model coefficients representing effect sizes of upstream wetland abundance, presence of algal patches, and presence of cyanobacteria on different water chemicals [NO$_3^-$, SRP, and conductivity (Cond)] in mid- to late succession in 2013 (A–C) and in late succession in 1995 (D and E) (results from model I). Red boxes indicate statistically significant effects [bootstrapped 95% confidence interval (CI) not including 0].
between local biological and/or physical processes and local nutrient concentrations and by the propagation of that influence in space (43). Such propagation of influence in space has been documented in streams at the local scale (e.g., ref. 29), but its effect on larger scale nutrient patterns has not been quantified, as is the case for changes over time. Here, we show that such internal spatial feedbacks could be as important as the geomorphic template in their influence on NO$_3^-$ concentration in the stream: By late succession, the ratio of control of nutrient concentration variability by internal regulation and by geomorphic template was 1:1 (Fig. 8). The intensification of the temporal feedbacks means that the system became more responsive to changes in NO$_3^-$ concentration in late succession (i.e., a small fluctuation in concentration invoked a quick return to an equilibrium concentration). This responsiveness likely results from intensified N limitation in late succession in Sycamore Creek, as observed in previous empirical research on the system (15). Resource limitation increasing the strength of internal feedbacks has been described in arid terrestrial ecosystems, where water constitutes the constraining resource and gives rise to self-organized vegetation patterns (e.g., refs. 20, 22). Sheffer et al. (49) showed that a semiarid shrub-grassland landscape exhibited self-organized vegetation patterns only when water was limiting; in contrast, the physical template determined vegetation patterns under sufficiently high precipitation. Although these regular patterns are formed via scale-dependent feedbacks, a mechanism different from the feedbacks we describe here, both studies demonstrate the role of broadly defined spatial self-organization (4) in forming spatial heterogeneity and show that the strength of self-organization intensifies with increasing resource limitation. Concentration-dependent effects were also observed for SRP, which suggests the existence of regulation mechanisms. However, no successional trend was observed for SRP, likely because SRP is subject to an additional control pathway (50) of sediment adsorption and desorption (51) that masks biological uptake.

The current paradigm for understanding nutrient spatial heterogeneity has almost exclusively focused on the effects of exogenous environmental drivers, considered for a snapshot in time. Although our study did support the importance of the geomorphic template in establishing spatial pattern (Fig. 5), we highlight here that internal regulation played an equally significant role in surface water chemical patterns (Fig. 8). Over successional time with a progressive reduction of surface discharge, the effect of groundwater inputs (i.e., groundwater is a higher fraction of total flow) was amplified by fourfold. However, the intensity of internal spatial feedbacks of NO$_3^-$ increased by a factor of eight, from 49% of the effect size of groundwater upwelling in early succession, to about 70% in midsuccession and mid- to late succession, up to 98% in late succession (Fig. 8). Meanwhile, biological uptake, an intensely studied and often pronounced mechanism driving spatial pattern in streams, had only a limited effect on longitudinal variation in nutrient concentrations (Fig. 4). Rivers and streams have generally been considered as open systems, subject to strong external environmental influences (38). We can therefore infer that it is highly likely that the kind of internal spatial feedbacks demonstrated in our study may play an even more important role in other ecosystem types where the effect of template heterogeneity is not as strong.

Methods

Study Site. This study was carried out in Sycamore Creek, a tributary of the Verde River located 32 km northeast of Phoenix, Arizona. The stream drains a catchment of 505 km$^2$ that ranges in elevation between 427 m and 2,164 m. The study site is a 10-km stretch of stream ranging from 600 to 700 m in elevation. Stream substrata consist of coarse sand and gravel that can be up to several meters deep in runps, as well as boulders and cobble in riffles, with limited reaches of exposed bedrock. The long-term (1905–2014) mean annual precipitation varies with elevation from 39 to 51 cm·yr$^{-1}$, but varies greatly across years (ranging from 2 to 92 cm·yr$^{-1}$). Precipitation is bimodally distributed through the year, with rainy seasons in winter (December–March) and summer (July–September); thus, the stream is frequently intermittent, with isolated perennial sections separated by large sections that are intermittently, especially in summer (52). N limits algal primary production during base flow, but P limitation has not been demonstrated and is unlikely (25). Growth of wetland vegetation (post-2000) also is N-limited (53).

Sycamore Creek experienced an ecosystem regime change around 2000, when cattle were removed from the watershed, with dominant gravel- and benthic vascular macrophytes transforming to a state with abundant riverine macrophytes (wetlands) (32). By 2013, around 40% of the 10-km main stem of Sycamore Creek was covered by patchily distributed wetland plants (33). Before wetland establishment (in the late 1990s), three surveys of the spatial patterns of water chemistry were completed in the 10-km main stem of Sycamore Creek by Dent and Grimm (54). These sampling dates represent three postflood successional stages (i.e., they differ in time after large winter floods that removed biomass, initiating succession) in the algae-dominated ecosystem state. In May 2013, after the ecosystem regime shift (wetland state), we repeated the water chemistry of Dent and Grimm (54) in the same 10-km stream reach, with the timing of the survey capturing a mid- to late (postflood) successional stage. These surveys collectively represent four successional stages (early to late) and two ecosystem states (algal- vs. microphyte-dominated).

Sample Collection and Analysis. The nutrient data used in this study were from two sources: existing data (51) and new data collected on May 31, 2013, all from the same section of Sycamore Creek. We replicated field techniques of Dent and Grimm (54), collecting duplicate samples of surface water in 60-ml tubes from the stream’s thalweg. Samples were taken at points 25 m apart,

![Fig. 6.](image-url)

(A) Linear relationship between extent of surface water (meters) and total volume of surface water (cubic meters). (B) Linear regression between the amount of surface water and the effective size of upwelling on NO$_3^-$ concentration (model I) before wetland establishment (1990s) and after wetland establishment (2013). After wetland establishment, the coefficient of upwelling was significantly lower than predicted by surface water volume (in red dashed-lined box).
and were collected as simultaneous as possible by 14 people arrayed along the 10-km stream segment. Each person walked upstream as he or she collected samples over ~700 m. All samples were filtered in the field within 2 h, between 0800 hours and 1000 hours. Locations at each 700-m overlap point were sampled at both the beginning and the end of the collection period to check for diel variation in nutrient concentrations. The magnitude of diel change was <10% of the range of concentrations observed and 2.5-fold the average variation between replicates, so we are confident that the spatial patterns we report were not confounded by temporal variation.

Filtered water samples were frozen until analysis. All water samples were analyzed within 3 wk for NO$_3^-$-N (hereafter, NO$_3^-$, but concentration is reported as mass N per volume), SRP (concentration reported as mass P per volume), and Cl$^-$. NO$_3^-$ and SRP were determined using a Lachat QC8000 Flow Injection Analyzer. We measured NO$_3^-$ using the cadmium reduction method (55) and SRP using the molybdate blue method (56). Cl$^-$ was also determined on the QC8000 Flow Injection Analyzer.

We then organized and reanalyzed the data collected from the same 10-km segment of Sycamore Creek studied by Dent and Grimm (54) in the 1990s. Those surveys represent three stages of postflood succession, 2.5 mo after a flood on March 6, 1995 (peak discharge = 113 m$^3$ s$^{-1}$); 9 mo after the same flood; and 2 wk after a flood on February 28, 1997 (peak discharge = 83 m$^3$ s$^{-1}$) (SI Appendix, Fig. S4). These dates were representative of mid-, late-, and early postflood successional conditions in the stream, respectively. Data in 2013 were collected 2.5 mo after a flood and corresponded to mid-succession (comparable to May 1995 data); however, the peak discharge of the flood in March 1995 was threefold larger than in May 2013. Moreover, there was a sustained relatively high flow in 1995 before the May survey (the mean daily discharge was 0.45 m$^3$ s$^{-1}$ on the survey date in 1995), whereas in 2013, discharge dropped to 0.45 m$^3$ s$^{-1}$ as early as March 28 and declined to 0 on the survey date. As a result, although both surveys were conducted 2.5 mo after the last flood, the 2013 survey was judged to be at mid- to late-successional stage. Whereas Dent and Grimm (54) measured conductivity, we analyzed Cl$^-$ instead in 2013. Both measures represent variation in a biologically inert constituent.

**Data for Covariates.** Two types of covariate data were collected. The first type was biological data. We surveyed the location, species (dominant species: Equisetum laevigatum, Papasul distichum, Schoenoeptolus americanus, Typha domingensis, and Juncus torreyi), and sizes of wetland patches along the 10-km study reach 2 wk after the 2013 water chemistry survey (SI Appendix, Fig. S5). One week before the survey, we recorded the presence or absence of filamentous algae and cyanobacteria at 25-m flagged intervals where water samples were to be taken. Dent and Grimm (54) recorded the presence or absence of filamentous algae and cyanobacteria in late successional time in 1995 in the same way. The second type of covariate data collected was data used to describe the physical template. Water permanent data were provided by E. Stanley, University of Wisconsin, Madison, WI (52). From May 1988 to February 1990, Stanley surveyed the same 10-km stream stretch and recorded the spatial extent and average depth of water monthly (22 consecutive monthly surveys). We calculated water permanence (percentage of time with surface water present within the 22-mo study period) along the stream using these survey data. The spatial locations of upwelling along the 10-km stretch of the stream were obtained from Dent et al. (10); they recorded upwelling zones at the reach, channel unit, channel subunit, and particle scale. Upwelling zones at the reach scale occur at transitions from unimproved to constrained valleys. Dent et al. (10) identified three such transitions as major upwelling zones (Fig. 1). Additionally, they used locations where water emerged downstream of a dry streambed as reach-scale upwelling, which they mapped during a dry period when the stream had not flooded for more than 18 mo. The upwelling locations at smaller spatial scales were also mapped; however, here, we assumed that only the reach-scale upwelling locations remain spatially fixed through bed-moving floods and only used these data. Finally, we recorded reach types (riffle, run, and pool; categorical) in the 2013 survey, as did Dent and Grimm (54).

**Statistical Methods.**

**Wavelet analysis.** We performed a wavelet analysis to decompose spatial scales of longitudinal variation in nutrient concentration, the results of which were used to infer putative environmental drivers. Wavelet analysis does not require the data series to be stationary, and is therefore particularly attractive, given the non-stationary nature of most ecological data (57). A full description of the wavelet technique can be found in an article by Torrence and Compo (38). Wavelet analyses were applied to all 12 nutrient series (i.e., three nutrient types × four surveys). A global assessment of the scale-specific properties of the decomposed signal was achieved by summing the mean of the squared wavelet coefficients across all locations to produce a scogram or GWS. After obtaining the corresponding wavelet spectra generated from wavelet analysis, we compared them using a multivariate method that defines an orthonormal basis maximizing the mutual covariance for each pair of wavelet spectra (59). Comparing the decomposition of the wavelet spectra onto this orthonormal basis enabled us to quantify the dissimilarity of space- and spatial-scale patterns (i.e., both the spatial scales and the spatial positions) among different nutrient species and among successional stages. We then used the constructed 12 × 12 dissimilarity matrix to calculate the mean dissimilarity exhibited by the main factors [i.e., nutrient species (NO$_3^-$, SRP, and Cl$^-$), successional stages], which allowed us to evaluate the relative importance of the main factors [similar to the method of Rouyery (59)]. Wavelet analyses were carried out using the “biwavelet” package (60) in R (61).

**MARSS models.** To quantify the relationships between the putative drivers and nutrient heterogeneity, we used MARSS models. We fitted MARSS models using the “MARSS” R-package (62), which provides support for fitting MARSS models to multivariate data via maximum likelihood, using an expectation-maximization algorithm. We constructed two different MARSS model structures: Model I quantified the relative influences of biological processes and the physical template on nutrient spatial patterns, and model II was used to quantify effects of the relative contribution by physical template and by internal spatial feedbacks.

**Model I.** A MARSS model includes a process model (Eq. 1) and an observation model (Eq. 2):

$$\begin{align*}
x_t &= Bx_{t-1} + Cc_t + w_t, \quad w_t \sim MVN(0, Q) \\
y_t &= Zx_t + A + v_t, \quad v_t \sim MVN(0, R)
\end{align*}$$

Data enter the model in $y$ (with $y_t$ being the log-transformed and z-scored nutrient concentration at sampling site $s$) and in $c$ (with $c_t$ being the covariate data at sampling site $s$, z-scored for continuous covariates). The total number of covariates included in MARSS models for different years varied, as detailed in the following paragraph. The data $y_t$ are a linear function of the “hidden” or true nutrient concentration $x_t$. Each element in $y_t$ is the observed concentration for three chemical species, each with two replicates (i.e., a 6 × 1 vector). Each element in $x_t$ is the true concentration for each physical template on nutrient spatial scales (i.e., a 3 × 1 vector). The effect of exogenous variables (i.e., the covariates representing physical drivers and biological processes) on concentration changes is $c$, a matrix of the linear effects of $c$, on $x_t$. $B$ is a 3 × 3 interaction matrix that models the effect of nutrients on each other (off-diagonal values) and on themselves (diagonal values). The covariance $w_t$ is a 3 × 1 vector of process error, representing the effects of environmental stochasticity and being modeled with a multivariate normal distribution (mean of 0, covariance matrix $Q$). In the observation model (Eq. 2), $v_t$ is a 6 × 1 vector of nonprocess (observation or measurement) errors, with errors at sampling site $s$ being multivariate normal with mean 0 and covariance matrix R. At each sampling point, we collected replicate samples, which allowed the
model to separate the two sources of error variance (observation vs. process error). $Z$ is a 6 × 3 matrix that relates time series to the different state processes. Finally, $A$ is a 6 × 1 “scaling” vector that allowed us to combine, in the same model, z-scored continuous covariates and non-z-scored categorical covariates. Covariates (C) included three physical variables [water permanence (continuous, unit [%]), reach types (pool, run, and riffle; categorical), and presence/absence of upwelling zones (binary)] and three biological variables [presence/absence of algae (binary; available for late succession in 1995 and 2013 surveys), presence/absence of cyanobacteria (binary; available for late succession in 1995 and 2013 surveys), and macrophyte abundance (i.e., percentage of cover of wetland patches 100 m upstream from each sampling site; available only in 2013; continuous, unit [%])). At the time of the early-successional survey in 1997, water was being pumped from a gravel pit beside the stream into the stream channel at a location in the middle of the study section. The chemistry of the pumped water differed significantly from the stream water at that point (56). We included the effect of the gravel pit as an additional covariate by designating all of the sampling upstream of the gravel pit as 0 and all of the points downstream as 1.

We selected the best model structure using AIC (Akaike information criterion with a correction for finite sample sizes) (63). In the Q matrix (Eq. 1), we compared models considering nutrient-specific process error with models considering a single process error across nutrients. In the B matrix (Eq. 1), we compared models with and without nutrient interactions. In the R matrix (Eq. 2), we compared models considering nutrient-specific observation errors with models considering constant observation errors (i.e., equal across all nutrient types). The best model structure (i.e., the one delivering the lowest AIC) was one that assumed both concentration-dependent effects and interactions among nutrients, plus nutrient-specific process and observation errors (SI Appendix, Table S5) on model comparison and selection.

**Model II.** Model II was a set of univariate state-space models constructed to partition the relative importance of internal spatial feedbacks and geomorphic template. To do so, we built a model for each chemical species at each successional stage (three chemical species × four successional stages = 12 models). Each model incorporated two types of drivers: variables describing the physical template and internal concentration-dependent spatial feedbacks. All of the covariates (continuous, water permanence; categorical, reach types and presence/absence of upwelling zones) in the model and nutrient concentration data were z-scored (SI Appendix, SI Materials and Methods). The first-order autocorrelation coefficient $b$ in model II can quantify internal spatial feedbacks of nutrients in a way that is analogous to density dependence in ecological communities (37), as we articulate below. A univariate autoregressive process can be expressed as

$$x_t = \alpha + bx_{t-1},$$

where $x_t$ is the log species abundance. Provided $b \neq 1$, this model has an equilibrium point given by

$$x_{eq} = \frac{\alpha}{1-b}.$$  \hspace{1cm} [4]

Starting from the initial point $x_0$, the following can be derived via recursion, after Ives et al. (37):

$$x_t = x_{eq} + b^t(x_0 - x_{eq}).$$ \hspace{1cm} [5]

The value of $x_t$ will converge to equilibrium $x_{eq}$ provided $|b| < 1$. The variable $b$ measures density dependence, or how fast the system is drawing populations back to equilibrium (more stability properties of the model can be found in the study by Ives et al. (37)). A $|b|$ value closer to 0 produces rapid returns to equilibrium, whereas $|b|$ closer to 1 results in a longer-lasting density dependence. In our study, $b$ describes how the concentration of a chemical species upstream influences the rate of concentration change of the same chemical species immediately downstream. This phenomenon is a “concentration-dependent effect” in space, analogous to the long known density-dependent effects over time. Whereas $b$ values closer to 0 suggest strong concentration dependence and quick return to an equilibrium concentration level, values close to 1 suggest concentration independence. A stochastic version of Eq. 5 is the univariate autocorrelation process:

$$X_t = \alpha + bX_{t-1} + \epsilon_t.$$ \hspace{1cm} [6]

Here, $X_t$ is the log abundance at $t$ and $\epsilon_t$ is the normal random variable with mean 0 and variance $\sigma^2$, and represents process error (model II is further described in SI Appendix, SI Materials and Methods).

Concentration-dependent feedbacks are an emergent property of biophysical and/or physical processes and can arise from several mechanisms. If nutrient concentration is high, biological consumption and/or physical advection may reduce downstream concentration; if nutrient concentration is low enough, nutrients may increase further downstream due to biological (e.g., $N_2$ fixation) and/or physical processes (e.g., desorption of P from sediments). To quantify such spatial feedbacks, model II excluded biological covariates because concentration-dependent feedbacks are realized via these processes. We kept the covariates describing the physical template (i.e., water permanence, reach types, presence/absence of upwelling zones) because these covariates are not controlled by nutrient concentration in surface water, but rather by geomorphic processes at much larger scales. We hypothesize that $NO_3^-$ spatial feedbacks have a biological nature (explained by biological uptake and release via decomposition-nitrification and $N_2$ fixation-mineralization-nitrification), whereas the spatial feedbacks of SRP are physical (explained by adsorption and desorption). Based on these premises, we tested the predictions with model II: (i) the $b$ value for $NO_3^-$ up-stream-downstream interaction would be significantly lower than 1, and (ii) as $NO_3^-$ becomes more limiting toward late succession, the $b$ value would diminish and approach 0. For conductivity and SRP, (iii) the $b$ value would be significantly lower than 1 and (iv) there would not be a linear trend over the ecosystem successional time. AICc was used to compare models, including physical template and internal spatial feedbacks, models with only internal spatial feedbacks, and models including only physical template (SI Appendix, Table S6).

We note that like most rivers and streams in arid and semiarid areas, Yacomo Creek is an intermittent stream; therefore, part of the stream was dry during the survey and no data were collected there. Methods for addressing these missing values in the dry sections for waterline analysis and MARKS models (model I and model II) are described in SI Appendix, SI Materials and Methods. We compared the extent to which our inferences would change by different approaches to deal with missing values. If inferences varied with the approach, we pointed out these differences. For all model I and model II results, 95% confidence intervals around maximum-likelihood covariate effects were obtained via 1,000 parametric bootstraps (62). Model residuals were examined via the autocorrelation function (62) (no significant autocorrelation remained in the model residual; SI Appendix, Figs. 56 and 57).

**Net Uptake Length.** To assess the intensity of biological activity, we applied an index, net uptake length (64), that reflects the rate of nutrient exchange with biota. To perform this assessment, we analyzed longitudinal nutrient concentration declines. We computed the first derivative of nutrient concentration above a threshold value to filter out noise in the data. Over moving windows of 100 m, 150 m, 200 m, and 250 m, we then extracted all of the positive values (so that concentration was decreasing downstream) and computed their mean. The result was an average downstream distance (in meters) required to see a concentration decline of 1 μg L$^{-1}$. This definition is different from uptake length in the nutrient spiraling concept (65), which is defined as the average downstream distance traveled by a nutrient molecule in dissolved form before being removed from the water column, because it likely includes both uptake and release processes. Our estimate of net uptake length using only decreasing downstream concentrations is conservative, because it might also include nutrient release from mineralization or groundwater inputs (i.e., groundwater concentrations of $NO_3^-$ and SRP are usually higher than surface water concentrations of $NO_3^-$ and SRP).

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