Ecosystem Spatial Heterogeneity: Formation, Consequences, and Feedbacks

by

Xiaoli Dong

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Graduate Supervisory Committee:

Nancy Grimm, Co-Chair
Rachata Muneepeerakul, Co-Chair
Janet Franklin
James Heffernan
John Sabo

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ABSTRACT

An understanding of the formation of spatial heterogeneity is important because spatial heterogeneity leads to functional consequences at the ecosystem scale; however, such an understanding is still limited. Particularly, research simultaneously considering both external variables and internal feedbacks (self-organization) is rare, partly because these two drivers are addressed under different methodological frameworks. In this dissertation, I show the prevalence of internal feedbacks and their interaction with heterogeneity in the preexisting template to form spatial pattern. I use a variety of techniques to account for both the top-down template effect and bottom-up self-organization. Spatial patterns of nutrients in stream surface water are influenced by the self-organized patch configuration originating from the internal feedbacks between nutrient concentration, biological patchiness, and the geomorphic template. Clumps of in-stream macrophyte are shaped by the spatial gradient of water permanence and local self-organization. Additionally, significant biological interactions among plant species also influence macrophyte distribution. The relative contributions of these drivers change in time, responding to the larger external environments or internal processes of ecosystem development. Hydrologic regime alters the effect of geomorphic template and self-organization on in-stream macrophyte distribution. The relative importance of niche *vs.* neutral processes in shaping biodiversity pattern is a function of hydrology: neutral processes are more important in either very high or very low discharge periods. For the spatial pattern of nutrients, as the ecosystem moves toward late succession and nitrogen becomes more limiting, the effect of self-organization intensifies. Changes in relative importance of different drivers directly affect ecosystem macroscopic properties, such as ecosystem resilience. Stronger internal feedbacks in average to wetter years are shown to increase ecosystem resistance to elevated external stress, and make the backward shifts (vegetation loss) much more gradual. But it causes increases in ecosystem hysteresis effect. Finally, I address the question whether functional consequences of spatial heterogeneity feed back to influence the processes from which spatial heterogeneity emerged through a conceptual review. Such feedbacks are not likely. Self-organized spatial patterning is a result of regular biological processes of organisms. Individual organisms do not benefit from such order. It is order for free, and for nothing.

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OVERVIEW

Landscapes, including both the biological components and the physical template, are heterogeneous. The cause of such spatial heterogeneity is one of the fundamental questions of landscape ecology (Turner 1989). Spatial heterogeneity has been mostly attributed to ecological responses to environmental gradients and/or geomorphic variation. For example, the spatial heterogeneity of shrubs at the forest-tundra ecotone was related to local topography (Ropars and Boudreau 2012), and spatial heterogeneity of nutrients in stream surface water was found to be dominated by the surface water-groundwater exchange (Dent and Grimm 1999). At the watershed scale, geomorphology, through its effect on the deposition of materials, flowpaths, and residence times, could influence the spatial distribution of macrophytes in rivers (Curie et al. 2007). Other factors, such as socio-economic, demographic, and cultural factors also influence the formation of biological patchiness (Black, Morgan, and Hessburg 2003).

In absence of such top-down influences, spatial heterogeneity can also emerge from a homogeneous template, via the mechanism of spatial self-organization. Spatial self-organization is a process where regular spatial patterns emerge from homogeneous initial conditions through internal local interactions. Self-organized patterns such as vegetation stripes (‘tiger bush’), labyrinths, spots (‘leopard bush’) and gaps on arid and semiarid ecosystems have been observed around the world (Rietkerk et al. 2002; Deblauwe et al. 2008). The causal mechanism for such ordered patterns involves scale-dependent feedbacks, which emerge from short-ranged facilitation and long-ranged competition for resources (Rietkerk and van de Koppel 2008).

Natural landscapes are typically heterogeneous. Spatial biological patchiness is usually a result of both external template heterogeneity and internal interactions and feedbacks (Sheffer et al. 2013). In addition, some ecosystems such as desert streams are characterized by high environmental temporal variability. The drivers (and their relative importance) of this biological patchiness might change depending on the interannual variation in environmental conditions. There are few research results on these topics.

Understanding the processes that generate the spatial heterogeneity is important for at least two reasons. First, spatial heterogeneity is intimately related to ecosystem functioning. Landscape heterogeneity has myriad influences on population dynamics (Newton, Woolnough, and Strayer 2008) and community structure (Dormann et al. 2007). It also influences ecosystem processes, such as nutrient loading to surface water (Strayer et al. 2003), nutrient retention in terrestrial ecosystems (Bennett, Carpenter, and Clayton 2005), and sediment loss (Ludwig et al. 2007). Strong relationships between landscape heterogeneity and ecosystem functioning suggest that spatial heterogeneity will affect the sustainability of ecosystem services.

Second, patterns do not equal processes. Individual processes do not affect patterns in a unique way; that is, different mechanisms may give rise to similar or same patterns. However, ecosystem response to disturbance may depend on specific formulations of the underlying mechanisms. Liu et al. (2012) compared two mechanically different models of regular spatial pattern formation in mussel beds. The two models produce very similar spatial patterns, but they have distinctively different responses to disturbance and to post-disturbance recovery. Because of this *non-unique relation* between pattern and underlying processes, it is imperative to know whether and how the focal ecosystem property depends on specific formulations of the underlying process from which the large-scale spatial heterogeneity emerges.

In this dissertation I studied the causes of spatial heterogeneity, considering the template effect and internal feedbacks, as well as their changes over time. My primary research question was: what explains the spatial heterogeneity in ecosystems? I examined different types of ecological components and explicitly took into consideration the temporal changes in drivers. Research was conducted primarily at Sycamore Creek, a stream in the Sonoran Desert in Arizona, where extensive work on ecosystem spatial heterogeneity in the past three decades laid the foundation for my work. The question was addressed through six chapters.

RESEARCH CHAPTERS

In **Chapter 1**, I studied the spatial distribution of macrophytes along a 12-km stretch of Sycamore Creek between 2009 and 2013. Sycamore Creek experienced ecosystem state change in around 2000, when cattle-grazing was terminated by the US Forest Service (Heffernan 2008). After that, the system shifted from gravel/algae dominated state to a state with abundant in-stream macrophytes. I used 5-year annual survey data on wetland abundance and spatial distribution combined with Bayesian hierarchical models to answer the question: whether and how does hydrological regime alter the effect of geomorphic template on wetland distribution? The results showed a stronger geomorphic template effect in drier years than that in wetter years.

Without a preexisting template effect, internal feedbacks alone can also give rise to plant spatial distribution (Kéfi et al. 2007). Positive feedback between wetland plants and sediments would increase the water holding capacity of wetland sediments, which improves the habitat condition for plant growth. The understanding on the interaction between physical template and internal feedbacks in giving rise to biological patchiness is very limited. In **Chapter 2**, I used 6-yr wetland survey data (2009 to 2014) from 12-km of Sycamore Creek, combined with a lattice simulation model to investigate the following questions: (1) how do template heterogeneity and internal local feedbacks (self-organization) interact to influence wetland spatial distribution? And (a) how do template heterogeneity and local facilitation interact to influence ecosystem robustness (including resistance to stress and capacity to recover)? The drivers of template heterogeneity and self-organization were both important and their relative importance varied linearly with the consequence of winter floods (quantified by the combined effect of the *timing* of a flood event and its *magnitude*: more frequent, later-occurring, and larger floods are associated with greater consequences). Local facilitation increased system's resistance to stress, but increased hysteresis (back shift from an undesirable state). Template heterogeneity, however, interacted with local facilitation to reduce hysteresis effect.

Wetlands are considered biogeochemical hotspots because their anoxic, organic-rich sediments are conductive to denitrification (McClain et al. 2003). Studied of in-stream macrophytes have often found significant nutrient retention (Schulz et al. 2003; Desmet et al. 2011). These studies generally integrate the effects of in-stream macrophytes over larger downstream distance (or areas). As a result, the effect of macrophytes on the spatial heterogeneity of nutrients remains uncertain. In **Chapter 3**, I explored the drivers of spatial pattern of nutrients in stream surface water and assessed the effect of wetland distribution. This study took advantage of existing data collected in 1990s by Dent and Grimm (1999), who took water samples every 25 m along the 12-km main stem of Sycamore Creek at three stages of post-flood successional time. When these surveys were done in-stream macrophytes were rare. By 2013 after cattle removal, about 40% of the stream (in length) was covered by wetland plants. I repeated their experiment in May 2013 along the same 12-km stretch of the stream. I asked (1) what explained the spatial heterogeneity of nutrients, in particular, I considered the effect of three categories of drivers, i.e., geomorphic template, biological processes, and self-organization, (2) did wetland cover influence spatial patterns of nutrients? And (3) how did the underlying drivers change over successional time. I used time-series methods, i.e., Multivariate Autoregressive State Space models and wavelet spectrum analysis to address these questions. Results showed that the geomorphic template played a dominant role in shaping spatial patterns of nutrients, whose effect size was an order of magnitude higher than that of in-stream biological processes. The effect of self-organization intensified over ecosystem successional time, as NO_3^--N became more limiting towards late succession. Wetland patches did not directly affect patterns of nutrient. However, I found evidence of an indirect effect of wetland plants via alteration of vertical hydrological gradient, which dampened the effects of upwelling zones on surface water chemistry.

In community ecology, there are two distinct families of theoretical models to explain species distribution in space. Models of niche differentiation are the basis for the vast majority of coexistence theories and have been used to explain the distribution and abundance of a wide range of taxa in both terrestrial and aquatic environments (Silvertown 2004). The second type of model invokes species that are ecologically equivalent and a dynamics governed by stochastic processes of extinction, immigration and speciation, i.e., the neutral theory of biodiversity (Hubbell 2001). In **Chapter 4**, I used aquatic invertebrate data collected from Huachuca Mountains located in Southern Arizona to test the validity of the neutrality assumption in environmentally dynamic systems. The river network in Huachuca Mountains is characterized by strong spatial and temporal heterogeneity. Spatially, it is a characterized with a configuration of intermittent, ephemeral, and perennial streams. Temporally, the precipitation varies both intra- and inter-annually. Application of neutral theory has been rare in environmentally dynamic systems (Rosindell et al. 2012). The data were collected between 2009 and 2012, representative of the hydrological regime in the area. I modified an existing spatially explicit neutral model developed by Muneepeerakul et al. (2008) to include the temporal variability at inter- and intra-annual scales, and tested the contribution of stochastic neutral processes under different hydrological conditions. The model fitting suggested that the contribution of neutral processes in shaping the biodiversity pattern varied in time, with higher explanatory power in either very dry or very wet periods.

In doing this project, I noticed problems with an important measure of species diversity pattern, i.e., β diversity. The species spatial turnover is expected to linearly decay when the distance between a pair community increases, if the metacommunity is controlled solely by dispersal (i.e., no environmental filtering effect). This is known as the distance decay relationship (DDR) (Morlon et al. 2008), and has been used widely in community ecology as a benchmark to infer whether the dominant process is niche or neutral in shaping species distribution in space (Condit et al. 2002). However, I found DDR is not always valid – sometimes species composition in a pair of communities farther away could be measured as more similar than a pair of closer communities. In **Chapter 5**, I systematically examined the effect of spatial configuration of habitat capacity on different measures of β diversity, including β diversity as turnover and as variation (Anderson et al. 2011). I created five different spatial configurations of habitat capacities, and used a spatially explicit neutral metacommunity model. I confirmed that spatial configurations of habitat capacities alone could cause non-monotonicity in DDR caused by variation in α diversity. This means that inferences of underlying processes shaping biodiversity patterns based on DDR may be erroneous in many existing studies. After accounting for variation in α diversity, spatial configuration of habitat capacities could introduce variation in landscape connectivity, which influences β diversity via spatial processes like dispersal.

An intriguing question related to spatial heterogeneity, but not addressed in landscape ecology, is: is it possible to have feedbacks from the outcomes of spatial heterogeneity to the process from which the spatial heterogeneity emerges? If yes, can these feedbacks *reinforce* ecological functioning (Fisher et al. 2007)? In Chapter 6, I addressed this topic with a conceptual review. I first contextualized the mechanism of spatial self-organization under a framework of propagation of ecological influence over heterogeneous landscapes, to bridge the conceptual gap between formation of ordered patterning and energy and material flow, the focus of ecosystem ecology. It is well accepted that ecosystem structure can emerge from local interactions among individuals, and that these structures carry certain functional consequences. However, the mechanisms of feedbacks, from the outcome of spatial pattern to individuals from which the pattern emerge, are seldom examined. I examined such feedbacks, and concluded that it is unlikely that the outcomes of the ordered patterning (i.e., altered ecosystem properties) would feed back to affect the local processes at the individual level from which the ordered patterning arises. The ordered pattern is formed as a result of regular biological activities, not because individuals did anything special. The pattern is "order for free."

SIGNIFICANCE

The six chapters represent a significant contribution to ecosystem ecology, especially in providing a spatially explicit perspective. While my primary focus was on the causes, I also investigated the consequences (Chapters 2 and 5) and feedbacks of ecosystem spatial heterogeneity (Chapter 6). (1) To understand the causes, I considered both template heterogeneity and internal feedbacks in forming spatial heterogeneity. Research in this area has been a challenge and has been rare so far, because these two categories of drivers are usually investigated from different methodological frameworks (statistical models *vs.* pattern formation mathematical models). (2) Because most patterns were surveyed repeatedly over time (Chapters 1, 2, 3, and 4), I was able to investigate explicitly how the relative importance of different drivers changed *over time*, either responding to changes in the external environment (e.g., hydrological regime in Chapters 1, 2, and 4) or to internal development of ecosystems (e.g., post-flood succession in Chapter 3). To my best knowledge, research on the temporal changes in underlying drivers is very rare. Such results directly challenge the temporal transferability of the understanding of pattern formation. (3) Changing drivers over time also directly influence ecosystem macroscopic properties. In chapter 2, I showed how the changing contribution of internal feedbacks and preexisting template effect could affect ecosystem regime shift and hysteresis. (4) I studied distinctive ecological components (nutrients, macrophytes, and aquatic invertebrates), falling within the fields of ecosystem ecology and community ecology. I demonstrated that spatial heterogeneity leads to consequences in both ecosystem properties (Chapter 2) and community properties (Chapter 5). (5) Lastly, I examined whether it is possible to have feedbacks from the consequences of spatial heterogeneity (i.e., ecosystem functioning) to the processes that generated the spatial heterogeneity to reinforce the consequences (Chapter 6). This is the first time the plausible mechanisms of such feedbacks were closely examined.

(First person "I" was used in the above Overview to ease writing. In truth, many collaborators contributed substantially to various chapters. The names of the coauthors, as well as the status of each chapter are listed below.)

PRODUCTS OF DISSERTATION CHAPTERS

CHAPTER 1

Dong, X., N.B. Grimm, J. Franklin, and K. Ogle. 2015. Temporal variability in hydrology modifies the influence of geomorphology on wetland distribution along a desert stream. *Journal of Ecology*. DOI: 10.111/1365-2745.12450.

CHAPTER 2

Dong, X., R. Muneepeerakul, and N.B. Grimm. Self-organization of macrophytes in heterogeneous fluvial landscapes. (*in preparation*)

CHAPTER 3

Dong, X., N.B. Grimm, and A. Ruhí. Disentangling influences of geomorphology, biology, and self-organization on stream nutrient patterns. *Ecological Monographs* (*in review*; Submitted on July 7th, 2015).

CHAPTER 4

Dong, X., R. Muneepeerakul, J.D. Olden, and D.A. Lytle. 2015. The effect of spatial configuration of habitat capacity on β diversity. *Ecosphere*. (*in press*)

CHAPTER 5

Dong, X. & R. Muneepeerakul. Neutral theory applied to desert stream network featured with variable hydrological regime. (*in preparation*)

CHAPTER 6

Dong, X. & S.G. Fisher. Order for nothing: ecosystem self-organization in space and time. (*in preparation*)

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CHAPTER 1

TEMPORAL VARIABILITY IN HYDROLOGY MODIFIES THE INFLUENCE OF GEOMORPHOLOGY ON WETLAND DISTRIBUTION ALONG A DESERT STREAM

ABSTRACT

1. Both geomorphic setting and dynamic environmental variables influence riverine wetland vegetation distributions. Most studies of species distributions in riverine systems emphasize either hydrological variability or geomorphic controls, but rarely consider the interaction between the two. It is unknown whether and to what extent the relationship between the geomorphic template and species distribution is modified by fluctuating environmental conditions.
2. This study examines how spatial patterns of riverine wetlands in a desert stream change in response to environmental shifts brought about by interannual variability in the hydrologic regime. We surveyed wetland spatial distribution and measured its abundance every June over five years (2009-2013) by recording patch size and presence/absence of five wetland plant species along the 12-km main stem of Sycamore Creek, Arizona, U.S.A. The study period encompassed a very large flood in January 2010, a wet year (2010), two average years (2009 and 2013), and two extremely dry years (2011 and 2012). We used a Bayesian statistical approach to analyze the relationship between geomorphic variables and wetland distribution under different hydrological conditions.

3. The geomorphic variables provided much greater explanatory power in dry years than in average to wet years. Hydrological conditions modified the interactions between geomorphic template and species distribution. Annual hydrological conditions affected the direction (i.e., positive or negative effect) and magnitude (i.e., the size and significance level of an effect) of these interactions, both of which gave rise to spatial patterns of wetlands. Ecosystem temporal variability, such as inter-annual and multi-year hydrological variability and longer-term ecosystem state changes, triggered complex species responses.
4. *Synthesis*: The effect of geomorphic setting on stream wetland plant distribution in this desert system is conditioned on the temporal variability in hydrology among years. Temporal transferability of the relationship between geomorphology and species distributions is therefore questionable.

Keywords: aquatic plant ecology; Bayesian modeling; environmental gradient; hierarchical; hydrological variability; plant–climate interactions; plant community structure; spatial heterogeneity; species distribution; vegetation.

INTRODUCTION

The distribution of plant species along stream-riparian ecosystems is influenced by both geomorphology and hydrological variability (Johnson 1994; Bendix & Hupp 2000). Geomorphology influences plant species distribution at multiple scales (Dixon, Turner & Jin 2002). At a local scale (i.e., vegetation patch level), feedbacks between sediment deposition and accretion and plant establishment directly influence species zonation patterns (Morris 2006), a process that occurs on relatively short time scales. On the other hand, broad-scale geomorphic setting, determined by the geometry of the drainage basin and landforms—including channel shape, elevation, drainage area, channel network structure, and valley floor width—influences species distribution indirectly. Geomorphic setting shapes spatial heterogeneity of environmental gradients (e.g., water depth, temperature, and light conditions), which act on plant distributions (Gregory *et al.* 1991; Porter 2000). In fluvial landscapes, hydrological variability—e.g., hydrological regimes, including the timing, intensity, and scale of hydrological events—also plays a major role in shaping species distributions. In contrast to the relatively static broad-scale geomorphic setting, hydrology is highly variable at multiple time scales (Sabo & Post 2008). At a long time scale (e.g., over a century), hydrological regime and geomorphology are intimately related, and hydrology shapes fluvial landforms (Poole 2002). At much shorter time scales (e.g., months, years, decades), hydrological impacts include mechanical damage to plants (Madsen *et al.* 2001), water saturation of soil (Bagstad, Stromberg & Lite 2005), and transport of sediments and propagules (Cellot, Mouillot & Henry 1998). Many studies have contributed to our understanding of the relative importance of the complex fluvial geomorphology and the highly dynamic hydrologic regime on species distributions in riverine ecosystems (Johnson 1994; Mertes, Daniel & Melack 1995; Muotka & Virtanen 1995; Hupp & Osterkamp 1996; Bendix & Hupp 2000; Hupp 2000; Górski & Buijse 2013).

Most studies of species distributions in riverine ecosystems emphasize either dynamic hydrological factors (e.g., Johnson 1994; Casanova & Brock 2000; Riis & Biggs 2003; Martinez & Le Toan 2007) or more static geomorphic controls (e.g., Zinko *et al.* 2005; Chen *et al.* 2006; Curie *et al.* 2007; Engelbrecht *et al.* 2007); rarely do they consider the interaction between the two. Broad-scale geomorphic template shapes environmental gradients. On the other hand, if we consider that a set of environmental variables (e.g., water depth, temperature, light) defines a multi-dimensional environmental space, it is reasonable to suppose that temporal variability modifies the ecosystem's position in that environmental space. For example, a transition between El Niño and La Niña years can relocate an ecosystem from a warm and wet region to a cooler and drier region in the environmental space. Such a shift in the environmental gradient, introduced by temporal variability, may alter the relationship between species distribution and the broad-scale geomorphic setting. To our knowledge, no studies have examined whether and to what extent the relationship between the geomorphic template and species distribution is modified by fluctuating environmental conditions. Testing the prediction that hydrological variability alters the degree to which the geomorphic setting controls species distributions is a central goal of this study.

If the relationship between geomorphology and species distribution can be modified by hydrological variability, the temporal transferability of the effect of geomorphology on species distribution becomes questionable. Such temporal transferability requires two assumptions: (1) constant environment and (2) pseudo-equilibrium between species distribution and the environment (referring to short-term equilibrium between species or communities and their environment (e.g., climate) within a specified and limited time frame (Guisan & Theurillat 2000). However, recent studies of ecosystem temporal variability have challenged these assumptions (Elith & Leathwick 2009; Zimmermann *et al.* 2009; Zurell *et al.* 2009). Most ecosystems are exposed to environmental temporal variability occurring at multiple temporal scales. Desert streams, in particular, are subject to high inter-annual variability in hydrology, with floods resetting community succession (Fisher *et al.* 1982) and drying disrupting community persistence (Stanley, Fisher & Grimm 1997). At a multi-year scale, these streams experience alternating dry and wet phases (Sabo & Post 2008; Sponseller *et al.* 2010). Major disturbances, like bed-moving floods (Stromberg, Fry & Pattern 1997), could push an aquatic ecosystem onto a new trajectory of change with long-lasting consequences for its structure. Such a system is unlikely to exhibit any sort of equilibrium between species and the geomorphic template. Additionally, recent theoretical treatments of ecosystem pattern formation suggest the importance of internal interactions and feedbacks in understanding the spatial structure of organism distributions (Rietkerk *et al.* 2002; van de Koppel *et al.* 2005). An observed species distribution is likely a manifestation of the combined effects of external physical constraints and internal feedbacks (Sheffer *et al.* 2013), which also govern the portfolio of alternative stable states (Carpenter *et al.* 2001; Scheffer & Carpenter 2003). For example, Heffernan (2008) provided evidence that wetlands and gravel-bed streams are alternative stable states in desert streams as a consequence of the positive feedback between macrophyte biomass and sediment stabilization. This implies that the same physical environment may yield different vegetation distribution patterns. Critical empirical investigations of the role of these various aspects of ecosystem temporal variability on the spatial distribution of wetland plants in stream ecosystems have not been done. The present study addresses this deficiency.

The organization of riverine wetlands along streams is strongly related to fluvial geomorphology, which determines the distribution of saturated areas and hydrological functioning in a catchment (Curie *et al.* 2007). The longitudinal pattern of stream flow is determined largely by catchment topography. On this relatively stable geomorphic template, the annual precipitation regime modifies the spatial heterogeneity of hydrology (e.g., spatial gradient of surface water depth, spatial distribution of dry sections) and sediment dynamics. In arid and semi-arid regions, high inter- and intra-annual precipitation variability results in very different hydrologic flows across years (Grimm 1994; Sabo & Post 2008; Sponseller *et al.* 2010). In this study, we focused on the spatial distribution of wetland vegetation along a desert stream, Sycamore Creek, Arizona, U.S.A. The system underwent an ecosystem state change from a gravel-dominated system to one covered by abundant in-stream wetlands around 2000, after cattle grazing ceased as a result of a change in U.S. Forest Service policy (Heffernan 2008). Using Sycamore Creek as a model system, we asked (1) how shifts of the system in environmental space influence the relationship between wetland spatial heterogeneity and the geomorphic template, (2) how different aspects of environmental temporal variability influence wetland distribution and its relation to the geomorphic template, and (3) whether internal biological feedbacks (e.g., species interactions, legacy effect) remain constant over time or change in response to fluctuations in the environmental setting. To address these questions, we conducted a five-year (2009-2013) survey of the dominant wetland species to quantify presence/absence and abundance along a 12-km section of the stream. The five years covered a range of hydrological conditions, including a wet year with a very large flood, two dry years, and two average years (Fig. 1.1). For each question, we made two predictions: one prediction tested the null hypothesis that environmental (hydrologic variability) has no influence on the relationship between the geomorphic template and wetland distribution, spatial heterogeneity, or internal feedbacks; and the other prediction was that these relationships change over time, tempered by changes in the environmental space occupied by the system in any given year. We conducted a Bayesian analysis of these data to evaluate the interactive roles of geomorphology, hydrological variability, and biotic feedbacks on wetland vegetation structure at different spatial scales.

MATERIALS AND METHODS

SITE DESCRIPTION

Our surveys were conducted along a 12-km segment of the main stem of Sycamore Creek, Maricopa County, Arizona, U.S.A. Sycamore Creek is a tributary of the Verde River that drains a watershed area of ~505 km^2 in the Tonto National Forest northeast of the greater Phoenix metropolitan area. The watershed receives 39-51 cm of annual precipitation (long-term means for lowland and headwater portions, respectively), in two distinct rainy seasons associated with winter frontal and summer monsoon storms. Due to high evapotranspiration, stream flow is intermittent in space and time (Stanley, Fisher & Grimm 1997), and perennial sections are shallow (10-50 cm), narrow (1-5 m), and support summer baseflow <0.05 $m^3 s^{-1}$. Sycamore Creek has a flashy hydrograph (i.e., characterized by sudden, dramatic increases in flow and rapid flood recession) typical of most arid catchments (Fig. 1.1a), and floods greater than 1 $m^3 s^{-1}$ are often sufficient to scour the channel and mobilize bed materials (Grimm & Fisher 1989).

Historically, riverine wetlands, characterized by slow flow rates, were a common feature of the arid drainages of Arizona (Hendrickson & Minckley 1984). However, because of increases in grazing pressure, climate variation, or interactions between the two, most of the wetlands disappeared in the late 19th and early 20th centuries. Since 2000, after the U.S. Forest Service eliminated grazing from much of the Sycamore Creek watershed, the system experienced a dramatic state change, from a gravel-dominated stream to one with ample in-stream vegetation (Heffernan 2008). The five most abundant wetland plant species are *Paspalum distichum* L. (knotgrass), *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller (chairmaker's bulrush), *Equisetum laevigatum* A. Braun (smooth horsetail), *Juncus torreyi* Coville (Torrey's rush), and *Typha domingensis* Pers. (southern cattail). Because of their dominance in this system, these five species were used as indicator wetland species in our study: *i.e.,* we recorded the abundance and distribution of these five indicator species to quantify wetland distributions. All five species are perennial plants, and while all of them can reproduce by seed, some also reproduce vegetatively. *P. distichum* reproduces mostly from rhizomes and stolons, *E. laevigatum* and *J. torreyi* also reproduce via rhizomes, and *T. domingensis* can reproduce by expansion of existing colonies.

The five years (2009 to 2013) during which this study was conducted were characterized by distinct hydrological conditions. Using the long-term hydrological data (1960-2013) available from the USGS gauging station on Sycamore Creek ("Sycamore Creek near Fort McDowell," ID: 09510200), we calculated the cumulative discharge of each year starting from the second the day of the survey in the previous year through the first survey date of the following year. This interval encompassed both summer floods and winter floods. Even though both winter and summer floods could influence wetland distribution and abundance, the effect of winter floods is likely to be much greater; winter floods lasted longer and their magnitudes were much greater (Fig. 1.1). However, although summer floods tend to occur at the time of year when wetland plants are past their peak biomass and beginning to senesce, they could influence root stock or seed banks. The median cumulative discharge for this twelve-month period was 9.9 million m^3. The year 2009 (21.2 million m^3) and 2013 (20.4 million m^3) were two average years, at the 68th percentile within the 53-yr record (calculated for the same 12-month interval across the entire record). These two years had similar amounts of total discharge and flood frequency and magnitude, except for the timing of the floods: the arrival of floods occurred about one month later in 2013 compared to 2009 (Fig. 1.1c). Conversely, we defined 2011 (3.7 million m^3) and 2012 (0.7 million m^3) as two dry years, at the 36th and 15th percentile of the 53-yr record. The largest peak discharge during June 2011 and June 2012 was only 2.4 m^3/s in December 2011 (Fig. 1.1d). The year 2010 was a wet year, with a cumulative discharge of 42.2 million m^3 (81st percentile in the hydrologic record). A large flood, the largest since the 100-year event of 1978, occurred in January 2010, with peak discharge of 439 $m^3\ s^{-1}$. Sampling years characterized by different hydrological conditions provided the opportunity to assess how the shift of an ecosystem's position in environment space may influence the relationship between the physical template and wetland distribution.

FIELD METHODS

We conducted surveys at the same time of year for each year from 2009 to 2013 (2009 June 15th, 2010 June 14th, 2011 June 13-14th, 2012 June 16th, and 2013 June 14th), roughly coinciding with the timing of near peak biomass. In addition to these annual surveys, we also conducted three additional "seasonal" surveys in a subset of years (January 2011, April 2011, and January 2012) using methods identical to those employed in the annual surveys. Surveys were conducted along the aforementioned 12-km stream channel and involved recording both presence/absence point data and patch attributes.

During each survey campaign, we recorded the presence/absence of indicator wetland species every 25 m within a band transect of ~1 m width (visually estimated) across the stream. These presence/absence point data provide information on the extent of vegetation dispersal and/or establishment along the stream channel.

Patch data provide information on the cover of wetland plants. We defined a wetland patch as a contiguous stand (<2 m separation between plants) greater than 4 m^2 and containing at least one of the five indicator wetland plants described above. In 2009, *Juncus torreyi* was not included due to low abundance. For each patch, we used a Garmin handheld Global Positioning System (GPS) (resolution is 5 m) to record the location of the upstream point of the patch and patch length. We recorded the species identities of the dominant and sub-dominant (<10% cover) plant species within each patch. For the dominant species, we measured patch length (longitudinal along the stream), width (lateral to the stream channel), and average plant height of the indicator species in the patch. In 2012 and 2013, we also measured the water depth within each patch and estimated the percentage of the patch area covered by water. Other patch geomorphic attributes that are assumed constant over our study period (*i.e.,* elevation, channel slope, and valley floor width [valley floors are composed of the active and secondary channels, floodplains, terrace, and alluvial fans (Grant & Swanson 1995)]) were extracted from a digital elevation model (DEM) and USGS topographic maps in ArcGIS 10.1 (ESRI 2012).

Water permanence (i.e., percent of time in a year when surface water is present at each location along the stream) was calculated from data collected by E. Stanley (Univ. of Wisconsin, personal communication) from the same 12-km segment of Sycamore Creek, which overlapped with our measurements of wetland distribution. From May 1988 to February 1990 (22 consecutive months), the extent of surface water was surveyed and recorded. We calculated the percentage of time over the 22 months when surface water was present, and used that value as a measure of the water permanence gradient along the stream. We argue that water permanence is a relatively unvarying feature of the geomorphic template, as it is controlled by drainage area and proximity of bedrock to the sediment surface. Similarly, we used known locations of upwelling zones (places where groundwater upwells into surface water, which usually support perennial flow) that were identified in the field across the 12-km survey area in the late 1990's (Dent, Grimm & Fisher 2001).

STATISTICAL ANALYSIS

We developed two different sets of models, one for the presence-absence point data, and the other for the patch distribution data. Each model was constructed to evaluate the role of geomorphic, environmental, and biotic variables on these wetland vegetation attributes.

Models for presence-absence point data

For the analysis of the presence-absence data for the indicator wetland species, let $y_{i,k,t}$ denote the occurrence (1 = present, 0 = absent) of indicator species k ($k = 1, 2, \ldots, 5$) at sampling point i ($i = 1, 2, \ldots, 440$) in year t ($t = 1, 2, \ldots, 5$ for 2009, 2010, …, 2013). The likelihood for $y_{i,k,t}$ is defined by Bernoulli distribution:

$$y_{i,k,t} \sim Bernoulli(p_{i,k,t})$$

A logistic regression was used to relate the probability of being present to geomorphic variables (i.e., E, S, V, and W) such that logit(p) = log(p/(1-p)) was defined by the following linear mixed effects model:

$$logit(p_{i,k,t}) = \beta_{0k,t} + \beta_{1k,t}E_i + \square_{2k,t}S_i + \beta_{3k,t}V_i + \beta_{4k,t}W_i + \lambda_t U_i + \sum_{j=1, j\neq k}^{5} (y_{i,j,t})\alpha_{kj,t} + \varepsilon_{b(i),t} + \gamma_{s(b(i)),t}$$

The coefficients, b, vary by species (k) and year (t), and b_1-b_4 describe the fixed effects of four continuous-valued geomorphic variables: elevation (E, m; centralized to zero: E – mean (E)), channel slope (S, unitless or m/m), valley floor width (V, m), and water permanence (W, %), and λ is the effect of being in an upwelling zone (i.e., $U = 1$ if upwelling zone, 0 otherwise). Biotic feedbacks were incorporated by allowing the presence-absence of each indicator species to potentially influence the presence-absence of other indicator species at point *i* (e.g., via competition or facilitation). That is, $a_{kj,t}$ describes the effect of the presence-absence ($y_{i,j,t}$) of wetland species *j* ($j \neq k$) on the occurrence probability of species *k* at time *t*. We also incorporated spatial random effects at two scales to account for unobservable (or latent) processes occurring at the band scale (via ε, see below) and the segment scale (via γ) (Fig. 1.2).

For the spatial effects, we determined the spatial scale based on two criteria. First, for the finer scale, we divided the stream into 22 bands (*b*), with each band capturing a relatively straight, 500-600 m portion of the stream channel between two curves (Fig. 1.2a). Second, the coarser segment (*s*) scale captures the alteration of constrained and unconstrained channels (Fig. 1.2b). In desert streams, valley-floor morphology varies from extremely narrow canyons, to expansive, unconstrained channels that spread over low-gradient landscapes. These two regions show differential susceptibility to and patterns of drying (Stanley, Fisher & Grimm 1997). We divided the whole 12-km mainstem of the stream into 5 segments that vary in length from ~2000-3000 m: $s = 1$ is relatively narrow, $s = 2$ is the region where the valley floor width increases, $s = 3$ is the region where the valley floor narrows, and the last two segments ($s = 4$ and 5) capture a relatively narrow section of the stream and a section with variable valley floor width (Fig. 1.2b).

Models for patch-scale vegetation cover

To estimate vegetation cover, we first divided the 12 km stream into 120 units, with each unit being 100 m in length. We used wetland patch data to calculate the per cent cover (c) of wetland patches in every 100-m unit along the stream channel. Given that c is constrained between 0 and 1, we logit-transformed c, and for observational unit i (i = 1, 2, …, 120) and time t (t = 1, 2, …, 5 years for 2009, 2010, …, 2013), we assumed logit(c) followed a normal distribution:

$$logit(c_{i,t}) \sim Normal(\mu_{i,t}, \sigma_t^2)$$

We defined the logit-scale mean (m) as a linear mixed-effects model with time-varying coefficients (b's and λ') and spatial random effects similar to the model for logit(p):

$$\mu_{i,t} = b_{0,t} + b_{1,t}E_i + b_{2,t}S_i + b_{3,t}V_i + b_{4,t}W_i + \lambda'_t U_i + \varepsilon'_{b(i),t} + \gamma'_{s(b(i)),t}$$

E, S, V, W, U, and all other subscripts are defined following the model for logit (p).

To analyze legacy effects, we used the same cover data (i.e., per cent cover of wetland patches supporting vegetation in every 100 m unit along the stream channel), and assumed logit(c) followed a normal distribution as described above. We used the wetland cover in 2009 as the baseline, and for each year after that, we constructed a linear mixed-effects model for the logit-scale mean (m):

$$\mu_{i,t} = b_{0,t} + L_t c_{i,t-1} + \varepsilon"_{b(i),t} + \gamma"_{s(b(i)),t}$$

$c_{i,t-1}$ is the wetland cover in the previous year (t = 2, …, 5 for 2010, 2011, …, 2013). And L_t is the legacy effect of the previous year's cover at stream unit i (i = 1, 2, …, 120). ε'' and γ'' are spatial random effects at band scale and segment scale similar to the presence/absence model and cover model described above.

Bayesian implementation

We implemented the generalized linear mixed-effects model (for presence-absence data) and linear mixed-effects model (for logit-scale cover) in a Bayesian framework. Crucial to this approach is the notion of transparency and flexibility, which allows explicit modeling of parameters at different hierarchies (Latimer *et al.* 2006). In the absence of relevant information to suggest otherwise, we specified standard, vague priors for model parameters (Gelman *et al.* 2013), and thus, the posterior distributions for all parameters were largely driven by the observed data. Three different types of priors were used in our models. First, for the parameters describing the effects of the geomorphic and biotic factors (e.g., the b, *b*, a, λ, λ', and *L* terms), we specified vague priors via normal distributions with large variances. Second, for the spatial random effects (i.e., the ε, ε', ε'', γ, γ', and γ'' terms), we assumed zero-centered normal priors with unknown variances such as *Normal*$(0, \sigma^2)$, where each of the four groups of random effects was associated with its own variance term. The variance term for each group varied by year (i.e., $\sigma_{\varepsilon,t}$, $\sigma_{\varepsilon',t}$, $\sigma_{\varepsilon'',t}$, $\sigma_{\gamma,t}$, $\sigma_{\gamma',t}$, $\sigma_{\gamma'',t}$). Third, for the variances associated with the logit(c) likelihood and the spatial random effects, we specified relatively non-informative inverse gamma priors.

We implemented the above models in OpenBUGS 3.2.1. (Spiegelhalter *et al.* 2003), an open-access software package for conducting Bayesian statistical analyses. OpenBUGS employs Markov chain Monte Carlo (MCMC) methods to sample parameter values from their joint posterior distribution. Three parallel MCMC chains were assigned relatively dispersed starting values, and run sufficiently long to achieve convergence and to obtain a posterior sample size effectively equivalent to >3,000 independent samples (for details on MCMC procedures, see Gamerman and Lopes 2006, Gelman *et al.* 2013). For each parameter, we computed the posterior mean and estimates of uncertainty via the 95% credible interval (CI), which is defined by the 2.5th and 97.5th percentiles.

Model diagnostics and comparison

We conducted an informal model goodness-of-fit assessment (following Ogle *et al.* 2006). For the presence/absence point model, a goodness-of-fit plot was derived according to the following steps: (1) we obtained the predicted probability of occurrence (p) for each point along the channel; (2) for each species and year, points were grouped according to their predicted probability of occurrence, with a fixed bin width of 0.01; (3) within each p bin, the fraction of points classified as "present" and the average value of the predicted p was calculated, yielding a plot of the observed fraction of points versus the average predicted probability of occurrence for each species. For the patch data, we compared the predicted versus observed percent cover for each year to evaluate the amount of variability in cover explained by the model.

We also assessed model sensitivity and the ability of the model to correctly predict the points with the presence of wetland plants (*i.e.,* positive points). We used prevalence of positive points in the empirical data as thresholds (Liu *et al.* 2005). Specifically, the point is defined as "predicted positive" if the posterior mean of the predicted occurrence probability is higher than the threshold, whereas the point is defined as "predicted negative" if lower. Sensitivity is calculated as the number of positive points correctly predicted by the model divided by the total number of positive points in sample (Fielding & Bell 1997). Receiver operating characteristics (ROC) analysis provides a threshold-independent assessment of the fit of model predictions (Hanley & McNeil 1982). ROC plots summarize the performance of a model as a tradeoff between sensitivity and specificity (the probability of correctly predicting a true absence). ROC plots display sensitivity (i.e., true positive rate) on the y-axis and false-positive rate (i.e., the probability of predicted presence where the species is observed to be absent) on the x-axis. The area under the ROC curve (AUC) then provides an integrated measure of the performance of the model. AUC ranges between 0.5 and 1.0. If the value is 0.5, the scores for two groups (i.e., true-positive rate vs. false-positive rate) do not differ, while a score of 1.0 indicates sensitivity increases without losing any specificity (the proportion of negatives correctly predicted as such). Therefore, high values of AUC reflect better model performance. These indices were calculated in R (R Core Team 2015), with the 'ROCR' package (Sing. 2015).

RESULTS

TEMPORAL AND SPATIAL PATTERNS IN STREAM WETLAND ABUNDANCE

Wetland distribution in Sycamore Creek was heterogeneous in space over the five-year study period. The stream channel between 3000 and 5000 m had almost no wetland establishment (Figs 1.3 and 1.4). The mean valley floor width across that stretch of the stream is about 260 m, much wider than the rest of the 12-km stream (average valley floor width ~ 90 m). However, the stream channel between 5000 and 7000 m had similar valley floor width, but supported abundant wetland cover (Fig. 1.4). Despite the high variability in wetland spatial distribution both in space and time, locations of some wetland patches have been stable (Fig. 1.3). We examined the legacy effect: the relationship between wetland cover and its distribution in the current and prior year. The legacy effect was significant for all years (the 95% CI of the coefficient did not contain zero), meaning that the location of wetlands and their cover in the previous year were a significant predictor of wetland cover in the current year. In the years without major floods, the previous year's wetland distribution explained a large amount of variance in the wetland distribution in the current year ($R^2 = 0.53$ and 0.50 for 2012 and 2013, respectively). For 2010 and 2011, values of R^2 were low (0.03 and 0.07), though the previous year's cover was still a significant factor. We also analyzed wetland fidelity, measured by the coefficient of variation (CV) of wetland cover for each 100 m stream unit over the 5-year period. The quadratic relationship between CV and mean of wetland cover (Fig. 1.3f) suggested that locations with high abundance of wetland cover stayed high over time, and those with low abundance stayed low.

Overall wetland abundance changed considerably among years (Fig. 1.3). After the large flood in January 2010, wetland cover decreased dramatically (Fig. 1.3d), reaching the lowest of the five years (~13%). In fact, a visual (qualitative) survey in March 2010 of several locations of high wetland fidelity showed very little evidence of surviving plants; however, regrowth from root stock occurred, so that cover reached 13% by June 2010. The highest cover was observed in the two dry years: 40% in 2011 and 45% in 2012 (Fig. 1.3d). There were only two small flood events in 2011 and no floods in 2012 between January and June (Fig. 1.1d). During the seasonal survey in January 2011, wetland plant cover was only 5% (living plants). Three months later, in April 2011, total wetland cover reached 18%, after which it increased to 40% in June. The only species with new, actively growing tips in January was *T. domingensis*.

Timing of floods directly influenced the abundance of *T. domingensis*. *T. domingensis* regenerated as early as January (this species occupied ~ 5% of the 12-km survey extent in January 2011 & 2012). Therefore, large floods (discharge > 1 $m^3 s^{-1}$) occurring in February and March could directly affect its abundance (Chen, Zamorano &

Ivanoff 2010). Comparing 2009 and 2013, which had similar hydrological conditions (Fig. 1.1c) except that floods in 2013 were one month later than those in 2009, the patch cover of *T. domingensis* in 2013 was only 70% of that in 2009 (Fig. 1.3c). In 2011 and 2012, there were no large floods after December, and these years had the highest observed abundance of *T. domingensis* (both absolute abundance and abundance relative to the other five species) (Fig. 1.3a,c). Dry years and the wet year also directly influenced *J. torreyi*. This species grows adjacent to the active stream channel, but not directly in water (i.e., parafluvial habitat). Therefore, an extensive dry area is favorable for the development of *J. torreyi*. Its abundance in the wet and average years was less than half of that in the dry years (Fig. 1.3a,c).

WETLAND SPECIES PRESENCE/ABSENCE: GEOMORPHOLOGY, BIOTIC INTERACTIONS, AND HYDROLOGICAL VARIABILITY

The Bayesian presence/absence point model sufficiently predicted the presence/absence of wetland plants (AUC values ranged between 0.8 and 0.9) (Table 1.1). However, AUC assessed the predictive power of the model at the point level, a very fine resolution (i.e., 25 m). As an informal evaluation of model fit, we used the coefficient of determination (R^2) from a regression of the observed fraction versus the predicted probability of occurrence at the 100-m scale. The R^2 values for this relationship ranged from 0.46 to 0.94 (Table 1.1), with observed versus predicted values falling around the 1:1 line (Fig. 1.5a). When various model diagnostic indices were assessed for individual years, the model performed better in the dry years (2011, 2012) than in the wet (2010) or average years (2009, 2013) (Table 1.1).

Both the direction and magnitude of the geomorphic effects varied among species and changed over time (years) (Table 1.2 and Fig. 1.6). The overall effect of channel slope (*S*) on the occurrence of the five indicator wetland species was significantly positive in 2009, and its effect on the occurrence of *E. laevigatum* was significantly positive when averaged over five years (Table 1.2). Elevation (*E*) was not a significant predictor of the presence of wetland plants overall, although the presence of *P. distichum* and *S. americanus* were significantly correlated (negatively and positively, respectively) with elevation. Water permanence (*W*) had a significant positive effect on species occurrence in all five years (averaging over all species), and exerted a significant positive effect on four out of five species (*J. torreyi* was the exception) across all years (Table 1.2). The magnitude of the effect of water permanence (*W*) varied significantly among the five wetland species (Fig. 1.6b). Upwelling zones (*U*) were a significant predictor of species presence only for *T. domingensis* in the dry year of 2012.

Species associations also changed from year to year (Fig. 1.7). Significant species associations can be attributed to two factors: the shared or opposite requirement for a particular physical environment (i.e., co-existence) and/or direct biological interactions (e.g., competition or facilitation) among species (Ovaskainen, Hottola & Siitonen 2010). Our model was not able to distinguish between these two causes, but even after accounting for geomorphic and spatial random effects, significant species associations remained. For example, species association patterns before the 2010 winter flood were quite different from the patterns after the flood. In particular, *T. domingensis* and *J. torreyi* were positively associated most years, and strongly so in the two dry years. The only significant negative association was found between *E. laevigatum* and *T. domingensis* in 2012 (Fig. 1.7).

The spatial random effects indicated significant unexplained spatial variability at multiple spatial scales that varied among years (Table 1.1; Fig. 1.8). After accounting for the effects of the geomorphic and biotic predictors, several significant band-scale spatial random effects emerged in all years, except for 2010 (only one band was significant) (Fig. 1.8). Significant segment-level spatial random effects still emerged after accounting for the geomorphic, biotic, and fine-scale band effects (Fig. 1.8), with least variation among segments (σ_s) occurring in 2010 and greatest occurring in the two dry years (2011 and 2012) (Table 1.1). Segment 2, which was the part of the stream where the valley floor widened in a downstream direction (Fig. 1.2b), had significantly lower probability of wetland occurrence across all five years. Conversely, segments 3 and 4, which are located in the part of the stream where the valley is narrowing downstream (Fig. 1.2b), had significantly higher probability of occurrence.

WETLAND PATCH ABUNDANCE: GEOMORPHOLOGY AND HYDROLOGICAL VARIABILITY

Similar to the presence/absence point model, the patch cover model predicted the distribution of wetland patches well for the two dry years, with R^2 values of 0.58 (2011) and 0.68 (2012). Models for the two average years explained less variance ($R^2 = 0.48$ and 0.51 for 2009 and 2013, respectively). The performance of the model was poor for the year of the large flood, 2010 ($R^2 = 0.27$; Table 1.1).

Elevation (*E*), channel slope (*S*), and valley floor width (*V*) had no significant effect on the distribution of wetland cover (Table 1.2). Water permanence (*W*) explained most of the variance in wetland cover across all years except for 2010 (Table 1.2), although effect size varied among years, with the largest effect occurring in the driest year (2012) (Fig. 1.6a). In general, places with greater water permanence were associated with higher cover of wetland patches. Finally, upwelling zones (*U*) exerted significant positive effects in 2012 and 2013, but only for *T. domingensis*.

Significant spatial random effects occurred in dry years, but they disappeared in average years or the wet year (Fig. 1.8). Greater values for σ_b and σ_s in dry years also indicated more evident spatial random effects (Table 1.1). In dry years, segment 3, where the valley floor narrowed sharply (Fig. 1.2b), had higher wetland abundance than expected (i.e., given the effects of the covariates included in the model) compared to the other segments (Fig. 1.8). The spatial effect at band scale was also most significant in the driest year, 2012 (Fig. 1.8). These results mirrored those of the presence/absence point model.

DISCUSSION

This study demonstrated a change in the relationship between species distributions and the geomorphic template due to changes in the environmental setting; specifically, in this case, the hydrological variability. That is, we found that the explanatory power provided by geomorphic variables (i.e., *E*, *S*, *V*, *W*, *U*) varied among years characterized by different hydrological conditions (Table 1.1). Geomorphic variables influence species establishment indirectly through their effects on the spatial distribution of temperature, light, saturation zones, groundwater upwelling, and nutrient availability (Dent, Grimm & Fisher 2001). These environmental gradients then directly influence the biological community. However, hydrological variability could alter the environmental gradients created by the geomorphic setting. For example, in dry years (e.g., 2011 and 2012), the geomorphic predictors, including water permanence, provided much greater explanatory power for wetland abundance and distribution (Table 1.1; Fig. 1.6). During such dry years, the effect of distribution of the saturation zones determined by the large-scale geomorphic characteristics was most evident. Wetland plants accumulated in these saturation zones, whereas the mortality of plants was high in the dry sections of the stream (hence low abundance). In the wet year, however, continuous surface water homogenized the flow patterns along the stream, weakening the relationship between the saturation gradient and wetland plant distributions.

Many studies have investigated the relative importance of hydrological and geomorphic impacts on species distributions in fluvial landscapes (e.g., Bendix & Hupp 2000; Hupp 2000; Górski & Buijse 2013; Stewart-Koster *et al.* 2013; Valente, Latrubesse & Ferreira 2013). In those studies, hydrologic variability over time was reduced to an integrated value for each sampling site (e.g., frequency of floods over 10 years, maximum floods within 5 years). Geomorphology and hydrologic variability were treated as two sets of variables independent of each other. This assumes that the geomorphology–species relationship is transferable in environmental space. In systems with high hydrological variability, such as desert streams, where the positions of the system in environmental space change drastically over time, the assumption of a stable relationship between geomorphology and species distribution is inappropriate. We therefore find support for our hypothesis that the relationship between the geomorphic template and species abundance and distribution can be modified by environmental temporal variability (in this case, hydrological variability).

Another reason for variable explanatory power of the geomorphic variables is that the degree to which the system approached a pseudo-equilibrium state likely varied among years. The magnitude of the spatial random effects at both scales was greater in dry years compared to the average years or the single wet year (Table 1.1; Fig. 1.8). This suggests a more homogenous wetland spatial distribution in average to wet years, which could have been caused by two inter-related processes: (1) as noted above, relatively abundant surface water in the wet and average years homogenized the spatial heterogeneity created by the saturation zones along the stream; and (2) severe flood disturbance and the timing of floods resulted in low wetland cover along the entire stream in wet year of 2010. Winter flood disturbances mobilize sediments and dislodge buried propagules, directly reducing vegetative reproduction in spring (Cellot, Mouillot & Henry 1998). Meanwhile, high flows in the wet year and even in the average years may reduce sites where wetland seeds could survive, while in drier years more streambed is exposed for seed establishment and germination. The low abundance of wetlands suggests that the system was likely farther away from species–environment pseudo-equilibrium in wet and average years than in dry years (Fig. 1.3b,d). The band-scale spatial effects capture the interactions between morphodynamics and hydrology in meandering rivers (Fig. 1.2). Interactions among flow movements, sedimentation processes, and vegetation create the spatial pattern of vegetation as well as shaping river channel morphology (Johnson 1994; Perucca, Camporeale & Ridolfi 2006). At the coarser segment scale (10^3 m), constrained and unconstrained sections alternate along the stream (Stanley, Fisher & Grimm 1997), and this determines the nature of sediment deposition and thus saturation area and residence time (Zinko *et al.* 2005; Chen *et al.* 2006; Curie *et al.* 2007), all of which could influence the spatial distribution of wetlands. However, the effects of processes at either spatial scale can only be fully manifested when wetland distribution is closer to species-environment pseudo-equilibrium.

Our study system experienced various aspects of hydrological variability, which gave rise to complex species responses. Some studies have suggested that the influence of timing and duration of flooding on riverine plant abundance depends on the fraction of the growing season flooded (Toner & Keddy 1997; Chen, Zamorano & Ivanoff 2010). This idea is relevant to our study in that abundance of *T. domingensis* was sensitive to the timing of the previous winter's floods. In 2011 and 2012, there were no large floods after December, and the highest abundance of *T. domingensis* was observed (Fig. 1.3b,d). In 2013, when the last winter flood was as late as March 9, *T. domingensis* cover was reduced to less than half that of its 2011 or 2012 cover (Fig. 1.3c). At a multi-year time scale, alternating wet and dry years may affect plant establishment from the seed bank by stimulating or inhibiting germination (Leck & Brock 2000), by modifying oxygen availability in the soil, or by desiccating aquatic plants or inundating terrestrial plants (Casanova & Brock 2000). However, a much longer-term dataset is needed to assess the impact of wet–dry cycles as well as disturbance timing on species abundance and distribution.

Flood magnitude is another aspect of the hydrologic regime that may influence vegetation (Vervuren, Blom & de Kroon 2003). While small floods result in fluctuations in wetland abundance from year to year, bed-moving floods, such as the one in January 2010 in Sycamore Creek, have longer-term consequences for vegetation composition and distribution. In the years after the 2010 100-year flood, we observed a major increase in the abundance of *T. domingensis*, yet the cover of other indicator wetland species did not recover (*P. distichum* and *S. americanus*) or only slightly recovered (*E. laevigatum*) towards their pre-2010 cover, even after four years. Similar long-term consequences of large disturbances have been observed in other studies. For example, Stromberg, Fry & Pattern (1997) found that in the three years following a 25-year flood in the Hassayamapa River, northwest of Sycamore Creek, riparian species composition shifted to increased abundance of wetland plants. This was because this single flood event lowered the floodplain surface relative to the water table, a factor critical to riparian plant composition in arid-land river systems.

Various aspects of the hydrological regime exert external constraints on species assembly, accompanied by stabilizing feedbacks between the biotic community and the local environment, including internal species interactions. Even though our model was not able to distinguish whether the detected species associations were caused by shared or opposite requirements for a particular physical environment or caused by direct biological interactions among species, the species association changed from year to year depending on hydrological conditions (Fig. 1.7). This could have resulted from the changed relative abundance of different species in different years (Fig. 1.3), which is likely to result in variations in the magnitude of biological interactions (e.g., competition, facilitation, etc.). Internal interactions involve not only interactions among species, but also feedbacks between abiotic environment and species. The theory of ecosystem alternative stable states (Carpenter 2001; Scheffer & Carpenter 2003) informs our understanding of ecosystem temporal variability as a result of internal feedbacks, including interactions among individual organisms and feedbacks between the environment and the organisms. Such a stabilizing mechanism is predicted to generate a negative relationship between wetland biomass and variability in biomass caused by flood disturbance (Heffernan 2008). The negative relationship between the mean and CV of wetland cover above a threshold amount (~15% cover in 100-m intervals; Fig. 1.3f) is consistent with this theoretical prediction. Below the threshold biomass (or cover) amount, places with low wetland cover stayed low (therefore, also low CV) in all five years; these are places constrained by geomorphic setting. Above the threshold, places with high wetland cover stayed high, as a result of density dependent self-stabilizing mechanism (Heffernan 2008). This mechanism is also consistent with the results from the legacy effect analysis: the previous year's distribution and abundance was significant for all the years, even after the big flood in the January of 2010. The quadratic relationship is evidence of a joint effect of the physical template and internal self-organization by vegetation patches (Sheffer *et al.* 2013). Additionally, ecosystem state-change theory suggests that an ecosystem could have more than one stable state, and the switch between states may involve a hysteresis effect (Sternberg 2001). In this case, flood magnitude would have to drop much lower than the threshold value for the system to return to the wetland state. Thus, either ecosystem state is resilient, and the same set of environmental conditions may correspond to totally different ecosystem states.

DATA ACCESSIBILITY

This study is a contribution to the long-term ecological research in environmental biology (LTREB) at Sycamore Creek, Arizona, USA, and the data are available online at https://caplter.asu.edu/data/data-catalog/?id=596.

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TABLE 1.1. Assessment of model performance for the presence/absence point model and the wetland patch cover model, as well as comparison of the model predictive power among years. Predicted mean and observed average in the presence/absence model refer to predicted probability and observed average proportion of occurrence, and in the patch cover model, they refer to predicted and observed average cover in each 100-m unit. The standard deviations, σ_b and σ_s, describe the residual spatial variability in each logit-scale variable (probability of occurrence and proportion cover) at the band (i.e., $\sigma_{\varepsilon,t}$ and $\sigma_{\varepsilon',t}$, fine spatial resolution) and segment (i.e., $\sigma_{\gamma,t}$ and $\sigma_{\gamma',t}$, coarse resolution) scale for each year. The coefficient of determination (R^2), model sensitivity, and AUC describe model goodness-of-fit, the ability of the (point) model to correctly predict points with presence of wetland plants (*i.e.,* positive points), and area under curve, respectively

	Predicted Mean	**Observed Average**	σ_b	σ_s	**R^2**	**Sensitivity**	**AUC**
Presence/absence Point Model							
Overall	0.20	0.20	-	-	0.94	0.83	0.84
2009	0.20	0.20	0.47	3.14	0.56	0.81	0.80
2010	0.10	0.10	0.54	1.07	0.46	0.79	0.81
2011	0.25	0.25	0.51	3.79	0.85	0.83	0.83
2012	0.27	0.27	0.73	4.29	0.83	0.82	0.88
2013	0.18	0.18	0.63	3.41	0.64	0.86	0.84
Patch Cover Model							
Overall	0.25	0.25	-	-	0.55	NA	NA
2009	0.22	0.22	0.13	0.16	0.48	NA	NA
2010	0.09	0.09	0.08	0.24	0.27	NA	NA
2011	0.36	0.35	0.16	0.33	0.58	NA	NA
2012	0.34	0.34	0.20	0.29	0.68	NA	NA
2013	0.26	0.26	0.13	0.18	0.51	NA	NA

TABLE 1.2. Summary of covariate effects in the presence/absence point model and the patch cover model. If significant ($p < 0.05$), the sign of the effect is indicated by –/+ for negative and positive effects; non-significant effects are indicated by *ns*. For the presence/absence model, the coefficients were indexed by both species and year; when listed under particular species, the effect was averaged over the 5 years; when listed under a particular year, the effect was averaged across the 5 species. Species codes are: EQLA = *Equisetum laevigatum*, PADI = *Paspalum distichum*, SCAM = *Schoenoplectus americanus*, JUTO = *Juncus torreyi*, and TYDO = *Typha domingensis*

Presence/absence point model					
Covariate*	**EQLA**	**PADI**	**SCAM**	**TYDO**	**JUTO**
E	*ns*	–	+	*ns*	*ns*
S	+	*ns*	*ns*	*ns*	*ns*
V	*ns*	*ns*	*ns*	+	–
W	+	+	+	+	*ns*
	2009	**2010**	**2011**	**2012**	**2013**
E	*ns*	*ns*	*ns*	*ns*	*ns*
S	+	*ns*	*ns*	*ns*	*ns*
V	*ns*	–	*ns*	*ns*	*ns*
W	+	+	+	+	+
U	*ns*	*ns*	*ns*	+	*ns*
Patch cover model					
Covariate	**2009**	**2010**	**2011**	**2012**	**2013**
E	*ns*	*ns*	*ns*	*ns*	*ns*
S	*ns*	*ns*	*ns*	*ns*	*ns*
V	*ns*	*ns*	*ns*	*ns*	*ns*
W	+	*ns*	+	+	+
U	*ns*	*ns*	*ns*	+	+

*Covariates: E = elevation; S = channel slope; V = valley floor width; W = water permanence; U = upwelling zone.

FIGURE 1.1. Hydrological conditions at Sycamore Creek, Arizona during the study period, including (a) daily discharge (the study period is indicated with a horizontal bar on the x-axis), (b) annual discharge (the study period is denoted by black bars), and cumulative daily discharge during (c) the survey years (2009-2013) with the summer flooding period and winter flooding period denoted by horizontal arrows, and (d) the two dry years (2011 and 2012). Data are from the USGS gauging station "Sycamore Creek near Fort McDowell" (ID: 09510200). Cumulative daily discharge is the sum of daily discharge from June 16th of the prior year until the survey date. A steep increase in cumulative discharge indicates a flood or series of floods.

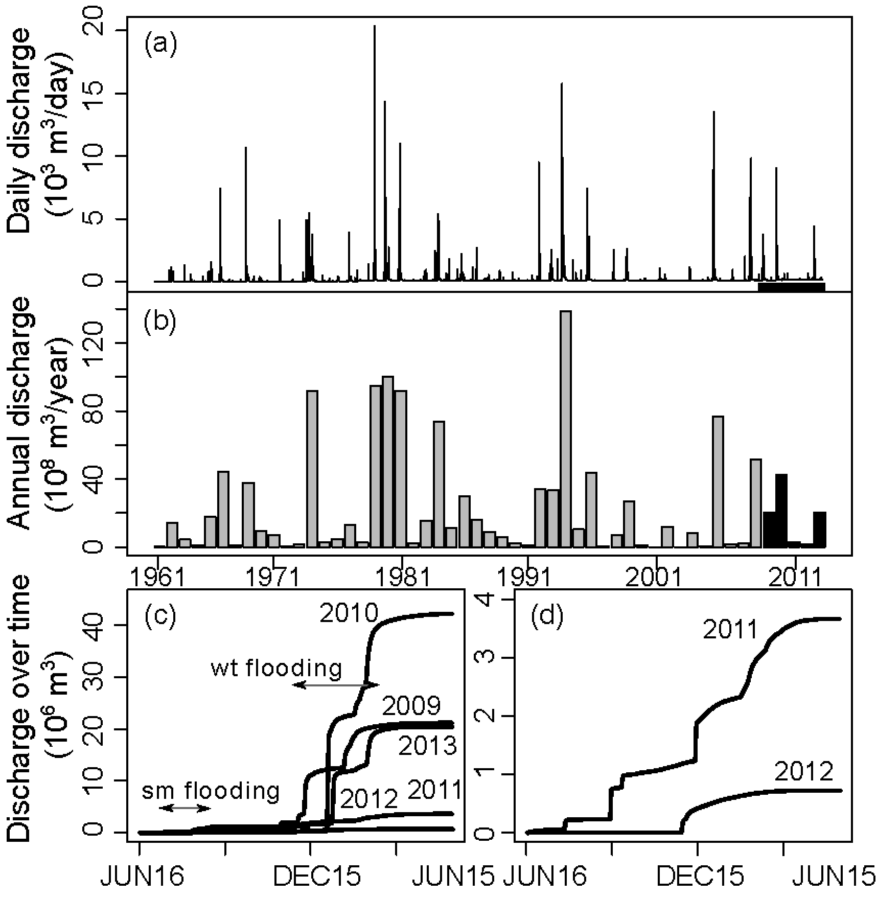


FIGURE 1.2. Schematic for the two spatial scales in the models: (a) fine-resolution band scale and (b) coarse-resolution segment scale.

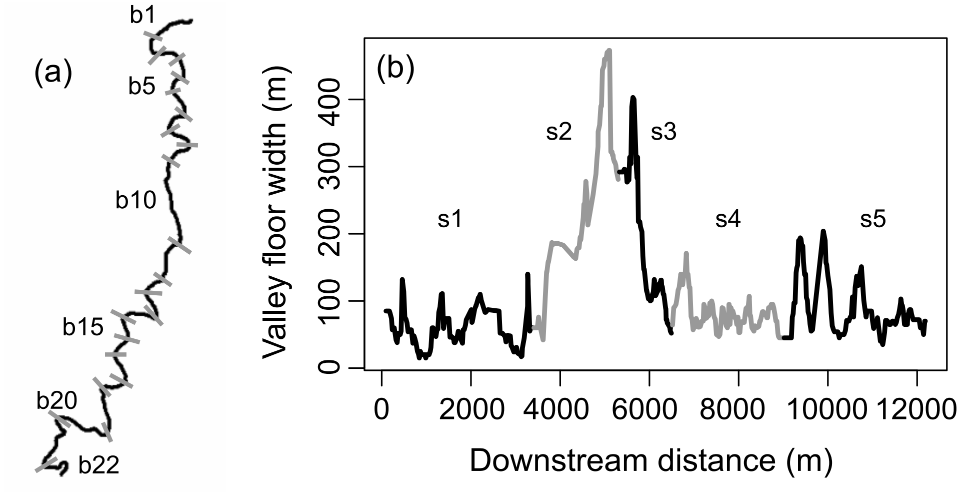


FIGURE 1.3. Changes in wetland cover and spatial distribution between 2009 and 2013 along the 12-km mainstem of Sycamore Creek in Arizona. (a) Changes in wetland occurrence by species. (b) Changes of wetland occurrence by year: percentage of surveyed points with at least one wetland species present. (c) Cover (%) by species between 2009 and 2013. (d) Changes of wetland cover: percentage of stream channel covered by at least one type of wetland patch. Note that *Juncus torreyi* was not surveyed in 2009. (e) The spatial distribution of wetland cover averaged over 5 years along the 12 km of the stream. Each point was the average wetland cover in a 100-m unit between 2009 and 2013. Symbol fill indicates coefficient of variation (CV). (f) The quadratic relationship between average CV and wetland cover. See Table 1.2 for species codes.

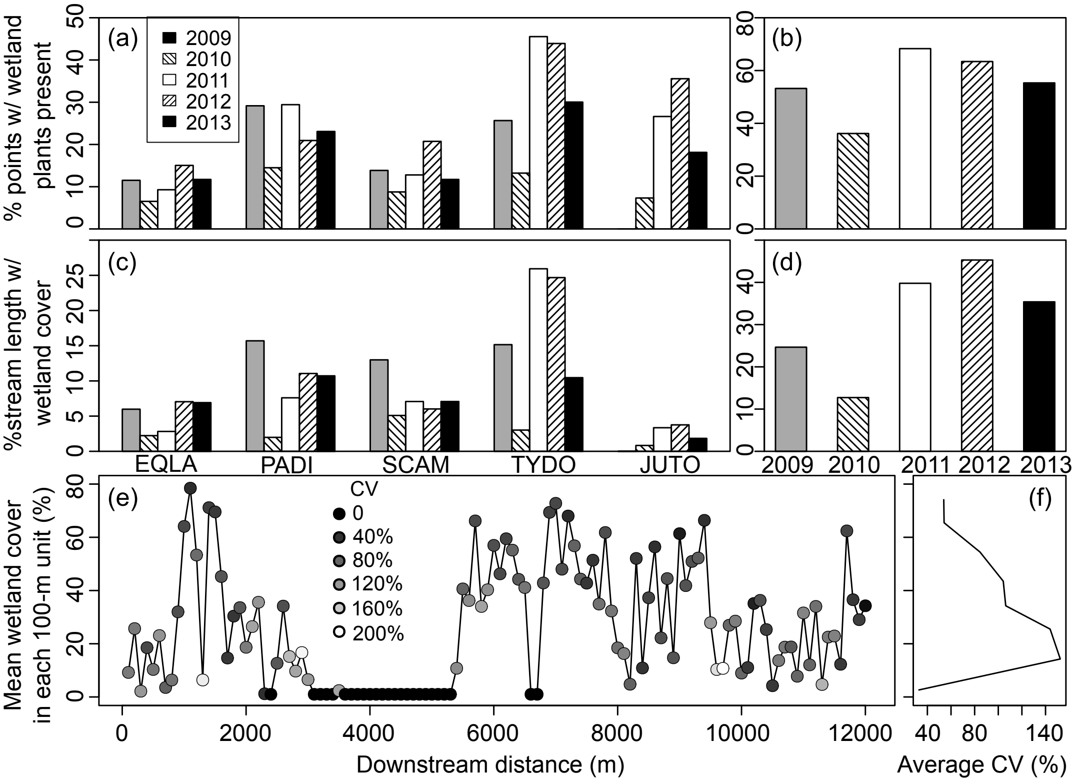


FIGURE 1.4. Spatial distribution of wetland patches along the channel in relation to valley floor width. The channel is divided evenly into 100-m units. The size of each point is proportional to the percentage of channel length covered by wetlands within each unit. The small gray points represent segments without wetland cover.

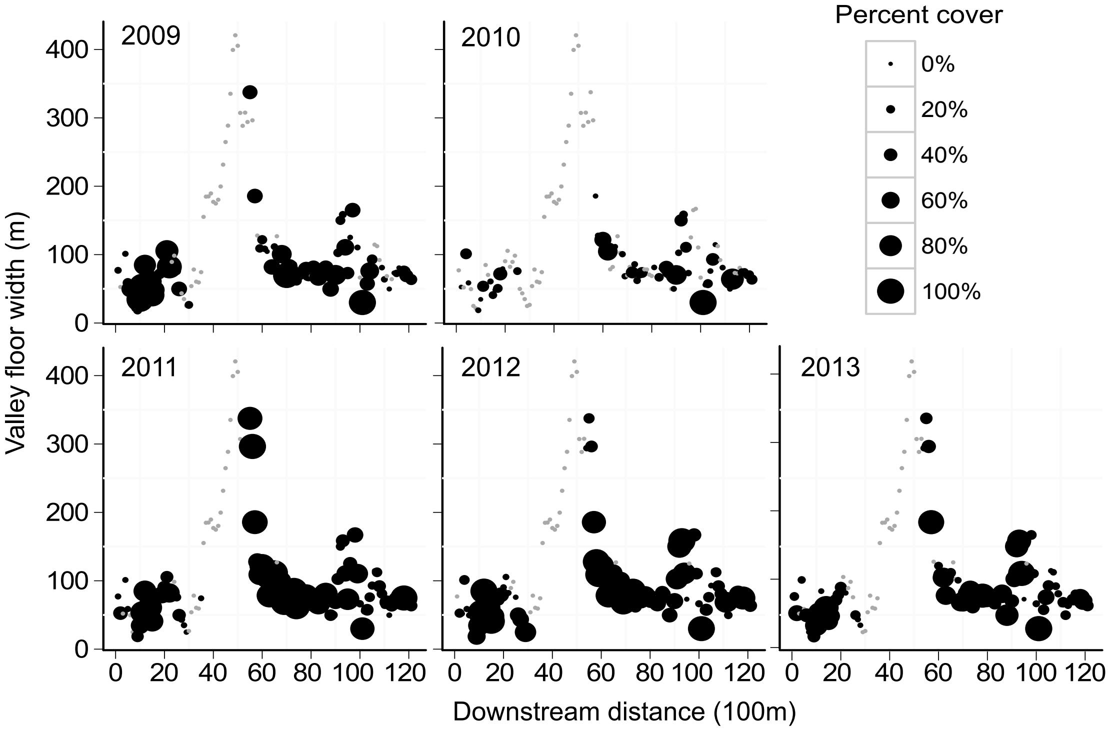


FIGURE 1.5. Observed versus predicted response variables for (a) the presence/absence point model and (b) the patch cover model. For the wetland cover model, the model fit was better in dry years (2011 and 2012) than in average years (2009 and 2013). The model goodness-of-fit was poorest for wetland cover in 2010. Dashed diagonal line is the 1:1 line.

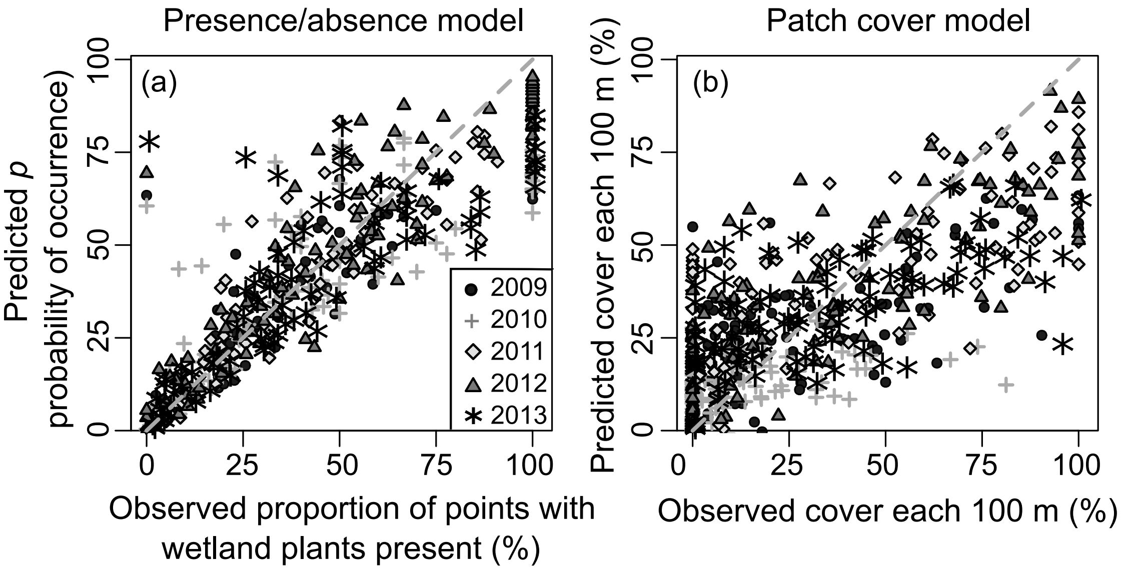


FIGURE 1.6. Posterior distributions for the effect of water permanence (a) in different years (results from patch cover model) and (b) for different species (results from presence/absence point model). See Table 2 for species codes. The vertical line at zero indicates the lack of an effect of water permanence.

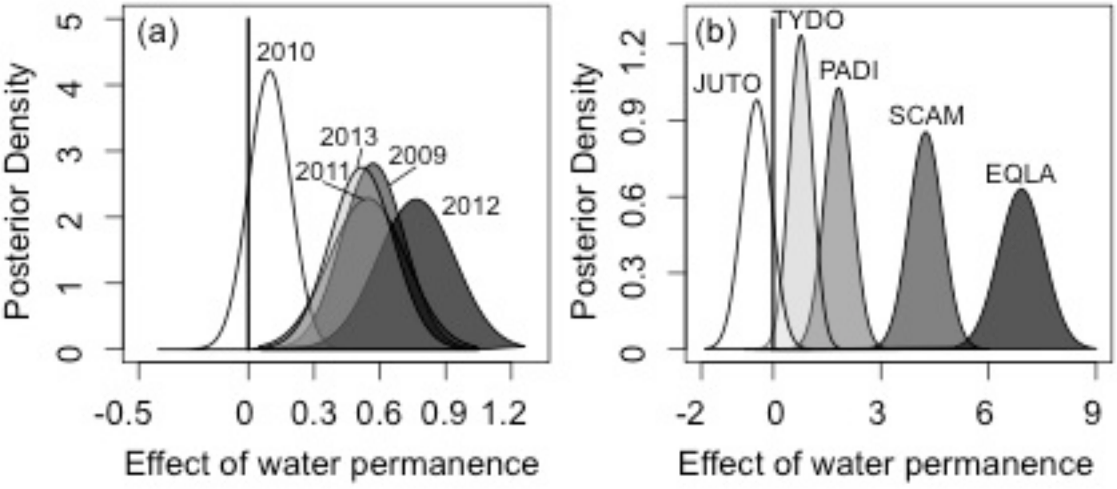


FIGURE 1.7. Species interaction effects changed among years. Dashed arrows indicate that the corresponding species-species effect was not significant, and solid arrows denote significant species associations. The black arrows represent a significant positive effect and the gray arrows represent a significant negative effect; arrow width is proportional to the effect size (i.e., the strength of the species associations). Species codes are: P = *Paspalum distichum*, S = *Schoenoplectus americanus*, E = *Equisetum laevigatum*, J = *Juncus torreyi*, and T = *Typha domingensis*.

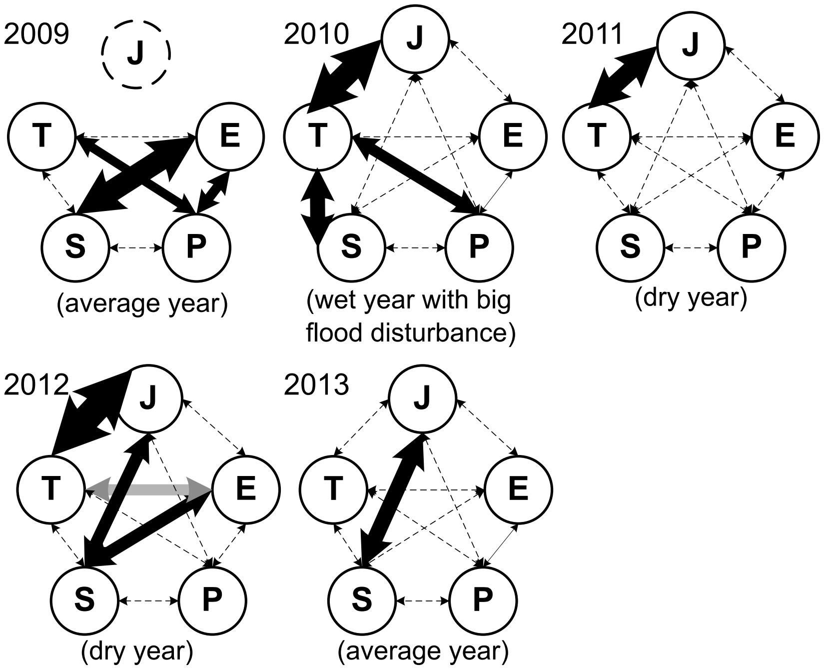
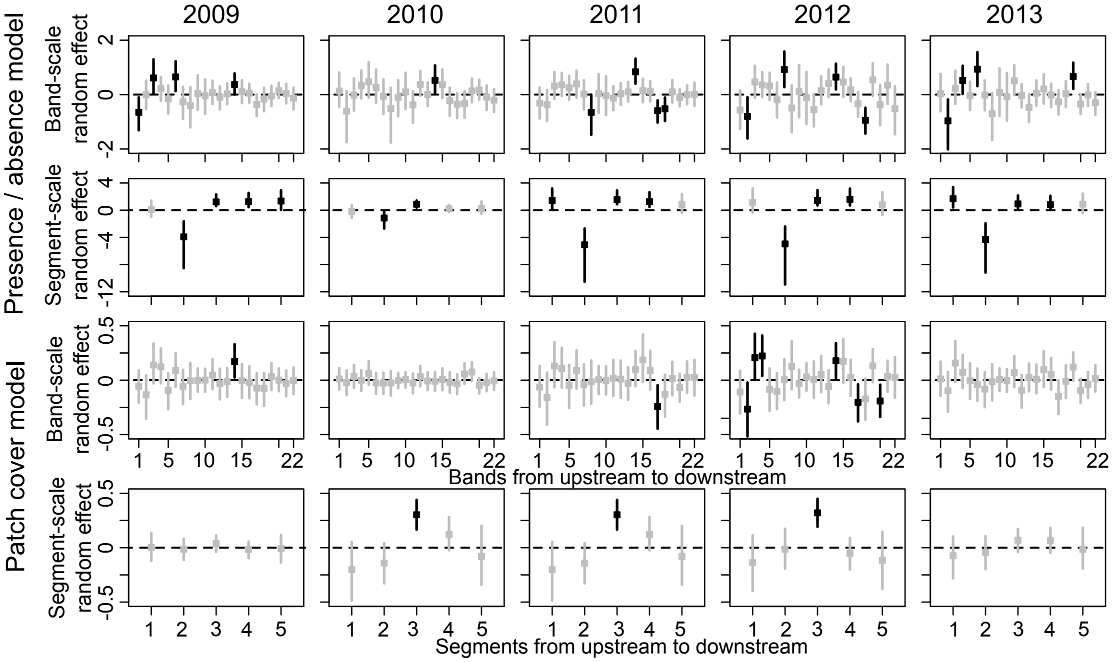


FIGURE 1.8. The posterior mean and 95% credible interval (CI) for the spatial random effects at fine-resolution band scale and coarse-resolution segment scale in presence/absence point model (upper two rows) and patch cover model (lower two rows) in different years. Significant random effects (95% credible interval does not contain 0) are marked as black, and non-significant effects are in gray.



CHAPTER 2

SELF-ORGANIZATION OF MACROPHYTES IN HETEROGENEOUS FLUVIAL LANDSCAPES

ABSTRACT

Both local interactions (self-organization) and the spatial heterogeneity of the physical template can influence biological patchiness in ecosystems. While there are abundant studies on the patterns formed by self-organization on landscapes where template heterogeneity is negligible, research on spatial self-organization in heterogeneous landscapes is rare, despite the fact that landscapes in nature are mostly heterogeneous. The relative importance of the two drivers might change in time, in response to changes in the external environment. This is especially relevant for systems experiencing high environmental temporal variability. We investigated the interaction between self-organization and template heterogeneity with 6-yr macrophyte patch distribution data collected from Sycamore Creek, a desert stream in Arizona, USA, a system that is highly variable both in space and in time. We used a lattice simulation model that includes both the spatial heterogeneity of the geomorphic template (template effect) and of the self-organization of plants (local facilitation effect). We showed that the strength of local facilitation and template effect first increased with the effective flood consequence (a metric we created to account for both the timing and magnitude of winter floods), and then leveled off. The system exhibited alternative states, catastrophic transitions, and hysteresis effects when the stress level exerted on the system changed. Self-organization reduced the tendency for the system to shift from vegetated to gravel state, by raising the threshold stress level and making the transition to gravel state more gradual; however, local facilitation increased ecosystem hysteresis. Template heterogeneity, in contrast, weakened hysteresis. Under different hydrological conditions, the role played by local facilitation and template heterogeneity varied. This directly influenced the robustness of the system, including its resistance to stress and recovery from an “undesirable” state. To our knowledge, this is the first study to show the relative influence of self-organization and template heterogeneity varying with external conditions.

Keywords: catastrophic shifts; desert stream; ecosystem resilience; hydrological variability; hysteresis; macrophytes; physical template; power-law distribution; self-organization; spatial heterogeneity.

INTRODUCTION

A landscape is a mosaic of biotic and abiotic patches, with consequences for some ecological functioning (Strayer et al. 2003; Dormann et al. 2007; Ludwig et al. 2007). Spatial patchiness results from processes at various spatial and temporal scales with complex cross-scale interactions (Peters et al. 2004). Fundamentally, two drivers, operating from the top down or the bottom up, are envisioned for the formation of biological patchiness (i.e., spatial heterogeneity of biological components in ecosystems): (1) a preexisting physical template (top-down) and (2) self-organization induced by internal feedbacks (bottom-up) (Deblauwe et al. 2008; Rietkerk and van de Koppel 2008; Liu et al. 2014). We will refer to these as the template effect and the local facilitation effect (i.e., self-organization), respectively. A typical example of top-down control is physical constraint. For example, vegetation expansion can be influenced by local topography (Ropars and Boudreau 2012), through its effect on local microclimate via elevation, lateral redistribution of water, and slope orientation (Monger and Bestelmeyer 2006). Template-induced vegetation patchiness can also be realized through vegetation biomass following resource spatial distribution (e.g., water, nutrients, organic matter) (Buxbaum and Vanderbilt 2007; Kohler et al. 2012; Manolaki and Papastergiadou 2012).

The second driver is the rise of spatial patterning from internal feedbacks, i.e., self-organization. Self-organization has been studied extensively in the past decade (HilleRisLambers et al. 2001; Rietkerk et al. 2002; van de Koppel et al. 2008; van de Koppel et al. 2005; Weerman et al. 2010). Ordered patterns of vegetation (e.g., spots, bands, labyrinths, and gaps) have been found in many ecosystems around the world (Rietkerk et al. 2002; Deblauwe et al. 2008). The causal mechanism for spatial self-organization involves scale-dependent feedbacks. In patterned vegetation, resource concentration underneath vegetation, where infiltration rate is high and evaporation rate is low, improves local condition for plants, but causes resource depletion farther away, leading to scale-dependent feedback (Rietkerk and van de Koppel 2008). Without the long-range negative feedback, local facilitation solely generates a scale-free patchiness (instead of periodic patterning with easily recognized geometric shapes), a pattern that can be described by a power law distribution (Scanlon et al. 2007; Kéfi et al. 2007). Previous research suggests that transition from power-law distribution to truncated power-law distribution (power-distribution with an exponential drop) can be used as a signal for ecosystem state change (Kéfi et al. 2011; Kéfi et al. 2010; Kéfi et al. 2007).

Studies on these self-organized spatial patterns (both regular and scale-free patterns) have been focused on homogeneous landscapes, where the template effect is absent or negligible. This is rare because most real landscapes feature heterogeneous substrates. Very few studies have considered the interactions between environmental template and spatial self-organization. Sheffer et al. (2013) developed a rock-soil mosaic framework, wherein the plant distribution is determined by the distribution of rocks. Only when the open soil area between rocks is large enough, did plants form self-organized patterns. Another study addressed the interaction between the spatial heterogeneity created by the termite mounds and vegetation biomass (Bonachela et al. 2015). Termite-mounds increase water infiltration and plant water use efficiency, and increase the resilience of these patterned Savannah ecosystems.

Self-organized systems often have altered ecosystem resilience. For example, mussel beds in ordered pattern are more resilient to wave disturbance and less prone to catastrophic collapse (Liu et al. 2014; van de Koppel et al. 2008). Self-organized salt marsh ecosystems are more resilient to strong wave attack on short timescales. On long timescales, self-organization may even lead to destruction of salt marsh vegetation (van de Koppel et al. 2005). Existing studies on the relation between self-organization and resilience are mostly from systems solely shaped by spatial self-organization. We have very limited understanding of how template heterogeneity may interact with self-organization to affect ecosystem resilience. The only study so far is by Bonachela et al. (2015), who found the spatial heterogeneity of termite mounds imposed on self-organization to increase the resilience of savanna ecosystems to climate change (lower precipitation).

In addition to internal feedbacks and external template effects, hydrological regime can also influence vegetation distribution and abundance, especially in environmentally dynamic systems (Riis and Biggs 2003). Hydrology directly determines the flow heterogeneity in fluvial landscapes. In water-limited ecosystems, at both ends of the hydrological spectrum (i.e., very dry or very wet), the landscape is relatively more homogeneous than in the intermediate condition. This suggests that the effect of the template may be altered by hydrology (Dong et al. 2015). Additionally, vegetation biomass varies over time in response to hydrology, and increased biomass is responsible for high sediment stability (Heffernan 2008), which improves the local habitat for plants as a consequence. Whether and how does hydrology alter the relative importance of self-organization and the template effect? How does that interaction influence ecosystem macroscopic properties? To our best knowledge, these questions have never been explored.

In this study, we addressed two questions: (1) what are the contributions of self-organization and template effect in shaping the spatial distribution of macrophytes along a desert stream in different years characterized by distinctly different hydrological regimes? And (2) how does template heterogeneity interact with self-organization to influence ecosystem robustness? To address these questions, we combined in-stream macrophyte data collected in a desert stream, Sycamore Creek, Arizona, USA, across 12-km stretch with a lattice model. Desert streams are highly variable in both space and time (Fisher et al. 1982; Stanley, Fisher, and Grimm 1997; Dent and Grimm 1999), making them ideal systems to investigate these questions. The data were collected during a six-year period (2009-2014), capturing the highly variable hydrology of the system. We will first present the construction of the lattice model, then we explore the behavior of the model over a gradient of template effect and local facilitation. We will then show how the combination of drivers hydrologically varying years influences ecosystem macroscopic properties.

METHODS

SITE DESCRIPTION

The study was carried out in Sycamore Creek, a tributary of the Verde River, 32-km northeast of Phoenix, Arizona, U.S.A. The stream drains a catchment of 505 km^2. Mean annual precipitation ranges from 39 to 51 cm yr^{-1} with high inter-annual variability, peaking bimodally in winter and summer. The stream is frequently intermittent, especially in summer (Stanley, Fisher, and Grimm 1997). Winter floods flush away almost all the biota in the system and reset ecosystem succession in the following spring

(Fisher et al. 1982). The system experienced state change in year 2000 (Heffernan 2008), when the U.S. Forest Service removed cattle grazing from the study area. Since then, wetlands have developed extensively in the system and their abundance and spatial distribution have changed substantially with the hydrological regime (Dong et al. 2015).

DATA COLLECTION

Data were collected from the 12-km mainstem of Sycamore Creek ranging from 600 m to 700 m in elevation between 2009 and 2014. The hydrology of the six years can be divided into three categories (Fig. 2.1; Table 2.1): 2010 experienced a 100-yr flood, with a peak discharge of 439 m^3 s^{-1} in the end of January and another flood as late as March (68 m^3 s^{-1}). All the wetlands had been removed after flooding. The years 2009 and 2013 were average years (Fig. 2.1a), with two or three medium-sized floods (peak discharge at 30-110 m^3 s^{-1}). The remaining three years, 2011, 2012, and 2014, were dry years, according to cumulative mean daily discharge (Fig. 2.1a). However, 2014 was wetter than 2011 and 2012, with one flood of peak discharge at 72 m^3 s^{-1} in early March. The driest year was 2012, with only one small flood (2.4 m^3 s^{-1}) in mid-December. This high hydrological variability is typical for Sycamore Creek.

Each year on June 15th (±3 days, peak biomass time of the year). We walked from upstream to downstream and recorded the location and size of each wetland patch. We used the five most abundant wetland species as indictor wetland species: *Equisetum laevigatum*, *Paspalum distichum*, *Schoenoplectus americanus*, *Juncus torreyi*, and *Typha domingensis*. We define a wetland patch as a patch with at least one of the five indicator species and whose area is greater than 4 m^2. If the gap between two patches is less than

1m, the two patches were assumed to be one continuous patch. We used hand-held GPS devices (with a resolution of 5m) to record the upstream location of that patch and the dominant species within it. We measured the average width and length of each patch.

Water permanence data were collected by E. Stanley (University of Wisconsin). She and her colleagues walked the same 12-km stretch of the stream every month for a consecutive 22 months between 1988 and 1989, and recorded the extent of surface water. We used that dataset and calculated the proportion of the time in the 22-month period when surface water was present for each location (resolution is 1m) along the stream. We assumed that the *relative* saturation gradient was unvarying because it is determined by the broad-scale geomorphic template. However, the absolute water permanence gradient could vary from year to year, depending on annual precipitation and temperature, which directly influence evaporation rate.

MODEL DESCRIPTION

The model is based on the assumption that two forces affect the distribution of macrophyte patches along the stream: geophysical template and local positive feedback between plants and sediments. We used water permanence (*wp*) gradient as geophysical template, as it was found to be the major variable determining wetland abundance and distribution in this system (Dong et al. 2015).

We used a power-law formulation to simulate the effect of preexisting template (*TP*) on the mortality rate:

$$TP_{i,yr} = wp_i^{\beta_{yr}}$$

The parameter β_{yr} is a year-specific parameter that represents the effect of water permanence on plant establishment rate. When $\beta_{yr} = 0$, it means there is no template effect. When $\beta_{\mathrm{yr}} = 1$, it means a linear relationship between water permanence and plant establishment rate exists. When $\beta_{yr} > 1$ and $\beta_{yr} < 1$, the relationship between water permanence and template effect is convex and concave, respectively. Water permanence influences the plant establishment rate, i.e., the transition probability for a cell to switch from empty state to vegetated state, w_{01}:

$$w_{01} = \varepsilon_{yr} q_d w p_i^{\beta_{yr}}$$

where q_d is the percent of vegetated cells neighboring an empty cell. We assumed that all dispersal occurred locally (we tried including global dispersal term, but it did not improve model performance, and it was almost constant among years). Here ε is the probability that a propagule from a neighboring cell disperses, lands on an empty cell, and successfully geminates when $wp = 1$. The neighbor size was assumed to be 4 meters (4 cells), with 2m upstream and 2m downstream. We tested the effect of size of the neighbor, and found the results of interest to be insensitive to it.

Local facilitation reduced the chance of plant mortality through positive feedback between plant biomass and water holding capacity of sediments beneath plants. Reduction of mortality is greater when there are more cells occupied by plants in the neighboring cells. We took advantage of the flexibility of the shape of power-law formulation to explore the relationship between the effect of local facilitation (self-organization, *SO*) and percent of vegetated cells in the neighborhood.

$$SO_{i,yr} = (1 - q_f)^{f_{yr}}$$

The parameter f_{yr} quantifies the effect of local facilitation. q_f is the percent of vegetated cells in the neighbor of a vegetated cell. Local facilitation influences the actual mortality rate of the plants, i.e., the transition probability of a cell in the lattice changes from vegetated to empty, w_{10}:

$$w_{10} = m_{yr}(1-q_f)^{f_{yr}}$$

where m is the mortality rate *without* any local facilitation effect for a particular year.

The model was simulated on a one-dimensional lattice. Even though we had two-dimensional patch data (both length along the stream and width perpendicular to channel), we did not use width information. The width of the patch was influenced by watershed morphology, i.e., the width of the terrace etc., which is beyond the scope of this study. We used periodic boundary conditions to avoid edge effects. The periodic boundary condition means that cells along an edge of the lattice will have neighbors along the opposite edge. The total number of cells $N = 12{,}000$, and each cell is 1 meter long. The lattice was updated asynchronously in order to approximate a continuous-time process (Durrett and Levin 1994). During each simulation, cells were randomly selected for update, with one time step equaling N^2 individual cell updates, until a statistical steady state was reached. When the difference of total number of vegetated cells in two states that are 200 time steps apart (after updating 12,000 cells 200 times) is less than 100 m, we assumed it had reached a statistical steady state.

We used two metrics – patch size distribution and gap size distribution, to quantify model goodness-of-fit, and determine the best parameter set for each year. To process the observed data, for each year, we lined up the wetland patch distribution by their positions along the 12-km stream, which were divided evenly into 12,000 cells.

Each cell was labeled as positive (with plant) or negative (without plant). We calculated the observed patch-size and gap-size distribution to compare with model results. Each error was estimated by the mean square deviation between data and predicted values normalized by the data variance. Total error was the sum of the two errors. We explored the parameter space within reasonable ranges, and calculated the total error for each parameter combination. The combination with minimum total error was selected as the best-fit parameter set. Using this procedure, we determined the best-fit parameter set for each year. Macrophytes start to germinate in late January in Sycamore Creek, and peak at about survey time. The values of parameters determined by model fitting should be interpreted as the *average* over the entire growth period, integrating the effect of early spring floods (e.g., March).

ANALYSES

We correlated the values of parameters to two aspects of hydrological regime: (1) effective flood consequences and (2) total wetness. We created a metric called "Effective Flood Consequence (EFC; m^3s^{-1})" as following: $EFC = \sum_{k=1}^{k=n} \tau_k Dis_k$. τ is the month-specific constant of a flood, determined by the time it occurred. If a flood occurred in March, $\tau = 1$, and if it occurred in February, January, December, and November, $\tau = 0.8$, 0.6, 0.4, 0.2, respectively. *Dis* is the peak discharge (m^3s^{-1}) of a flood event, and *n* is the total number of winter floods before the survey date (Table 1). Later-occurring, larger, and more frequent floods constitute larger effective flood consequence. Index (2) total wetness indicates how much surface water was present in that year. The index was calculated as the cumulative mean daily discharge (m^3) from the beginning of the water year (October 1st) to the survey date (Fig. 2.1a). These two aspects of hydrology were not entirely independent (Fig. 2.1b). A flooding year is very likely to be a wet year; however, the wet-dry gradient is also influenced by evaporation, which is closely related to temperature. Effective flood consequence was designed to capture the differential effect of floods on plants occurring at different times.

We used a numerical procedure to detect the tendency for catastrophic transition and hysteresis in response to a gradual increase and a subsequent decrease with a hypothetical stressor (such as grazing), which could change the mortality rate, *m*. Mortality rate first increased from 0.01 to 0.9 by small steps of 0.02 (45 steps in total), and then decreased from 0.9 to 0.01 by steps of 0.02. After each of these increments, the model was simulated until they reached statistical steady state. Seady-state cover was saved for each step. In this paper, we use the term “forward shift” to mean shift from gravel to vegetated state, and “backward shift” to mean from vegetated to gravel state.

Using this numerical procedure, we explored the effect of local facilitation and template heterogeneity on the ecosystem’s response to external stress. To determine the effect of local facilitation, we created (i) models with and without local facilitation, and (ii) models with different degrees of local facilitation. To determine the effect of preexisting template heterogeneity, we constructed three different templates: (1) heterogeneous template: using the original water permanence gradient; (2) random template: created by randomizing the spatial distribution of the original water permanence gradient; and (3) homogeneous template: using the mean of the original water permanence as water permanence for all 12,000 cells. We used the model to analyze the system’s robustness, which considered two components: “resistance” to stress and perturbation and “recovery” from an undesirable state (Levin and Lubchenco 2008). Lastly, we analyzed the robustness of the system under actual hydrological conditions between 2009 and 2014. Specifically, “resistance” was quantified by the critical stress level (m^*), at which the system shifted from vegetated to gravel state, “recovery” was measured by the degree of system hysteresis, and “robustness” referred to both effects.

RESULTS

PATCH SIZE DISTRIBUTION

Few empirical phenomena obey power laws for all values of x in practice. More often the power law applies only for values greater than some minimum x_{min} (Clauset, Shalizi, and Newman 2009). In such cases we say that the *tail* of the distribution follows a power law. In this study, when we say patch size distribution follows power laws, we mean the tail of distribution. The patch size distribution fitted power-law distribution well for all six years (Fig. 2.2). However, we observed evident drops in the tail of the distribution in the two dry years, 2011 and 2012, indicating the absence of large-sized patches (Fig. 2.2). This was not likely to be caused by finite-size effect, since the largest patch size (200 – 300 m) was two orders of magnitudes smaller than the system size.

MODEL FIT AND PARAMETER INTERPRETATIONS

For the model-goodness of fit, the mean total error of six years was 0.1 (Table 2, Fig. 2.2). Model fit for 2010 patch size was not as good, with total error of 0.22, compared to the other five years, whose total error < 0.1. The model predicted patch sizes larger than observed for 2010 (Fig. 2.2).

We examined the correlation of the parameter values with both metrics of hydrology, i.e., the dry-wet gradient and the effective flood consequence. Consistently across all four parameters (*m*, ε, β, *f*), the effective flood consequence was a better explanatory variable (i.e., higher R^2 values).

Parameter *m* was year-specific mortality rate without local facilitation. *m* value was significantly negatively corrected with the effective flood consequence of each year (Fig. 2.3a). Drier and less flooded years were associated with higher *m*. ε was the year-specific probability that a propagule from the neighboring cells disperses, lands on an empty cell, and successfully geminates and establishes when *wp* = 1. ε was also negatively correlated with the effective flooding consequences, i.e., higher ε in years with less flooding years. For both *m* and ε, when the value of effective flood consequence kept increasing (i.e., in the year 2010), the value leveled off (Fig. 2.3a and b).

The effect of template heterogeneity can be influenced by two factors: plant responsiveness to the water permanence gradient and the *actual* template heterogeneity in a given year. We assumed that plant responsiveness to water permanence stays the same, because it is determined by plant physiology, which is not likely to change significantly at the time scale of our study. *Actual* template heterogeneity could however change from year to year, influenced by the annual precipitation and average temperature of the year (related to evaporation rate). The water permanence data collected in 1988-1989 used in the model could be used as a benchmark (hereafter, “benchmark water permanence gradient”), but it does not necessarily represent the actual water permanence gradient for the years we studied. In the model, the template effect is defined as: the difference in *potential* plant establishment rate at the wettest place (*wp* =100%) and at the driest place

(wp =13.64%) in the benchmark water permanence gradient, i.e., 1^{β}-$(13.64\%)^{\beta}$. By this definition, since the lowest water permanence in our system is not zero, the magnitude of the template effect can therefore be measured by β. The potential plant establishment rate at wp = 100% is 1. The actual establishment rate can be influenced by many variables and was modified by the year-specific parameter ε, i.e., $\varepsilon(wp)^{\beta}$.

When the value of 2010 was not considered, the effect size of template was significantly positively correlated with effective flood consequences, i.e., greater β values in more flooded years ("more flooded" means more frequent, larger, and later-occurring floods) (Fig. 2.3c). The template effect in 2010 was largest, but lower than the value predicted by the linear model (Fig. 2.3c). The relationship between template effect and water permanence varied among years (Fig. 2.4a). In dry years, the curve was concave (β <1), which suggested the establishment rate was most sensitive in the lower water permanence area. In wet years, the curve was convex ($\beta > 1$), indicating a higher sensitivity of plant establishment at high water permanence sections.

Local facilitation was quantified as the percent of reduction of mortality by the existence of plants in the neighboring cells, and can be measured by the value of f, i.e., greater f value, larger reduction in the mortality rate, and greater local facilitation effect. The strength of local facilitation (f) was also positively correlated with effective flooding consequences (Fig. 2.3d), i.e., stronger local facilitation in wetter years. When the effective flood consequence exceeded ~200 $m^3 s^{-1}$ (i.e., year 2010), the value of f leveled off (Fig. 2.3d). All f values were much lower than 1 (mean = 0.16), indicating a strong threshold effect associated with the effect of local facilitation as a function of q_f (percent of neighboring cells occupied by plants). The reduction was weak, until a threshold q_f

was reached, above which the mortality dropped drastically (Fig. 2.4b). Such threshold effect was more evident in drier years (i.e., smaller f value) (Fig. 2.4b).

CATASTROPHIC TRANSITIONS AND HYSTERESIS

The model exhibited alternative stable states and hysteresis when the external stress exerted on the system first increased and then decreased. Below we report the effect of template heterogeneity and local facilitation on these macroscopic properties of systems.

Effect of local facilitation – The effect of local facilitation was demonstrated by (i) comparing the behavior of models with different degrees of local facilitation (Fig. 2.5); and (ii) comparing the behavior of the models with and without local facilitation (Fig. 2.6). In the model without local facilitation, we first incrementally raised the level of stress (by increasing m) exerted on the system. The system shifted from vegetated to gravel state (i.e., backward shift) *abruptly* at m_b*. After including local facilitation, the transition from vegetated to gravel state became gradual (Fig. 2.6f) and occurred at a much higher m value (Fig. 2.6c). Stronger local facilitation was associated with greater m* (Fig. 2.5c). We then gradually reduced the level of stress. The system shifted from gravel back to vegetated state (i.e., forward shift) at m_f*, and m_f* was much lower than m_b*, exhibiting a hysteresis effect. Hysteresis was stronger in models with higher degree of local facilitation (Fig. 2.5b), and was significantly higher than models without local facilitation (Fig. 2.6b). Regardless of the degree of local facilitation, the shift from gravel to vegetated state was more abrupt than from vegetated to bare state (Fig. 2.5a, d, g).

Effect of template heterogeneity – The effect of template heterogeneity was demonstrated by comparing the behavior of models with heterogeneous, random, and homogeneous templates. The difference in the template did not have a noticeable influence in the backward shift, but it influenced the forward shift. The system with the homogeneous template showed strongest hysteresis effect, followed by the random template, and weakest hysteresis effect was found in the heterogeneous template (Fig. 2.7c). Additionally, the sensitivity of vegetation recovery to the decreases in m varied with templates: highest sensitivity in heterogeneous template and lowest in homogeneous template (Fig. 2.7c). The effect of template was irrelevant when local facilitation was absent, and was weak at low f (Fig. 2.7a and b). The effect of template heterogeneity was intensified when local facilitation was stronger (Fig. 2.7). Lastly, regardless of the construct of the template, the forward shift was much more abrupt than the backward shift (Fig. 2.7).

ROBUSTNESS OF THE SYSTEM UNDER REALISTIC HYDROLOGICAL CONDITIONS

We evaluated the system's robustness against hydrological condition over the six years (Fig. 2.8a). The system in the condition of 2011 and 2012 had the highest resistance to stress, with highest critical m (Fig. 2.8b). The system in the 2010 condition had the lowest resistance and highest hysteresis, indicating lowest system robustness (Fig. 2.8b and c). The system under the condition of 2009 had the lowest hysteresis effects, with very low resistance to perturbation.

DISCUSSION

EFFECT OF TEMPLATE HETEROGENEITY

Preexisting template heterogeneity exerted an important effect on plant distribution, but its effect varied with hydrology (effective flood consequence). Average and wet years showed stronger template effect on *potential* plant establishment. This could be explained by the changes in the actual water permanence gradient in years with different hydrological conditions. In average and wet years, water permanence is likely more heterogeneous than that in dry years. Dong et al. (2015) found stronger geomorphic template effect on macrophyte abundance in drier years. Their definition of template considers ε, i.e., the difference in the *actual* plant establishment in the driest and wettest places. Here, we found high ε value in dry years and low ε in wet years, consistent with findings by Dong et al. (2015). The specific mechanism of this effect varied among years. In wet years, plant establishment was most sensitive to water permanence in more saturated areas. In dry years, however, it was most sensitive at less saturated zones.

Template heterogeneity increased ecosystem robustness by decreasing the hysteresis and increasing the recovery rate (Fig. 2.7), making it more likely to shift back to the vegetated state. This is similar to the results of van Nes and Scheffer (2005), where they examined several ecosystem regime shift models, and suggested that spatial heterogeneity may weaken the tendency for large-scale catastrophic regime shifts. In reality, the ecosystem is much more heterogeneous than we considered in the model. Other than the heterogeneity of water permanence, the stream is characterized by alteration of constrained canyon and wide valley reaches at the broad scale, longitudinal arrangement of riffle-run-pool, and heterogeneity of the channel substrata. Microtopography, aspect, side channels, and distribution of upwelling zones that introduce the heterogeneity of nutrient availability all contribute to the heterogeneity of the physical template. As suggested by Hastings and Wysham (2010), most of these indicators (the 'general leading indicators') are unlikely to occur in a wide range of ecosystems because systems including nonlinearities and environmental variability might not exhibit smooth potentials, on which the general leading indicators depend. In our system, even after the 100-year flood in the winter of 2010, the system still maintained a wetland-gravel mosaic.

The forward shift to vegetated state was much more abrupt than the backward shift. This may come from differential sensitivity to mechanisms and parameters in the two shifts, and may have implications for the scale of the underlying mechanisms. In the forward shift, when cattle grazing was removed from the system, it led to large-scale regeneration of in-stream macrophytes in around 2000 within a very short period. This is similar to a large-scale pest outbreak. For instance, a rinder pest epidemic decimated most large herbivores in much of the South of Africa leading to large-scale regeneration of woodlands for a few decades (Dublin, Sinclair, and McGlade 1990). However, the back-shift (woodland destruction) happened only on local scales by humans and sometimes-high density of elephants, and has been proceeding gradually. In our system, as shown by the model, the spatial heterogeneity increased the tendency for the system to recover to the vegetated state. Spatial heterogeneity allows vegetation to sustain and spread locally, making the shift to gravel state very slow.

EFFECT OF LOCAL POSITIVE FEEDBACKS

Local facilitation, measured by the percent reduction of mortality induced by neighboring plants, increased nonlinearly when patch size expanded (Fig. 2.4b). The effect of local facilitation was stronger in average and wet years than it was in dry years (Fig. 2.3d). In the two dry years when we did the survey, we observed a considerable amount of plants died because of severe drought. This suggests that in dry years, local facilitation was overwhelmed by high mortality (Fig. 2.3a) due to lack of water. For average years, the system was not as dry, and local feedback could still effectively reduce plant mortality. But increasing wetness would not continue to increase the strength of local facilitation (Fig. 2.3d).

Local facilitation altered ecosystem resistance by increasing the threshold stress level (Fig. 2.5c). It also made the decline of vegetation much more gradual (Fig. 2.6f), because patches of vegetation are more easily maintained. Heffernan (2008) demonstrated at the *patch* scale, local facilitation increased the resilience of in-stream macrophytes to floods. Here, we showed that the internal feedbacks were also critical at the *whole ecosystem* level.

While local facilitation made the system less vulnerable to shifts to the gravel state, it enhanced the hysteresis effect (Fig. 2.7f). An analysis by Rietkerk et al. (2002) illustrates that alternative stable states between vegetated and bare land may occur over a range of precipitation levels. This is because in the absence of vegetation there is no local concentration of water, which is essential for plant survival in water-limited ecosystems. Once lost, vegetation patches do not easily recover, hence, the hysteresis effect. While external template heterogeneity can reduce hysteresis, self-organized heterogeneity generated by internal feedbacks by biota may in fact promote such phenomena (Rietkerk et al. 2004; van Nes and Scheffer 2005).

In our model, facilitation can be considered as a combination of physical and biological processes occurring in the local environment of a plant. It does not trigger effects farther away. This is different from the regular patterning found in many ecosystems. In those cases, the pattern arises from scale-dependent feedbacks, which not only includes local facilitation, but also long-ranged competition for limiting resource. Kéfi et al. (2011) suggested that in systems totally determined by local positive feedbacks, patch size distribution can be used as a signal for ecosystem phase transition. With an increasing level of stress (e.g., increased grazing or decreased precipitation), patch size distribution shifts from power-law, to truncated power-law, then to exponential distribution. Therefore, it is argued that patch size distribution can be used to assess ecosystem health, or equivalently, the level of stress exerted on it. The application of this theory is probably limited. We found that wetland patches size distributions in the two driest years were characterized by evident exponential drop (Fig. 2.2). This is probably caused by the physical constraints imposed by the template heterogeneity – the expansion of patch size is interrupted in places where water permanence is too low to support plants. While mathematical models could show clear evidence of the association between changes in patch size distribution and stress level exerted on ecosystems, real ecosystems are commonly spatially heterogeneous, and in such ecosystem abrupt changes are probably much more complex.

TEMPORAL VARIABILITY AND ECOSYSTEM CHANGES

Internal feedbacks and external environment together shape biological patchiness in an ecosystem (Sheffer et al. 2013). Both template heterogeneity and the environmental temporal variability constitute the external environment, and influence biological patchiness and ecosystem change. Template heterogeneity interacts with internal feedbacks to influence ecosystem resilience (Bonachela et al. 2015). Exogenous temporal variability (e.g., disturbances and environmental changes) could either cause a direct change in system state or trigger changes in the internal feedbacks that are critical to ecosystem resilience (Dent, Cumming, and Carpenter 2002; Turnbull et al. 2012). Temporal variability not only interacts with internal feedbacks, it also alters template heterogeneity, and consequently, template - internal feedback interactions. The dynamic nature of the underlying drivers and their interactions have been rarely studied, but could be important in predicting ecosystem responses to disturbances or stress. Changes in the composition and relative strength of the drivers could alter broad-scale ecosystem properties, such as the ability to resist external stress and its recovery capacity from an undesirable state (Fig. 2.8). One of the basic questions in ecology is to understand how spatial patterns influence ecosystem properties, such as resource retention (Ludwig et al. 2007). For other ecosystem properties, such as ecosystem resilience, our research indicates that only knowing the spatial patterns is not enough. It is essential to also understand whether and how ecosystem resilience depends on underlying pattern-generating processes, and how these processes vary over time.

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TABLE 2.1. The timing and peak discharge of winter flood events in the six-year study period (2009 – 2014). Data were obtained from the monitoring gauge USGS #09510200 Sycamore Creek near Fort McDowell, AZ, located about 1 km downstream of the surveyed 12-km section of the stream.

Year	**Peak discharge ($m^3 s^{-1}$)**	**Flood dates**	**Days to survey**
2009	29.2	Nov-28	199
	33.1	Dec-18	180
	109.3	Dec-26	171
	87.8	Feb-10	125
2010	438.9	Jan-21	145
	68.2	Mar-08	99
2011	27.6	Dec-30	168
	0.85	Mar-02	106
2012	2.41	Dec-14	185
2013	9.26	Dec-16	182
	72.5	Jan-28	139
	36.8	Mar-09	98
2014	72.5	Mar-02	105

TABLE 2.2. Year-specific model goodness-of-fit (total error) and parameter values used in the best-fit model for each year

Parameters	2009	2010	2011	2012	2013	2014
m	0.18	0.16	0.32	0.36	0.26	0.28
ε	0.61	0.59	0.86	0.86	0.78	0.78
β	1.52	2.00	0.50	0.30	1.00	0.90
f	0.20	0.22	0.08	0.10	0.16	0.22
totErr	0.098	0.222	0.063	0.088	0.067	0.065

FIGURE 2.1. (a) Cumulative mean daily discharge (from Oct 1st of the previous year to the survey date) of the six-year study period labeled with wetland cover in the corresponding year. Each abrupt increase in discharge represents a flood event. (b) The correlation between effective flood consequence and cumulative average daily discharge. Different years are labeled with different colors.

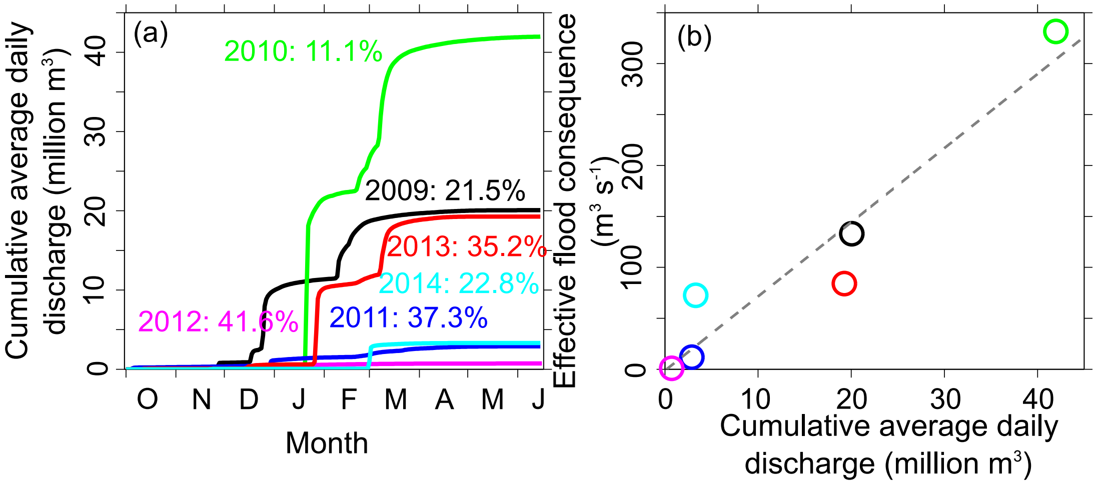


FIGURE 2.2. Model goodness-of-fit for patch size and gap size distribution between 2009 and 2014. The observed patch size distributions were fitted with power-law distributions (the red dashed line), with γ being the exponent. *a* on the x-axis is a given patch size, and y axis is the number of patches greater than the patch size *a* in the system.

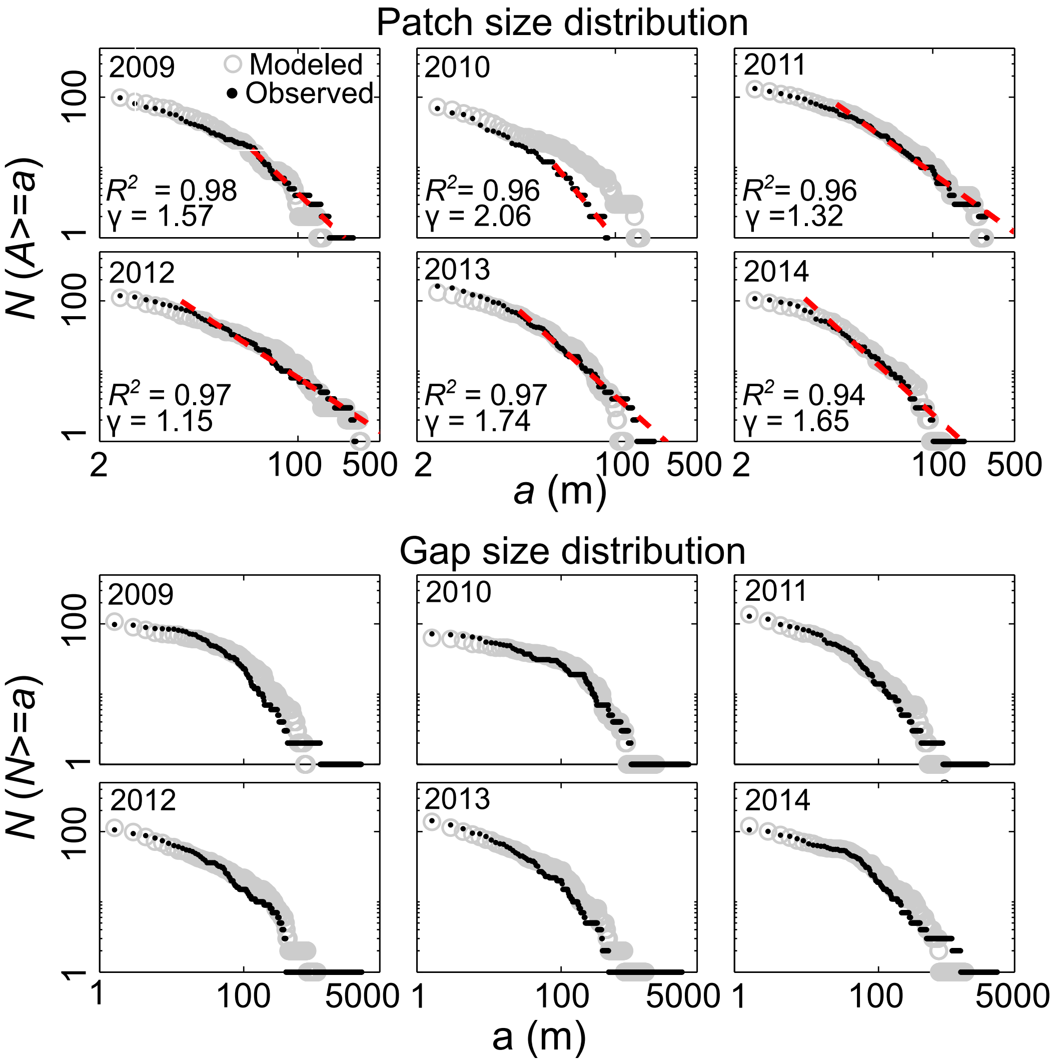


FIGURE 2.3. The relationship between the parameter values (*m*, *f*, β, ε) and the effective flood consequences. Linear regression model fitted well (black dashed line, provided with the R^2 value), when the parameter values for the year 2010 (labeled with red cross) were not included. After the parameter value of the year 2010 was considered, the relationships were not linear (blue line).

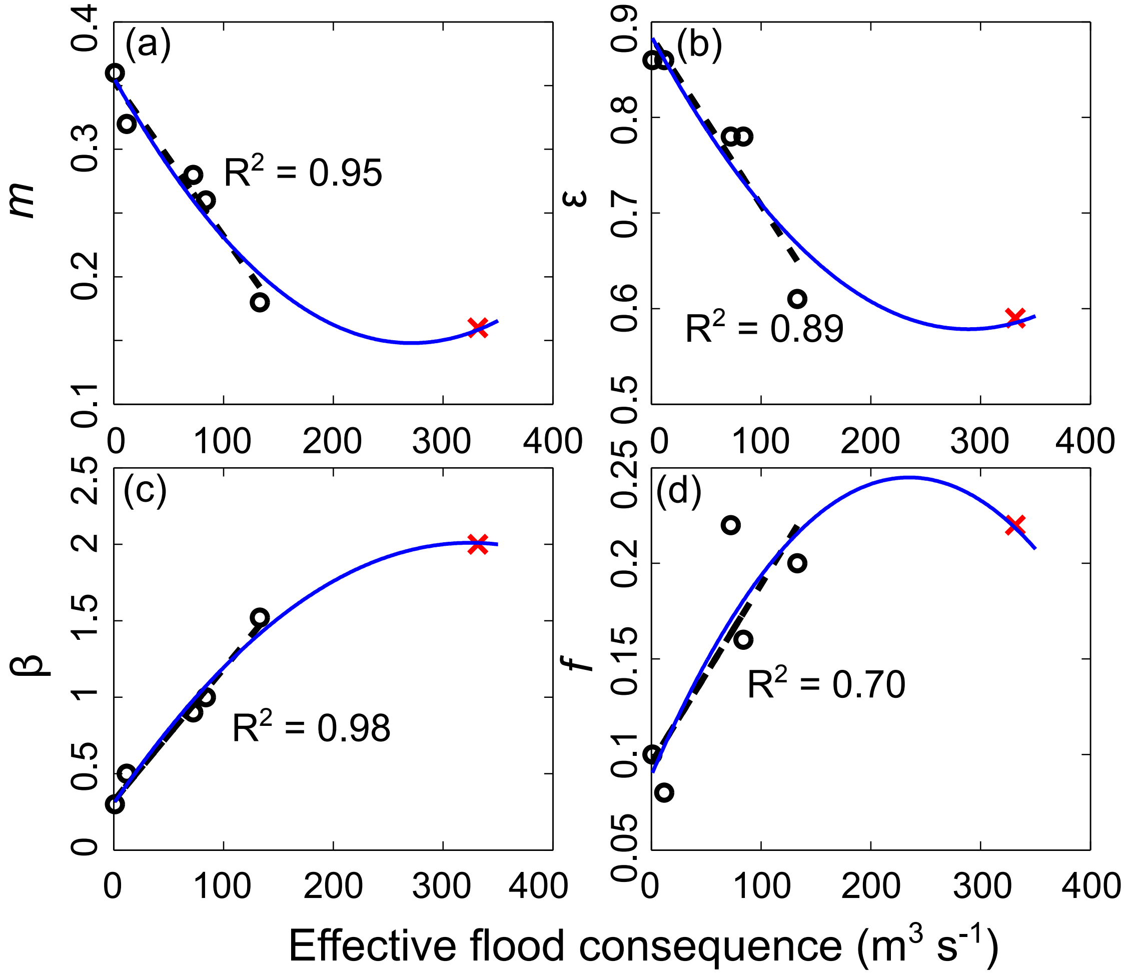


FIGURE 2.4. (a) The effect of template on potential establishment rate as a function of water permanence gradient in six years. The area to the right of the black dashed line denotes the range of average water permanence observed and used in the model, i.e., 13.6% to 100%. For each year, the difference between the value on y-axis when *wp* = 13.6% and when *wp* = 100% represents the template effect of that year. (b) The effect of local facilitation as a function of percent patch cover in the neighboring cells (upstream 2m and downstream 2m) in each year. In the model, the neighbor size = 4 meter. Therefore, the actual values of *q* were discrete, and equaled to [0, 0.25, 0.5, 0.75, 1], labeled by the open circles on the continuous function.

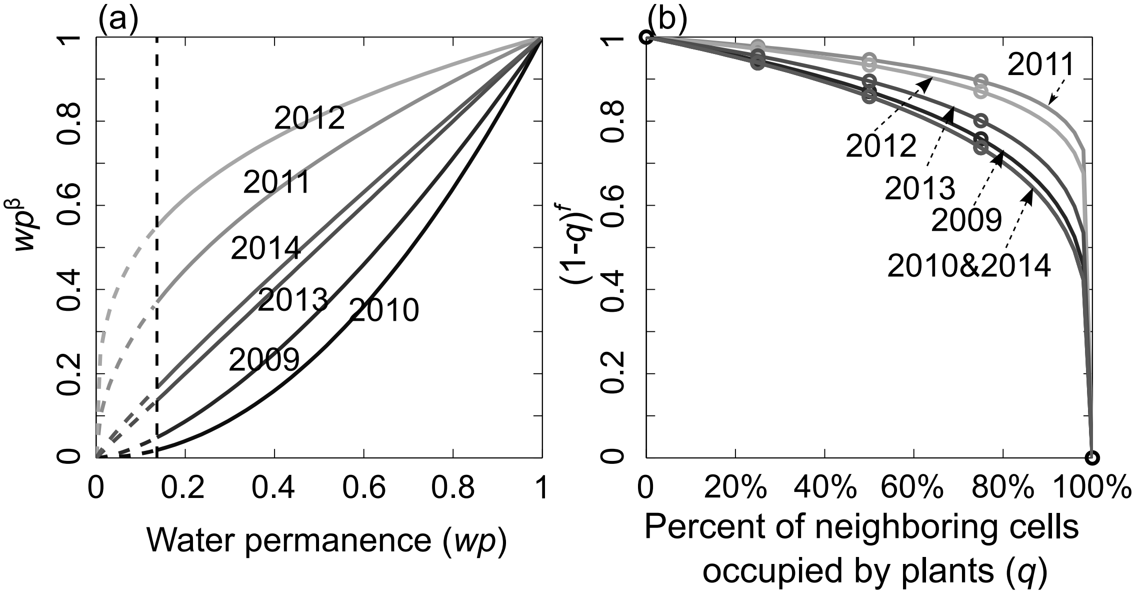


FIGURE 2.5. The effect of local facilitation on catastrophic shifts and hysteresis. Arrows in (a), (d) and (g) mean the progressive changes of vegetation cover when *m* first increased from 0.01 to 0.95, and then gradually decreased to 0.01. Hysteresis in (b) and (i) were quantified as the difference between the *m* value at which the system arrived at the gravel state when *m* increased, and the *m* value when the system started to recover to vegetated state when *m* decreased. *m** in (c) and (h) is the value of *m* when the system shifts from vegetated state to gravel state as *m* increased from 0.01. "Graduality of recovery" in (e) was measured as the difference between the *m* value when the system started to recover from gravel state and when it reached 100% vegetation cover, as *m* increased. "Graduality of decline" in (f) was measured as the difference between the *m* value when the vegetation began to decline and when all the vegetation disappeared from the system, as *m* increased, For all the simulations, $\beta = 0.90$.

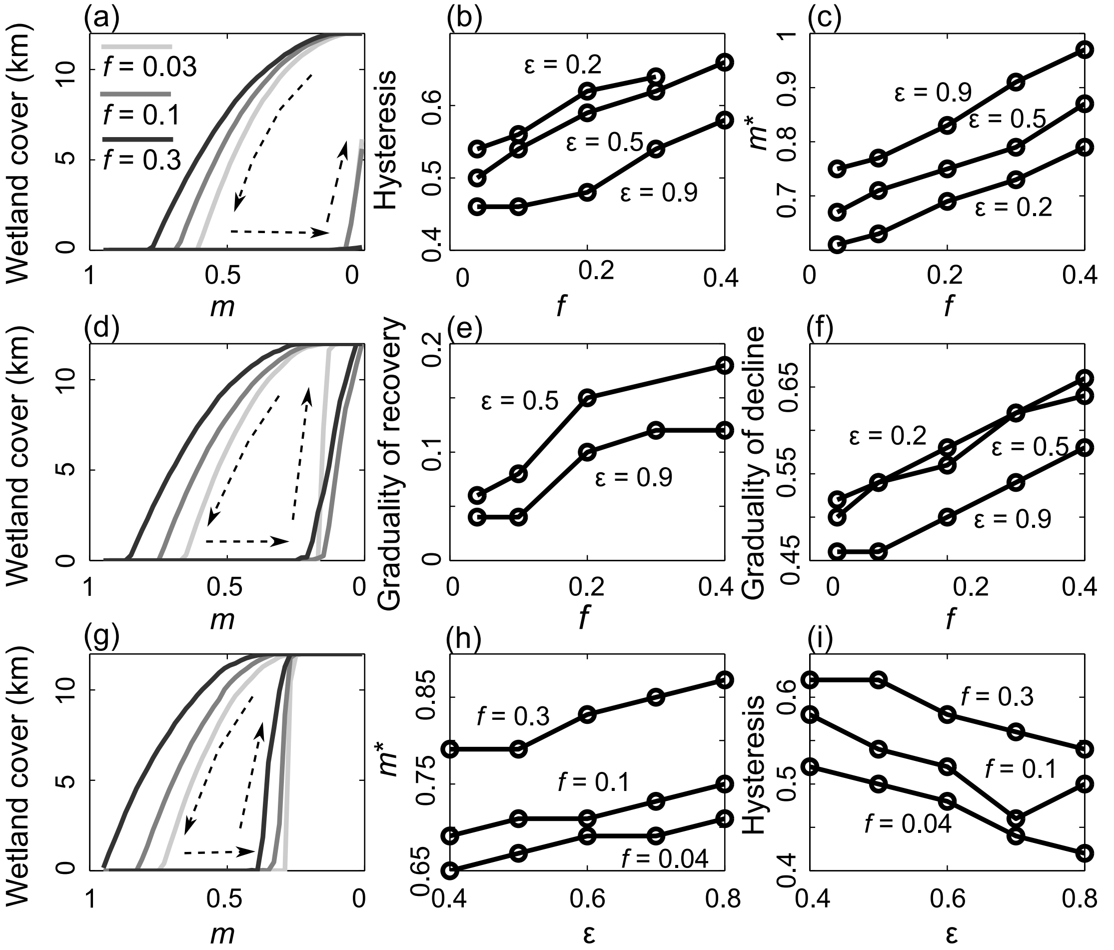


FIGURE 2.6. The effect of local facilitation on ecosystem regime shifts and hysteresis demonstrated with the result of the model with and without local facilitation (self organization). The results of model *without* local facilitation are presented in red. The description of panels and figure legends are the same as in Figure 2.5.

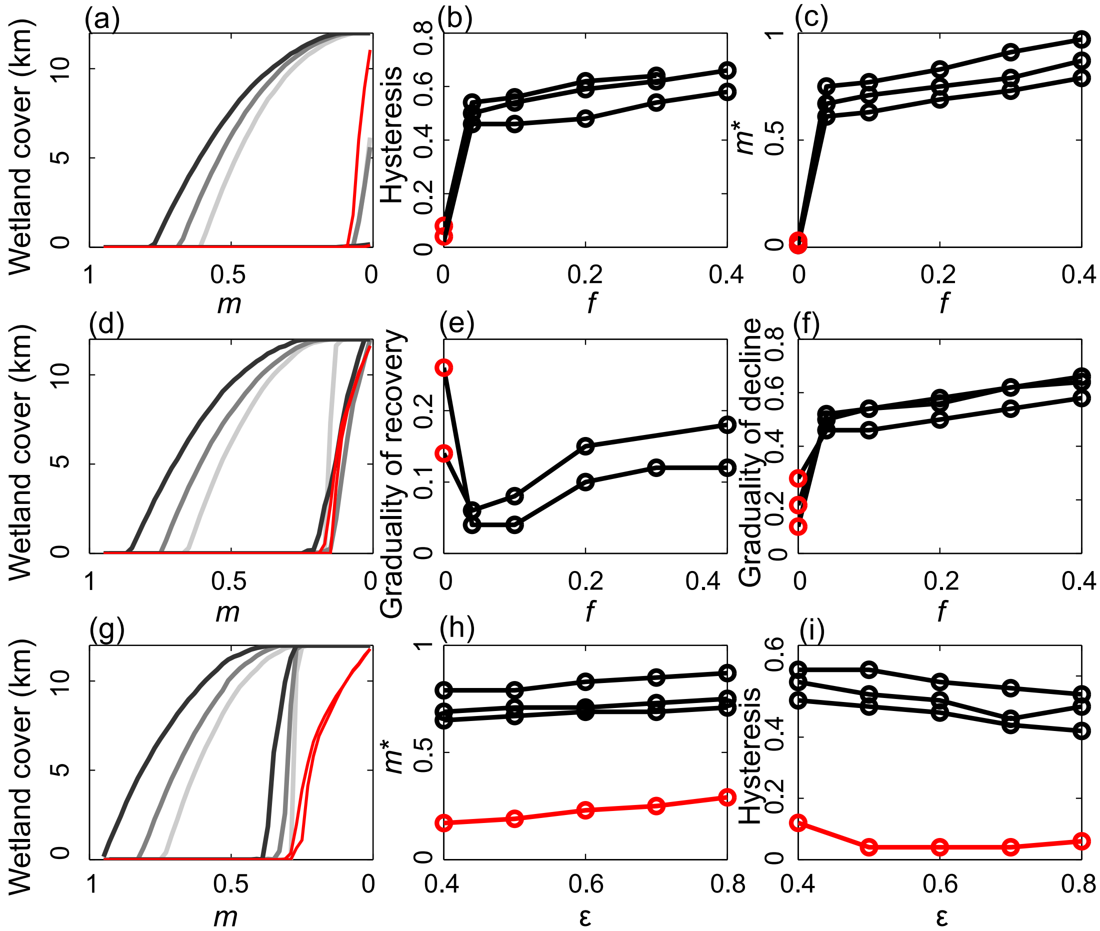


FIGURE 2.7. The effect of template heterogeneity (homogeneous, random, and heterogeneous template) on catastrophic shifts and hysteresis, when there is no local facilitation (a) and when local facilitation was present (*f* = 0.04, 0.1) (b and c). β = 0.9 and ε = 0.7 were fixed for all the simulations. The arrows illustrate hysteresis by showing that starting from *m* = 0.01 and progressively increasing *m*, a transition to gravel state occurred. If we then decrease *m* to its original value, the transition back to vegetated state will not take place until a much smaller *m* is reached, i.e., hysteresis. The *m* value at which the system recovers from gravel state differs among systems with different templates, and such difference among templates increases with *f* value.

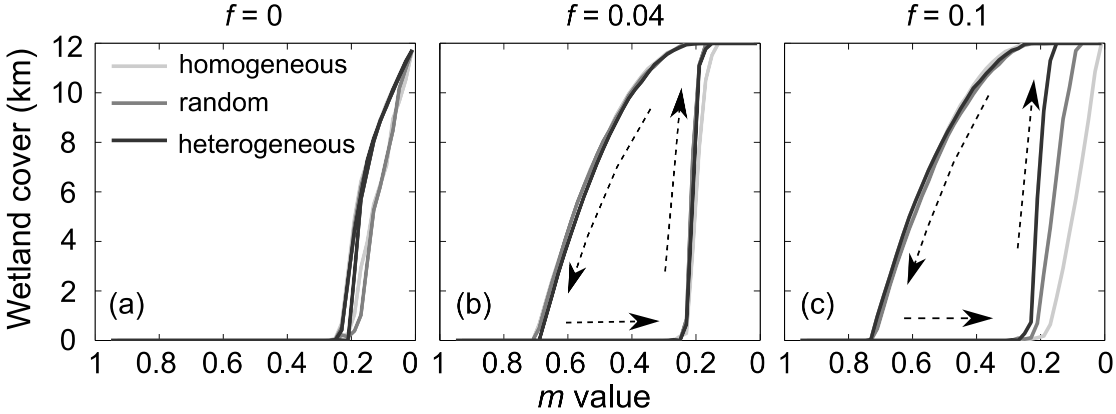
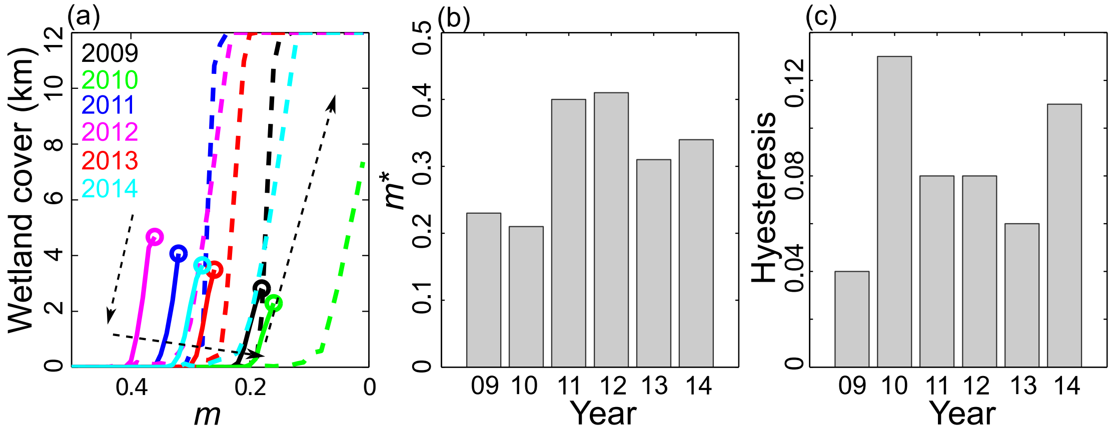


FIGURE 2.8. The robustness of the system under different hydrological conditions between 2009 and 2014. (a) Model started at the initial condition with the vegetation cover of a given year, gradually increased stress level by increasing *m*, until it reached gravel state. Then the model decreases the stress level, until the system reaches the absorbing state with 100% vegetation cover; (b) *m** - the critical *m* value when the system reached gravel state when external stress increased for each year; and (c) hysteresis effect (the difference in *m* value when the system reached gravel state and when the system started to recover) in each year.



CHAPTER 3

DISENTANGLING INFLUENCES OF GEOMORPHOLOGY, BIOLOGY, AND SELF-ORGANIZATION ON STREAM NUTRIENT PATTERNS

ABSTRACT

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 spatio-temporal scales at which these processes operate hinder a precise understanding of how this spatial heterogeneity is generated and maintained through time. Our goal was to quantify the spatial structure and the relative importance of three categories of drivers: physical template, biological processes, and self-organization. Since stream flow is unidirectional, time-series analyses can be applied to analyze spatial longitudinal data along the channel, allowing quantification of the independent roles of the three drivers. Here we revisited Sycamore Creek, an intermittent desert stream in Arizona (USA) that experienced an ecosystem shift (from a gravel/algae- to a vascular plant-dominated system) in 2000 as a consequence of cattle removal. We conducted high-resolution spatial nutrient surveys in surface water along a 10-km stretch of the stream, over four visits spanning 18 years (1995 – 2013) that represent different successional stages and pre- *vs.* post- wetland states. Wavelet transform analyses were used to identify the spatial scales of the underlying drivers of variation in nutrient patterns and their variation over ecosystem successional time. Subsequently, Multivariate Autoregressive State-Space models were fitted to quantify the influences of the three drivers. Contrary to our expectations, we did not find a direct effect of wetland establishment on nutrient spatial patterns. Wetlands, however, had a significant indirect effect on nutrient patterns by modifying the vertical hydrological gradient, which in turn altered surface water–groundwater exchange. Overall, geomorphic influences were about one order of magnitude higher than biological influences. Self-organization, manifested through feedbacks between biotic patch configuration and nutrient concentration, increased in strength over ecosystem successional time. To our knowledge, this is the first study to disentangle the relative influences and interactions among these drivers and their changes over successional time. This study advances the notion that the mechanisms causing spatial heterogeneity in ecosystems are complex; hence, cross-scale interactions and feedbacks among system elements should be considered when attempting to infer underlying processes from observed patterns.

Keywords: desert stream; ecosystem succession; geomorphology; multi-scaled drivers; nutrients; spatial heterogeneity; self-organization; spatial scales; state-space models; wavelets; wetland.

INTRODUCTION

The relationship between pattern and process is a long-standing topic of investigation in ecology (Watt 1947, Turner 1989, Turner 2005, Gaston and Blackburn 2008). One of the fundamental questions underlying the study of pattern-process relationships is, to what extent are patterns determined by local conditions (e.g., soil and climate in terrestrial ecosystems; salinity and flow in oceans) and to what extent are they self-organized (Levin 1999)? A major challenge to fully understanding spatial heterogeneity is that multiple factors and processes, operating across a range of spatial scales, contribute to it, and their relative contributions may change over time. The multiplicity of kinds of factors and scales of influence hinders quantification of the unique influence of each driver (O'Neill et al. 1986, Levin 1992, Pickett and Cadenasso 1995, Chave 2013, Nash et al. 2014). In this study, we used patterns of nutrient concentration in a desert stream across different successional stages as a model system to disentangle the influence of three basic drivers of spatial heterogeneity: physical template, biological processes, and self-organization (Mcintyre et al. 2011, Schoelynck et al. 2012, Stella et al. 2013; Stewart et al. 2014, Bonachela et al. 2015). We used novel quantitative approaches to examine the unique influences of these drivers, the spatial scales at which they operate, and their changes over ecosystem successional time.

Rivers and streams are open ecosystems. Stream surface-water chemistry is highly influenced by the physical environment (Poole 2002) and by the other subsystems to which surface water is connected, both longitudinally, vertically, and laterally (Dent et al. 2001, Bencala et al. 2011, Zarnetske et al. 2011). Longitudinally, tributary junctions can bring water with different chemistry into a stream. Vertically, the hyporheic zone is an interface zone connecting surface water to the groundwater aquifer (Stanford and Ward 1993, Boulton et al. 1998). Subsurface water has a distinct biogeochemical signature and may alter that of stream water (Jones and Holmes 1996, Hill et al., 1998, Dent et al. 2001). The locations of upwelling and downwelling zones are determined by geomorphic features at multiple spatial scales. They can be influenced by broad-scale catchment geomorphology and local bed surface topology, such as changes in background groundwater discharge rate, sediment hydraulic conductivity, channel slope, depth to bedrock, and depth of alluvium (Thibodeaux and Boyle 1987, Gooseff et al. 2006, Hester and Doyle 2008). In the lateral dimension, streams are hydrologically connected to the riparian zone, the floodplain, and the upland portions of the catchment (Martí et al. 2000, Krause et al. 2007, Bencala et al. 2011). Riparian zones represent 'nutrient filters,' removing various chemical constituents from water as it moves from the upland catchment to the stream (Lowrance et al. 1984, Daniels and Gilliam 1996, Dosskey et al. 2010). At smaller scales, stream sinuosity can result in exchanges between the stream and its floodplain or parafluvial zone. Collectively, connections among subsystems in the riverine landscape form the physical template that influences patterns of nutrients in stream surface water.

Stream nutrients are not only influenced by the physical subsystems connecting to the surface water, but are also modified by in-stream biological processes (Peterson et al. 2001, Mulholland and Webster 2010). Many studies have documented the longitudinal declines in nutrient concentration (Hill 1979, Peterson et al. 2001, Tank et al. 2008). Algal uptake rates vary with nutrient availability, light, water velocity, and temperature, and may represent a primary pathway of nitrogen retention (e.g., Grimm 1987, Hall and

Tank 2003, Johnson et al. 2013). In-stream wetland patches are more complex in their relation to stream nutrient concentrations. During the growing season, a substantial amount of nitrogen (N) and phosphorus (P) can be taken up by vascular plants from sediments (Schulz et al. 2003, Riis et al. 2012). However, comparisons of stream reaches with different macrophyte cover showed that macrophytes have limited influence on water column nutrient concentration (either N or P) (O'Brien et al. 2014). Macrophytes may affect nutrient dynamics over a longer term, by locking up nutrients in biomass and extending the nutrient turnover period compared to algae (Simon et al. 2007, Riis et al. 2012). In-stream macrophytes alter the accumulation of fine sediments and reduce vertical hydrological exchange (Madsen et al. 2001), which in turn could dampen the biogeochemical signature of groundwater on surface water. Nitrogen fixation (i.e. N_2 to organic N) is another potentially important biological process contributing to variation in surface-water N concentration, whose influence varies spatially and seasonally (reviewed by Marcarelli et al. 2008). Because biological processes are themselves controlled by different factors that vary spatially, they may exert significant influences on the spatial heterogeneity of nutrient concentrations in streams.

A third class of driver is self-organization. Spatial heterogeneity can emerge even in homogeneous landscapes via self-organization (Levin 1999), when local feedbacks between resources and biological communities lead to biological patchiness. Self-organized biological patterns have been studied extensively in the last decade in water-limited systems (e.g., Valentin et al. 1999, Rietkerk et al. 2004, Schmitz 2010, Deblauwe et al. 2011). Mathematical models (e.g., Lefever and Lejeune 1997, Rietkerk et al. 2002, Borgogno et al. 2009) and field observations (e.g., Valentin et al. 1999, Becker and

Getzin 2000, Deblauwe et al. 2011) show that plants can form regular patterning, driven by the local feedbacks between biomass and the limiting resource, water. In streams, nutrients (nitrogen and phosphorus) also represent a limiting resource (Grimm and Fisher 1986, Tank and Dodds 2003, Johnson et al. 2009, Hill et al. 2010). Elevated stream nutrient concentrations at upwelling zones induce the formation of algal patches that take up those nutrients (Valett et al. 1994), resulting in low nutrient concentrations downstream. Low stream NO_3^- simulates N-fixing Cyanobacteria, which may raise NO_3^- concentrations further downstream, inducing the development of algal patches (Henry and Fisher 2003). A better understanding of the processes that influence spatial patterns in nutrient concentrations should consider the effect of self-organized patch configuration (Fisher et al. 1998). However, to our knowledge, no studies have yet investigated self-organization and its potential significance for nutrient patterns.

On top of these three drivers, the formation of spatial heterogeneity in desert streams is intimately dependent on the hydrological regime, which could be regarded as an overriding variable. In desert streams after winter floods, surface flow declines rapidly as a result of high rates of evapotranspiration (Stanley et al. 1997). The reduction in flow accentuates the effect of both geomorphic and biological processes on the spatial heterogeneity of nutrients. At a multi-year time scale, desert streams experience high interannual hydrological variability. Hydrological regime, which determines the stream-upland connection, affects the nutrient inputs from the catchment and thereby sets a nutrient limitation ‘status’ (Grimm and Fisher 1992).

Most of the processes and variables described above have been studied relatively well in isolation. However, little is known about how they collectively influence spatial heterogeneity, and even less is known about how their relative contributions may change over time, responding to the changing environment (e.g., hydrology as described above) and successional stages. Classical successional theory does not address changes in spatial heterogeneity over time (e.g., Odum 1969, Vitousek and Reiners 1975). The first real acknowledgement of spatial heterogeneity in the context of ecosystem succession dates back to Bormann and Likens (1979), the idea of "shifting-mosaic steady state". Although studies on how ecosystem spatial heterogeneity changes over successional time are limited (but see Armesto et al. 1991, Cadenasso et al. 2006), results are intriguing. For instance, Cain et al. (1999) suggested that nutrient spatial heterogeneity in dunes decreased during succession. In contrast, Dent and Grimm (1999) observed increasing nutrient heterogeneity over post-flood succession in Sycamore Creek. Understanding the cause of such contrasting patterns likely requires understanding how the contributions of the underlying drivers change over successional time.

Our study capitalizes on prior surveys of nutrient heterogeneity over successional time in Sycamore Creek, Arizona (Dent and Grimm 1999). Those surveys were done during the 1990's, when gravel substrates and benthic algae predominated and wetland plants were scarce. Since 2000, when the U.S. Forest Service eliminated cattle grazing from the study area, the abundance of wetland plants in the active channel of Sycamore Creek increased dramatically (Heffernan 2008). By 2013, around 40% of the 10-km section surveyed was covered by patchily distributed wetland plants (mainly *Equisetum laevigatum*, *Paspalum distichum*, *Schoenoplectus americanus*, *Typha domingensis*, and *Juncus torreyi*). In May 2013, we repeated Dent and Grimm's (1999) survey in the same 10-km stream reach. Collectively, the resulting data represent both different successional stages (early, mid, and late succession) and the two ecosystem states (before vs. after wetland establishment) that have been observed in this system in the past two decades. Here, we addressed the general questions of how observed nutrient patterns are linked to underlying processes, and how the unique influences of their drivers, hierarchies, and feedbacks, change over ecosystem successional time. In particular, we asked: (Q1) are spatial patterns of nutrients influenced by wetland establishment? (Q2) What spatial patterns, in terms of patch size and scales, emerge during succession? (Q3) What is the relative importance of physical and biological drivers, and what role does self-organization play (if any) in influencing these nutrient patterns? Finally, (Q4) how do the underlying processes and the manifested patterns change over successional time?

We examined these questions in a novel way, by applying time-series methods (wavelets analysis and Multivariate Autoregressive State-Space [MARSS] models) to evenly spaced longitudinal data. Wavelets allowed us to precisely describe the multi-scaled variation in nutrient concentration, hence the spatial scales at which the underlying processes operate. In turn, MARSS models allowed us to quantify the processes that shape nutrient patterns, and therefore any changes in the identity, direction, and extent to which these drivers influence nutrient concentration, both over successional time and before and after wetland establishment (i.e., 1990s vs. 2013). Collectively, these methods allow us to integrate different types of data (nutrients, geomorphic, biological) spanning a range of spatial and temporal scales. Overall, they allow us to relate observed nutrient spatial patterns to the underlying processes causing them in an explicit, quantitative way (Fig. 3.1).

METHODS

STUDY SITE

This study was carried out in Sycamore Creek, Arizona, a tributary of the Verde River located 32 km northeast of Phoenix, Arizona (USA). The stream drains a catchment of 505 km^2 that ranges in elevation between 427 and 2164 m. The study site is a 10-km stretch of stream ranging from 600 m to 700 m in elevation. Stream substrata consist of coarse sand and gravel that can be up to several meters deep in runs, and boulders and cobble in riffles, with limited reaches of exposed bedrock. The long-term mean annual precipitation varies with elevation from 39 cm yr^{-1} to 51 cm yr^{-1} but varies greatly among years (ranging from 2 cm yr^{-1} to 92 cm yr^{-1}, with a coefficient of variation of 35% over the past 100 years). Precipitation is bimodally distributed 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 dry out completely, especially in summer (Stanley et al. 1997). Nitrogen limits primary production during baseflow; phosphorus limitation has not been demonstrated and is unlikely, with long-term average concentration always exceeding 20 μg L^{-1} (Grimm and Fisher 1986).

SAMPLE COLLECTION AND ANALYSIS

The nutrient data used in this study were from two sources: (1) existing data (Dent and Grimm 1999); and (2) new data collected on May 31st, 2013 in the same section of Sycamore Creek (2.5 months after a March 8th flood, with a peak discharge of 36.8 m^3 s^{-1}) (Fig. 3.2). We replicated field techniques from Dent and Grimm (1999), collecting duplicate samples of surface water in 60-ml tubes from the stream's thalweg. Samples were taken at points 25 m apart, and were collected as simultaneously as possible by 14 people arrayed along the 10-km stream segment. Each person walked upstream as they collected samples over ~700 m. All samples were filtered in the field within two hours, between 8am and 10am. Locations at each 700 m overlap point were sampled both at beginning and end of the collection period to check for diel variation in nutrient concentrations. Magnitude of diel change was <10% of the range of concentrations observed, so we were confident that the spatial patterns reported here were not confounded by temporal variation.

Filtered water samples were frozen until analysis. All water samples were analyzed within three weeks for NO_3^--N (hereafter, NO_3^-, but concentration is reported as mass N per volume), soluble reactive phosphorus (SRP; concentration reported as mass P per volume), and chloride (Cl^-). NO_3^- and SRP were determined using a Latchat QC8000 Flow Injection Analyzer. We measured NO_3^- using the cadmium-reduction method (Solorzano 1969), and SRP using the molybdate blue method (Wood 1967). Cl^- was also determined on the Lachat QC8000.

We then organized and re-analyzed the data collected from the same 10-km segment of Sycamore Creek studied by Dent and Grimm (1999) in the 1990s. They did surveys in three stages of post-flood succession, on May 22nd 1995, 2.5 months after a March 6th, 1995 flood (peak discharge was 113 $m^3 s^{-1}$), on December 7th 1995, 9 months after the same flood, and on March 17th 1997, 2 weeks after a flood on 28 February 1997 flood (peak discharge = 83 $m^3 s^{-1}$) (Fig. 3.2). These dates were representative of middle, late, and early successional conditions in the stream, respectively. Data collected in 2013 corresponded to mid-succession, comparable to May 1995 data; however, the peak discharge of the flood in March 1995 was three times larger than that in May 2013. Moreover, there was a sustained relatively high flow in 1995 before the May survey (the mean daily discharged measured at the USGS gauge #09510200 1.5 km downstream of the survey section was 0.45 $m^3 s^{-1}$ on the survey day in 1995), while in 2013, discharge dropped to 0.45 $m^3 s^{-1}$ as early as March 28th, and declined to zero on May 21st. As a result, although both surveys were conducted 2.5 months after the last flood, the 2013 survey was at a mid-to-late successional stage. While Dent and Grimm (1999) measured conductivity, in 2013 we analyzed Cl^- instead to represent a biologically inert parameter.

ANCILLARY DATA

Two types of supplementary data were collected. (1) Biological data: wetland, algal, and Cyanobacteria distribution data were collected from field surveys in 2013. The spatial distribution of algae and Cyanobacteria (presence-absence) was surveyed one week before the water chemistry survey. Spatial distribution of wetland plants was determined two weeks after the water chemistry survey. We surveyed the location of wetland patches along the 10-km study reach, and recorded species identities and patch sizes of wetland plants. In late succession in 1995, Dent and Grimm (1999) recorded presence-absence of filamentous algae and N fixers at each point where water samples were taken. (2) Physical condition: water permanence data were provided by E. Stanley (personal communication; University of Wisconsin). From May 1988 to February 1990 (22 consecutive months) Stanley surveyed the same 10-km of stream, and recorded the spatial extent and average depth of water monthly. We calculated water permanence (percentage of time with surface water present within the 22 month study period) along the stream from these survey data. Upwelling locations along the 10-km stretch of the stream were identified by Dent and Grimm (2001) using vertical hydrological gradient measurements in the field. We recorded reach types (i.e., riffle, run, and pool) in the survey in 2013, as did Dent and Grimm (2001).

STATISTICAL METHODS

Wavelet analysis

To decompose the spatial scales of nutrient distribution on sampling data, we performed wavelet analyses. Wavelets are a time-frequency decomposition of non-stationary, aperiodic, and noisy signals (Cazelles et al. 2008). Although primarily applied to time series, wavelets have also been applied to the analysis of spatial patterns (e.g., Rosenberg 2004, Mi et al. 2005, Keitt and Urban 2005). Our intent in using wavelet analyses in this study was to reveal the spectral structure of the longitudinal nutrient variation, which would inform us about (1) the spatial scales of the underlying processes, and (2) the specific locations where these processes occurred. We used this information to infer the possible environmental drivers underlying spatial variation. A full description of the wavelet technique can be found elsewhere (Torrence and Compo 1998).

Wavelet analyses were applied on all 12 nutrient series (i.e., three nutrient types × four surveys). After obtaining the corresponding wavelet spectra, we compared them using a multivariate method that defines an orthonormal basis maximizing the mutual covariance for each pair of wavelet spectra (full description of the method can be found at Rouyer et al. (2008). 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, Cl^-] and successional stages), to evaluate the relative importance of the main factors (similar to Rouyer et al. 2008). Wavelet analyses were carried out using the ‘biwavelet’ package (Gouhier and Grinsted 2013) in R (R Development Core Team 2015).

MARSS model

To quantify the relationships between the putative drivers (i.e., covariates) and nutrient heterogeneity, and to determine the relative importance of these drivers across different successional stages and ecosystem states, we used multivariate autoregressive (MAR) models. In ecology, MAR models have been mainly employed to quantify the effects of environmental drivers on population growth rates and community dynamics (reviewed by Hampton et al. 2013). MAR models rely on theory about the patterns of temporal correlation that emerge from environmental drivers and species interactions (Ives et al. 2003), and use these patterns to estimate the effects of external drivers and internal interactions on community dynamics. Moreover, state-space versions of MAR models (i.e., MARSS models) allow inclusion of observation error. Parsing out observation (i.e. non-process) from process error is important in ecological applications because ignoring observation error can drastically change inferences about underlying processes (Knape and de Valpine 2012). Therefore, in our case MARSS allowed us to partition the variation in nutrient concentration data due to measurement error from the variation due to true changes in concentration. We fitted MARSS models using the 'MARSS' R-package (Holmes et al. 2014), which provides support for fitting MARSS models with covariates to multivariate data (here, nutrient concentration data downstream) via maximum likelihood, using an Expectation-Maximization algorithm.

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

$$x_{i,s} = Bx_{i,s-1} + \sum_{k=1}^{k_{yr}} C_{i,k} c_{k,s} + w_{i,s}; w_{i,s} \sim MVN(0, Q_s) \quad (Eq.1)$$

$$y_{i,s} = Zx_{i,s} + v_{i,s}; v_{i,s} \sim MVN(0, R_s) \quad (Eq.2)$$

Data enter the model as y (with $y_{i,s}$ being the log-transformed concentration of nutrient type i at sampling site s) and as $c_{k,s}$ (the covariates k at sampling point s; the total number of covariates included in MARSS models for different years varied, as detailed in the following paragraph. $y_{i,s}$ is a linear function of the "hidden" or true nutrient concentration $x_{i,s}$. The effect of exogenous variables (i.e., the covariates), such as physical drivers and biological processes, on concentration changes, was included in c_s. Values of $C_{i,k}$ are coefficients that indicate the effect of covariate k on the concentration of nutrient i. $\mathbf{B}$ is a 3×3 interaction matrix that models the effect of nutrients on each other (off-diagonal values) and on itself (diagonal values). $w_{i,s}$ is the process error, representing the effects of environmental stochasticity and being modeled with a multivariate normal distribution (mean of 0, variance-covariance matrix $\mathbf{Q_s}$). In the observation model (Eq. 2), v is a vector of non-process (observation) errors, with errors at sampling site s being multivariate normal with mean 0 and covariance matrix $\mathbf{R_s}$. $\mathbf{Z}$ is a 6×3 matrix to relate observation points to the different state processes.

Covariates (c_s) included three physical drivers, i.e., water permanence (continuous, unit: %), reach types (i.e., pool, run, riffle; categorical), and presence/absence of upwelling zones (binary), and three biological drivers, i.e., presence/absence of algae (binary; available for late succession in 1995 and 2013 survey), presence/absence of cyanobacteria (binary; available for late succession in 1995 and 2013 survey), and macrophyte abundance (i.e., per cent cover of wetland patches 100 m upstream from each sampling site; available only in 2013; continuous, unit: %).

We compared several model structures using AICc (Akaike information criterion with a correction for finite sample sizes) (Burnham and Anderson 2002). In the **B** matrix (Eq. 1), we compared models with and without nutrient interactions (using an *identity* **B** matrix for the without-interactions model). 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). For the **Q** matrix, we also compared models considering nutrient-specific process error with models considering a single process error across nutrients. We used AICc to select the best model structure, i.e., the one minimizing AICc (see similar application in Ward et al. 2010; Ruhí et al. 2015). The state variables were all natural-log transformed first, and then z-scored to allow comparison of effect sizes and interaction strengths across surveys and across nutrient types (Holmes et al. 2014). The effects of covariates were assessed via 95% confidence intervals (1,000 bootstrap samples).

Like most rivers and streams in arid and semi-arid areas, Sycamore Creek is an intermittent stream in space and time, and therefore, part of the stream was dry during the survey, hence no data were collected there. We compared the extent to which our inferences would change by different approaches to deal with “missing” values. Methods for addressing these “missing” values in the dry sections for wavelet analysis and MARSS models are described in Appendix A.

Net uptake length

To assess the intensity of biological activity, we applied an index- net uptake length (Martí et al. 1997), that reflects the rate of nutrient exchange with biota. To do this, we analyzed downstream nutrient concentration declines. This is different from uptake length in the nutrient spiraling concept (Newbold 1981), which is defined as the average downstream distance travelled by a nutrient molecule in dissolved form before being removed from the water column, as it likely includes both uptake and release processes. We computed the first derivative of nutrient concentration (above some threshold value to filter out noise in the data) over a moving window size of 100 m, 150 m, 200 m, and 250 m (i.e., 4, 6, 8, and 10 data points). We then extracted all the positive values (so that concentration was decreasing downstream) and took the mean of these. By estimating uptake lengths for N and P across the four surveys, we were able to compare the general pattern of uptake over successional stages and before & after wetland establishment. The result is an average downstream distance required to see a concentration decline of 1μg L^{-1}. This is the *net nutrient uptake length* (unit: meter). This analysis excluded points between which nutrient concentration increased, as these could indicate either release processes or groundwater inputs, or both. Our estimate of net uptake length using only the positive values is conservative, as it might also include groundwater input (for NO_3^- and SRP groundwater concentrations are usually higher than those of surface water).

RESULTS

PATTERNS OF NUTRIENT HETEROGENEITY

Nutrient concentrations were extremely variable in space (CV as high as 145%; Table 3.1 and Fig. 3.3). We monitored surface-water nutrient concentration ~biweekly in Sycamore Creek at a single location for 23 y (between 1976 and 1999), and CV of NO_3^- concentration over that time period was only twice that over 10 km of space in middle succession on a single day (CV over 23 yr = 207% for 434 samples, CV over 10 km = 104% for 399 samples). This pattern of temporal variation was similar to that reported by Dent and Grimm (1999) for the shorter time period. The pattern of overall spatial variation in concentrations (CV) was highest for NO_3^-, followed by SRP, and lowest for conductivity, regardless of successional stage. If we had taken water samples from sections of the stream that were less well mixed than the thalweg (e.g., edges, backwaters, etc.), spatial variation may have been even higher than this. This is contrary to conventional wisdom that stream water is well mixed and poses challenges to any stream monitoring studies that rely on a single station.

EFFECT OF WETLAND ESTABLISHMENT AND SUCCESSIONAL CHANGES ON SPATIAL PATTERNS OF NUTRIENTS

During the survey in 2013, 40% of stream channel in length was covered by wetland patches (Appendix E), affording us an opportunity to evaluate the influence of wetlands on nutrient spatial pattern. Little difference was found in conductivity before and after wetland establishment. A large sine-wave curve was observed across all four surveys (Fig. 3.3). In contrast, SRP patterns changed dramatically with wetland establishment (Fig. 3.3). Mean SRP concentration increased by 60% after wetland establishment (same successional stage). In contrast, mean NO_3^- concentration was similar before and after wetland establishment (Table 3.1). Spikes of NO_3^- concentration were found in the same upwelling locations, regardless of the timing of the survey (Fig. 3.3). Increased SRP and an unchanged NO_3^- created a lower N to P ratio (N:P), i.e., from 0.5 to 0.3, hence intensifying N limitation (Table 3.1).

Net uptake lengths of both NO_3^- and SRP were shorter after wetland establishment (Fig. 3.4), regardless of the size of the moving window used in the analysis. For SRP, the net uptake length of SRP with wetlands present was much shorter than the same mid-succession stage without wetlands, and even shorter than that in late succession without wetlands. This indicates a more rapid net SRP uptake in the presence of wetlands.

Wavelet analysis revealed the spatial scales of the underlying processes causing nutrient spatial heterogeneity. The analysis revealed a strong influence of upwelling zones on NO_3^- patterns (Fig. 3.7). A global assessment of the scale-specific properties of the decomposed signal independent of spatial location was achieved by summing the mean of the squared wavelet coefficients across all locations to produce a scalogram or Global Wavelet Spectrum (GWS). The GWS showed a large amount of variance at coarser spatial scales and little variance at finer scales (Table 3.2; Fig. 3.5). GWS of NO_3^- signals showed two distinct peaks at spatial scales of approximately 1 km and 3 km, except during early succession, when the 1 km-peak was absent (Table 3.2; Fig. 3.5). For SRP and conductivity, only one peak was observed in GWS over successional time (Table 3.2; Fig. 3.5). The maximum GWS for SRP was reached at a spatial scale between

1.5 km and 1.8 km (Table 3.2; Fig. 3.5). Wavelet power spectrum analysis of wetland abundance and its GWS showed that the spectrum powers peaked at spatial scales of ~700 m and ~2,500 m in the downstream distances of 5 – 7 km and between 7-10 km, respectively (Table 3.2; Figs. 3.5 and 3.7). The distinctive difference between these scales and those described by the GWS of nutrients indicates that different processes contribute to nutrient *vs.* wetland patterns.

Using the 12×12 dissimilarity matrix of the wavelet spectra of 12 nutrient patterns, we examined the mean dissimilarities in the space-spatial scale patterns of nutrients. This allowed us to evaluate the impact of the two key factors of interest (i.e., nutrient types and successional stages) on the spatial variability of nutrients. Results showed that SRP patterns varied most with successional stage, followed by NO_3^- and conductivity (Fig. 3.6a). In addition, differences in spatial patterns among nutrient species increased as succession proceeded (Fig. 3.6b).

RELATIVE EFFECTS OF DRIVERS DURING SUCCESSION

The best MARSS model was the one considering nutrient-specific observation errors, nutrient-specific process errors, and both concentration-dependent effects and interactions among different nutrients in the **B** matrix (Appendix B). Upstream wetland abundance was not a significant factor in explaining the NO_3^- or Cl^- spatial patterns. We explored wetland abundance across a variety of upstream distances (scales = 25m, 50m, 75m, 100m, 125, and 150m), but at none of these scales was a wetland effect statistically significant (only results at 100m-scales are shown; Fig. 3.8). Presence/absence data for algae and Cyanobacteria were available only for late succession in 1995 and for mid-succession in 2013. Algal communities showed a significant negative effect on NO_3^- concentration in 2013 (Fig. 3.8). In late succession, presence of algae did not significantly affect NO_3^- or SRP concentrations; however, the effect of nitrogen fixers on NO_3^- was positive and significant (Fig. 3.8).

In general, upwelling influenced NO_3^- concentration one order of magnitude more than did biological processes (the value of the covariate at 10^0 *vs.* 10^{-1}, respectively) (Figs. 3.8 and 9). The upwelling effect on NO_3^- concentration was significant in all four surveys, and its effect size increased from early to late succession (Fig. 3.9). Before wetland establishment, the upwelling effect was negatively correlated with the amount of surface water in the stream (Fig. 3.10a). However, with wetlands present this effect size decreased, showing significantly lower values than those predicted by the amount of surface water at the time the survey was conducted (Fig. 3.10b). Similarly, the effect of upwelling on SRP was greatest in late succession, and significantly positive in early- and mid-succession before wetland establishment. However, upwelling zones showed no significant effect on SRP patterns when wetlands were present. We also examined other physical drivers, including water permanence and reach types (i.e., riffle, run, and pool). These could influence nutrient spatial patterns in some surveys, but no driver had an explanatory power as strong as that of upwelling (Appendix C and D).

The **B** matrix in the MARSS model informed us of the interactions among nutrients. The diagonal values of the **B** matrix can be interpreted as the effects of nutrient concentration on rate of change of the same nutrient (analogous to “density dependence” in population ecology). In the pre-wetland state, these values decreased from early to late succession for NO_3^-, indicating a stronger concentration-dependent effect towards late succession (i.e., an increase in NO_3^- would trigger, on average, an immediate decrease in NO_3^- downstream) (Fig. 3.11). This effect became more apparent in late succession (i.e., B_{11} values far below 1 [Fig. 3.11]). In contrast, diagonal values of the **B** matrix did not show a successional trend in SRP or COND. However, maximum likelihood and 95% confidence intervals of B_{22} and B_{33} were lower than 1 (where 1 would reflect concentration independence), indicating some regulation of these nutrient concentrations in the system. The off-diagonal values of the **B** matrix estimated interaction strengths between the different nutrients. We found a positive effect (mean = 0.08, 95% CI=0.02 – 0.15) of SRP concentration on NO_3 in mid succession, both before and after wetland establishment (Appendix C and D).

DISCUSSION

Implementing a multi-scaled approach to understanding of ecological patterns is challenging but necessary if we are to produce general predictions (Chave 2013, Nash et al. 2014). At each scale, patterns are results of multiple processes. Effectively disentangling the roles played by top-down physical template effects, internal biological processes, and bottom-up self-organization is essential for understanding how ecosystems are assembled and predicting how they may change over time (van Nes and Scheffer 2005, Smith et al. 2010, Weerman et al. 2011, Wohl et al. 2014). In this study, we identified the spatial scales of the underlying drivers of nutrient spatial patterns, and separated the relative influences of the physical drivers, biological processes, and self-organization over successional time. We found that the physical template is paramount in explaining variation in nutrient patterns in this stream, being one order of magnitude higher than biological processes. We also found feedbacks between biological patchiness and NO_3^- concentration forming patch configuration along the stream to influence NO_3^- concentration. This is self-organization. We quantified this self-organization and found that its strength intensified over ecosystem successional time. Finally, by comparing two ecosystem states (*i.e.* before and after wetland establishment), we found no direct effect of wetland establishment. Instead, wetlands influenced nutrients *indirectly* by accumulating fine sediments that in turn affected surface water–groundwater exchange (upwelling) (Fig. 3.11b).

EFFECTS OF WETLANDS ON SPATIAL HETEROGENEITY OF NUTRIENTS

Wetlands are considered biogeochemical hotspots because their anoxic condition and organic-rich sediments are conducive to denitrification (McClain et al. 2003). Studies of in-stream vascular macrophyte patches have often found significant nutrient retention there (Schulz et al. 2003, Desmet et al. 2011). These studies generally integrate the effects of in-stream macrophytes over larger downstream distances (or areas) to calculate total uptake. Thus, the influence of these macrophytes on nutrient *spatial* patterns remains uncertain. Despite the fact that ~40% of the stream was covered by wetland plants in 2013, we found no evidence that wetland patches affected spatial patterns of NO_3^- directly. In contrast, algal uptake had a significant negative effect on NO_3^- (Fig. 3.8), even though the amount of N stored in algae is much lower than that in vascular plants. Across the surveyed section, about 40 kg N and 3 kg P were stored in wetland plants (aboveground biomass only) while macro-algae stored about 12 kg N and 1 kg P (Appendix A). Although more nutrients are associated with vascular macrophytes, algae take up nutrients directly from surface water, whereas sediments are the major source of nutrients for wetland plants (Nichols 1983). This dampened exchange of NO_3^- between pore and surface water (Johnston 1991) is consistent with our finding that the local effect of wetlands on surface water nutrients is undetectable.

Although we did not find any *direct* effect of wetlands on nutrient spatial patterns, we found an *indirect* effect of wetlands through upwelling. The effect size of upwelling on NO_3^- in 2013 was significantly lower than predicted by the amount of surface water (Fig. 3.10). We suggest that this is a result of hydrogeomorphic changes that occurred during wetland development. While upwelling zones provide high nutrient concentrations, they are also places with high abundance of wetlands (Dong et al. *in press*). Dense wetland plant formations trap and accumulate fine sediments (Cotton et al. 2006), leading to a reduced vertical hydrological gradient, and thus to a lower hydrological exchange than would otherwise occur (Heffernan et al. 2008). In addition, wetlands create an anoxic hyporheic environment, which elevates denitrification in hyporheic sediments, leading to low NO_3^- (Heffernan et al. 2008). Reduced exchange and denitrification are consistent with a reduced effect of upwelling zones on NO_3^-. A previous mechanistic study of the impact of a riparian shrub, *Baccharis salicifolia*, on NO_3^-implicated plants in stimulating denitrification via organic root exudates, but did not show major effects on hydrologic exchange (Schade et al. 2001). Further research should focus on how biogeomorphic change affects hydrologic exchange on nitrogen cycling processes. Our study demonstrates a shift of mechanism at different spatial scales (Levin 1992, Chave 2013). At the patch scale, wetlands alter biogeochemical patterns via processes such as denitrification, uptake, and decomposition. At larger scale, sedimentation and subsequent modification of hydrological connectivity may shape biogeochemical patterns.

As with NO_3^-, we observed no direct effects of wetlands on SRP, but wetlands almost always affected upwelling. SRP net uptake length in 2013 was very short, similar to that observed in late succession (Fig. 3.4), suggesting a rapid uptake of SRP. This could result from adsorption of SRP by the large surface area and high concentrations of Fe and Al oxides of the fine sediments and organic matter accumulated in wetland patches (Reddy 1998). Comparing the same mid-succession stage before and after wetland establishment, mean SRP concentration in 2013 (44 $\mu g\ L^{-1}$) was much higher than before wetland establishment (28 $\mu g\ L^{-1}$). This is very likely related to the inter- and/or multi-annual hydrological regime. The long-term (1978 to 1999) average concentration of SRP in May in Sycamore Creek shows high interannual variability (Appendix G). Winter precipitation and ensuing floods import P from the upland catchment, but the effect of floods decreases as flood frequency increases (Martí et al. 2000). Low mean SRP in 1995 can be explained by the four consecutive preceding wet years. Conversely, the two very dry years before 2013 could explain the higher SRP observed that year. The increased SRP in 2013 may also result from the establishment of wetland vegetation. O'Brien et al. (2014) measured nutrient uptake and retention in reaches of differing macrophyte cover and before & after experimental removal of macrophytes. They found that P uptake was *negatively* related to biomass of macrophytes. While our study explains spatial variation in nutrients over the short term, understanding long-term mean nutrient levels requires extended monitoring of hydrology and biogeochemistry of the system (Lindenmayer and Likens 2009), beyond which we were able to do here.

CHANGES IN THE SPATIAL SCALES OF UNDERLYING DRIVERS DURING SUCCESSION

The spatial scales at which geomorphic drivers operate are determined by the geomorphic template. For example, major upwelling zones and groundwater input peaks were about 3 km apart, which contributed to the spatial scale of 3 km (Figs. 3.5 and 7). On the other hand, the spatial scale of the influence of a biological process is determined by the process rate and by the propagation rate of its consequences on the pattern of interest (Reiners and Driese 2001). Both of these may change over successional time. Patches with processes characterized by distinctive spatial scales collectively influence patterns of nutrient concentrations (Fisher et al. 1998). Over successional time, the hierarchical structure of the underlying drivers may change, and this may in turn manifest through changes in the spatial patterns of nutrients.

We used the spatial scales identified by wavelet transform to infer the operant drivers. This approach is gaining increasing attention and is an effective means to identify scales in ecological studies (e.g., Keitt and Urban 2005, Vargas et al. 2010). Upwelling and nitrogen fixation influence NO_3^- concentration at two spatial scales. Peaks in the NO_3^- concentration pattern occurred at major upwelling zones, and repeated themselves every ~3 km (Fig. 3.3), generating a stable peak at ~3 km spatial scale in the GWS for NO_3^- (Fig. 3.4). The spatial scale at which nitrogen fixation occurred varied between 0.75 and 1.5 km (Fig. 3.5). According to Grimm and Petrone (1997), nitrogen fixation in late succession in Sycamore Creek is about 2 mg m^{-2} hr^{-1}. This translates to approximately 1.5 km (assuming mean flow velocity is 300 m hr^{-1}, and average water depth is 0.2 m) for NO_3^- to increase by 50 μg L^{-1} (consistent with the small peaks in late succession [Fig. 3.3; Table 3.2]). Cyanobacteria are usually absent in early spring (Grimm and Petrone 1997), but over seasonal and successional time, rate of nitrogen fixation, flow velocity, and areal coverage of nitrogen fixers tend to increase. Therefore, the spatial scales of N fixation changed over successional time (Fig. 3.5). Alternatively, the signal at a spatial scale between 0.75 and 1.5 km could be generated from bedform-driven upwelling zones, which occur in concave locations of the channel (channel slope decreases, becoming flatter, which causes subsurface water to upwell to the surface (Harvey and Bencala 1993). This signal became stronger as surface water (dilution water) declined towards late succession.

Compared to NO_3^-, SRP showed higher variability as a function of successional time (Figs 3.3, 3.5, and 3.6a). The first maximum GWS was reached at a spatial scale between 1.5 km and 1.8 km in the pre-wetland state (Fig. 3.5). For the post-wetland state, the first maximum was reached at about a 1.2-km scale (Fig. 3.5). For SRP, adsorption-desorption equilibrium between sediments and overlying water column often plays an important role in P dynamics (Diaz et al. 1994; Hoffman et al. 2008; Richardson 1985). A desorption rate of 1.7 – 2.5 μg L^{-1} day^{-1} would increase SRP concentration by 10 μg L^{-1} within a 1.2 km to 1.8 km downstream distance (Table 3.2). This desorption rate is within the range observed in other streams and rivers (e.g., Philip 1988, House et al. 1995).

The potential of wavelet transform analyses is particularly attractive given the nature of ecological and environmental data, and the relationship between them. In ecology, wavelet transform analyses have often been used in time-series analysis. Cazelles et al. (2005) used wavelet analyses to demonstrate the association between El Niño, precipitation, and dengue epidemics in Thailand. Vargas et al. (2010) explored the time scale at which environmental variables (soil moisture and temperature) correlate with soil respiration using wavelets. Recknagel et al. (2013) applied this approach to analyze the population dynamics of phytoplankton in relation to physical and biological determinants. Here we used wavelet analysis on spatial data (instead of time series) and showed its effectiveness in understanding nutrient spatial patterns and their scale-specific drivers.

RELATIVE INFLUENCES OF PHYSICAL, BIOLOGICAL AND SELF-ORGANIZATION EFFECTS

Three broad categories of drivers, i.e., physical template, biological processes, and self-organization, are generally examined in explaining ecological spatial patterns (e.g., Mcintyre et al. 2011, Schoelynck et al. 2012, Stella et al. 2013, Stewart et al. 2014, Bonachela et al. 2015); however, no studies have so far examined them together to separate the relative contribution of each and their changes over ecosystem successional time. Rivers and streams are open ecosystems, highly influenced by their physical environment (Dent et al. 2002, Poole 2012). In Sycamore Creek, the effect size of upwelling was about one order of magnitude higher than the direct effect of biological processes on NO_3^- concentrations (Figs. 3.8 and 3.9). This indicates a dominant role for the geomorphic template in shaping patterns of NO_3^- in stream ecosystems.

The observed spatial heterogeneity of nutrients in streams is the longitudinal integral of the interactions between the underlying geomorphic template, internal biological processes, and local feedbacks between patch configuration and nutrients, i.e., self-organization. The consequences of physical drivers and biological processes on nutrients propagate downstream with flowing water. Elevated nutrient concentration at upwelling zones increases algal biomass, which efficiently reduces nutrients downstream. The resultant low concentration of stream NO_3 triggers nitrogen fixation even further downstream. Such local feedbacks, between biological patches and nutrient concentrations, self-organize to form spatial configurations of biological patches along the stream. The **B** matrix from the MARSS model provides evidence of the effect of self-organization on NO_3^- patterns (Fig. 3.11). The concentration of nutrients creates concentration-dependent effects in space, similar to density-dependent effects in population dynamics over time (Ward et al. 2010). This means that a high NO_3^- concentration is followed by a rapid decrease, and a low NO_3^- concentration that then triggers a rapid increase of NO_3^- downstream owing to nitrogen fixation (Fisher et al. 2004). The concentration-dependent effect on NO_3^- is caused by self-organization of patch configuration, and is realized through feedbacks between biological patch formation and local nutrient concentration as described above.

From early to late succession, the concentration-dependent effect on NO_3^- increases (Fig. 3.11), suggesting stronger self-organization towards late succession. The stronger self-organization towards late succession is rooted in biological responses to more severe global N limitation in Sycamore Creek. This is consistent with findings on vegetation patterns in arid terrestrial ecosystems, where water is the constraining resource (e.g., Valentin et al. 1999, Rietkerk et al. 2004, Schmitz 2010, Deblauwe et al. 2011). At sufficiently high precipitation, vegetation patchiness follows the pattern dictated by the template. Only when water becomes limiting does the landscape show self-organized vegetation patchiness (Sheffer et al. 2013). Similarly, in Sycamore Creek, as N became increasingly limiting over succession, self-organization became stronger. Although concentration-dependent effects were also observed for SRP and conductivity, no successional trend was observed, likely because the extra physical/chemical control pathway for dissolved phosphate (Froelich 1988), which does not exist in N dynamics.

The effect of such self-organization reduces spatial heterogeneity of nutrients; however, spatial heterogeneity of nutrients in Sycamore Creek was observed to increase towards late succession (Dent and Grimm 1999). This is because as succession proceeds, reduction of surface water amplifies the effect of groundwater input. Because the geomorphic template is the dominant driver of nutrient spatial patterns in the stream, as a net effect, spatial heterogeneity increases with successional time. In terrestrial ecosystems, where the influence of the geomorphic template is not as strong, heterogeneity of nutrients is driven by changes in the plant composition and structure during succession, hence observed heterogeneity decreases (Gross et al. 1995, Cain et al. 1999, Yankelevich et al. 2006).

Studies of self-organization have so far focused on homogeneous landscapes or landscapes where the template effect is negligible. Most landscapes in nature are heterogeneous however, and biological patchiness is affected by both the physical template and by local feedbacks (Schmitz 2010). The manner in which the physical template and self-organization act in concert to shape spatial pattern had never been studied to our knowledge, until Sheffer et al. (2013). They developed a unifying framework for understanding the relative importance of self-organization and the physical template in terrestrial vegetation patchiness, and suggested that vegetation patchiness in any landscape is likely to result from a mixture of patchiness induced by the physical template and by self-organization. Here we provide the first example of such a mechanism in riverine landscapes, and demonstrate how self-organization of biological patch configuration affects stream nutrient concentrations. More work along this line from a variety of ecosystems would be lucrative.

CONCLUSIONS

This study provides a comprehensive framework for understanding nutrient spatial patterns by integrating hydrological regime, physical template, biological processes, self-organization, and their changes over ecosystem successional time. Taking advantage of the characteristics of our data (i.e., one-dimensional, evenly spaced), we applied time-series methods (wavelets and MARSS) to spatial patterns. An accurate understanding of ecological spatial patterns requires a multi-scaled approach (Holmes et al. 2005, Dibble et al. 2006, Bisigato et al. 2009). We quantified the spatial scales of processes correlated to the variation in nutrient concentrations using wavelet transform analyses, and showed how the relevant scales for processes changed over time. Further, using MARSS models we quantified the relative influences of each of three drivers (geomorphic template, biological processes, and self-organization). Patterns of nutrient concentrations in the stream were predominantly controlled by the geomorphic template. We found wetlands, often considered biogeochemical hotspots, did not have a direct effect on nutrient patterns; however, they indirectly altered spatial patterns of nutrients via their hydrogeomorphic effects, especially sedimentation. We reported, for the first time, the effect of self-organization of biological patch configuration on nutrients. Self-organization intensified during succession as nutrients became increasingly limiting. By incorporating reciprocal changes between pattern and process (i.e., self-organization), ecologists may contribute to higher-order theory about feedbacks between ecosystem structure and functioning (Fisher et al 2004, Corenblit et al. 2010). Nutrient patterns, the relevant scales of drivers, and the internal feedbacks and self-organization all change over ecosystem successional time. This study thus provides an explanation of the components of ecological complexity in both space and time.

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TABLE 3.1. Water chemistry characteristics over the 10-km stretch of Sycamore Creek. All values are calculated on the basis of *n* sample locations; values at each sample location are based on two analytical replicates. Data for1995 and 1997 are from Dent and Grimm (1999).

Characteristics	**Unit**	***n***	**Mean**	**SD**	**CV (%)**
Early succession (2 week post-flood)/1997Mar					
NO_3^--N	µg/L	398	219	158	72
SRP	µg/L	398	17	7	42
Conductivity	µS/cm	396	379	14	4
N:P	-	398	28	11	-
Middle Succession (2 months post-flood)/1995May					
NO_3^--N	µg/L	399	6	6	104
SRP	µg/L	399	28	6	20
Conductivity	µS/cm	399	402	19	5
N:P	-	399	0.5	0.5	-
Late succession (9 months post-flood)/1995Dec					
NO_3^--N	µg/L	260	35	51	145
SRP	µg/L	260	28	13	44
Conductivity	µS/cm	260	488	68	14
N:P	-	260	3	4	-
Middle Succession (x months post-flood)/2013May					
NO_3^--N	µg/L	449	7	10	144
SRP	µg/L	449	44	19	43
Cl^-	mg/L	449	15	2	17
N:P	-	449	0.3	0.16	-

TABLE 3.2. Summary of the spatial scales of nutrient signals over successional time detected by wavelet analysis, and the inferred underlying processes based on $\frac{\Delta C[\mu g / L]}{R[mg / (m^2 \cdot hr)] \times Z[m]} \times V_{flow}[m / hr]$, where ΔC is the local concentration peak of the nutrient in interest, R is the process rate (e.g., nitrogen fixation rate or desorption rate), Z is average water depth, and V_{flow} is flow velocity. Two spatial scales were detected in the NO_3^- pattern, and one spatial scale was detected in SRP pattern.

Nutrient species	**NO_3^-**		**SRP**
Spatial scale	3 km	0.75-1.5 km	1.2-1.8 km
Changes over time	No	Appear in mid-succession, and change with time	Yes
Inferred contributing process	Groundwater upwelling	Nitrogen fixation	Desorption
Reasoning	The spacing between major upwelling zones is ~3 km	ΔC = 50 μg L^{-1}; R = 2 mg m^{-2} hr^{-1}; Z = 0.2 m; V_{flow} = 300 m hr^{-1};	ΔC = 10 μg L^{-1}; R = 1.7-2.5 mg m^{-2} hr^{-1}; Z = 0.2 m; V_{flow} = 300 m hr^{-1};

FIGURE 3.1. Flow chart of the design of the study, from data collection, to the corresponding analysis methods, results, inferences based on the results, and how the questions were answered.

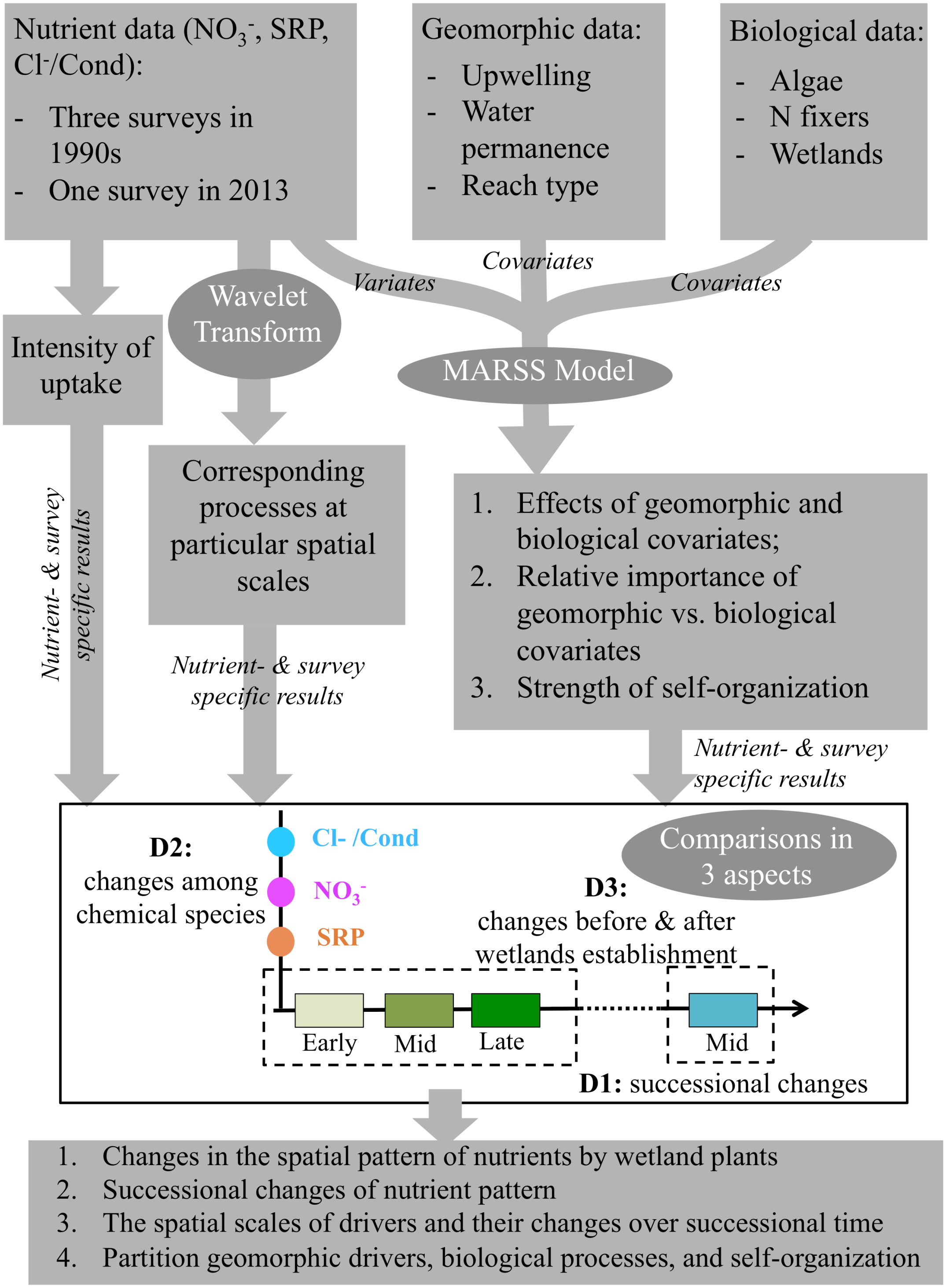


FIGURE 3.2. Hydrograph of the three years (1995, 1997, and 2013) when surveys were done. The data were from USGS gauge #09510200 located about 1.5 km downstream of the surveyed section of Sycamore Creek. The *y*-axis is the integral of daily average discharge between October 1st and the survey date of that water year. Survey dates are marked with gray triangles.

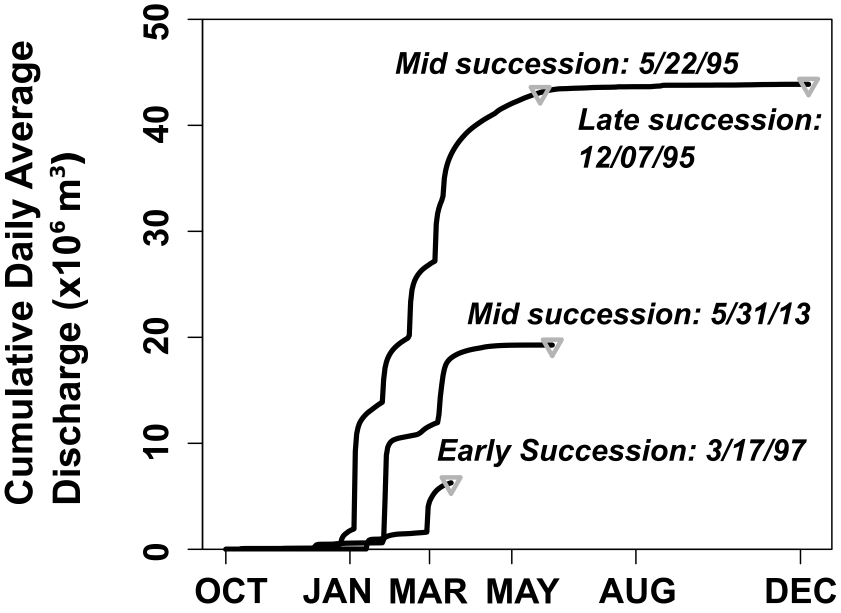


FIGURE 3.3. Spatial patterns of nutrient concentration in Sycamore Creek over 10 km across four stages of post-flood succession (i.e., early succession in March 1997; mid-succession in May 1995; late succession in December 1995; and mid-succession with wetlands present in May 2013). In the 2013 survey, we measured chloride (Cl^-) concentration instead of conductivity.

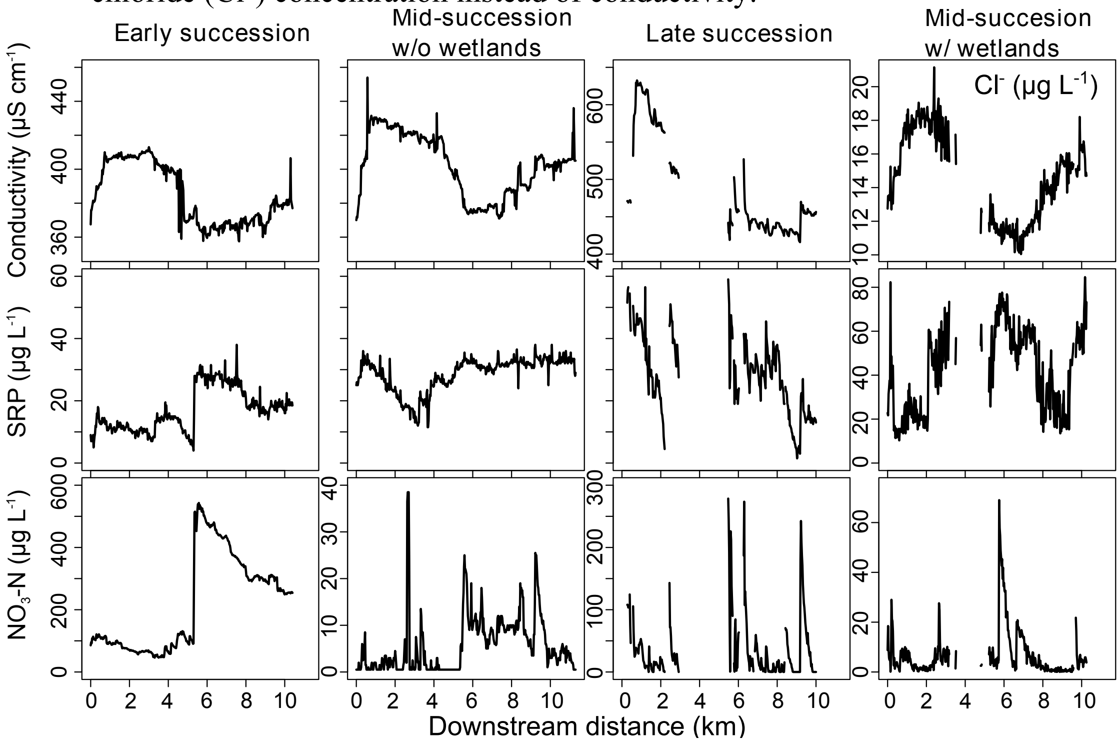


FIGURE 3.4. Comparison of the net uptake length of NO_3^- and SRP across four surveys. The moving window (MW) size used did not change the relative pattern of the uptake length in successional time, but changed the absolute net uptake lengths. Four moving window sizes were used 100m, 150m, 200m, and 250m. “E” – early succession; “M”- mid-succession in 1995; “L”- late succession; “M-W” – mid-succession with wetland patches.

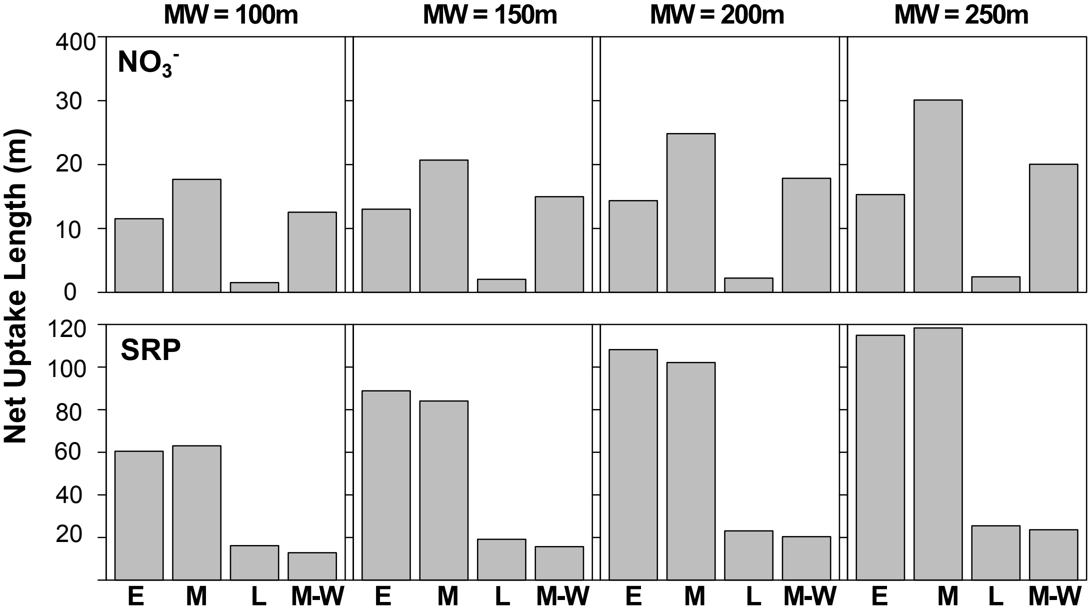


FIGURE 3.5. Global wavelet spectra (GWS) of NO_3^-, SRP, and conductivity across four surveys (a-c) and the GWS for wetland abundance distribution (d).

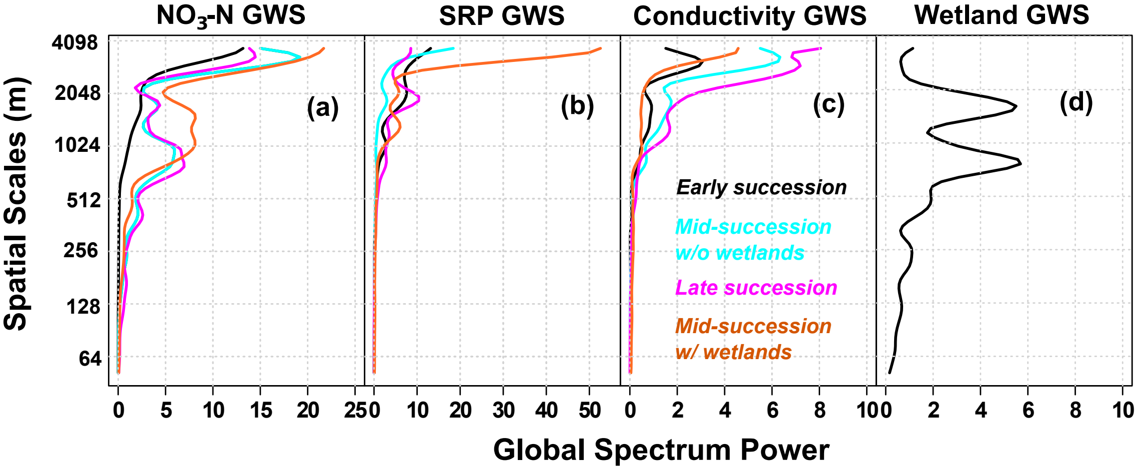


FIGURE 3.6. Boxplots of the mean dissimilarity between the wavelet spectrum of each chemical variable – showing the effects of successional stage (a) and the mean dissimilarity between the wavelet spectrum of each successional stage – showing the effect of chemical types (b).

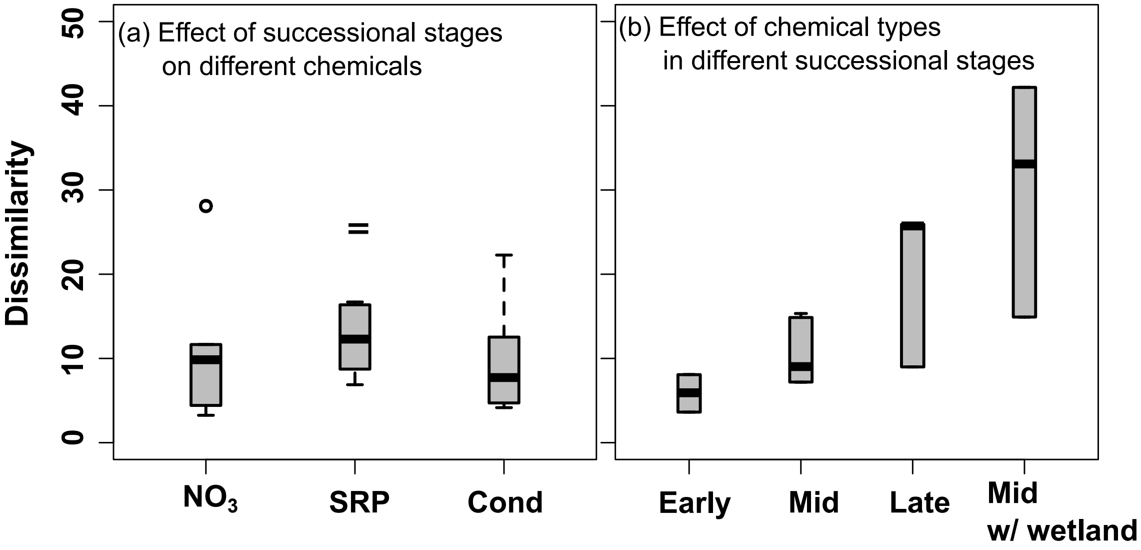


FIGURE 3.7. Wavelet spectrum analysis of three types of water chemistry in four surveys (four rows) and the wetland abundance distribution in 2013 June, two weeks after the water chemistry survey. Statistically significant results (based on random noise) inside the labeled 95% confidence interval are enclosed in white dashed lines. Image colors are a representation of wavelet spectrum power (WPS). The dashed white U-shaped line is the cone of influence (COI), below which edge effects limit confidence in results. The x-axis shows downstream location (m); the y-axis shows spatial scale (m). For the dry section, we used ARIMA model to estimate the "missing data" in those sections (Appendix A).

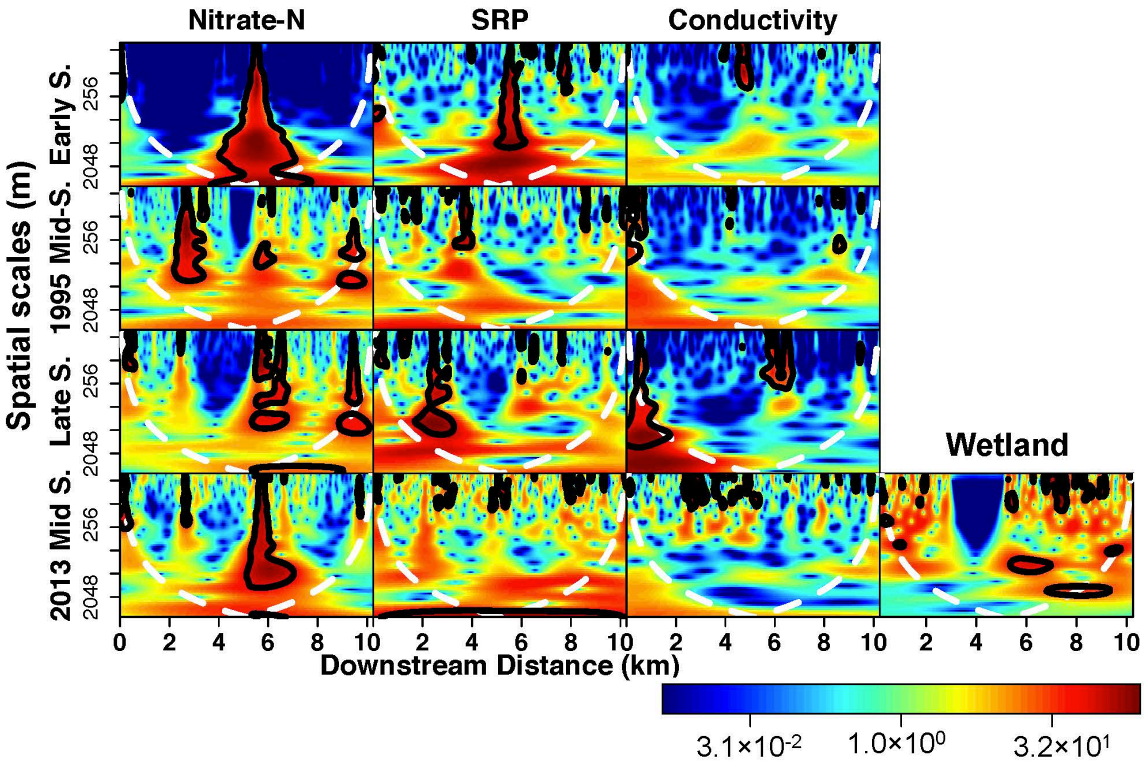


FIGURE 3.8. The effect size of upstream wetland abundance, presence/absence of algal patches, and presence/absence of cyanobacteria on different water chemicals (NO_3^-, SRP, and conductivity) in mid-succession in 2013 and late-succession in 1995. Statistically significant effects (the bootstrapped 95% confident interval did not include 0) are labeled with *.

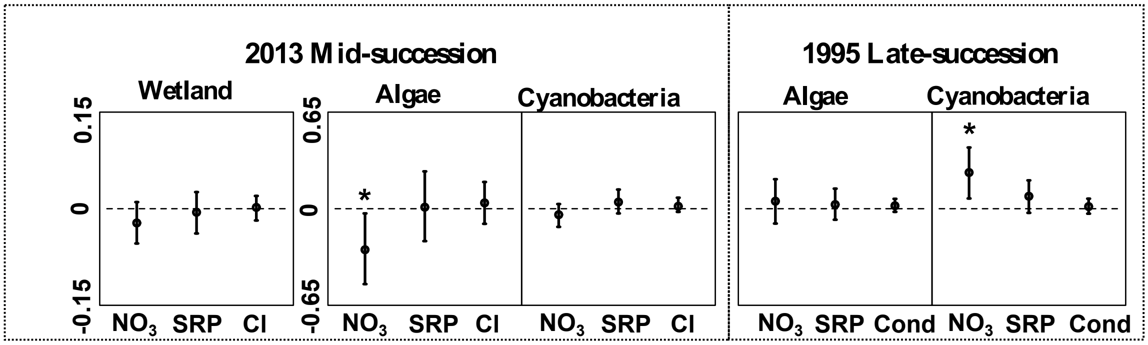


FIGURE 3.9. The concentration-dependent effect of different water chemistry across four surveys, i.e., the maximum likelihood of the diagonal values of **B** matrix in MARSS models, and the corresponding 95% confidence interval (CI) obtained from 1000 bootstrap samples. All values were between 0 and 1: within this range, smaller values denote stronger effects of concentration on the rate of change of concentration downstream. E: early succession; M: mid-succession in 1995; L: late succession; M-W: mid-succession with wetland patches.

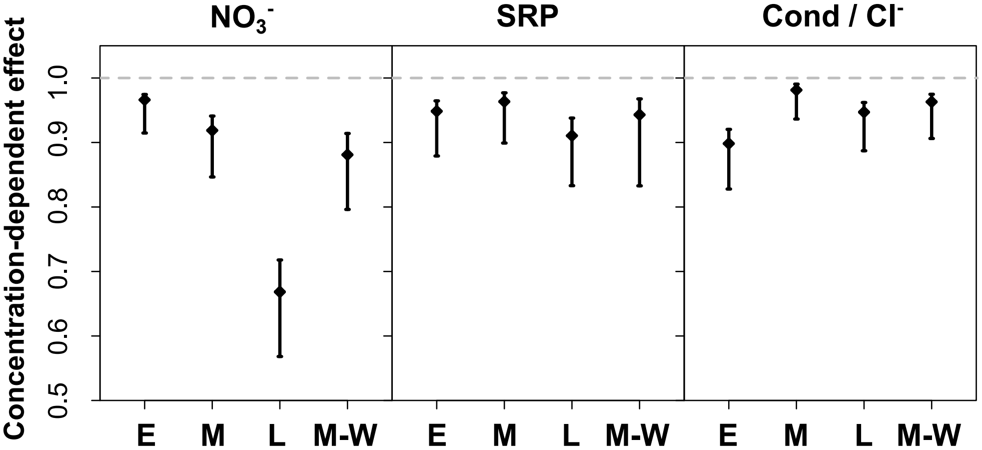


FIGURE 3.10. Maximum likelihood estimate of the coefficients of upwelling on surface water chemistry across four surveys with 95% confidence intervals. E: early succession; M: mid-succession in 1995; L: late succession; M-W: mid-succession with wetland patches.

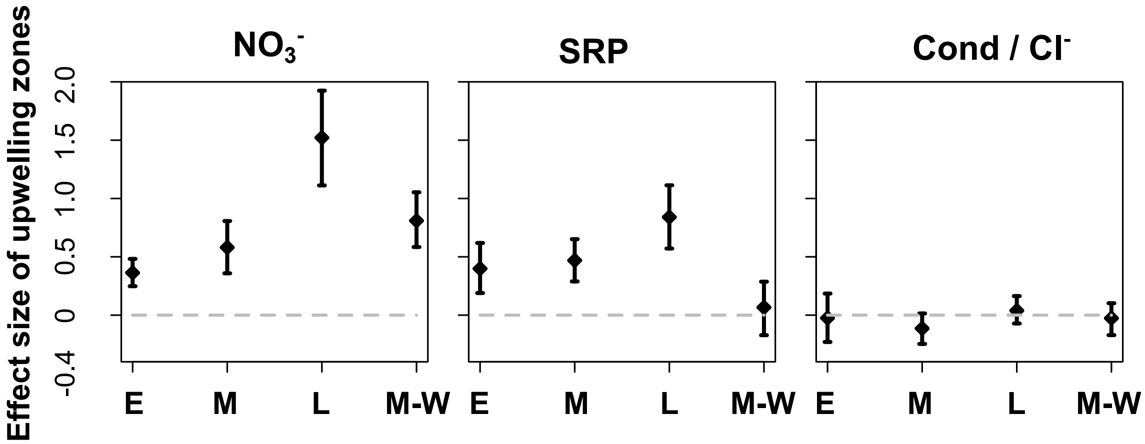
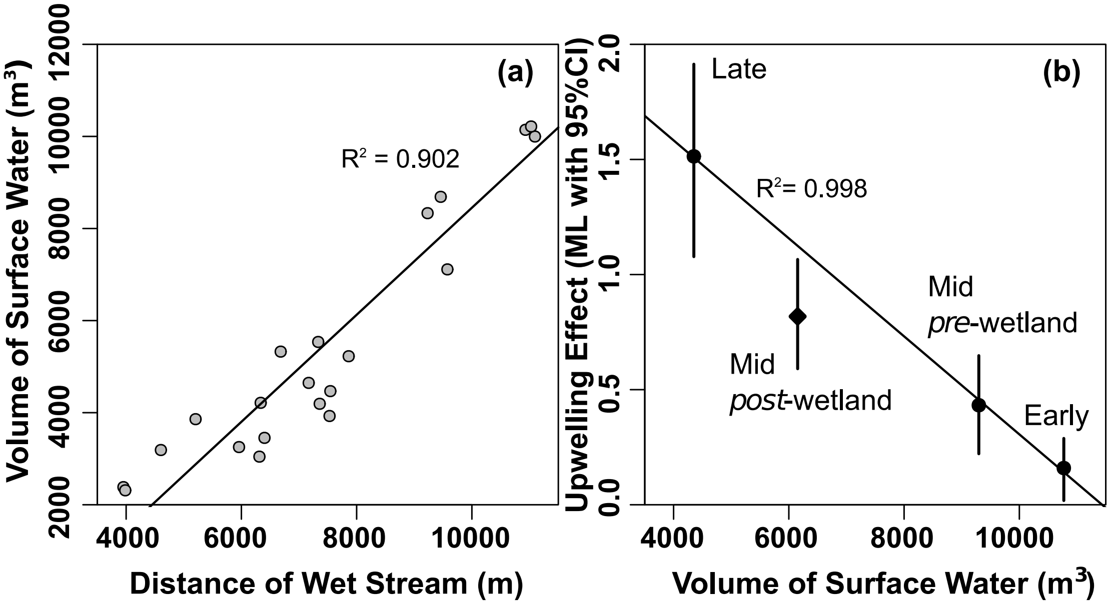


FIGURE 3.11. The effect of upwelling on NO_3^- was lower than predicted by amount of surface water. (a) Linear relationship between the extent of surface water and the total volume of surface water. (b) The coefficient of upwelling on NO_3^- concentration was linearly correlated with the amount of surface water before wetland establishment in 1990s. However the coefficient of upwelling was significantly lower in 2013 than the amount predicted by surface water volume.



CHAPTER 4

THE EFFECT OF SPATIAL CONFIGURATION OF HABITAT CAPACITY ON BETA DIVERSITY

ABSTRACT

Patterns of β diversity are commonly used to infer underlying ecological processes. In this study, we examined the effect of spatial configuration of habitat capacity on different metrics of β diversity, i.e., β diversity measured as turnover and as variation. For β diversity as turnover, a monotonic species spatial turnover pattern is typically considered as a benchmark for species distributions driven only by dispersal process. Deviations from a monotonic curve are attributed to local environmental filtering (i.e., the same environmental factors affecting different species differently). However, we found non-monotonicity in species spatial turnover in models without environmental filtering effect. This non-monotonicity was caused by variation in α diversity, introduced by spatial configuration of habitat capacity. After applying a recent null-model approach—designed to tease out the effect of variation in α diversity—species spatial turnover remained non-monotonic. This non-monotonicity makes it problematic to use species spatial turnover to infer the underlying processes for species distribution, i.e., whether it is driven by environmental filtering or dispersal processes. Spatial configuration of habitat capacity also influences landscape connectivity. Small-habitat capacity sites may constrain movements of organisms (i.e., dispersal) between sites supporting high capacity habitats. We showed that in a landscape where small-habitat capacity sites were located in positions important for dispersal (e.g., in the center as opposed to on the edge of a landscape) has a higher spatial variation of species composition, hence, higher β diversity. Ecologists who use different measures of β diversity should be aware of these effects introduced by spatial configuration of habitat capacity.

Keywords: β diversity; habitat capacity; landscape connectivity; monotonicity; similarity indices; spatial configuration; species spatial turnover.

INTRODUCTION

A burgeoning challenge in ecology is to distinguish among the many dimensions of species diversity. Increased scientific activity has centered on the study of beta (β) diversity – broadly defined as the variation in species membership among locales – because it provides a direct link between local biodiversity (α diversity) and regional species pool (γ diversity) (Whittaker 1960, Whittaker 1972) and it has numerous implications for conservation (Olden 2006). Ecologists frequently use β diversity to infer processes that structure species assemblages spatially (Vellend 2010). However, landscape heterogeneity, one aspect of which is manifested as spatial variation in habitat capacity (defined as the potential number of individuals a site can hold) among sites, can make it difficult to infer processes from observed β diversity patterns. Variation in habitat capacity introduces, among other things, differences in α diversity among sites via the simple effect of random sampling. As a result, variation in α diversity can generate spurious similarities or differences between locales, i.e., β diversity (Lennon et al. 2001, Koleff et al. 2003, Baselga 2007, Chase et al. 2011).

Beta diversity is expressed both in terms of species turnover and variation (Anderson et al. 2011). Species turnover refers to the rate of change in community structure along a given gradient, such as the distance decay relationship (DDR) describing decreasing taxonomic similarity with geographic distance (e.g., Qian and Ricklefs 2007, Brown and Swan 2010). Ecologists expect monotonic decay of species spatial turnover to occur when a system is predominantly controlled by dispersal limitation, whereas deviations from DDR (i.e., “peaks” and “valleys” in the species spatial turnover) indicate the importance of local environmental filtering on species occurrence (e.g., Condit et al. 2002, Anderson et al. 2013, Bogan et al. 2013). β diversity as variation is captured by Whittaker's original measures ($\beta_W = \gamma/\bar{\alpha}$) or the mean dissimilarity index (such as Bray-Curtis and Sorensen dissimilarity index) among communities ($\bar{d} = \frac{1}{m}\sum_{i,j<i} d_{ij}$, $m = N(N-1)/2$ is total sample units) (Anderson et al. 2011). Greater values indicate higher variation in species composition across space. In this study, we examine how the validity of the inferences about ecological processes based on different measures of β diversity may be compromised by the spatial configuration of habitat capacity in a landscape. We define spatial configuration of habitat capacity (hereafter SCHC) as the spatial arrangement of sites with different habitat capacities in a landscape.

Various methods exist to correct for the effects of variation in α diversity on estimates of β diversity. It should be noted that these effects relate to the dependence of β diversity on the differences of α diversity between sites *within* a system; and they are not the same as the effects arising from the differences of the mean α diversity (i.e., averaged across all sites within a system) *between* different systems. The latter issue is related to the comparability of β diversity measures among systems with different mean α diversity, and has been addressed by several authors (e.g., Jost 2007, Jost et al. 2010, Baselga 2010). Our study addresses the first issue: the dependence of β diversity on the differences of α diversity between sites within a system (e.g., Lennon et al. 2001, Koleff et al. 2003, Baselga 2007). Chase et al. (2011) recently developed a null-model approach, originally proposed by Raup and Crick (1979), to detect whether different species compositions among sites result from variation in α diversity or from other ecological processes (e.g., deterministic environmental filtering and stochastic dispersal). However, this approach was developed for a pair of local communities, and its effectiveness and validity when applied to all pairwise combinations of communities in a landscape have not yet been systematically investigated.

Spatial configuration of habitat capacity also influences landscape connectivity. For example, low capacity habitats in the landscape matrix may constrain movements (i.e., dispersal) between locations supporting high capacity habitats. Greater connectivity among habitats allows immigration from others sites to offset local extinction events, leading to higher a diversity but lower variability in community composition across the landscape (i.e., lower β diversity). By contrast, lower connectivity can isolate habitats, leading to lower a diversity but higher species turnover (i.e., higher β diversity) (Hubbell 2001, Economo and Keitt 2010, Carrara et al. 2014). Although the influence of landscape connectivity for community composition is widely appreciated (Chase and Ryberg 2004, Chave and Norden 2007, Minor et al. 2009), few studies have considered the sole effect of habitat spatial configuration on β diversity.

In this paper, we examine how the quantification and interpretation of β diversity patterns are influenced by the spatial configuration of habitat capacity. Addressing this question through the analysis of empirical data is challenging because many known and unknown ecological processes are in operation. Therefore, we examined the effects of SCHC on β diversity patterns using simulated landscapes that are free from the effects of environmental filtering. A set of communities comprised a metacommunity on this landscape, and we assumed that the locales that supported the communities differed only in their habitat capacity. As a result, species distributions—and the corresponding β diversity patterns—would be controlled solely by dispersal and not by differences in the ecological niche requirements of species.

The SCHC gives rise to spatial variation in α diversity, which subsequently affects β diversity patterns (Lennon et al. 2001, Koleff et al. 2003, Baselga 2007, Chase et al. 2011). If the influence of α diversity can be effectively removed, β diversity patterns should have the following properties in the hypothetical landscape free from the effect of environmental filtering (Fig. 4.1). First, β diversity as turnover should conform to the monotonic decay relationship describing how species similarity decreases with spatial distance. Second, β diversity, measured as either turnover or variation, should be statistically indistinguishable across landscapes with different spatial configurations of habitat capacities. Although these two predictions may appear intuitive, it is unclear whether frequently used β diversity measures conform to these properties. We systematically investigated the effects of SCHC on the robustness of these two properties by implementing a neutral metacommunity model (see, e.g., Hubbell 2001 and Muneepeerakul et al. 2008) in the no-niche hypothetical landscapes described above.

METHODS

We systematically investigated the effects of SCHC on estimates of β diversity by applying a neutral metacommunity model (Muneepeerakul et al. 2008) in one-dimensional landscapes (e.g., such as a stream) with different spatial configurations of habitat capacity (Fig. 4.2). In the “uniform” configuration, all sites had identical habitat capacity. In the “gradient” configuration, habitat capacity increased linearly along a hypothetical gradient. In the “random-shuffle” configuration, we randomized the spatial distribution of habitat capacities along the gradient. In the “V-shaped” configuration, habitat capacity was set high at both ends and low in the middle of the gradient; this is akin to a stream system in which the headwater receives much rainfall and the downstream end connects to a large river, while the middle reaches are intermittent streams (e.g., Bogan et al. 2013). In the “hump-shaped” configuration, habitat capacity was large in the middle and small at the two extremes of the gradient—akin to an edge effect such as the boundaries of a forest experiencing more external pressure than its interior. All five configurations had the same average habitat-capacity size of 514, and thus the same total habitat capacity. All configurations except for the uniform configuration were built from the same set of habitat capacities, but they were configured differently in space (Fig. 4.2). The biggest sample-size discrepancy (i.e., ratio of largest to smallest habitat capacity) in the four non-uniform configurations was about 20.

The metacommunity consisted of 30 local communities, with a distance between neighboring sites of 1 arbitrary distance unit. The dispersal kernel was assumed to be a two-sided exponential distribution:

$$K_{ij} = Ce^{-L_{ij}/a}$$

where K_{ij} is the probability that an organism produced at site j arrives at site i after dispersal; C is a normalization constant to ensure that for every site j , $\sum_i K_{ij} = 1$, i.e., no organisms traveled out of the metacommunity. L_{ij} is the distance between two habitats, and a was the characteristic dispersal distance. At each time step, a randomly selected individual died and the resources that previously sustained that individual became available to sustain a new individual. With probability v, the diversification rate, the empty spot was taken up by a new species (the diversification rate is a per-birth rate and is due to speciation or to immigration of a new species from outside the metacommunity). With probability 1-v, the empty spot was occupied by a species already existing in the system. In the latter case, the probability P_{ij} that the empty spot in site i would be colonized by a species from habitat j was determined as follows:

$$P_{ij} = (1 - v)\frac{K_{ij}H_j}{\sum_{k=1}^{N} K_{ik}H_k}$$

where K_{ij} is the dispersal kernel, H_k is the habitat capacity of site k, and N is the total number of sites (i.e., communities). All the organisms in site j had the same probability of colonizing the empty spot at site i where the death took place. Each site was assumed to be always saturated at its habitat capacity.

We explored five characteristic dispersal distances (a = 1, 4, 8, 12, 16) at the diversification rate $v = 0.0010$. In the metacommunity's initial state, the distribution of species composition was random. We ran the model until it reached a statistically steady state (when there is no directional trend in the mean α diversity or total species richness with simulation time steps).

Results from the neutral metacommunity model were used to calculate different β diversity measures. Three commonly-used measures of β diversity were considered: Sorensen dissimilarity index based on species presence/absence data, Bray-Curtis dissimilarity index based on species abundance data, and the more recent Chao-Sorensen dissimilarity index based on species abundance data, which was originally created to address the issue of under-sampling rare species (Chao et al. 2005). For each configuration, we had 500 replicates (from 500 realizations of the same neutral metacommunity model) to calculate the mean and 95% confidence interval for each dissimilarity index at any particular pairwise distance.

Next, we tested the effectiveness of Chase et al.'s (2011) null-model approach, which was supposed to remove the effect of variation in α diversity. The calculated index is called pairwise β_{RC}. The β_{RC} metric expresses the magnitudes by which communities deviate from a stochastic null expectation. β_{RC} uses a randomization approach to estimate the probability of which pairwise communities have less observed number of shared species between two communities, containing α_1 and α_2 species respectively, than SS_{exp}. SS_{exp} is the expected number of shared species of a pair of communities by randomly drawing α_1 and α_2 species from a known species pool. The random draw was repeated 99,999 to create the SS_{exp} distribution. β_{RC} therefore calculates the probability that SS_{obs} is lower than SS_{exp} by chance (i.e., a dissimilarity index).

We used the four pairwise dissimilarity indices described above to calculate β diversity as turnover and as variation (Anderson et al. 2011). For β diversity as turnover, we used the slope between pairwise species similarity and pairwise geographical distance as a direct measure of turnover (e.g., Qian and Ricklefs 2007). We also considered the relative strength of the relationship (r^2) between species similarity and distance, as recommended by Anderson et al. (2011). To examine the non-monotonicity in the plot of species spatial turnover (*x* axis is pairwise distance, and y axis is *dissimilarity* index), we defined that if there exists a mean at larger pairwise distances statistically lower (Welch-Satterthwaite *t* test; $p < 0.01$) than a mean at smaller pairwise distance (meaning that species composition is more similar for the communities farther apart), it is considered to be non-monotonic. For β diversity as variation, we considered the classic metrics of β diversity, including Whittaker's proportional β diversity ($\beta_W = \gamma/\bar{\alpha}$) and the additive model of β ($\beta_{ADD} = \gamma - \bar{\alpha}$) (Lande 1996, Crist and Veech 2006), as well as multivariate measures of β diversity (i.e., the mean of the pairwise dissimilarity indices), which are based on pairwise resemblance of species among habitats (Anderson et al. 2011). Since the classic β diversity is directly derived from α and γ diversity, we investigated the effects of SCHC on α and γ diversity as well.

RESULTS

SCHC INTRODUCES NON-MONOTONICITY TO SPECIES SPATIAL TURNOVER

By design, a neutral metacommunity model is free from the effects of environmental filtering, and thus patterns of spatial species turnover are shaped solely by stochastic dispersal. Therefore, we expect monotonic decay in species similarity with pairwise distance (or monotonic increase in species *dissimilarity* with pairwise distance) (Fig. 4.1); however, we found little evidence for this relationship (Fig. 4.2). Species turnover was non-monotonic when measured by the traditional presence/absence-based Sorensen index and the abundance-based Bray-Curtis index (Fig. 4.2). Chao index, however, showed less evidence for non-monotonicity in species spatial turnover across different configurations (Fig. 4.2). The non-monotonicity observed was caused by the variation in α diversity among the communities induced by the SCHC.

THE NULL MODEL APPROACH IS NOT EFFECTIVE IN SEPARATING Α FROM β DIVERSITY

Next, we tested the effectiveness of Chase et al.'s (2011) method to disentangle α from β diversity in spatially explicit context. We tested this method in two steps. First, we tested it using a randomly assembled metacommunity without dispersal limitation. The dispersal-free metacommunities were created by randomly selecting species from a common pool of a given regional diversity ($\gamma = 200$). Each species had the same probability of being selected and was assigned to local communities until the local habitat capacity was reached. The random assembly of species was repeated 500 times for each configuration. Our results demonstrated two main findings. First, the mean pairwise similarity across 500 realizations was 0, indicating no difference from a random assemblage (Chase et al. 2011). Second, the slope of turnover curve was 0, with an intercept of 0 (Fig. 4.3). These results suggest that the Chase et al. (2011) method was effective under random species assemblages, i.e., no dispersal introduced. It is worth noting that the confidence intervals were of varying widths, but all were wide (Fig. 4.3).

In the second step, we included dispersal limitation in creating metacommunities at landscapes of different SCHCs, and expected that β_{RC} would exhibit a monotonically increasing pattern in all configurations. Contrary to our expectation, in the hump-shaped and gradient configurations, we found that species turnover was non-monotonic (Fig. 4.3). We also found that the confidence interval generally became wider with increasing pairwise distance. Despite the widening confidence intervals, the non-monotonicity in species turnover curve was still statistically significant (Fig. 4.3).

SCHC CAUSES DIFFERENCES IN β DIVERSITY ACROSS METACOMMUNITIES

We assessed the effect of SCHC on β diversity across metacommunities to determine whether, after correcting the effect of α diversity by Chase et al.'s (2011) method, β diversity is statistically indistinguishable across landscapes with different spatial configurations of habitat capacities. To do this, we examined both types of β diversity: turnover and variation (Anderson et al. 2011).

We found that the slope between species similarity and geographical distance differed among varying configurations of the landscape (Figs. 4.2 and 4.3), and Chao index and β_{RC} did not conform to the linear models (i.e., very low r^2 values when the relationship was non-monotonic). We found that Whittaker's β_W and Lande's β_{Add} were also influenced by SCHC (Table 4.1; Fig. 4.4). Mean pairwise dissimilarity indices were also significantly different across configurations (Table 4.1; Fig. 4.4). Higher values were found in the V-shaped configuration and lower values in the hump-shaped configuration (Fig. 4.4). We also found that SCHC caused differences among metacommunities in both mean α diversity and γ diversity, especially in mean α diversity (Table 4.1; Fig. 4.4). Mean α diversity was much higher in the hump-shaped configuration than in the V-shaped configuration (Fig. 4.4). By contrast, mean γ diversity was slightly lower in the hump-shaped configuration than in the V-shaped configuration (Fig. 4.4).

DISPERSAL LIMITATION CHANGES THE EFFECT OF SCHC

We examined two effects of SCHC: (1) its effect on the *shape* of species turnover curve (i.e., whether it is monotonic), and (2) its effect on the *value* of β diversity, both as variation and turnover, across metacommunities (Fig. 4.1). Both effects varied with the strength of dispersal limitation (Table 4.1; Figs. 4.2 and 4.3). Non-monotonicity was more evident when dispersal was more widespread according to the three traditional indices (Fig. 4.2). For β_{RC}, which corrects for α diversity variation, SCHC had greater effects on the shape of species turnover when dispersal was more local (Fig. 4.3). When dispersal limitation was absent, the shape of species turnover across different configurations was similar (Fig. 4.3), suggesting little effect of SCHC. In terms of SCHC's effect on β diversity across metacommunities, the influence of SCHC was more pronounced when dispersal was more local (Table 4.1), i.e., the difference in β diversity among metacommunities caused by SCHC is amplified when the dispersal was more local. We explored five levels of dispersal limitation, but only reported result for two; all the patterns reported here hold for the rest three dispersal levels.

DISCUSSION

The interdependence of β and variation in α diversity is well established in the literature (e.g., Koleff et al. 2003, Jost 2007, Chase et al. 2011). One contribution of our study is to examine how spatial configuration of habitat capacity may affect different measures of β diversity in spatially explicit context, beyond just one pair of communities, through its influence on the variation in α diversity. We found that traditional similarity indices, be they incidence- or abundance-based were highly sensitive to the SCHC (Fig. 4.2). Even with only dispersal limitation in the model, patterns of species turnover measured by these indices were non-monotonic. Non-monotonicity, such as "peaks," "valleys," and "plateaus" (e.g., Condit et al. 2002, Anderson et al. 2013, Bogan et al. 2013), in species spatial turnover has been used as evidence for local environmental filtering processes shaping community composition and distribution. We did not observe non-monotonicity in the species spatial turnover measured by Chao index (Fig. 4.2). Our findings imply that, when local habitat capacities in the landscape are not uniform (a common occurrence), analyses of spatial turnover based on these frequently used similarity indices should be interpreted with care because they are at risk of inadvertently conflating ecological processes with confounding effect by α diversity in their conclusions.

The methods available to remove the influence of α diversity variation seem ineffective for the β diversity patterns discussed here. For example, Chase et al.'s (2011) null-model approach, which was designed specifically to correct for the effect of variation in α diversity on β diversity, is useful for deciding whether the community assemblage is significantly different from a random assemblage. But it was developed for a single community pair; our results show that it is not readily transferable for comparisons among all pairs at landscape scales (Fig. 4.3). Nonetheless, β_{RC} has already been applied at landscape scales in many very recent studies (e.g., Akasaka and Takamura 2012, Bernard-Verdier et al. 2012, Anderson et al. 2013, Siepielski and McPeek 2013).

Why can't β_{RC} be extended to more than one pair? The calculation of β_{RC} is based on comparing the value of SS_{obs} with the probability density distribution of SS_{exp}. The probability density distribution of SS_{exp} is generated by repeated random sampling for a pair of communities with given α diversity levels. Inevitably, α diversity levels vary across different community pairs. Different α diversity combinations result in different shapes of the SS_{exp} distribution (i.e., skewedness and variance) (Chase et al. 2011).

Variation in the shape of SS_{exp} distribution makes comparison among different pairs problematic.

We note that β_{RC} is highly sensitive to SS_{obs}. When SS_{obs} falls near the peak of SS_{exp} distribution, a small change in the value of SS_{obs} results in a disproportionally large change in the value of β_{RC} (see Fig. 4.5 and its caption for an example)—even a change in its sign. In reality, under-sampling of rare species could easily result in such small fluctuations in the value of SS_{obs} collected in the field. Therefore, β_{RC} are not reliable for inferring underlying ecological processes. To demonstrate this problem, we took two pairs of communities in the hump-shaped configuration as an example (Fig. 4.6). The first pair consists of the two communities at both ends (i.e., communities 1 and 30), and the second pair consists of communities 12 and 18, which are much closer to each other than the first pair. After removing the effect of variation in α diversity, we expected the second pair to be more similar in species composition, i.e., having a lower β_{RC}; instead, it was less similar (Fig. 4.6). Accordingly, this could lead to an interpretation that ecological processes other than dispersal are at play where there is none.

Another reason that SCHC causes complications in interpreting β diversity patterns is the spatial autocorrelation between the SCHC and dispersal. It is useful to see this through a lens of the effects of variation in habitat capacity. The variation in habitat capacity affects patterns of spatial turnover in two ways. First is a random sampling effect: if the overall species richness is fixed, two habitats with larger and more equal carrying capacity are likely to have a greater proportion of common species, hence a higher similarity value. Second is the spatial correlation between SCHC and dispersal. Corrective methods such as null-model shuffling (Kraft et al. 2011) effectively remove the random sampling effect, but not the spatial autocorrelation effect. Therefore, the effectiveness of these methods depends on species' dispersal capacity, which is difficult to estimate in reality, consequently, difficult to correct.

Another contribution of our study was that we confirmed the effect of SCHC on β diversity via its effect on landscape conductivity. The hump-shaped landscape and V-shaped landscape have same total habitat capacity; however, in the V-shaped landscape, the sites with lower habitat capacity level are located in the center of the landscape, and these lower-habitat-capacity sites are located on the edge of the landscape in the hump-shaped landscape. Smaller habitat capacity in the center of the landscape greatly reduces landscape connectivity, similar to bottleneck effect, and increases isolation among sites. As a result, the local species diversity is low (low mean α diversity), but the species composition is more spatially variable, i.e., higher β diversity (Fig. 4.4). By fixing the overall landscape carrying capacity, and only changing the spatial arrangement of habitats of different size, we demonstrated the significant effect of SCHC on different measures of β diversity. This mechanism is often neglected in interpreting β diversity patterns.

As the upshot of our investigation, we recommend that for ecologists who wish to use the shape of species spatial turnover to infer underlying ecological processes, Chao index is currently the best choice. According to our study, Chao index is considerably more robust than traditional similarity indices: it exhibits no or very weak non-monotonicity when only dispersal limitation is present. One possible explanation for this robustness is that SCHC influences spatial patterns of rare species, and the Chao index was already designed to minimize sensitivity to rare species (Chao et al. 2005). That said, the Chao index is not completely insensitive to the SCHC effects (Fig. 4.2). Our findings suggest that when inferring ecological explanations from β diversity patterns, researchers should take into account not only the commonly considered deterministic and stochastic processes (e.g., species adaption to habitat quality, dispersal, extinction, and speciation), but also the effects of spatial configuration of habitat capacities, which alters patterns of β diversity by introducing variation in α diversity and influencing landscape connectivity, which further influences dispersal limitation and other spatial processes.

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TABLE 4.1. Effects of the spatial configuration of habitat capacity (SCHC) measured by *F* (3, 1996) values on β-diversity, mean α diversity, and γ diversity at two levels of hypothetical dispersal. The smallest *F* (3, 1996) value was 6.3, when ***P* = 0.003. All other *F* values were greater than that, hence, much more significant effect of SCHC.

Dispersal levels	**Multivariate measure of β as variation**				**Classic measure of β**		**α and γ**	
	Sorensen	Bray-Curtis	Chao	β_{RC}	β_{Add}	β_W	Mean α	γ
1-unit	4806.4	9822.0	5357.1	7366.6	194.7	3330.3	2509.6	76.5
8-unit	13.8	89.5	6.3	194.8	130.0	1387.0	1158.0	45.7

Notes: For each configuration (total four different configurations, not including homogeneous configuration), 500 replicates (i.e., 500 realizations of the neutral metacommunity model) were used. γ diversity = ~200.

FIGURE 4.1. Schematic representation of the effect of spatial configuration of habitat capacity (SCHC) on β diversity – testing the validity of the two properties of β diversity when the metacommunity is controlled only by dispersal.

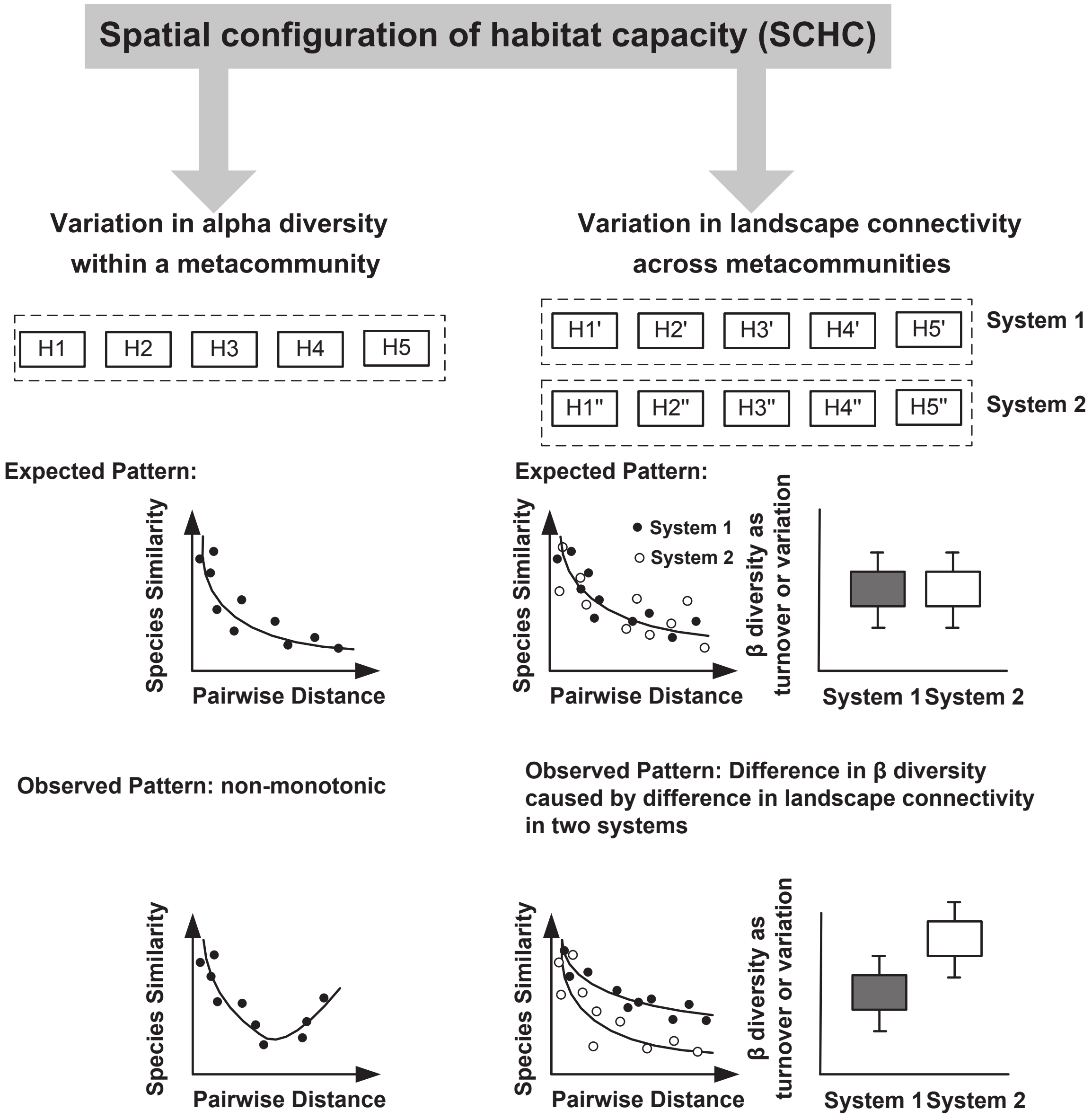


Figure 4.2. Effect of spatial configuration of habitat capacity (SCHC) on species spatial turnover at two levels of dispersal limitation (solid red line: 1 distance-unit; solid blue line: 8 distance-units).

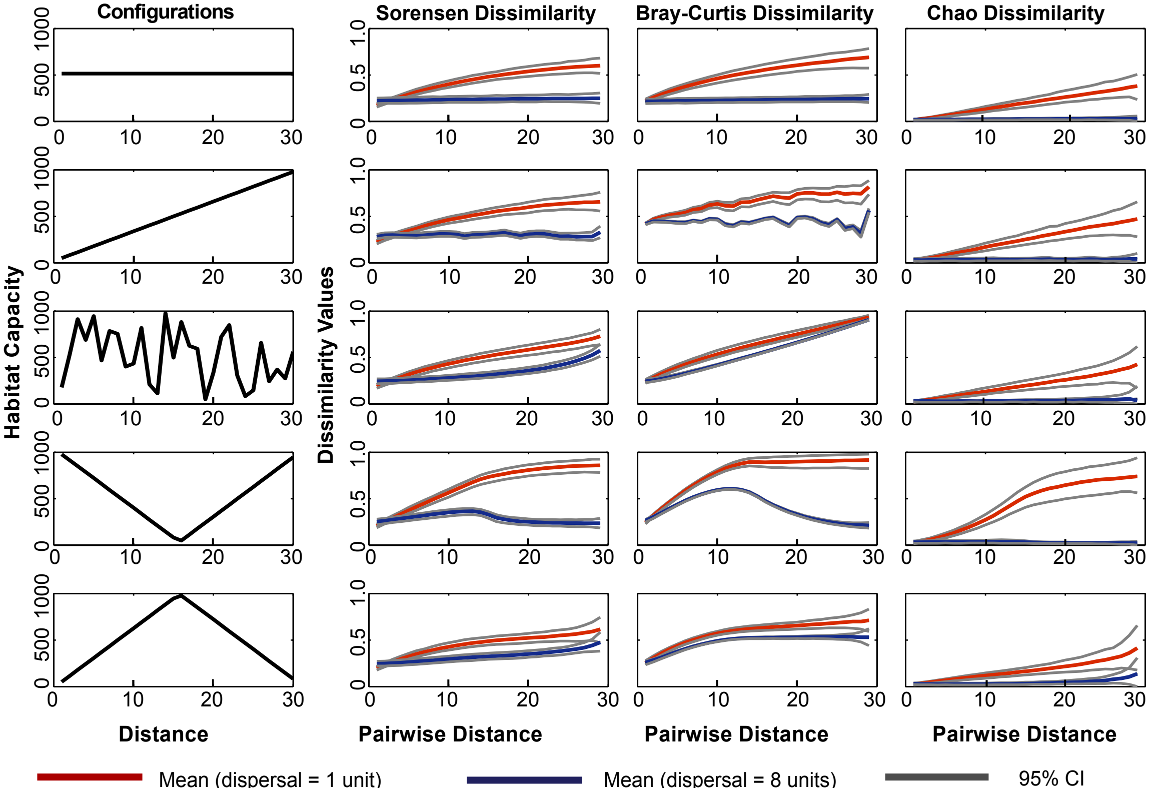


FIGURE 4.3. Patterns of β_{RC} at different levels of dispersal distance (no dispersal, dispersal distance = 1 unit and 8 units; γ diversity = ~200).

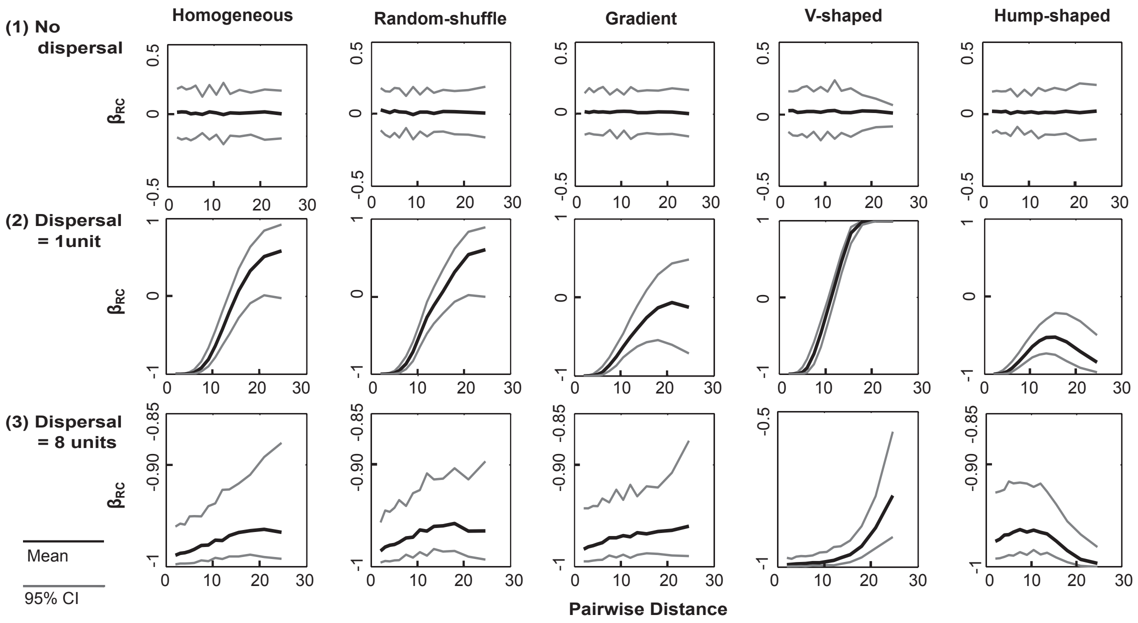


FIGURE 4.4. The influence of SCHC on β diversity as variation, measured by classic metrics of species diversity (mean α, γ, β_{Add}, and β_w) and mean of dissimilarity indices (Sorensen dissimilarity index (SDI), Bray-Curtis dissimilarity index (BCI), Chao dissimilarity index, and β_{RC}). The results were based on 500 realizations of the neutral metacommunity model with a characteristic dispersal distance of 1 unit.

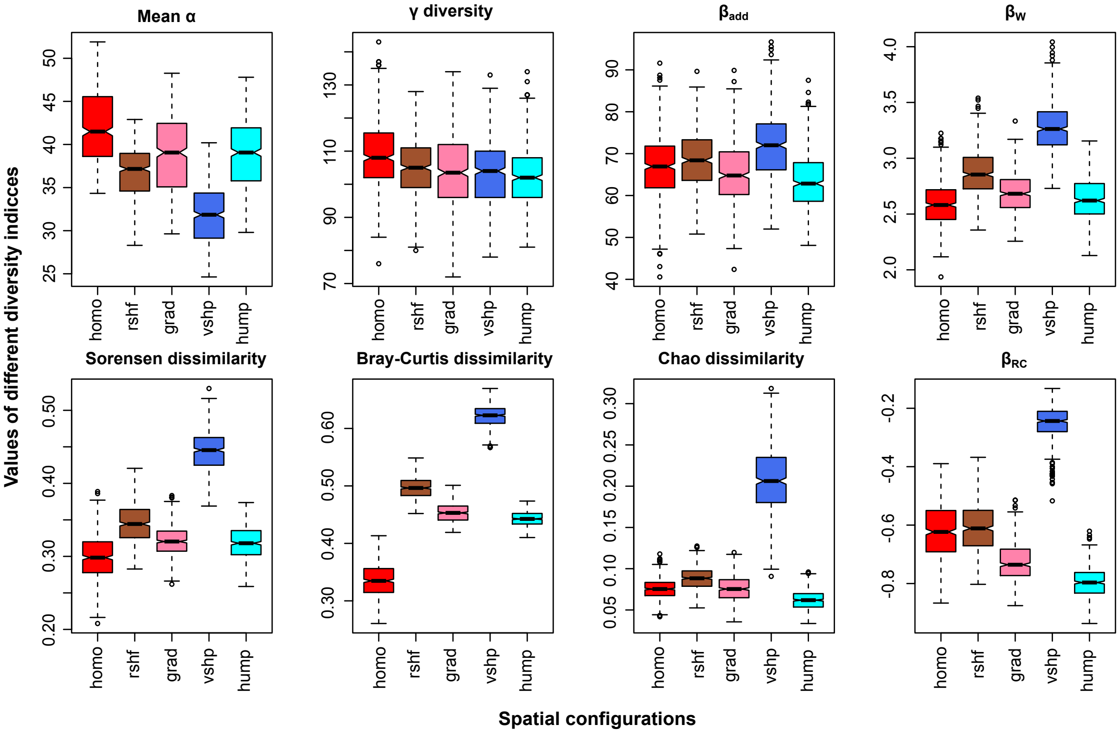


FIGURE 4.5. Sensitivity of β_{RC} to small changes in observed shared species (SS_{obs}) when the value of SS_{obs} falls within or near the peak of SS_{exp} distribution. SS_{exp} distribution was created by 99,999 repeated random draws of α_1 and α_2 species from a known species pool. The γ diversity of 204 was taken from one of the neutral metacommunity model realizations in the V-shaped configuration with dispersal distance of 8 units.

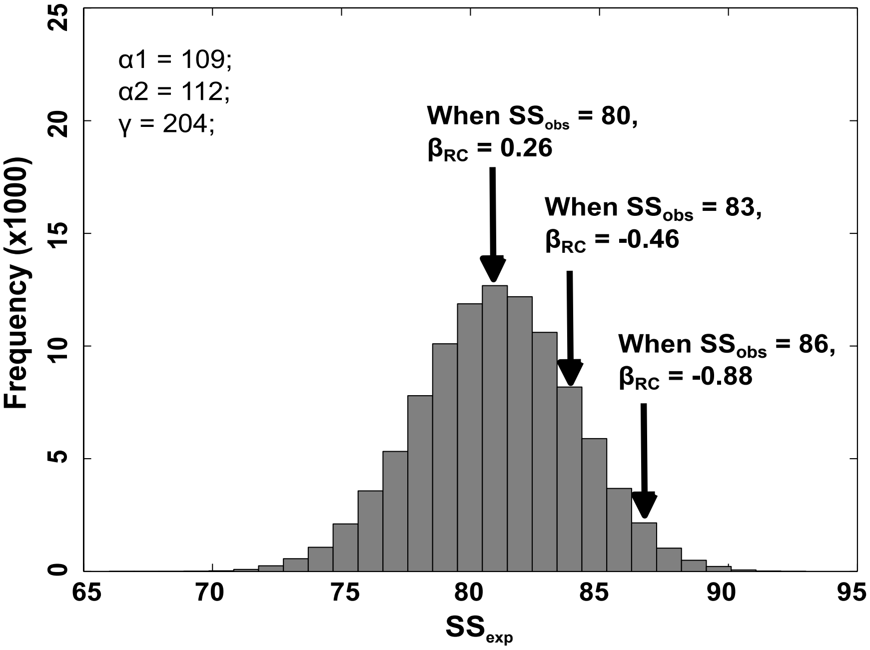
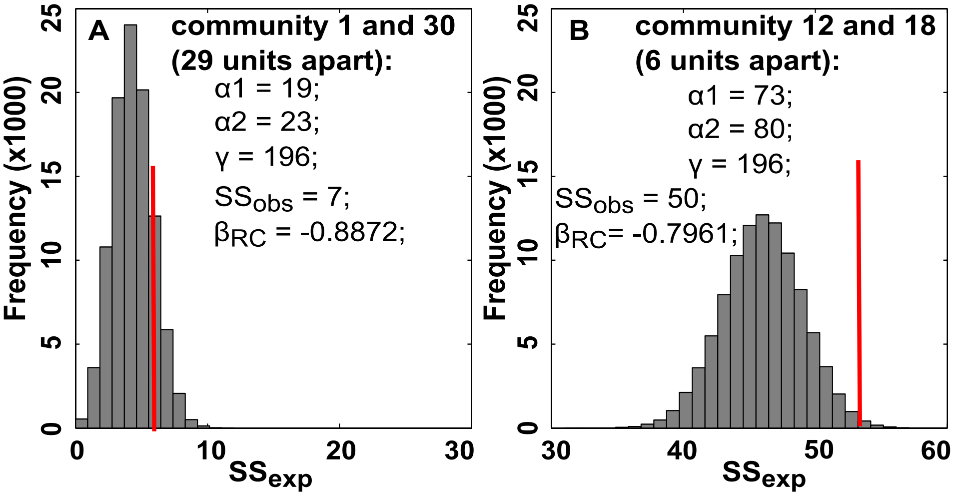


FIGURE 4.6. Influence of the shape of SS_{exp} distribution on β_{RC}. The two pairs of communities shown are from the same neutral model realization: (A) the pair of communities with 29 units apart; and (B) the pair of communities with 6 units apart. Red bars indicate the number of observed shared species.



CHAPTER 5

NEUTRAL THEORY APPLIED TO A DESERT STREAM NETWORK CHARACTERIZED BY VARIABLE HYDROLOGICAL REGIMES

ABSTRACT

Neutral models are dynamic, and should explain patterns in both space and time; however, little work has been done on the effects of neutral processes in dynamic environments. We constructed neutral models with different levels of temporal variability, and compared model results with freshwater invertebrate data collected in a desert river network in Arizona, USA, between 2009 and 2011 across eight sampling seasons in 20 sites. Model performance was improved by including temporal variability, especially inter-annual hydrological variability, although only marginally. Regardless of the parameter values used in the model, the relative fits for eight sampling seasons did not change. This failure can be ascribed to the particular formulation we used to model the temporal variability: it might be missing some important aspects of temporal structure, such as legacy effects of disturbance in time or cross-scale interactions. Alternatively, results may suggest that the relative importance of niche and neutral processes varied in time depending on hydrological conditions at the time of sampling. Model fit decreased with increasing discharge (i.e., wetter), except in the summer 2010, when discharge was very high. This suggested that neutrality is important when the stream discharge is either very high or very low. At either extreme, the spatial pattern of flow is relatively more homogeneous; hence, niches overlap more and the system is closer to neutrality. At intermediate discharge levels, spatial heterogeneity is highest, niche overlap is least. Overall, freshwater invertebrate communities in desert streams, characterized by strong spatial heterogeneity, high temporal dynamics, and low species richness, are dominated by environmental selection.

Keywords: biodiversity; desert stream; dispersal; hydrological variability; metacommunity; neutral theory; river network.

INTRODUCTION

Neutral theory in community ecology (Hubbell 2001) has progressed substantially during recent years and the arguments both for and against it have matured (Rosindell et al. 2011). Neutral theory makes a controversial “neutrality assumption”: all individuals within a particular trophic level have the same chances of reproduction and death regardless of their species identity (Hubbell 2001). Ecologists increasingly appreciate the merits of neutral theory (Alonso et al. 2006; Adler et al. 2007), both in a philosophical and technical sense. Philosophically, the assumption of ecological equivalence is parsimonious, only to be replaced by more complex mechanisms when data convincingly tell us so. Technically, neutrality functions as an approximation that may work well for macroscopic properties at appropriate spatial and temporal scales (Holt 2006). However, few ecologists believe that the world is neutral – all biologists know that species differ in many exquisite and complex ways. On the contrary, empirical evaluation of neutral theory has shown many limitations (McGill et al. 2006). However, not all limitations are attributable to the neutrality assumption – some may be caused by the particular model formulation employed. For example, a spatially explicit neutral model has been shown to give a much better description of species-area relationships than the original spatially implicit version (Rosindell and Cornell 2007).

Neutral theory of biodiversity was originally spatially implicit. It envisioned a well-mixed metacommunity (“mainland” of potential immigrants) and a separate local community (“island”) (Hubbell 2001). Explicit consideration of spatial structure represented a significant advance (Rosindell and Cornell 2007). Volkov et al. (2007) considered several (instead of one) local communities, to provide a more realistic description of metacommunity. Further developments in the form of networks of patches were extensions of these ideas that provided even greater realism. This type of model was applied to fish communities in river networks, where it produced excellent fit to both species richness pattern and species spatial turnover (Muneepeerakul et al. 2008). More model extensions and relaxation of assumptions other than neutrality are needed to truly explore the domain of applicability of the neutrality assumption (Etienne 2007).

One assumption to relax is the temporally static setting employed in many neutral models. Neutral theory is dynamic, which means that it should explain biodiversity patterns not only in space, but also in time. However, little work has been done on the effects of neutrality in dynamically changing environments, as pointed out in a recent review for the neutral theory at "age 10" (Rosindell, Hubbell & Etienne 2011). Keil et al. (2010) studied population dynamics in a patch-based neutral model and showed that neutral theory can reproduce Taylor's power law relating the mean and variance in population size for a given species. Adler (2004) used 35 years of data from permanent plots in Kansas grasslands to test the ability of neutral models to produce observed species-area relationships (SARs) and species-time relationships (STRs). The model could generate realistic SARs or STRs, but not both simultaneously. The author attributed the failure of the model to "large interannual variation in resources in the system", which was not included in the model.

Environmental temporal variability is an important force driving community dynamics (Taylor and Warren 2001; Urban 2004; Gouhier et al. 2010). This is especially true for certain ecosystem types, such as stream ecosystems, whose species composition and abundance are heavily influenced by the hydrological regime at multiple time scales

(Smith et al. 2003; Boix et al. 2010; Poff et al. 2010). Temporal variability itself is a strong environmental filter in shaping community structure (Poff and Ward 1989). The effects of environmental temporal variability have received considerable attention in the literature on population and community processes (Rodriguez-Iturbe et al. 2009; Chesson 2000). How useful or valid is the neutral process in such variable environments in capturing biodiversity patterns? To our best knowledge, this question has never been investigated.

In temporally variable ecosystems, dispersal capacity and disturbance regime (both frequency and size) could interact to shape biodiversity patterns (Roxburgh et al. 2004). Population size shrinks during disturbance, freeing up niches. Species with strong dispersal capacity could quickly colonize empty niches in post-disturbance recovery. Under high-frequency disturbances, better dispersers can persist, while under low-frequency disturbance, differences between better dispersers and poorer dispersers are less evident. The interaction between dispersal capacity and disturbance regime could directly influence patterns of both species richness and abundance.

Neutrality may be more pertinent in some environments than others (Gravel et al. 2006; Holt 2006; Scheffer and van Nes 2006). The relative importance of competitive vs. stochastic exclusion creates a continuum from niche-structured communities to neutral structure. In heterogeneous landscapes, the species tend to have non-overlapping niches, and niche differentiation is likely to be the dominant process affecting species abundances. In contrast, the validity of neutrality assumption is thought to increase in more homogeneous landscapes as a result of increasing niche overlap, and hence, intensified competition (Gravel et al. 2006). Environmental temporal variability could induce landscape heterogeneity. For example, streams in desert river networks have different levels of water permanence, and flow heterogeneity is lowest under both very dry and very wet conditions (Dong et al. 2015). The contribution of neutral process in shaping biodiversity pattern is therefore likely to vary in time in such ecosystems.

In this study, we tested the neutral theory in an environmentally dynamic ecosystem. We used a dataset of aquatic invertebrates collected between 2009 and 2011from a river network located in southern Arizona. The system is characterized by high heterogeneity both in space and time. Spatially, the river network is formed by a spatial configuration of ephemeral, intermittent, and perennial streams with different levels of water permanence. Temporally, precipitation changes greatly over seasons and across years, which consequently influences hydrological connectivity in the landscape. We included temporal variability at two time scales (intra- and inter-annual) in spatially explicit neutral models. We tested two specific hypotheses and predictions: (1) including temporal variability improves performance of neutral models in an environmentally dynamic system; and (2) performance of models is influenced by hydrological conditions (i.e., the wet-dry gradient), because of the combined effects of hydrology on hydrological connectivity, dispersal, and flow heterogeneity of the river network.

METHODS

SITE AND CLIMATE DESCRIPTION

The data for this study were collected in the Huachuca Mountains located in southeastern Arizona, U.S.A. (Fig. 5.1). Mean annual precipitation in the region is about 35 cm, but is highly variable from year to year (Fig. 5.2a). Precipitation is strongly bimodal within a year, with roughly 60% of precipitation occurring during brief, intense summer (July-September) monsoon storms and 40% during more prolonged, moderate-intensity winter (November-April) storms (Fig. 5.2b). During the study period, summer storms produced much higher discharge peaks that rapidly declined, whereas a single winter storm in 2010 produced prolonged high discharge. Winter and spring runoff during 2009 and 2011 was low.

The aquatic invertebrate data were collected across eight sampling seasons, from 2009 to 2011, during the summer and winter high-flow periods and the fall low-flow period (Fig. 5.3a). 2010 had significantly higher discharge than the other two years; the lowest discharge was observed in 2009. The samples were taken from 20 sites in Huachuca Mountains (Fig. 5.1), covering perennial, intermittent, and ephemeral streams. In each sampling season, only a subset of all 20 sites was visited and sampled. Detailed descriptions of data and sampling methods can be found elsewhere (Bogan and Lytle 2007).

RIVER NETWORK CHARACTERISTICS AND STREAM TYPES

We used data from the NHDPlus Version2 to delineate the boundary of the San Pedro watershed draining the Huachuca Mountains. It contains a total of 561 catchments and streams (Fig. 5.1). Catchment area and streams were also directly extracted from the NHDPlus Version2.

Headwater streams in the Huachuca Mountains are spring-fed and thus perennial. Downstream of these perennial headwaters, streams flow across alluvial fans with a gravel substrata where surface water losses to evaporation and infiltration are high, and streams become intermittent. Surface flow in these intermittent streams persists for weeks to months after precipitation. Further downstream, the water table never rises to the level of the stream bed and flow becomes ephemeral. Surface flow occurs for very short periods (< 1 day) in response to extreme precipitation events. Below the alluvial fans, perennial rivers flow through incised fluvial floodplains. Regardless of stream type, all streams are prone to flooding and drought disturbance.

To identify the hydrological type for each stream in the river network, we constructed a classification tree model using field sensor data on water permanence (the sensor data from Jaeger and Olden (2012), with detailed description therein). We used three categories of flow permanence: 0 (ephemeral), 1 (intermittent), and 2 (perennial or near-perennial), as a function of geology, cumulative drainage area, and elevation. The geology data (i.e., the types of mineral) were collected from USGS (Arizona Geology Layer: http://mrdata.usgs.gov/geology/state/state.php?state=AZ; and North American Geology Layer for Mexico via ArcGIS: http://www.arcgis.com/home/item.html?id=2967ae2d1be14a8fbf5888b4ac75a01f). The Geology data layer was imposed on the catchment delineation layer so that each catchment in the river network was labeled with its major mineral type, which was used as one of the input variables for the classification tree model to determine the hydro-type of each stream (Fig. 5.1). The analysis was carried out in R (R Core Team 2014) with the package ‘tree’ (Ripley 2015). It is important to note that the sample size for the classification tree model was low – only 25 sensors, hence, water permanence for 25 streams (compared to a total of 561 streams within the whole drainage area), and sensors were concentrated within a relatively small area (Fig. 5.1), which did not necessarily capture the variability of the large drainage areas.

QUANTIFYING HYDROLOGICAL TEMPORAL VARIABILITY

We used the discharge data within the study period (2009-2011) to determine the duration of high flow and low flow periods in a year (Fig. 5.2b). There are six USGS gauges located within the boundary of the watershed (STAID 09471400, 09471380, 09471310, 09470800, 09470750, and 09470700; Fig. 5.1). Based on the discharge regime from the six gauges between 2009 and 2011, we estimated 16 weeks for the duration of the winter high flow period, 12 weeks for the summer high flow period, and 12 weeks each for spring and fall low flow periods for an average year (Fig. 5.2b).

We obtained the spatial gradient of precipitation across the watershed from USGS National Atlas GIS data for annual precipitation (Fig. 5.1). This represented the precipitation spatial gradient in an average year. We extracted the precipitation for each catchment within the watershed. To simulate the inter-annual variability in precipitation, we obtained annual precipitation data (non-spatial) between 1922 and 2014 from NCEP North American Regional Reanalysis (NARR) by National Oceanic & Atmospheric Administration (NOAA) for this area. We used a first-order autoregressive model to fit this long-term dataset:

$$PT_{yr} = \varphi PT_{yr-1} + w_{yr}$$

, where *PT* was annual precipitation, φ was the coefficient (i.e., lag 1 autocorrelation), and *w* was the noise term, which captured the stochasticity. We fitted w_{yr} with different distributions, and a gamma distribution was the best fit, with shape parameter $k = 3.40$, and scale parameter $\theta = 4.95$.

ESTIMATING HABITAT CAPACITY

We used the product of precipitation and watershed area (PT×WA) as the kernel to explore the relationship with α diversity for each sampling with observed data. We found that α diversity first increased with PT×WA, then decreased, with a heavy tail (Fig. 5.4). We used a transformed gamma distribution to fit the relationship between α diversity and PT×WA. This way, we can use the product of precipitation and watershed area for each catchment to infer its local species richness. However, we needed habitat capacity, not local species richness. To get that, we used the species-area relationship (actually the "species-*habitat capacity*" relationship) to infer habitat capacity of each catchment (HC_i) based on the estimated α diversity (α_i):

$$HC_i = (b\alpha_i)^a$$

where a and b parameters were to be determined by model fit.

DESCRIPTION OF NEUTRAL METACOMMUNITY MODEL

Four model variants were constructed with different levels of complexity of temporal variability: (1) Basic Model - model without any temporal variability; (2) Seasonal Model - model included seasonality; (3) Annual Model - model includes inter-annual variability; and (4) Full Model - model included both seasonality and inter-annual variability. All four models explicitly included the river network structure (Fig. 5.1).

Basic Model was similar to the model developed by Muneepeerakul et al. (2008), which included stochastic dispersal, reproduction, mortality, and speciation. Using the river network, we determined the distance matrix for dispersal. First, we extracted two different types of distance: channel distance (i.e., distance along the channel) and Euclidean distance (i.e., shortest distance between the middle points of a pair of streams). To decide which to use, we plotted the relationship between species similarity and pairwise distance, measured with both types of distances. We expected a distance decay relationship (Morlon et al. 2008). We found species similarity decreases with Euclidean distance, but not with channel distance (Fig. 5.5). This suggested that the dominant dispersal mechanism for the species in this meta-community was likely areal dispersal, instead of in-stream drift. Using a manipulative experiment in the same system, Bogan and Boersma (2012) showed that about 1/3 of taxa documented from neighboring streams arrived at isolated experimental pools within two weeks via aerial dispersal, lending support to the areal dispersal mechanism.

The metacommunity consisted of 561 local communities. The dispersal kernel was assumed to be bivariate Students' *t* or "2Dt" kernel (Clark, Silman, and Kern 1999), which can be written as

$$K_{ij} = C_j \frac{p}{\pi l_0^2 [1 + \left(\frac{L_{ij}}{l_0}\right)^2]^{p+1}}$$

where K_{ij} is the probability that an organism produced at site *j* arrives at site *i* after dispersal; *C* is a normalization constant to ensure that for every site *j*, $\sum_i K_{ij} = 1$, i.e., no organisms traveled out of the metacommunity. L_{ij} is the Euclidean distance between two habitats. l_0 is the distance where, after dispersal, the ratio between its offspring and those at the origin location is $2^{-(1+p)}$. This dispersal kernel is determined by two parameters, l_0 and p. It was chosen because 2Dt kernels can exhibit a wide range of different behaviors from the heavy-tailed Cauchy kernel when p approaches 0 to the thin-tailed Gaussian kernel when p approaches ∞ and others in between.

At each time step, a randomly selected individual died (with probability m) and the resources that previously sustained that individual became available to sustain a new individual. With probability v, the diversification rate, the empty spot was taken up by a new species (the diversification rate is a per-birth rate and is due to speciation or to immigration of a new species from outside the metacommunity). With probability $1-v$, the empty spot was occupied by a species already existing in the system. In the latter case, the probability P_{ij} that the empty spot in site i would be colonized by a species from habitat j was determined as follows:

$$P_{ij} = (1-v)\frac{K_{ij}H_j}{\sum_{k=1}^{N} K_{ik}H_k}$$

where K_{ij} is the dispersal kernel, H_k is the habitat capacity of site k, and N is the total number of sites (i.e., communities). All the organisms in site j had the same probability of colonizing the empty spot at site i where the death took place.

Seasonal Model was modified from the Basic Model by including the intra-annual variability in habitat capacity, introduced by the alteration of the high-flow period and low-flow period. We included seasonal variability by changing habitat capacity among four different flow periods, and set the mean annual precipitation constant across years. From one flow period to the next, habitat capacity of each catchment changes. If the habitat capacity increases, there will be sites available to be occupied in that catchment.

These unoccupied sites will be recolonized with a probability of *r*. The recolonizing species can be from species already existing in the metacommunity with probability 1-*v,* or from new species with probability *v*. The recolonization occurs in each time step until all the unoccupied sites are taken. In another case, if the habitat capacity decreases from one flow period to the next, a randomly selected set of individuals, whose number equals the difference of habitat capacity in two flow periods, die. All the other processes in the Seasonal Model were the same as they were in the Basic Model.

Perennial streams were assumed to have the same habitat capacity in all four seasons, equal to the value estimated by PT×WA (Fig. 5.4). The habitat capacity for intermittent and ephemeral streams varied among seasons, modified by a season-specific weight. The values of the weights were estimated from the observed species richness data for corresponding stream types.

The Annual Model was developed from the Basic Model with incorporation of inter-annual variability in habitat capacity introduced by interannual variability in precipitation, which was simulated using the first-order autoregressive model described previously. From one year to the next, when the mean precipitation changes, it changes the habitat capacity of each catchment (as described above, HC_i was estimated by the product of precipitation and catchment area). As with the Seasonal Model, if habitat capacity increases, unoccupied sites appeared in the first time step of a year, and will be recolonized with a probability of *r*. The recolonizing species can be from species already existing in the metacommunity with probability 1-*v,* or from new species, with probability *v*. Recolonization occurs in each time step until all the unoccupied sites are taken. If habitat capacity decreases from one year to the next, a randomly selected set of individuals, whose number equals to the difference of habitat capacity in two years, die.

The Full Model simulated both seasonality and inter-annual hydrological variability. It basically is a combination of all the processes in Seasonal and Annual Models. What is different is that the duration of each flow period changes every year, i.e., the increase or decrease in the duration of the high flow periods is proportional to the increase or decrease of the precipitation in that year compared to precipitation in an average year.

Each time step in the model represented one week, and it took about 80,000 time steps (about 1500 y in model time) to reach statistical steady state, i.e., when the biodiversity pattern became stabilized, showing no directional trend in the mean local species richness or the total species richness. After the model reached steady state, we ran another 1000 y of model time to calculate average patterns.

QUANTIFYING MODEL GOODNESS-OF-FIT

We used patterns of α and β diversity (measured by Chao similarity index (Chao et al. 2005)) to assess the fit between observed and modeled results from the Full Model. The best-fit parameter set was chosen by the following procedure. We ran several simulations with different sets of parameters distributed over a wide meaningful range. For every simulation, we computed the error between data and model for the two biodiversity patterns: α and β diversity. The error for pattern k, E_k ($k = 1, 2$), was estimated by the mean square deviation between data and predicated values normalized by the data variance; this can be expressed as follows:

$$E_k = \frac{\sum_{i=1}^{N_k}(x_{k,i} - \hat{x}_{k,i})^2}{\sum_{i=1}^{N_k}(x_{k,i} - \langle x_k \rangle)^2}$$

where N_k was the number of data points used in fitting pattern k, $x_{k,i}$ and $\hat{x}_{k,i}$ were data point i (data points from all eight sampling events across three years) of pattern k and its predicted value, respectively, and $< x_k >$ the mean value of the data points of pattern k. We then defined the total error, *TE*, of each parameter set as $E1 + E2$. TE was used as a metric to decide model goodness-of-fit, and models with lower *TE* fit better with data. The parameter set with minimum *TE* was selected, and was the best-fit parameter set (Table 5.1).

The comparison between model results from the Full Model and observed pattern was done at different aggregated levels: (1) among-season comparison: observed data were averaged over three years to be aggregated by season to compare with results from the Full model that were aggregated by season across different years; and (2) among-year comparison: observed data were aggregated by years to compare with results from the Full Model that were aggregated by year. To get the model results by year to match the three sampling years, we selected years with similar hydrological condition in the model. We first calculated the quantile of annual precipitation of each year (2009 to 2011) within the simulated precipitation series (1000 y at model steady state). For each year, we expanded the range of that year's quantile until 10 simulated years fell within that range. We used that 10-y modeled results to calculate the average patterns and compared them with the patterns of the corresponding sampling year.

We used best-fit parameters from the Full Model in the Seasonal Model, Annual Model, and Basic Model. This was because we assumed there was only one best parameter set characterizing the underlying processes of the system, regardless of the model construct. For example, characteristic dispersal distance should be the same value regardless of the way temporal variability was constructed in different model variants.

All the simulations were carried out in MATLAB 7.10.0 (The MathWorks Inc. 2000). Spatial maps and data were processed in ArcGIS 10.1. (ESRI 2012).

ANALYZING VARIABLES INFLUENCING MODEL PERFORMANCE

Based on the model goodness-of-fit, we explored variables that could potentially influence model performance: hydrological condition, dispersal mechanism of species in the metacommunity, and the spatial range of the metacommunity. To test the effect of dispersal mechanism (approach), all the species (272 in total) were categorized into two groups according to their dispersal mechanisms at their adult stage: aquatic and aerial dispersal. We then evaluated the relationship between the proportion of species of different dispersal mechanisms and model performance. For hydrology, we calculated mean discharge for different seasons, years, and stream types, to correlate with model performance. The spatial range of the metacommunity was quantified by calculating the average pairwise distance of all sampled sites in each sampling season.

RESULTS

Overall, the predictive capacity of the neutral models – all four models – was not satisfactory (based on *TE* value described in Methods) in predicting the biodiversity patterns of aquatic invertebrates in the river network of Huachuca Mountains (Tables 5.2 and 5.3; Figs 5.6 and 5.7). Nonetheless, including temporal variability, seasonality and/or inter-annual variability, did improve model performance. Not surprisingly, the Full Model, with explicit modeling of both seasonal and inter-annual variability, provided best predictive capacity (Table 5.2). The model performance was slightly better after including inter-annual variability, compared to including seasonality (Table 5.2), indicating that the effect of interannual variability likely played a more important role than did seasonality in shaping species abundance and distribution in this system. The basic model, which did not include any temporal variability, has the poorest performance among all model variants, with its total errors greater than 1 (Table 5.2). Additionally, the importance of including temporal variability was also supported by the fact that errors between the aggregated observed data and the aggregated result from the Full Model are less than those from the model variant with the same variability as the data aggregation. For example, when the year- and season- specific results from the Full Model were aggregated by season across years, its fits were consistently better than the fit by Seasonal Model. The same is true for the comparison between the aggregated annual results from Full Model and the results from the Annual Model (Table 5.2). Lastly, the model prediction for the pattern of α diversity was generally much better than that for the pattern of β diversity (Table 5.2; Figs 5.6 and 5.7).

Using the result from the Full Model, we evaluated model fit across different variables, i.e., season, year, and stream types, to assess how the model performance varied in these dimensions. The fits of α diversity pattern were still generally better than that of β diversity (Table 5.4). For α diversity, the driest year in all three years (2009) had the poorest fit. The fit was slightly better for 2011 than for 2010. The poorest fit for β diversity occurred in the wet year 2010. By cross-season comparison, the summer high flow period had the poorest fit for both α and β diversity, and the fall low flow period had the best fit for both patterns. Lastly, the model performed much better in predicting biodiversity patterns in perennial streams than it did for non-perennial streams (Table 5.4).

We then checked the year- and season- specific result from the Full Model (Table 5.3; Fig. 5.8). For the pattern of α diversity, the best fit occurred in 2010 summer, the high flow period in a very wet year and poorest fit in 2009 summer and 2011 fall, whose total errors were greater than 1. For the pattern of β diversity, fall 2011 also had the poorest fit, whereas the best fits were for 2010 summer and 2011 winter (Fig. 5.8).

Interestingly, the relative predictability of the model for each sampling event did not change with the combinations of parameter values used (Fig. 5.8). The absolute model goodness-of-fit could be improved or worsened depending on the values of parameters, but the pattern of relative model goodness-of-fit did not change. This applied to both the fit for α diversity and for β diversity patterns (Fig. 5.8).

We analyzed the relationship between model goodness-of-fit and different observed variables, including hydrology, species dispersal capacity, and the spatial range of the metacommunity, to evaluate their effects on model performance and thus the validity of the neutrality assumption.

Hydrology – the model performance was poorest for the intermediate range of discharge. When the mean daily discharge of the sampling month was below 3 $m^3 s^{-1}$ (~100 cfs), the model's ability to predict the α and β patterns decreased with the discharge, i.e., better fit in lower-discharge periods (Fig. 5.3b). However, when the mean daily discharge reached about 7 m^3 s^{-1} in the summer high flow period of 2010, a very good model fit was obtained (Fig. 5.3b).

Dispersal mechanisms – we extracted sites, which were sampled repeatedly in all three seasons within the same year, to compare how the proportion of the aerial dispersal species changed. Within the same year, these streams had a notable increase in the proportion of aerial dispersal species in the low flow period (i.e., fall) compared to that in the high flow period (i.e., summer or winter). For example, in 2010, data showed that the proportion of the aerial dispersal species decreased from 91%, to 74%, and to 69% when mean daily discharge increased from 0.74 m^3 s^{-1} to 1.8 m^3 s^{-1} to 7.4 m^3 s^{-1} across three sampling seasons. Regardless of the apparent negative correlation between the discharge and the abundance of aerial dispersal species, there was no significant correlation between the proportion of aerial dispersal species in the metacommunity and the model goodness-of-fit (Fig. 5.9).

Spatial range of the sampling sites – in each sampling seasons, the subset of sampling sites varied. In some seasons, the sampling sites were more scattered than others. When the sampling sites were more scattered in space, the performance of the model for β diversity was better. When the sites were more spatially clustered, the total error increased notably (Fig. 5.10). However, the variability of the total error was large when the spatial range was short (Fig. 5.10b). This correlation only applied to predictions of β diversity patterns, not for α diversity patterns.

DISCUSSION

Including temporal variability in the neutral model for aquatic invertebrate species in an environmentally dynamic system did improve model performance. This suggests that the neutrality assumption is not always to blame for unsatisfactory fit – it could be that the particular formulation of the model is to blame (i.e., here whether or not to include temporal variability). However, despite being spatially and temporally explicit, the Full Model's predictive capacity was limited at best (Tables 5.1, 5.2, and 5.3). Regardless of the parameter values used, the model goodness-of-it for certain sampling periods was consistently better than others (Fig. 5.8). This implies that certain aspects of temporal variability may be still missing. Using a spatially implicit neutral model, Etienne (2007) found that a separate local community can fit species abundance in a single forest plot, but cannot simultaneously fit species abundances in three distinct forest plots with the same parameters. His result highlighted the potential importance of explicit spatial structure, as the model used was only spatially implicit. Our results, on the other hand, suggested the importance of temporal variability. We modeled seasonality and inter-annual variability by varying the habitat capacity with precipitation (variation in precipitation seasonally and annually). However, just like in explicitly defining a spatial structure, defining the temporal structure itself is difficult. Other more complex hydrological effects such as legacy effect of hydrological disturbance (Parsons et al. 2005) and cross-scale interactions (Peters et al. 2004) could be playing a role in influencing habitat capacity and species neutral processes. These could be introduced to the model, while still retaining the neutrality assumption. Alternatively, the difference in model fit for different sampling periods could be caused by the actual variation in the relative importance of neutral vs. niche processes in determining biodiversity.

Gravel et al. (2006) and Scheffer and van Nes (2006) showed that community structure reflects both niche organization and neutrality. These studies suggest that the emergence of near-neutral suites of species is more likely in species-rich communities. The validity of the neutrality assumptions increases with species richness, as a result of increasing niche overlap, hence intensified competition (Gravel et al. 2006). Based on this, we could expect some communities to be species rich and niche dominated, because of a highly heterogeneous environment that enables low niche overlap; or we could expect some species-poor communities to be neutral because of a homogeneous environment that increases niche overlap. Our findings lend support to this hypothesis. We found that in both very low and very high discharge periods, the model fit was much better than hydrological condition closer to the central tendency (Fig. 5.3). When stream flow is very low or very high, the whole landscape is more homogeneous (uniform low (or zero) or high stream flow), hence, more niche overlap occurs and the system is closer to neutrality.

Neutrality is more pertinent to some taxa and environmental settings than others (Gravel et al. 2006; Holt 2006; Scheffer and van Nes 2006). In places where the environment is relatively homogeneous, species richness is high, and the taxa possess strong capacity for long-ranged dispersal, neutrality is shown to be stronger (Gravel et al. 2006). However, desert streams are strongly heterogeneous in space and highly dynamic in time, subject to frequent disturbance including both drought and floods. Additionally, desert streams have much lower insect species richness than streams of other? biomes

(Vinson and Hawkins 2012). In terms of dispersal, freshwater invertebrates can be categorized as active or passive, but in general the dispersal limitation is strong (Bilton et al. 2001; Bohonak and Jenkins 2003); long-distance dispersal is achieved through animal vectors, such as birds (Green and Figuerola 2005), but it is not the dominant dispersal approach. All these attributes suggest that aquatic invertebrate communities in desert streams are likely dominated by environmental selection and the contribution of neutral processes is minimal (Clarke et al. 2008; Grönroos et al. 2013). Our findings agree with these corollaries.

Several lines of evidence in our study indicate a strong influence of niche processes in shaping the biodiversity patterns in dryland streams. In addition to finding the best parameter set for all eight sampling events simultaneously, we also extracted the best-fit parameter for *each* sampling event. This still did not significantly improve the fit (Table 5.3; Figs. 5.6, 5.7, and 5.8). This indicated the strong roles played by niche processes. The models performed better for perennial streams than for the intermittent or ephemeral streams (Table 5.4). This difference was likely due to the unique hydrological regime of non-perennial streams, which strongly selects for species that adapt to that particular regime. Bogan and Lytle (2011) monitored two study pools seasonally for eight years, and found that the stream pool communities underwent a catastrophic regime shift in community structure after a transition to intermittent from perennial flow, suggesting dominant roles of hydrology in determining community structure. In another study, Bogan et al. (2013) found that communities with similar hydrological conditions were much more similar to each other, compared to communities that were located closer by in distance, but with different hydrological conditions.

In ecosystems with high temporal environmental variability, it is very likely that species are not in equilibrium with the environment. Such transient periods may happen after a large disturbance (in our model, both drought and floods are disturbances, when habitat capacity shrinks drastically [Fig. 5.4]), when the number of unoccupied sites is too high. When the next disturbance occurs, there are still sites unoccupied. The frequency and magnitude of disturbance and the recolonization capacity of species interact to shape biodiversity patterns (Roxburgh et al. 2004). We tested this with different combinations of environmental stochasticity and recolonization rates. As stochasticity increases (i.e., high variance of annual precipitation) local species richness decreases, because species do not disperse fast enough to occupy the empty sites. When the recolonization rate increases, the metacommunity can handle higher levels of stochasticity and maintain a high mean α diversity (Fig. 5.11).

Neutral models have proved useful as an approximation for some macroecological patterns and as a null model for others. In this study, we used neutral theory as an approximation to species abundance and distribution patterns. The result was not satisfactory in terms of model fit, but still informative. Analysis of model performance in different dimensions informed us of the conditions when niche processes might be important and when neutral models may provide a better approximation. This is the first study to introduce explicit temporal dynamics to a spatially explicit neutral model and to apply that model to a system that is spatially and temporally dynamic. Testing the results against aquatic invertebrate community data showed that neutrality is limited in such systems. Unlike introducing spatial structure, temporal structure (temporal variability) itself is a strong environmental filter, especially when that variability is hydrological.

Species usually adapt to a particular hydrological regime, and species composition is quite different in perennial and intermittent flow regimes.

Neutral theory is driven by questions on how important the difference among species is in understanding broad-scale patterns of species distribution and abundance. It is not meant for exact site-by-site comparisons, which may not work well as shown in our study (e.g., the pairwise local species richness comparison). We did find a better fit in sampling events when the sampling sites were more scattered in space (Fig. 5.10), which suggests that there might be a certain spatial scale above which neutrality is important.

The relative importance of niche and neutral processes varies across systems, taxa, spatial scales, and it also varies *in time* for the same system and taxa at the same spatial scale as a result of altered landscape heterogeneity, as we demonstrated in this study. While model performance varied, overall, the contribution of neutral processes in shaping biodiversity patterns in desert ecosystems, characterized by high spatial and temporal variability, is limited.

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TABLE 5.1. List of parameters in the model, their ecological interpretations, and their values used in the best-fit models

Parameters	Meaning	Value
a	Exponent in species-area relationship	1.05
b	Slope in species-area relationship	60
p	Dispersal parameter in the 2Dt kernels	0.40
l_0	Dispersal parameter in the 2Dt kernels; l_0 is the distance where, after the dispersal, the ratio between its offspring and those at the origin location is $2^{-(1+p)}$	350
v	Speciation rate	0.0002
d	Morality rate	0.10
r	Recolonization rate	0.60

TABLE 5.2. Model goodness of fit for the four models with different complexity for temporal variability. For the cases of seasonality only, annual only, and no temporal variability, observed data were compared against results from two models. For example, for “Seasonality only”, the observed data were compared with the predictions from the seasonal model, and from the full model; we aggregated season- and year-specific results from full model to obtain the average result for each season (across three years).

	Seasonality & Annual	**Seasonality only**		**Annual only**		**No temporal variability**	
	Full Model	Full Model	Seasonal Model	Full Model	Annual Model	Full Model	Basic Model
α diversity	0.64	0.73 *sm =1.07; †wt =0.86; ‡fl =0.64;	1.01 sm = 1.49; wt = 0.94; fl = 0.61;	0.68 §$y09$ = 0.67; ‖$y10$ = 0.59; ¶$y11$ = 0.57;	0.84 $y09$ = 0.73; $y10$ = 1.41; $y11$ = 0.61;	1.00	1.48
β diversity	0.84	0.93 sm = 1.05; wt = 0.98; fl = 0.80;	0.98 sm = 1.08; wt = 1.02; fl = 0.86;	0.90; $y09$ = 0.80; $y10$ = 1.00; $y11$ = 0.80;	0.95 $y09$ = 0.97; $y10$ = 1.00; $y11$ = 0.80;	1.01	1.07

*summer; †winter; ‡fall; §year 2009; ‖year 2010; ¶year 2011

TABLE 5.3. Performance of the Full Model (measured by total error) for prediction of pairwise α diversity and β diversity (Chao similarity index) across the eight sampling seasons

Metrics	**Model**	**Summer**			**Fall**			**Winter**	
		2009	2010	2011	2009	2010	2011	2010	2011
α diversity	*best-fit for all eight sampling events*	9.98	0.51	0.56	0.54	0.53	2.28	1.12	0.70
	best-fit for each sampling event	1.08	0.18	0.33	0.32	0.35	2.13	0.84	0.54
β diversity	*best-fit for all eight sampling events*	1.19	0.64	0.92	0.58	0.79	2.80	1.00	0.44
	best-fit for each sampling event	0.82	0.37	0.88	0.55	0.77	1.13	0.92	0.29

TABLE 5.4. Model goodness of fit (Full Model) for different seasons, years, and stream types

Variable	Categories	α diversity	β diversity
Season	Fall	0.64	0.80
	Summer	1.07	1.05
	Winter	0.86	0.98
Year	2009	0.67	0.80
	2010	0.59	1.00
	2011	0.57	0.80
Stream type	Perennial	0.68	0.78
	Non-perennial	1.21	1.36

FIGURE 5.1. Map of a portion of the San Pedro watershed draining the Huachuca Mountains, including streams labeled with hydro-types (i.e., perennial, intermittent, and ephemeral streams), catchments, precipitation, sampling points, locations of six USGS gauges within the watershed, and locations of sensors for recording water permanence.

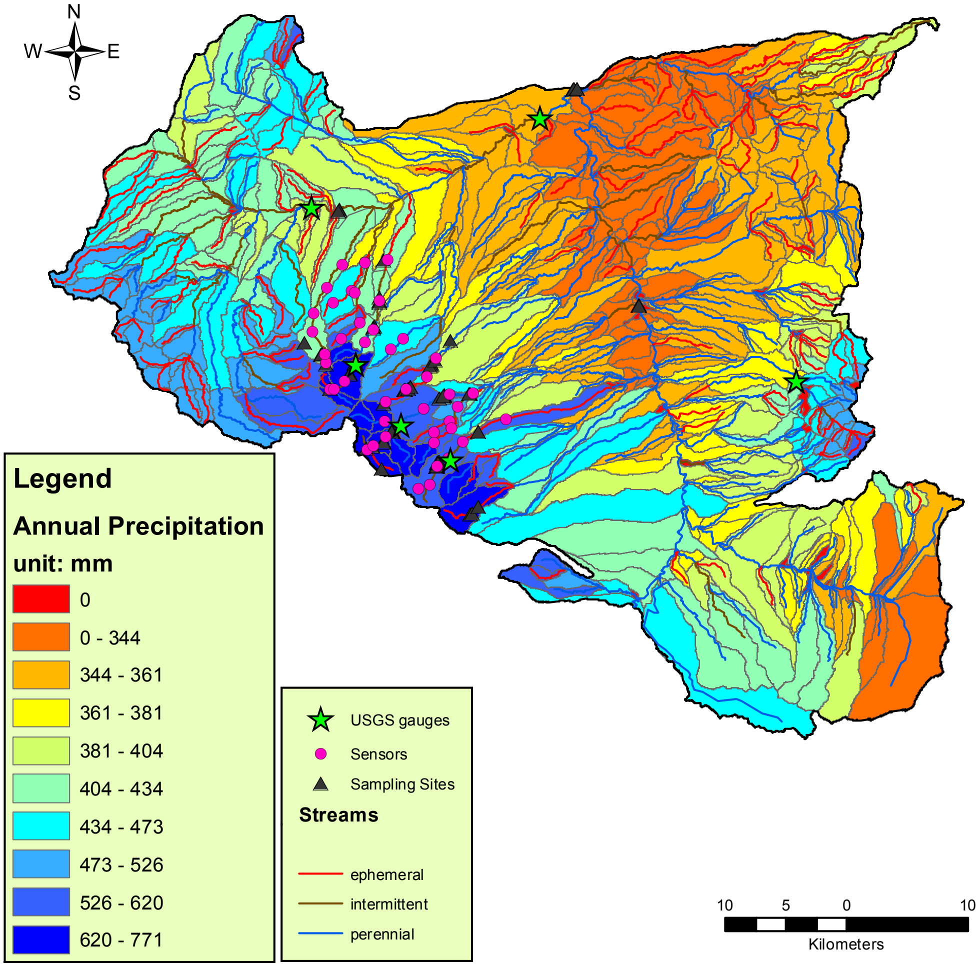


FIGURE 5.2. Observed hydrological regime of inter- and intra-annual variability and hydrological regime used in the model. (a) Observed annual precipitation (1923-2003) and predicted mean annual precipitation using first-order autoregressive model with a gamma residual; (b) normalized discharge from the six USGS gauges within the study area between 2009 and 2011 (the study period), and the modeled durations of the four flow periods (seasons).

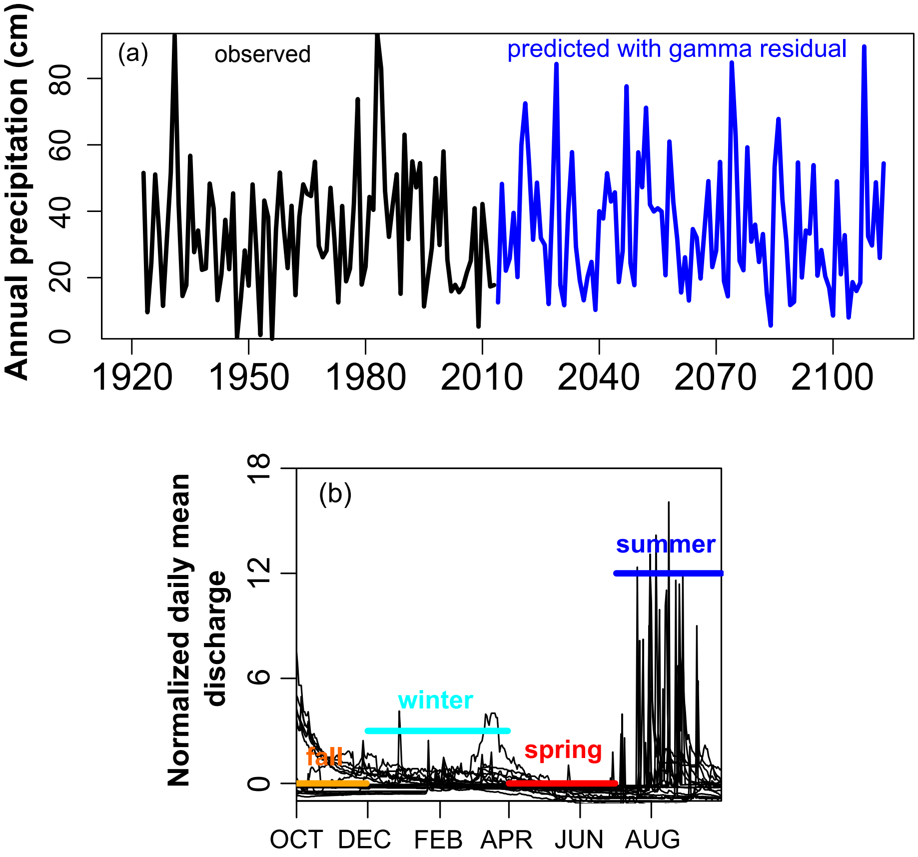


FIGURE 5.3. The effect of hydrology on the model performance. (a) The average daily discharge in the seasonal sampling periods over three years; and (b) relationship of model fits for those seasons in which a reasonable fit was obtained, vs. seasonal discharge.

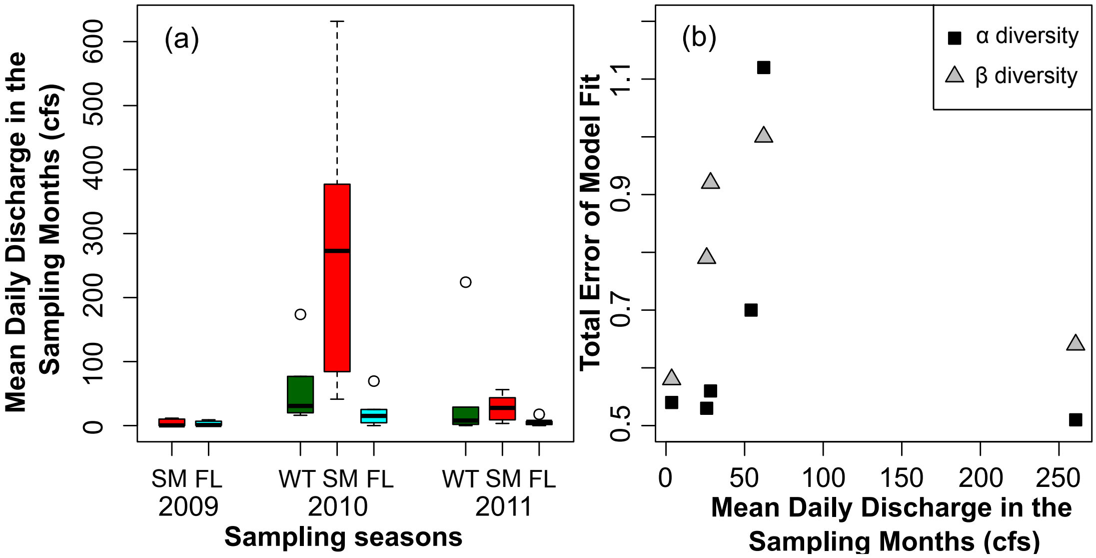


FIGURE 5.4. Transformed gamma distribution fitting the relationship between the product of watershed area and annual precipitation and local species richness. This relationship was further used to estimate habitat capacity for each site. The gray crosses were the observed data points, and black line was the best fit by minimizing total error between predicted and observed local species richness.

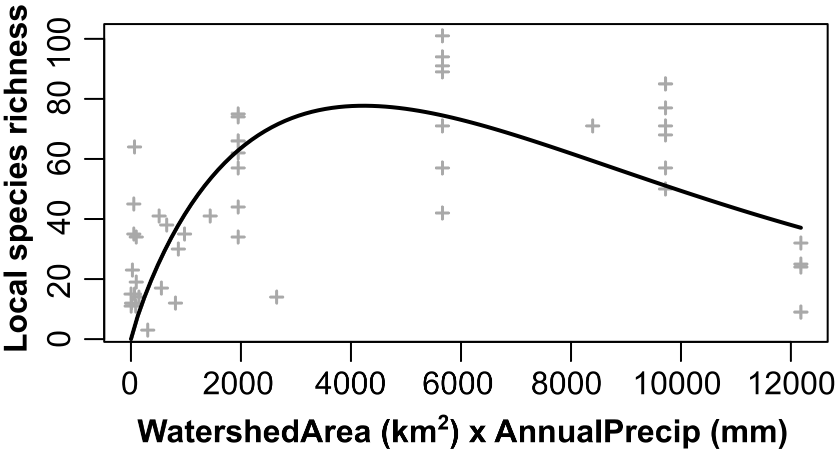
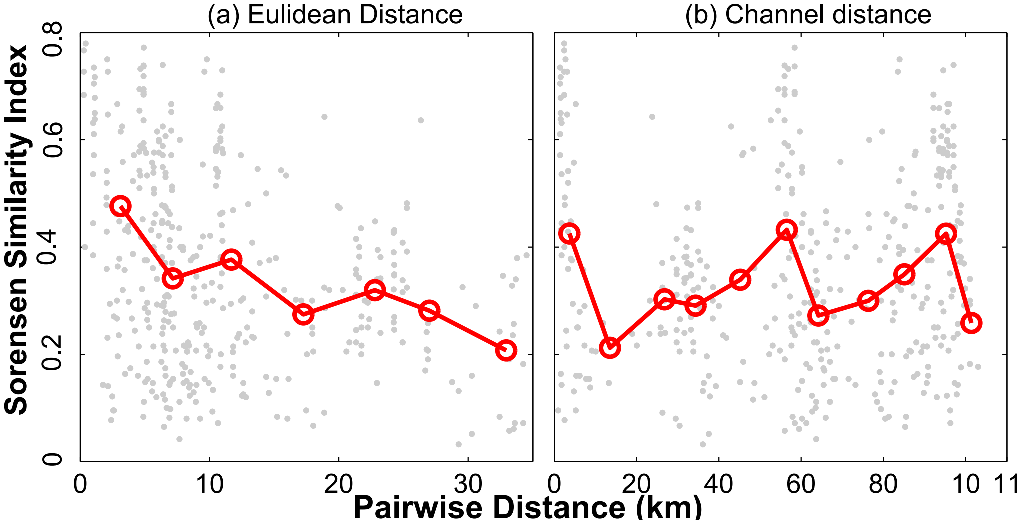


FIGURE 5.5. The observed pattern of β diversity plotted against pairwise (a) Euclidean distance and (b) channel distance. The gray closed dots in the plots were the actual observed data, and the red open dots were the average Sorensen similarity values for every 5km for the (a) Euclidean distance and every 10km for the (b) channel distance.


(a) Eulidean Distance

(b) Channel distance

FIGURE 5.6. Model goodness-of-fit for local species richness (LSR) for each sampling season from the best-fit Full Model (same parameter set for *all* sampling seasons; open circles) and from the best-fit model for each sampling event (one parameter set for *each* sampling season; gray “×”).

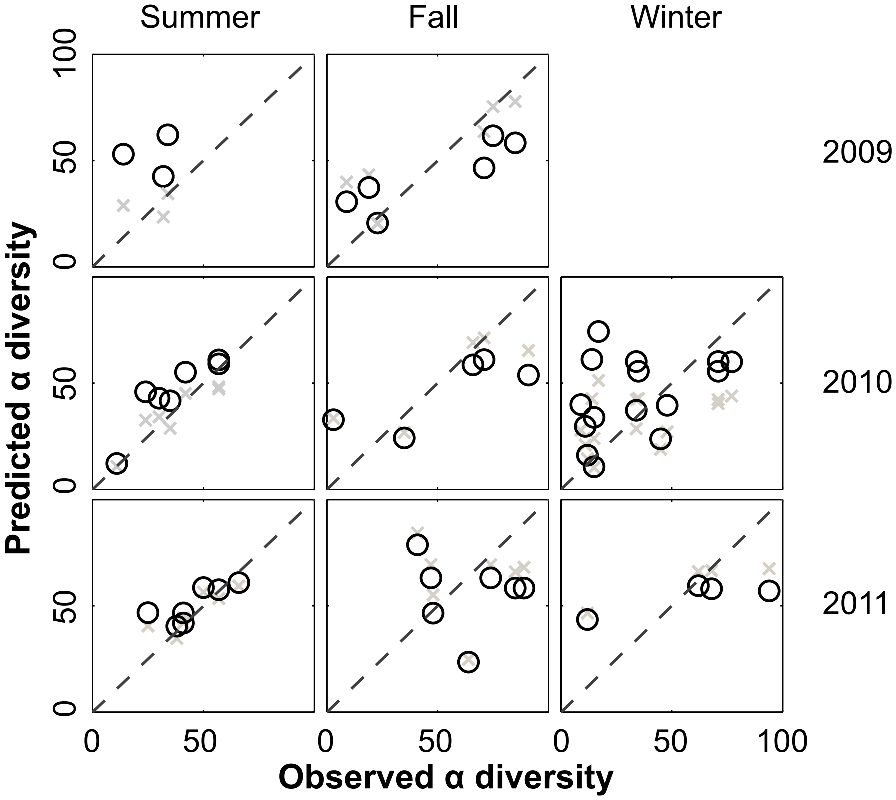


FIGURE 5.7. Model goodness-of-fit (Full Model) for β diversity pattern for each sampling season the best-fit Full Model (same parameter set for *all* sampling seasons; open circles) and from the best-fit model for each sampling event (one parameter set for *each* sampling season; gray “×”).

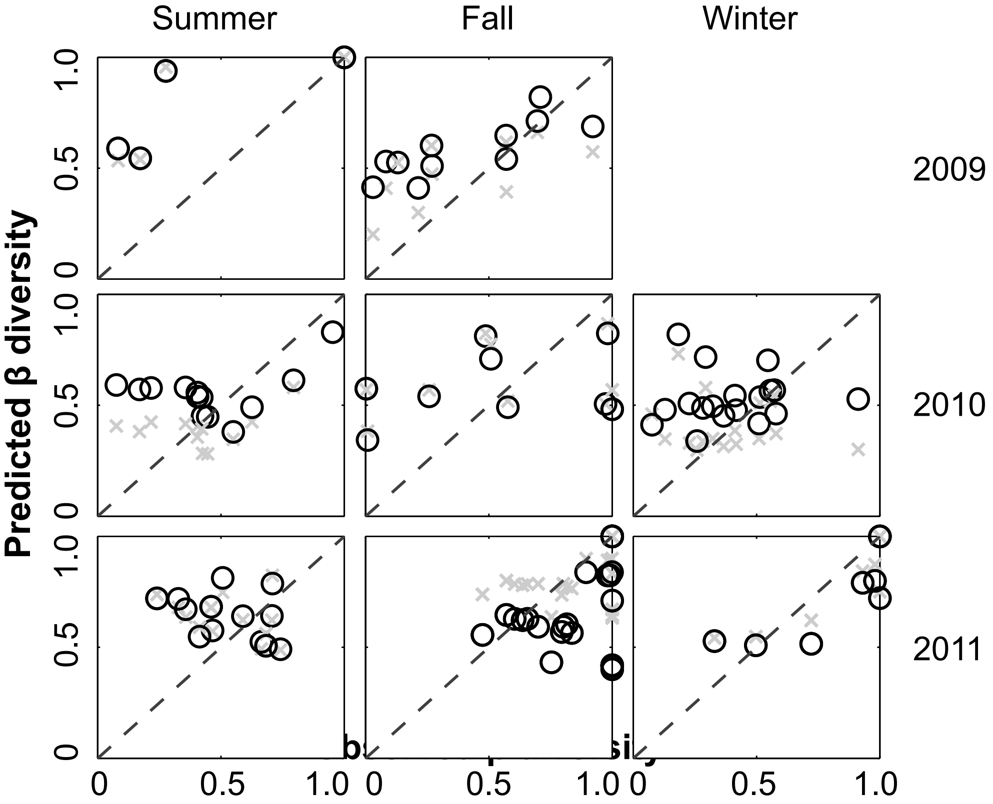


FIGURE 5.8. The total error of the Full Model fitted with 28 different parameter sets (parameter list in Table 4) for (a) α diversity pattern, and (b) β diversity pattern across 8 sampling events in three years.

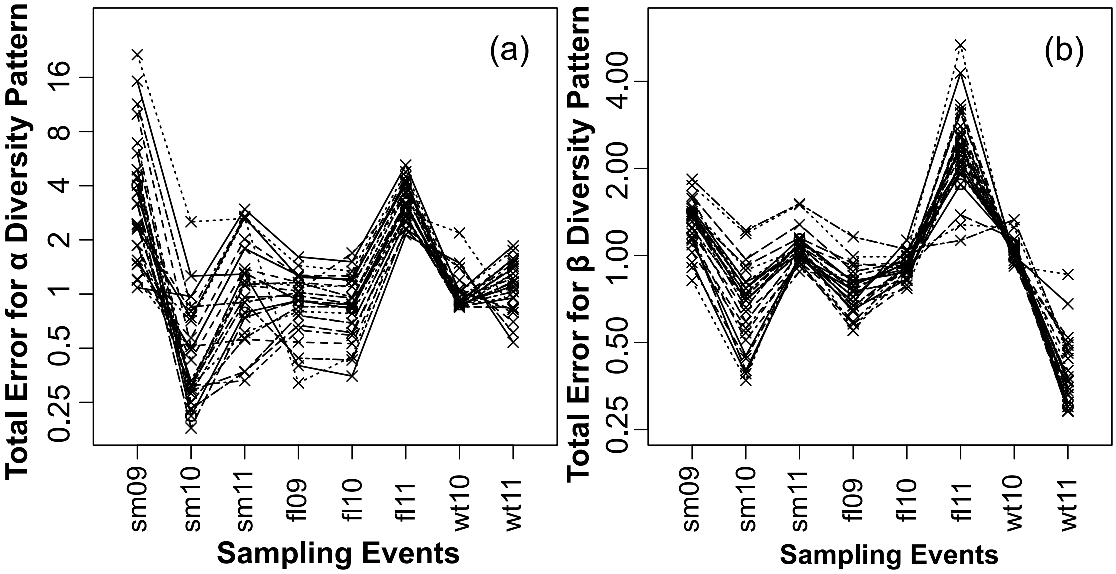


FIGURE 5.9. No significant correlation existed between the proportion of aerial-dispersal species measured by abundance (a) and by species richness (b) in a metacommunity and the model goodness-of-fit for both α diversity and β diversity patterns.

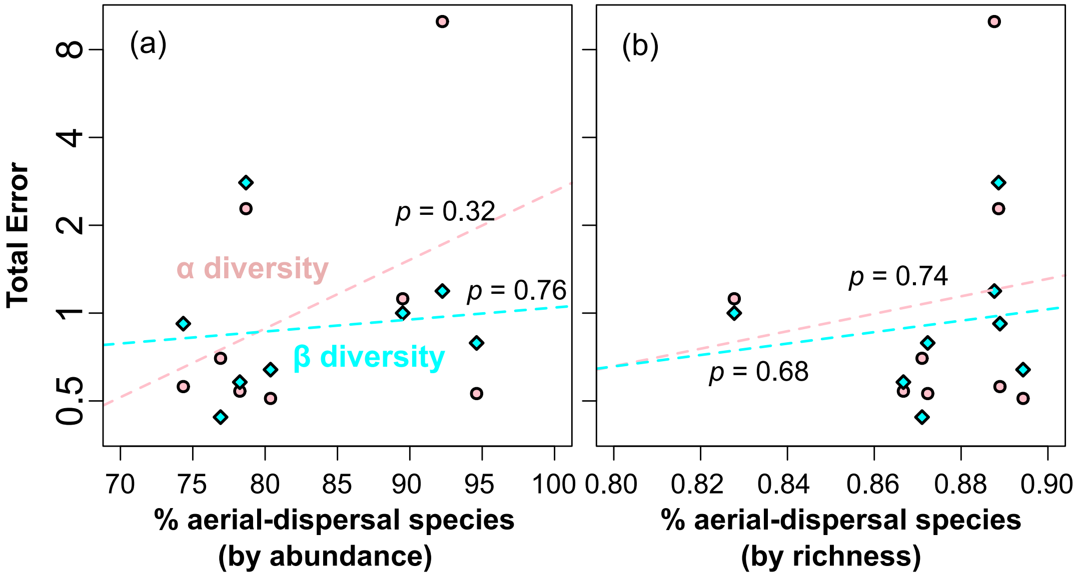


FIGURE 5.10. The spatial scale influences the performance of the model. (a) At sampling site level, the error of β diversity decreased with the pairwise distance between two sites. The light gray dots were results for all the pairs of sampling sites across all eight sampling seasons, and the black dots were the averaged results. (b) At aggregated sites level, the total error of model predictability of β diversity decreases with the average pairwise distance of all sampling sites within one sampling event.

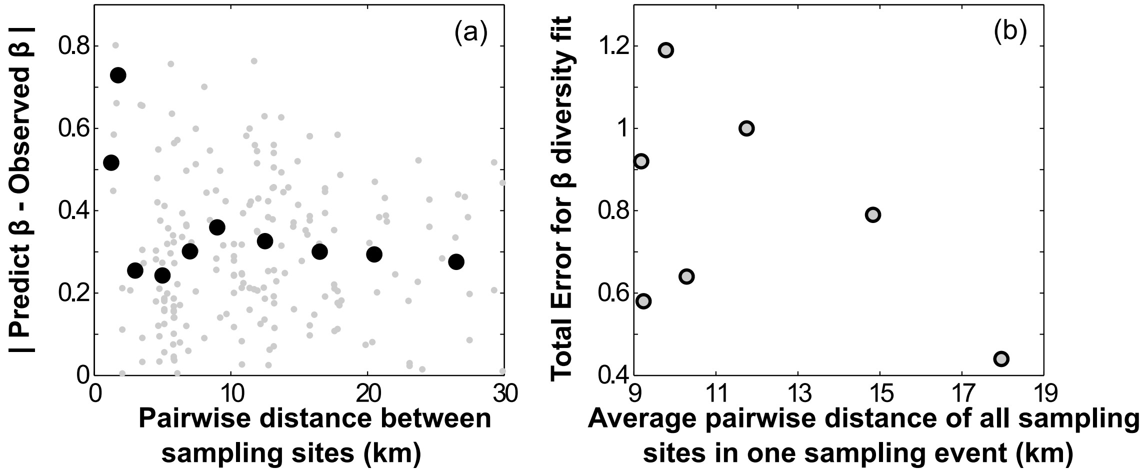
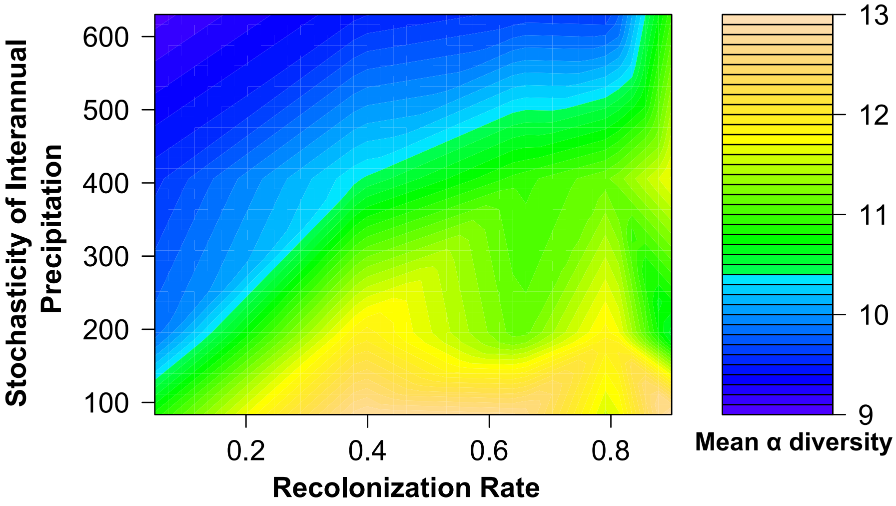


FIGURE 5.11. Rainfall stochasticity (measured by the variance of the gamma noise in the interannual precipitation in mm) and recolonization rate interact to influence the mean local species richness in the metacommunity.



CHAPTER 6

ORDER FOR NOTHING: ECOSYSTEM SELF-ORGANIZATION IN SPACE AND TIME

ABSTRACT

Self-organization has become an increasingly important theory for understanding ecosystem spatial heterogeneity. Here, we contextualize the mechanism of spatial self-organization under a framework of propagation of ecological influence over heterogeneous landscapes, to bridge the conceptual gap between formation of ordered patterning and energy and material flow, the foci of ecosystem ecology. The mechanism of self-organization, i.e., scale-dependent feedbacks, is essentially propagation of a particular type of ecological influence along flow paths (defined as the pathways along which causes and effects move) across a landscape. We demonstrate how to use this framework to systematically analyze the interplay between template heterogeneity (the preexisting spatial structure of landscapes) and self-organization. Template heterogeneity can influence all three of these aspects: information flow, flow path structure, and responses of the ecological target. This integration of organismal patterns with energy and material flow provides a platform for broad application of spatial self-organization in ecosystem ecology and for understanding ecosystem self-organization in a more realistic setting, by taking into consideration the spatial heterogeneity and temporal variation of the environment.

The central element of spatial self-organization is feedback, a fundamental element of complex adaptive systems theory. Ecosystems are considered complex

adaptive systems, which means that macroscopic system properties and patterns emerge from interactions among components and feed back to influence the subsequent development of those interactions. It is well accepted that ecosystem structure can emerge from local interactions among individuals, and that these structures carry certain functional consequences. However, the mechanisms of feedback, from the outcome of spatial pattern to individuals from which the pattern emerge, are seldom examined. We present a logical framework to examine such feedbacks, and conclude that it is unlikely the outcomes of ordered patterning would feed back to affect local processes at the individual level, from which ordered patterning arises. The ordered pattern is formed as a result of regular biological activities. The pattern is “order for free.” It is also “order for nothing” — in other words, there is no evolutionary reward returned to individuals that “build” the structure.

Keywords: complex adaptive systems theory; ecosystem functioning; feedbacks; flowpath; propagation of influence; resource retention; self-organization; spatial heterogeneity; temporal variability.

INTRODUCTION

Landscapes are typically heterogeneous, and this heterogeneity confers certain functional consequences. The classic perspective on spatial heterogeneity of ecological components (e.g., animals, plants, nutrients, and microbes) emphasizes the local physical conditions set by the landscape as the main determining factor (Ropars and Boudreau 2012; Buxbaum and Vanderbilt 2007; Manolaki and Papastergiadou 2012). But heterogeneity can also arise from a homogeneous initial condition through interactions among the components. This spatial self-organization has been used to explain formation of regular patterns by organisms via the mechanism of scale-dependent feedbacks. Much less research has been done to understand how self-organization may have influenced energy and material flows across a landscape, the core of ecosystem ecology. Here, we propose a conceptual framework to bridge the current gap between spatial pattern formation and ecosystem ecology.

Self-organized patterns emerge from internal interactions and further influence ecosystem macroscopic properties, such as resource retention. But is there feedback from the consequences of spatial patterns to the actions of individual from which the patterns arise? Furthermore, if such feedbacks exist, can they reinforce ecosystem functioning, as suggested by Fisher et al. (2007)? While feedback is a central feature of complex adaptive systems (Levin 2005; Levin 1998), plausible mechanisms are seldom explored. Our second goal is to explicitly examine the mechanisms for feedbacks from the outcome of self-organized patterns to the pattern formation.

Existing studies of spatial self-organization are mostly exclusively carried in ecosystems with negligible preexisting spatial heterogeneity (via an effect of variation the underlying physical structure, i.e., a template effect) and without temporal variability (but see Bonachela et al. 2015; Sheffer et al. 2013). Real ecosystems, however, are spatially heterogeneous and/or temporally variable. We assert that current applications of spatial self-organization theory are therefore limited and have missed multiple opportunities to contribute to understanding the dynamics and functioning of ecosystems. We analyze the mechanisms of interactions between preexisting template heterogeneity and self-organization in the framework of propagation of influences along flowpaths. Additionally, we discuss how temporal variability might affect spatial self-organization. This is the third goal of this review – to demystify self-organization and broaden the scope of its application in real complex ecosystems.

ORIGIN OF SPATIAL HETEROGENEITY

Ecosystems were first studied as a "black box," wherein ecosystem ecologists measured inputs and outputs of material and energy without explicit reference to spatial heterogeneity (Odum 1957; Fisher and Likens 1972; Bormann et al. 1977). In contrast, ecology has a long tradition of understanding the spatial pattern of organisms at a variety of scales (Watt 1947; Whittaker 1956; Curtis 1959; Bormann and Likens 1967). Consideration of spatial dynamics received increased attention in the late 1970s and 1980s with the ascendance of landscape ecology (Steele et al. 1978; White 1979; Paine & Levin 1981; Pickett and White 1985). The emergence of landscape ecology brought a particular focus to spatial heterogeneity with attempts to link it with its functional consequences. Two "black box" ecosystems of the exact same components could have quite different ecological functioning, if the components are arranged differently in space! For example, sediment losses from a semiarid savanna landscape in Australia are determined by the spatial arrangement of grassy and bare soil areas (Ludwig et al. 2007). Spatial heterogeneity is shown to enhance species survival during climatic perturbations (Virah-Sawmy et al. 2009). Theoretical models suggest that spatial heterogeneity could alter the threshold of ecosystem state change (van Nes and Scheffer 2005).

Landscape ecology also addresses the causes of the spatial heterogeneity (Turner 1989; Turner 2005). How do biotic and abiotic variables (processes) produce landscape patterns? The focus has been to relate landscape patterns to *top-down template effects* imposed by environmental, biophysical, and socioeconomic variables. Black et al. (2003) assessed the role of several economic, demographic, cultural, climatic, topographic, and geologic factors in forest spatial pattern changes in the northwest United States. Their results showed that biophysical factors are important, but human social factors are overriding in influencing forest pattern changes. Suarez-Rubio and Thomlinson (2009) suggested that the bird abundance and distribution in Puerto Rico was related to biophysical condition characteristics of patches and urbanization matrix at the landscape scale. Sponseller et al. (2014) showed that organic nitrogen in streams and rivers in Sweden was closely related to broad-scale gradients in state factors (e.g., temperature, precipitation), and spatial heterogeneity of nitrate was connected to gradients of anthropogenic inputs (e.g., agriculture).

Other than the commonly studied top-down template effects, spatial heterogeneity can arise in many ways, and always includes some *stochasticity*. One of the fundamental questions about spatial heterogeneity is how much of it is due to chance and how much is determined by environmental variation (Levin 1999). An extreme example is encompassed in the unified neutral theory of biodiversity (Hubbell 2001), which assumes that one does not need to invoke environmental variation and selection to explain certain macroscopic patterns of biodiversity. Rather, biodiversity can arise from stochastic dispersal, speciation, mortality, and reproduction. Individuals are equally subject to all these processes regardless of their species identity (the neutrality assumption). Spatially explicit versions of neutral models have been applied to river networks for fish communities (Muneepeerakul et al. 2008) and aquatic invertebrates (Dong and Muneepeerakul, *in prep.*).

Spatial heterogeneity can also arise from a homogeneous template by the process of *self-organization*. There is burgeoning interest in the formation of ordered patterning in the past two decades, as regular patterning has been observed in many different ecosystems around the world. For example, in many arid ecosystems, vegetation forms regular stripes (‘tiger bush’), labyrinths, spots (‘leopard bush’), and gaps (Rietkerk and van de Koppel 2008). Striking spatial patterns have also been observed at alpine tree lines in the Rocky Mountains. Stands of Engelmann spruce and sub-alpine fir were found to grow in narrow, parallel rows perpendicular to the prevailing winter wind direction (Billings 1969). In mussel beds on intertidal flats, patterns develop at two scales, banded patterns occurring at the ecosystem level, and net-shaped patterns at the scale of individual mussels (van de Koppel et al. 2005; Liu et al. 2014). In all of these cases, self-organization has been implicated as a primary cause of the spatial pattern.

DEFINITION OF SELF-ORGANIZATION

The term “self-organization” was originally introduced by Immanuel Kant to characterize the unique properties of living organisms in 1790. No external force, no divine architect is responsible for the organization of nature; the internal dynamics of the being itself are sufficient. Only in the 20th century did self-organization begin to acquire the promise of a physically based understanding, with the advent of cybernetics and the mathematical triumphs of nonlinear dynamical systems theory (Keller 2005). The late 1980s brought a noteworthy addition to the concept, namely, Per Bak’s notion of “self-organized criticality” (Bak et al. 1987): a system organizes itself into a critical state by its intrinsic dynamics, independent of any control parameter. Since then, the term “self-organization” rapidly spread to other fields and served both its original biological meaning and its later application in engineering. In the past two decades, self-organization has been a buzzword in ecology. While the common core of self-organization is macroscopic structure and functioning arising from interactions among components, the emphasis of different definitions varies.

In his book *Fragile Dominion* (Levin, 1999) and other work (e.g., Levin 1998; Levin 2003; Levin 2005), Simon Levin characterized “self-organization” as “development of a complex adaptive system” based on simple local rules that govern how the systems change in response to “past and present conditions.” Self-organization is characterized by localized interactions among components and it is an autonomous process that arises from those interactions, reinforcing the structural arrangements by the flow and interactions among the components (Levin 1998). This definition of self-organization describes a continuum of changes in the ecosystem over time. Temporal development of ecosystems is realized through cross-organizational feedbacks: macroscopic patterning and properties emerge from interaction among components, and feed back to influence the subsequent evolution of those interactions.

More recently, in ecosystem ecology, there is a rising interest in understanding the ordered patterning observed in many ecosystems, via the mechanism of *spatial self-organization*. Here, self-organization is defined as a process in which ordered spatial patterning at the global level of a system emerges solely from local interactions among individuals (Camazine et al., 2003). Spatial self-organization emphasizes (1) the formation of ordered spatial patterns featuring periodic geometric units (such as stripes, spots, rings) and (2) scale-dependent feedbacks as the underlying mechanism. It does not touch upon any temporal development of the system or cross-organizational level feedbacks, as did the definition by Levin. Reconciliation of these two approaches is overdue.

MECHANISM OF SPATIAL SELF-ORGANIZATION

Self-organized regular spatial patterns described above arise by the mechanism of scale-dependent feedbacks. Scale-dependent feedbacks couple short-range positive feedbacks with long-range negative feedbacks (Rietkerk and van de Koppel 2008). Depending on the sources for “activation” and “inhibition”, there are two basic mechanisms for scale-dependent feedback: one is through resource concentration and the other is related to divergence of physical stress, as detailed below.

Ordered patterning is often found in environments where resources are limiting. In resource-limited environments, the positive feedbacks result from the local interaction between consumer and its limited resource (usually water or nutrients), which result in large-scale depletion of the limiting resource, i.e., negative feedbacks. In arid systems, for example, infiltration of water is locally enhanced by plant presence, which improves the local condition for plant growth, while at a longer distance, competition for water between plants is the dominant process (Couteron and Lejeune 2001; Rietkerk et al. 2002). Self-organized patterns resulting from this mechanism disappear when the resource is no longer limiting. Regular patterning is also found in environments with physical stress, such as freshwater macrophyte patches in lowland streams and rivers (Schoelynck et al. 2012), which are exposed to shear stress. At short range, divergence of physical stress by plants enhances sediment accretion, and at long-range, it forms erosion troughs around the plant tussock, which restrict lateral expansion of vegetation. This phenomenon was demonstrated by Bouma et al. (2009) in a lab flume. Erosion decreases as sediment accumulates in the plant tussock, which improves local habitats. Meanwhile, in the area away from vegetation, erosion greatly increases. Rietkerk and van de Koppel (2008) suggest that in scale-dependent feedback, only the long-ranged negative feedback is essential for regular pattern formation. Short-ranged positive feedbacks between plants and their local environment give rise to scale-free patterns, which can be described by power-law clustering (Scanlon et al. 2007).

CONSEQUENCES OF SELF-ORGANIZED PATTERNS

Studies of self-organized spatial patterns have revealed several macroscopic consequences. The banded vegetation in arid and semiarid ecosystems can retain more runoff and sediments than non-patterned ecosystems (Ludwig et al. 1999; Ludwig et al.

2005). Self-organized landscapes exhibit catastrophic shifts among different ordered patterns responding to different levels of stress (e.g., precipitation) (Rietkerk et al. 2004). Patterned mussels in intertidal flats are more resilient to wave action and have higher productivity at landscape scales than mussels in non-patterned forms (van de Koppel et al. 2008). However, whether self-organization leads to increased resilience and stability or to increased vulnerability may vary depending on the ecosystem involved. No other studies have yet tested this hypothesis. Van de Koppel et al. (2005) found that self-organization induced by local positive feedbacks between clay accumulation and plant growth improved the functioning of salt marsh ecosystems on short time scales. On long time scales, however, self-organization led to the destruction of salt marsh vegetation. Mathematical models predict that patterned mussel beds become more resilient to wave disturbance, but are more vulnerable to regime shifts at high wave disturbance rates (van de Koppel et al. 2005).

THE IMPORTANCE OF INFORMATION FLOWS AND FLOW PATHS IN GENERATING PATTERN

Scale-dependent feedbacks were discovered in studies of ordered patterning, and the concept has been applied exclusively to those cases. Ecosystem ecologists have yet to fully embrace these approaches. Self-organization is studied more as a driver of organismal distributions, with little mention of its effect on material flows across landscapes. We propose that scale-dependent feedbacks fall under the broader aegis of propagation of ecological influences in space (Reiners and Driese 2001, 2004). Scale-dependent feedback requires flow paths, which define the patterns of connectivity that shape the information distribution underlying heterogeneity. Flow paths are ubiquitous and are defined as the pathways along which information transports. Information here is defined as any propagation of causes and effect within a system, with a consequence for ecological components involved in forming spatial structure. It could take the form of differential concentrations of a limiting resource (a non-limiting resource is not effective information, because its differential levels are inconsequential). For example, plants accumulate nutrients (in oligotrophic peatlands) or water (in arid ecosystems) and improve local conditions, causing a small-scale positive feedback. This local resource accumulation leads to depletion of resources at large scale, which causes a negative feedback (Rietkerk et al. 2002; Rietkerk et al. 2004; Eppinga et al. 2008). The information could also be in the form of differential levels of physical stress. In streams, clumps of vegetation obstruct water flow, which locally improves growth condition; however, the influence of vegetation clumps propagates downstream, leading to increased erosion outside the vegetation clump, which limits plant growth (Temmerman et al. 2005; Hiemstra et al. 2006; Larsen et al. 2007; van Wesenbeeck et al. 2008; Weerman et al. 2010).

Ecosystems are characterized by flows: flows of nutrients and energy, flows of materials, and flows of information. Flows provide the interconnections between parts and link a random collection of species into an integrated whole, an ecosystem in which biotic and abiotic components are tied together (Levin 1999; Fisher and Welter 2005). Consequences of ecological processes propagate across a landscape along flowpaths (Fisher et al. 2004). It is along these flow paths that scale-dependent feedbacks occur.

Explicit consideration of flow and flow path could generalize scale-dependent feedbacks beyond current application to the formation of ordered patterning. A systematic study of mechanisms for interactions between self-organization and preexisting spatial heterogeneity would encompass three types of mechanism: (i) self-organization can be interrupted or enhanced by modification of the information flow along flowpaths in space (Fig. 6.1). For example, stream flow links subsystems longitudinally (e.g., tributary), laterally (e.g., riparian and floodplain), and vertically (e.g., groundwater exchange). If a nutrient is limiting in the stream, nutrient concentration can then become the signal organizing vegetation patch configuration (e.g., alteration of nitrate-consuming patches [e.g., algae] and nitrate-generating patches [e.g., Cyanobacteria]). The information content, i.e., the variation in nutrient concentration, can be easily modified by input from adjacent subsystems with different nutrient levels. This will interrupt the self-organized patch configuration along the stream. (ii) The information content could also be altered by changed local interaction between information and the ecological components themselves. For example, termite mounds enhance plant water use efficiency (Jouquet et al. 2011; Seymour et al. 2014) and change soil texture, which alters water infiltration (Jouquet et al. 2011; Bottinelli et al. 2014). These processes alter the local interactions between limiting resource (i.e., water) and plants, which indirectly modify the information. Such alterations intensify and stabilize the self-organized pattern of plants (Bonachela et al. 2015). (iii) The structure of the flow path along which influences propagate could be altered to influence spatial self-organization. For example, Sheffer et al. (2013) found that at the landscape scale, the vegetation followed the preexisting physical template of rock-soil distribution and self-organized pattern only appear in the soil patches between rocks. In this case, the existence of rocks interfered with the information flow at a landscape scale and modified self-organization.

Propagation of influence occurs not only within a single community, but also across ecosystems, contributing to the zonation of biological communities on landscapes at broad scales. The example of the formation of spatial configuration of algal and Cyanobacteria patches mentioned in the previous paragraph illustrates this. Another example is the interaction between coral reefs, seagrass meadows, and mangrove forests in tropical coastal areas (Gillis et al. 2014). Coral reefs provide physical protection from wave action, allowing seagrasses and mangroves to develop in the shallows behind them. Meanwhile, seagrasses and mangroves trap sediments and absorb nutrients from flow paths traversing the hinterland to the reefs. These are long-distance interactions, as reviewed recently by van de Koppel et al. (2015).

FEEDBACKS FROM ECOSYSTEM PROPERTIES TO INDIVIDUALS

We described above how spatial patterns could emerge from local feedbacks. The resultant patterning has further functional consequences, including ecosystem properties, such as the ratio of ecosystem production and respiration (P/R ratio), stability, resource retention capacity, and resilience to disturbance (Odum 1969). Ecosystems are considered complex adaptive systems, which means that "*spatial patterns emerge from, and feed back to affect, the actions of adaptive individual agents*" (Levin 1998; Levin 2005). Even though this definition of complex adaptive systems has been widely used, the central part of it, i.e., feedback that crosses levels of organization (between ecosystem level and individual level), has seldom been examined closely. Is there feedback from the consequent ecosystem property to the actions of individuals that generated the pattern, to intensify the patterning and/or to reinforce ecosystem functioning? If so, what are the effective mechanisms for such feedbacks?

We use ecosystem resource retention as an example of an ecosystem property. Ecosystem nutrient retention is a collective property proposed by Odum (1969) to change over successional time. The patterned landscape allows for greater productivity than a landscape with homogeneous distribution at the same rainfall rate, *i.e.,* higher resource retention capacity and lower runoff (Aguiar and Sala 1999; Ludwig et al. 1999). In order for the macroscopic property to feed back to influence individuals or the actions of individuals, the ecosystem resource retention capacity must in some way exert its effect on the process involved in spatial self-organization at the individual level in the first place. Before we address this question of whether ecosystem properties affect actions of individuals, let us first ask, why do patterned landscapes have higher resource retention capacity?

The higher resource retention capacity of a patterned landscape results from its spatial structure, or the spatial configuration of vegetated and open patches (Ludwig et al. 2007). Spatial self-organization optimizes the use of the limiting resource, and the system is at the equilibrium between the spatial patterning and the level of resource limitation ("equilibrium" means that the geometric shapes match the level of stress; for example, in arid ecosystems, as precipitation decreases, the pattern of plants shifts from gaps, to stripes, to spots, with increasingly lower vegetation cover; Rietkerk et al. 2004). A decrease in precipitation may cause the patterned vegetation to degrade and lose biomass.

As a consequence, the proportion of rainfall that infiltrates into the soil decreases (van de Koppel et al. 1997), which results in a transition to an alternative stable state (e.g., when resource limitation decreases, the pattern may shift from periodic spots, to labyrinths, to gaps, and to stripes; Rietkerk et al. 2004). On over-grazed hillslopes in semiarid landscapes, both runoff and sediment yields increase as the spatial pattern of vegetation coarsens, and increased runoff and sediment yields make the vegetation pattern even coarser (Bautista et al. 2007). This kind of positive feedback could eventually lead to desertification. Indeed, Okin et al. (2009) use the length of connected pathways (i.e., flow paths) to explain ecosystem desertification. Positive feedbacks between erosion and plant mortality increase the length of connected pathways. When the length of a flow path is above a threshold value, connectivity created by flow paths has a negative effect on plant survival and growth, resulting in further lengthening of flow paths and increased desertification.

Other than the effect of the spatial structure, do individuals in patterned landscapes themselves retain more resource, and thereby contribute to increased ecosystem retention capacity? The studies reviewed above suggest that spatially structured landscapes have greater retention of resources, but do not tell us about the effects on individuals. Do individual organisms inhabiting patterned landscapes retain more resource than individuals in non-patterned landscapes? Van de Koppel et al. (2008) reported that over three weeks, the growth rate of individual mussels that occurred in a patterned beds were not significantly different from isolated mussels. Bautista et al. (2007) monitored surface runoff and sediment yields for 45 months in nine closed plots at El Ventós Experiment catchment in Spain, and found an inverse relationship between patch density and runoff. However, after controlling for the effect of grain size and connectivity of landscape, no relationship between patch density and runoff was found. These studies imply that individuals in ordered patterning do not take up more resources than individuals in non-patterned landscapes, even though the patterned landscape *as a whole* retains more resources than non-patterned ones. We conclude that the explanation for altered resource retention capacity in patterned landscapes does not reside at the individual level. Instead, it originates from the differences in landscape patterns (e.g., patch configuration and flow path length).

We contend that, in fact, there is no mechanism for individuals in patterned landscape to retain more resource than individuals in non-patterned landscapes. The ordered patterning is an accidental consequence of the regular biological processes of plants (or other agents that form the patterning). Plants establish somewhere in the landscape, modify the soil texture, and improve the local habitat condition, which naturally leads to lower level of resource concentration away from plants. When the resource is limiting, local processes generate a consequent depletion of that particular limiting resource. This causes a negative feedback at long range via propagation of influence. These are regular biological processes occurring in any kind of landscape. Thus scale-dependent feedback is likely a more general explanation for spatial complexity in ecosystems than previously considered, and it also plays a role in structuring systems that have more complex non-regular spatial patterning (van Wesenbeeck et al. 2008). Ordered patterning is a result of these regular biological processes when other conditions are met (such as a relatively homogeneous template).

Individuals in patterned landscape do not invest anything to create the ordered patterning. Ordered patterning comes at no cost ("*order for free*"; Kauffman 1995).

At the individual level, when genetic mutations occur, they are associated with certain phenotypes. If the individual is better off with that phenotype, the frequency of that gene will increase in the population. Future mutations that further improve the fitness of this particular trait will be selected for. As a result, that particular trait will be *enhanced* and *intensified*. This represents feedback from "functioning" to individuals (i.e., genes) from which the "pattern" (phenotype) emerged. Such feedbacks are realized because of differential reproduction and selection at the individual level. However, such selection does not exist at the ecosystem level: there is no "birth-reproduction-death" cycle for ecosystems. Ecosystem level selection (Dunbar 1960) or at least group selection (Wilson 1983; Stevens, Goodnight, and Kalisz 1995; Price 2012) is still debatable. Moreover, the pattern is formed not because individuals did anything special. There is no gene responsible for spatial self-organization. The pattern is "*order for free*", but it is also "*order for nothing*" in that there is no evolutionary reward returning to individuals that "build" the structure. Without reward to individuals that do the organizing, self-organization would be limited in the extent to which it can shape the structure and functioning of ecosystems. However, these limits are currently unknown.

WHAT FEEDBACKS *ARE* POSSIBLE?

Ecosystems and the biosphere are complex adaptive systems, from which patterns emerge, and then feed back to affect the actions of adaptive individuals (Levin 1998). An important feature of such systems is the sustained diversity of components (Gell-Mann

1994). However, with spatial self-organization, such diversity or heterogeneity of composition is usually neglected – only one species is considered. Therefore, feedback from the outcome of the spatial structure to the actions of individuals that lead to the spatial structure is not likely. However, the self-organization of complex adaptive systems considers a community and the interactions and changes of *many* species over time. When the diversity of species composition in a real ecosystem is considered, the conclusion may be different (Levin 1999; Levin 2005).

When multiple species are considered, the feedbacks from the outcome of the spatial structure to the spatial structure are likely to happen. In ecosystems, ecological activities of single species in communities can lead to great changes in the environment (both biotic and abiotic). This leads to further changes in the candidate species for likely community assembly and interactions. Such feedbacks from the outcome of the actions of individuals to these same individuals are rooted in adaptation and selection at the individual level in a system characterized by a diversity of species, which is in turn reflected in differential reproduction. Over time, the result is a change in species composition. When an ordered vegetation patterning occurs, the environment for the community living in this landscape is changed, e.g., the landscape retains more resource and has higher productivity, compared to the non-patterned landscape. This will necessarily change the community on this landscape, including its species composition, abundance, and richness. Evolution proceeds. Gene frequencies change. The altered community structure will then influence the organisms that formed the pattern at the first place. This completes the feedback loop from the outcomes of spatial structure to spatial structure itself. However, such feedback loop does not provide a mechanism for this outcome to affect the plants in such a way as to alter the spatial pattern one way or another (e.g., reinforcing the functioning). As there is no gene for structure formation, it cannot be differentially selected.

A TRADITION OF WISHFUL THINKING IN ECOSYSTEM SCIENCE

Using ecosystem nutrient retention as an example, Fisher et al. (2007) hypothesized reciprocal feedbacks between function and form, and asked whether the process of retention of nutrients could feed back to influence the spatial structure of an ecosystem in a direction that enhances function. The studies on ecosystem directional changes can be traced back to Odum (1969), who hypothesized directional and predicable changes in many ecosystem properties over successional time. Some of the specific predictions were later rejected by empirical studies (e.g., Vitousek and Reiners 1975). But the general idea that ecosystems could self-organize to benefit organisms over time persisted. Similarly, Gaia failed as a model for understanding nature, because it treats the biosphere as if it were selected for its macroscopic properties (Lovelock and Margulis 1974). These views of ecosystem change are rooted in a tradition of wishful thinking and rely on unspecified mechanisms such as group selection.

While biological components are an important part of ecosystems, ecosystems are also complex systems in nature and include dynamic abiotic elements as well. Therefore, dynamics of ecosystems must be rooted in laws of evolution/natural selection, biophysical laws, and systems theory. Complex systems can have interesting emergent properties resulting from simple local interactions among a diversity of components. One of these emergent properties is called self-organized criticality, which was proposed by physicist Per Bak (Bak et al. 1987). A system self-organizes to the edge of stability such that a slight perturbation will cause collapse (think about the collapse and reorganization of sand piles). This view simply takes ecosystems as dynamical systems, without considering the biological nature of the system's components. The most recent theory of complex adaptive systems emphasizes feedbacks that cross levels of organization, wherein macroscopic structure and properties emerge from and feed back to the action of individuals. While there is plenty of evidence showing how actions of individuals result in macroscopic structure and property, feedbacks from structures and system properties to individuals are likely implausible, as we reasoned in the previous sections. Despite this, complex adaptive system theory still provides one of the most promising frameworks to understand the organization and dynamics of ecosystems. It considers abiotic and biotic components, includes variation and adaptation of organisms in an evolutionary view, and adopts a systems perspective.

SELF-ORGANIZATION AND NATURAL SELECTION

Both self-organization and natural selection can generate order. Stuart Kauffman in his book, *At Home in the Universe* (1995), wrote that self-organization is a different source of order than natural selection. It is "*order for free.*" A pure Darwinist might argue that order could arise only after evolutionary trial-and-error. However, self-organization is "*the origin of the very ability to evolve*," because "*stability can't be imposed from outside by natural selection – it must arise from within as a condition of evolution itself.*" Holland (1976) proposed that natural selection is an emergent process of self-organization founded on birth-reproduction-death cycles.

The formation of ordered pattern by living organisms in ecosystems is no different from that by physical objects, except that the rules of local interactions among biological organisms are subject to both physical and biological laws (which are defined by natural selection at the individual level). Self-organization is the root source of order and exists without biology, e.g., on Mars (Bishop 2007), hence without natural selection. The ordered pattern is formed by the relentless operation of self-organization, without the need to invoke selection at any level.

SPATIAL AND TEMPORAL HETEROGENEITY INFLUENCING SELF-ORGANIZATION

Preexisting spatial heterogeneity (i.e., the template) influences self-organized patterns. When template heterogeneity is absent or moderate, self-organization buffers the underlying heterogeneity to form ordered patterning (van de Koppel et al. 2005). However, what happens when template heterogeneity is pronounced? We summarized three basic ways in which self-organization and template heterogeneity could interact previously (i.e., by directly changing the information content, by altering the flow path structure, and by modifying local interactions; Fig. 6.1). So far, only three studies have attempted to address this issue (i.e., Sheffer et al. 2013; Liu et al. 2014; Bonachela et al. 2015) with only modest success. More research is clearly needed.

On a continuum of systems ranging from being totally self-organized to being entirely determined by the landscape template, how does ecosystem resilience vary? Liu et al. (2014) evaluated state transitions under homogeneous and heterogeneous resource conditions by comparing results from a model explicitly considering a gradual depletion of algae (the prime food of mussels) from the seaward boundary of the mussel bed, with results from models not including this gradual consumption. They found that alternate stable states existed when the algal gradient was lacking but were absent under conditions of algal depletion. In contrast, Bonachela et al. (2015) reported on an interaction between vegetation self-organization and spatial heterogeneity of termite mounds. The extra layer of spatial heterogeneity imposed by termite mounds enhanced resistance of dryland habitats to climate change (drier climate with less precipitation). The consequences of interaction between self-organization and template heterogeneity were thus opposite in these two studies. To understand how self-organization interacts with template variation to affect ecosystem properties, such as resilience, it is important to know whether and how the focal ecosystem property depends on specific formulations of the underlying process through which the large-scale physical context interacts with self-organization.

Self-organization is a process – it takes time for feedbacks to occur and for spatial patterns to form. The environment on which it plays out is heterogeneous in space and variable in time. Ecosystems are exposed to frequent environmental fluctuations, some of which are disturbances, such as fire, floods, or grazing. Environmental fluctuation in time is analogous to landscape heterogeneity in space. Here, we call it temporal heterogeneity. Just like in preexisting spatial heterogeneity, temporal heterogeneity can also shape the spatial distribution of biological patches.

A Forest fire model provides a classic example illustrating temporal regime of disturbance shaping the spatial patterns of forest tree patches (Drossel and Schwabl 1992). In the model, starting with an empty model lattice, trees gradually appear. Lightning strikes may chance upon a tree, and burn it and its connected cluster. The cluster is localized because landscape connectivity is well below the percolation threshold. As time goes by, more trees grow until percolation occurs. When any tree in the cluster is hit by lightning the entire cluster can be burned. This eliminates the spanning cluster so that the system no longer percolates. Over time as more trees appear this process plays out repeatedly. The system oscillates around the critical point. Given enough time, the forest self-organizes to a state in which it has a power-law distribution of the sizes of clusters (and fires). Another example is flooding. As with the forest fire model, an empty lattice is colonized by stream macrophytes, with frequent flood disturbance. Unlike the forest fire model, where large tree patches are more susceptible to big fires, large and dense macrophyte patches are *less* susceptible to floods (Heffernan 2008; Bouma et al. 2009). Above threshold patch size and plant density, the removal rate by floods decreases nonlinearly. At the beginning, patches formed by plants are small, and are easily removed by floods; however, as plants continue to develop, small patches connect and form larger patches. This nonlinearly increases the force required for floods to remove plants. Here, the temporal configuration of the flood size (flood regime) shapes the patch size distribution of macrophytes.

The effect of temporal heterogeneity on spatial self-organization is more poorly known than the effect of preexisting spatial heterogeneity. We propose that some existing conceptual elements of understanding of spatial heterogeneity and self-organization can be borrowed to explore the effect of temporal heterogeneity on spatial patterns, and we illustrate here with an example. The disturbance regime in time is analogous to the size of soil patch between rocks in the soil-rock mosaic framework described by Sheffer et al. (2013). When the plant-patch size is much smaller than the size of a soil patch, plants will interact and self-organize to form ordered vegetation patterns between rocks. Similarly, when the interval between two disturbances is long enough, ecosystems can self-organize over time. In the soil-rock mosaic framework, at the landscape level, vegetation follows the physical template by occupying the network of soil patches. In temporal self-organization, the ecosystem assembly in the long term is determined by the disturbance regime. Lastly, water availability in the area open for plant growth is determined by the size of soil patches. Specifically, the redistribution of rainfall in a rock-soil landscape results in a differential increase of water content in the soil patches. Small patches have soil-water content significantly higher than large patches. Differential degrees of water limitation determine the shape of the repeated pattern (e.g., spots or bands). Similarly, the disturbance regime is related to distribution of resource in time. For example, Sycamore Creek, a desert stream in Arizona, is nitrogen limited (Grimm and Fisher 1986). Floods wash the nitrogen accumulated in the upland to the stream. This nitrogen is highest after floods. The hydrological regime, which determines the stream-upland connection, affects nutrient inputs from the catchment and thereby sets a nutrient limitation 'status' (Grimm and Fisher 1992). Frequent floods are related to frequent small pulses of releases of nutrient limitation. Infrequent large floods are related to large increases of nutrients in the system. In this way, the disturbance regime influences the level of resource limitation and the time allowed for self-organization to occur, both of which influence ecosystem self-organization.

ECOSYSTEM SELF-ORGANIZATION

Ecosystems consist of both biotic and abiotic components and self-organization occurs both in physical environments (e.g., branched river networks, spacing between mountain ridges, distribution of catchment sizes, and soil structure) and among biological organisms (e.g., plant, animal, and microbe). It is all of these components and the complex interactions and feedbacks among them that make an ecosystem. The self-organization of different components of ecosystems occurs at different spatial and temporal scales, and in response to different signals (e.g., the information that organizes one ecological component might be just white noise to another). Different types of ecological components differ in their intrinsic motivation to move, in their motilityand navigation abilities, and in their response to external factors (Holyoak and Casagrandi 2008; Nathan 2008). But they occur simultaneously within an ecosystem. Currently, most research has been focusing on the self-organization of one type of ecological component, which cannot really be considered as *ecosystem* self-organization.

Self-organization of different ecological components could occur at similar temporal and spatial scales. In the example of the plant distribution in savanna ecosystems with preexisting termite mounds (Bonachela et al. 2015), the spatial distribution of termite mounds was taken as a preexisting template. However, studies on spatial distributions of mounds showed that the older colonies were regularly distributed as influenced by intraspecific competition (Korb and Linsenmair 2001). It may be that termite mounds simply act as a template to influence the self-organization of plants, but alternatively, the two mechanisms of pattern formation may interplay with each other in time. Do distinctively different self-organization processes occurring at similar spatial and temporal scales interact with each other? How? What are the consequences of such interactions, structurally and functionally? Answers to these questions need further research.

In other cases, self-organization of ecological components occurs at distinctively different spatial and temporal scales. The rock-soil mosaic framework of Sheffer et al. (2013) can be generalized to model whole watersheds. Watersheds consist of soil planes that are embedded within hard-rock mountain ridges, within which are many source-sink spatial relationships. On the other hand, the emergence of evenly spaced ridges and valleys (and therefore, the distribution of sizes of catchment areas) is one of the most striking examples of self-organization in landscapes at broad scales (Perron et al. 2009). The shape of catchments can greatly influence water chemistry, each catchment being characterized by a distribution of travel times, reflecting the diverse flow paths available by which rainfall can move to the stream (Kirchner et al. 2000; Kirchner and Neal 2013). The travel time of water and nutrients through a catchment influences the retention of both. Resources received by soil planes in the watershed further influences its self-organized spatial structure, and further affects flow paths, resource retention, and a host of other processes at various spatial and temporal scales, many in the realm of ecosystem properties.

SUMMARY

Ordered pattern arises from homogeneous landscape through spatial self-organization, a phenomenon observed widely around the world in many ecosystem types. Such patterns have functional consequences, as we have discussed, altering ecosystem productivity, resource retention capacity, and ecosystem resilience. These ecosystem properties emerge from the spatial structure at the landscape level, not from processes at the individual level. We reasoned that the outcomes of ordered patterns are not likely to feed back to the actions of individuals, which give rise to spatial patterning in the first place. Ordered patterning is a result of regular abiotic or biological behaviors of individual agents: individuals do not invest anything to "build" these patterns, nor do they (differentially) benefit from them. It is order for free, and also order for nothing for individuals. Order for nothing means that spatial self-organization, while an important mechanism for the formation of spatial heterogeneity, does not provide a mechanistic basis for directional (teleological, cybernetic) change in ecosystems.

We propose that the mechanism of spatial self-organization – scale-dependent feedback – falls within the broad theory of propagation of ecological influence in heterogeneous landscapes (Reiners and Driese 2001). The key aspects of propagation of influence are information flow (i.e., influence), the processes that modify the information, and flow path through/over which information travels (Fisher and Welter 2005). Contextualizing spatial self-organization in the theory of propagation of influence bridges the conceptual gap between current work on pattern formation (which focuses on organisms and their spatial structure) and ecosystem ecology, which considers the flow of material, energy, and organisms. This provides a general framework to systematically study the interaction between spatial self-organization and template heterogeneity: how template heterogeneity may influence information flow, the process generating the information, and the flow path by which information travels. Such a framework may lead to a much broader application of the concept of spatial self-organization in ecosystem ecology and a leap in understanding of ecosystem self-organization in a more realistic setting, one that takes into account the spatial and temporal heterogeneity of the environment, beyond current studies on conspicuous two-dimensional patterning.

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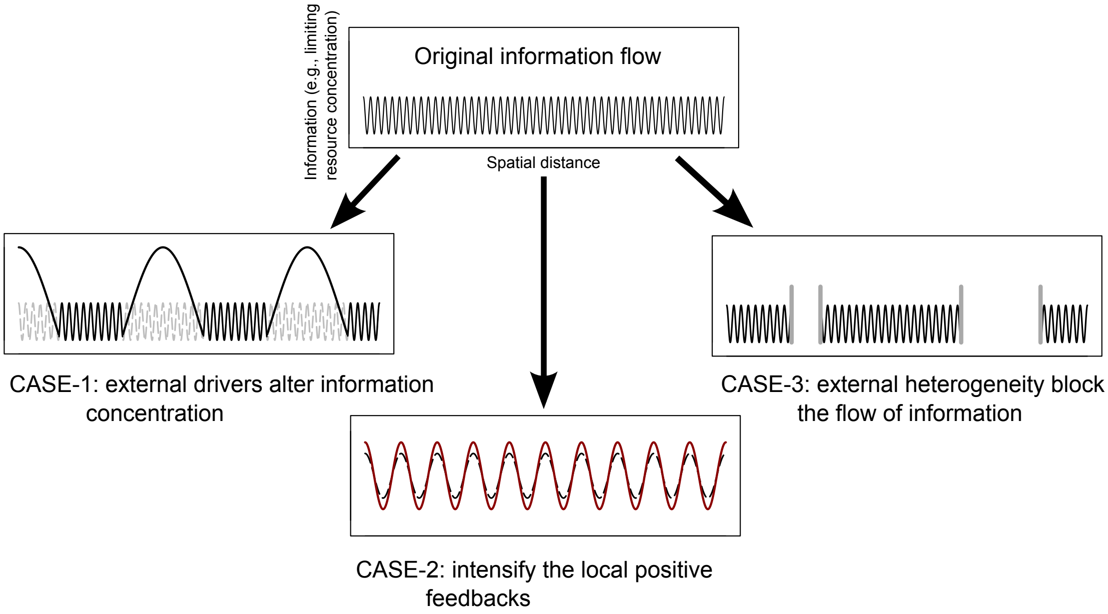
FIGURE 6.1. A conceptualization of the three approaches preexisting heterogeneity interplaying with spatial self-organization (1) external drivers directly alter the information content in the flowpath. Example of this could be stream tributary joining the main channel or groundwater inputs, directly altering the concentration of the limiting resource; (2) intensify the local positive interactions (the example of termite mounds in savanna ecosystems as reviewed in the text: termites increase plant water use efficiency in water limited ecosystems); and (3) alter the flowpath structure (the example soil-rock mosaic example in the text: rocks blocks the propagation of information flow).



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APPENDIX A

SUPPLEMENTARY METHODS USED IN CHAPTER 3

ADDRESSING "MISSING" DATA IN THE DRY SECTIONS

Because surface water was not continuous in late succession in 1995 and in 2013 mid-succession, no water samples were collected in the dry section of the stream. The dry section occurred between 3 km and 6 km, which divided the stream into two continuous wet sections. Wavelet analysis does not tolerate missing data (Saunders et al. 2005). We used two methods to deal with the missing data to cross-validate the results from wavelet analysis. (1) We estimated nutrient concentrations in the dry sections ("*ARIMA estimate*" approach). For NO_3^- concentration in dry sections, we first used autoregressive integrated moving average models (ARIMA) to fit the data. From observations of the dry section data in other surveys where water did not dry out, we found that the dry section barely had any big fluctuations in the concentration of NO_3^- and the overall NO_3^- concentration was low. So we set the average NO_3^- concentration to be 2.5 $\mu g\ L^{-1}$, and used the best ARIMA model from the data to predict the NO_3^- concentration in the dry section in late succession of 1995 and mid-succession of 2013. For conductivity data, we used similar ARIMA method to estimate the autocorrelation in the data, but we also superimposed the big sine-wave curve, which we observed in other surveys where surface water was continuous, to the whole dataset for estimation. For SRP concentration, we first calculated the slope between the SRP concentration in the last water sample before the dry section and the SRP concentration in the first water sample after section. We then added the autoregressive noise estimated from best ARIMA model to the data predicted from the linear model. (2) In the second approach, we did not estimate the "missing data", instead, we left out the dry sections of the stream, and only used a subset of the data, where the samples were continuous ("*subset*" approach). We ran wavelet analysis on the two continuous wet sections upstream and downstream of the dry section separately.

For the MARSS model, since the missing values are nonrandom, the standard methods (reviewed by Horton and Kleinman 2007) to estimate missing data in time series data (in our study, spatial auto-correlated data) do not apply in our case. We also used two methods to cross-validate the results. (1) We took out the dry section in the datasets of 1995 late succession and 2013 mid-succession, and connected the two wet sections of the stream together; we then run MARSS on the connected whole dataset ("*connected-pseudo-complete*" approach). In this method, we included a covariate to indicate before and after dry section, similar to the covariate of pit effect used in the early succession model. All the sampling points collected upstream of the big dry section were labeled 0's, and all the points downstream of the dry section were labeled 1's. (2) In the second approach, we took out the dry section in the dataset, and run MARSS separately on each continuous wet section of the stream ("*subset*" approach).

For results from both MARSS and wavelet analysis, we reported the general results invariant of approaches used to deal with "missing data." If the results were not consistent across different approaches, we pointed out the differences by reporting both results.

ADDRESSING THE PIT EFFECT IN THE EARLY SUCCESSION IN 1997

When the survey in early succession was done, 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 (Dent and Grimm 1999). We included the effect of the pit by designating all the sampling sites upstream of the gravel pit as 0 and all the points downstream as 1.

ESTIMATING THE N AND P IN THE ABOVEGROUND BIOMASS OF WETLANDS

Wetland survey was carried out two weeks after the survey of water chemistry. We measured the length and average width of wetland patches along the same 10 km of the stream. We also recorded the dominant wetland species within each patch. In the whole system, the dominant wetland species are *Equisetum laevigatum*, *Paspalum distichum*, *Schoenoplectus americanus*, *Typha domingensis*, and *Juncus torreyi*. The total wetland areas for each in 2013 were, respectively, 1761 m^2, 2386 m^2, 1878 m^2, 2378 m^2, and 429 m^2. We used 200 g dry mass m^{-2} for approximation (Hudon 2006). Average N and P content were estimated as 15 mg N (g dry mass)$^{-1}$ and 1.2 mg P (g dry mass)$^{-1}$ (Verhoeven and Schmitz 1991). We estimated a total N of 39.74 kg and total P of 3.18 kg fixed in the aboveground biomass of wetlands in the beginning of June 2013 across 10 km of the stream.

ESTIMATING THE N AND P IN THE FILAMENTOUS ALGAE

We surveyed the presence and absence of filamentous algae along with taking water samples every 25 meters across the 10 km section of the stream. 33% out of 400 points had algae present. We assumed the average width of the wet stream channel to be 2 m. While 33% of the surveyed points had algae present, this did not mean that 3.3 km of the stream channel was covered by algae. We assumed that half of the total area of the 3.3 km stream was covered by algal mat, which was 3,300 m^2. According to (Fisher et al. 1982), in Sycamore Creek, 60 days after the winter flood, the biomass of algae was about 150 g m^{-2}. We estimated the N and P by using 5% N content and 0.5% P content in the algal dry mass. This resulted in 12.37 kg N and 1.24 kg P fixed in the biomass of algae in the 2013 survey across 10 km of the surveyed stream. This is about one third of the aboveground N and P in the macrophytes.

CROSS-WAVELET ANALYSIS OF THE SPATIAL PATTERNS OF WETLAND ABUNDANCE AND NUTRIENT PATTERNS

We constructed Cross Wavelet Transform (XWT), which will expose the common wavelet spectrum power in space-spatial scale plane (i.e., spatial position on x-axis and spatial scale on y-axis). The detailed description of the method can be found in (Grinsted et al. 2004). The purpose of this analysis in our study is to explore shared signal by wetland distribution and spatial patterns of nutrients in 2013. Also, analyzing the cross wavelet of nutrients and wetland distribution across four surveys sheds light on the changes in patterns of nutrient caused by wetland establishment in the system. We did not find any noticeable changes in the cross-wavelet analysis in different successional stages for either NO_3^- or SRP (Appendix F).

APPENDIX B

SUPPLEMENTARY TABLE 1

TABLE 1. Summary of the model selection of different structures of MARSS model using AICc. We examined the two approaches to deal with missing values ("connected-pseudo-complete" approach and "subset" approach; when "subset" approach was used, results were shown for both the first part of the continuous wet stream, *s1*, and the second part of the continuous wet stream *s2*). We tried combinations of different structures for **B**, **Q**, and **R**. *s* is the "chemical type specific" and *c* is short for constant parameters for different chemical types. The combination of *s*, *s*, *s* is set as the minimum AICc value, and other combinations of **B**, **Q**, and **R** are compared against this AICc values. In most cases, *s, s, s* had the lowest AICc, except for a few cases, where the values were in bold. ΔAICc = AICc-min(AICc).

Model		**Early Succession**					**Mid-succession *w/o* Wetlands**					**Late Succession**					**Mid-succession *w/* Wetlands**				
		B	Q	R	AICc	ΔAICc	B	Q	R	AICc	ΔAICc	B	Q	R	AICc	ΔAICc	B	Q	R	AICc	ΔAICc
Connected	1	s	s	s	-2594.5	0	s	s	s	425.3	0	s	s	s	-1586.8	0	s	s	s	2442.7	0
	2	s	s	c	-998.3	1596.2	s	s	c	831.9	406.6	s	s	c	-974.3	612.4	s	s	c	2634.5	191.9
	3	s	c	s	-2592.3	2.2	s	c	s	451.3	26.0	s	c	s	-1221.7	365.1	s	c	s	2450.8	8.2
	4	s	c	c	-930.9	1663.6	s	c	c	915.7	490.4	s	c	c	-606.5	980.3	s	c	c	2703.9	261.3
	5	c	s	s	-2594.7	**-0.3**	c	s	s	439.5	14.2	c	s	s	-1553.5	33.2	c	s	s	2447.9	5.3
	6	c	s	c	-997.1	1597.4	c	s	c	849.3	424.0	c	s	c	-939.1	647.6	c	s	c	2654.3	211.6
	7	c	c	s	-2593.1	1.4	c	c	s	466.9	41.6	c	c	s	-1188.2	398.5	c	c	s	2457.0	14.3
	8	c	c	c	-932.3	1662.2	c	c	c	929.8	504.5	c	c	c	-574.0	1012.7	c	c	c	2711.6	269.0
s1	1	s	s	s	-257.0	0	s	s	s	399.6	0	s	s	s	-702.9	0	s	s	s	1350.6	0
	2	s	s	c	318.4	575.4	s	s	c	705.2	305.5	s	s	c	-492.6	210.4	s	s	c	1380.6	30
	3	s	c	s	-219.6	37.3	s	c	s	428.8	29.2	s	c	s	-550.5	152.5	s	c	s	1347.1	**-3.6**
	4	s	c	c	492.2	749.2	s	c	c	820.8	421.2	s	c	c	-342.4	360.5	s	c	c	1386.5	35.9
	5	c	s	s	-252.3	4.7	c	s	s	413.9	14.3	c	s	s	-686.8	16.1	c	s	s	1344.0	**-6.6**
	6	c	s	c	330.7	587.7	c	s	c	726.2	326.6	c	s	c	-476.3	226.7	c	s	c	1376.1	25.5
	7	c	c	s	-213.5	43.5	c	c	s	434.0	34.4	c	c	s	-524.9	178.0	c	c	s	1342.9	**-7.8**
	8	c	c	c	496.1	753.1	c	c	c	827.5	427.9	c	c	c	-316.4	386.5	c	c	c	1381.9	31.2
s2	1	s	s	s	-502.4	0	s	s	s	1216.2	0	s	s	s	96.6	0	s	s	s	1624.5	0
	2	s	s	c	572.7	1075.1	s	s	c	1812.1	595.8	s	s	c	150.2	53.6	s	s	c	1652.8	28.3

3	s	c	s	-360.6	141.8	s	c	s	1274.2	58.0	s	c	s	110.3	13.7	s	c	s	1630.6	6.1
4	s	c	c	705.7	1208.1	s	c	c	1910.6	694.3	s	c	c	162.7	66.1	s	c	c	1674.7	50.1
5	c	s	s	-504.2	**-1.9**	c	s	s	1225.3	9.1	c	s	s	98.3	1.7	c	s	s	1634.3	9.9
6	c	s	c	576.3	1078.7	c	s	c	1846.8	630.6	c	s	c	151.4	54.9	c	s	c	1667.7	43.1
7	c	c	s	-364.7	137.6	c	c	s	1275.3	59.0	c	c	s	109.7	13.1	c	c	s	1637.4	12.9
8	c	c	c	706.6	1209.0	c	c	c	1918.8	702.6	c	c	c	161.9	65.3	c	c	c	1681.6	57.1

APPENDIX C

SUPPLEMENTARY TABLE 2

TABLE 2. Comparison of MARSS results using different approaches to deal with missing data in the dry section of the stream in the late-succession in 1995. *subset* approach: we left out the dry section of the stream, and only used a subset of the data, where the samples were continuous. *connected-pseudo-complete* approach: we included a covariate to indicate before and after dry section. The section upstream of the big dry section was labeled 0's, and the section downstream of the dry section was labeled 1's. The two sections were connected and MARSS models were run on the connected pseudo-complete dataset. The coefficients that were statistically significant were in bold.

	ML.Est	**Std.Err**	**low.CI**	**up.CI**	**ML.Est**	**Std.Err**	**low.CI**	**up.CI**	**ML.Est**	**Std.Err**	**low.CI**	**up.CI**
	s1 ("*subset*")				*s2* ("*subset*")				"*connected-pseudo-complete*"			
R_N	0.00689	0.000904	0.005146	0.00883	0.00401	0.000423	0.00317	0.00487	0.004899	0.000398	0.004164	0.005741
R_P	0.00510	0.000639	0.003835	0.006326	0.01096	0.001136	0.00882	0.01327	0.008215	0.000679	0.006976	0.009546
R_C	0.000343	0.0000443	0.000259	0.000426	0.00458	0.000469	0.0037	0.00553	0.000288	0.0000228	0.000243	0.000334
B_{NN}	**0.579**	**0.0700**	**0.391**	**0.672**	**0.705**	**0.0540**	**0.559**	**0.770**	**0.668**	**0.0393**	**0.568**	**0.718**
B_{NP}	-0.0213	0.0397	-0.090	0.0648	-0.0519	0.0401	-0.123	0.0363	-0.0467	0.0259	-0.0959	0.00425
B_{PN}	**0.136**	**0.0701**	**0.029**	**0.299**	0.0331	0.0567	-0.069	0.157	0.0630	0.0397	-0.00292	0.1529
B_{PP}	**0.944**	**0.0417**	**0.820**	**0.977**	**0.871**	**0.0411**	**0.751**	**0.911**	**0.910**	**0.0276**	**0.833**	**0.938**
B_{CC}	**0.964**	**0.0287**	**0.872**	**0.985**	**0.700**	**0.0508**	**0.576**	**0.765**	**0.947**	**0.0194**	**0.887**	**0.962**
Q_N	0.293	0.0388	0.206	0.358	0.380	0.0402	0.294	0.449	0.361	0.0291	0.294	0.407
Q_P	0.0982	0.0129	0.0688	0.120	0.213	0.0237	0.161	0.255	0.155	0.0135	0.125	0.177
Q_C	0.0232	0.00294	0.0168	0.0281	0.384	0.0407	0.290	0.455	0.0310	0.00246	0.0256	0.0352
UPW_N	**1.739**	**0.305**	**1.153**	**2.328**	**1.237**	**0.289**	**0.683**	**1.828**	**1.513**	**0.215**	**1.078**	**1.914**
UPW_P	**0.807**	**0.176**	**0.477**	**1.158**	**0.798**	**0.222**	**0.374**	**1.257**	**0.811**	**0.137**	**0.530**	**1.072**
UPW_C	-0.142	0.0850	-0.307	0.0200	**1.360**	**0.287**	**0.817**	**1.931**	0.0718	0.0583	-0.0381	0.194
WTP_N	-	0.0776	-0.138	0.172	0.00114	0.0551	-0.114	0.101	-	0.0441	-0.0972	0.0773

	0.00169								0.00679			
WTP_P	-0.0431	0.0440	-0.138	0.0328	-0.00363	0.0434	-0.101	0.0709	-0.0247	0.0298	-0.0890	0.0265
WTP_C	-0.00353	0.0223	-0.0373	0.0512	-0.0796	0.0549	-0.195	0.00881	0.00888	0.0132	-0.0157	0.0372
RCH_N	**-0.298**	**0.102**	**-0.500**	**-0.104**	-0.114	0.101	-0.317	0.0704	**-0.241**	**0.0814**	**-0.410**	**-0.0921**
RCH_P	-0.0601	0.0634	-0.185	0.0614	-0.0540	0.0784	-0.208	0.0959	-0.0556	0.0556	-0.157	0.0611
RCH_C	-0.0557	0.0328	-0.129	0.00148	-0.0590	0.0995	-0.257	0.136	0.0218	0.0263	-0.0236	0.0808
CYN_N	**0.306**	**0.117**	**0.0740**	**0.532**	0.255	0.156	-0.0561	0.555	**0.263**	**0.0950**	**0.0744**	**0.445**
CYN_P	0.0376	0.0649	-0.0943	0.165	0.227	0.115	-0.00901	0.445	0.0906	0.0597	-0.0301	0.206
CYN_C	-0.00173	0.0309	-0.0654	0.0588	-0.0855	0.152	-0.381	0.204	0.0156	0.0269	-0.0360	0.0730
ALG_N	0.0895	0.122	-0.146	0.330	0.0334	0.108	-0.174	0.251	0.0545	0.0829	-0.108	0.214
ALG_P	0.0217	0.0732	-0.118	0.173	-0.00279	0.0843	-0.163	0.167	0.0301	0.0556	-0.0800	0.146
ALG_C	**0.0683**	**0.0344**	**0.002036**	**0.134**	0.0440	0.107	-0.159	0.265	0.0214	0.0238	-0.0229	0.0716
DRY_N									0.103	0.0821	-0.0488	0.266
DRY_P									-0.0284	0.0589	-0.162	0.0698
DRY_C									**-0.0808**	**0.0327**	**-0.169**	**-0.0438**

APPENDIX D

SUPPLEMENTARY TABLE 3

TABLE 3. Comparison of MARSS results using different approaches to deal with missing data in the dry section of the stream in the mid-succession in 2013. *subset* approach: we left out the dry section of the stream, and only used a subset of the data, where the samples were continuous. *connected-pseudo-complete* approach: we included a covariate to indicate before and after dry section. The section upstream of the big dry section was labeled 0's, and the section downstream of the dry section was labeled 1's. The two sections were connected and MARSS models were run on the connected pseudo-complete dataset. The coefficients that were statistically significant were in bold.

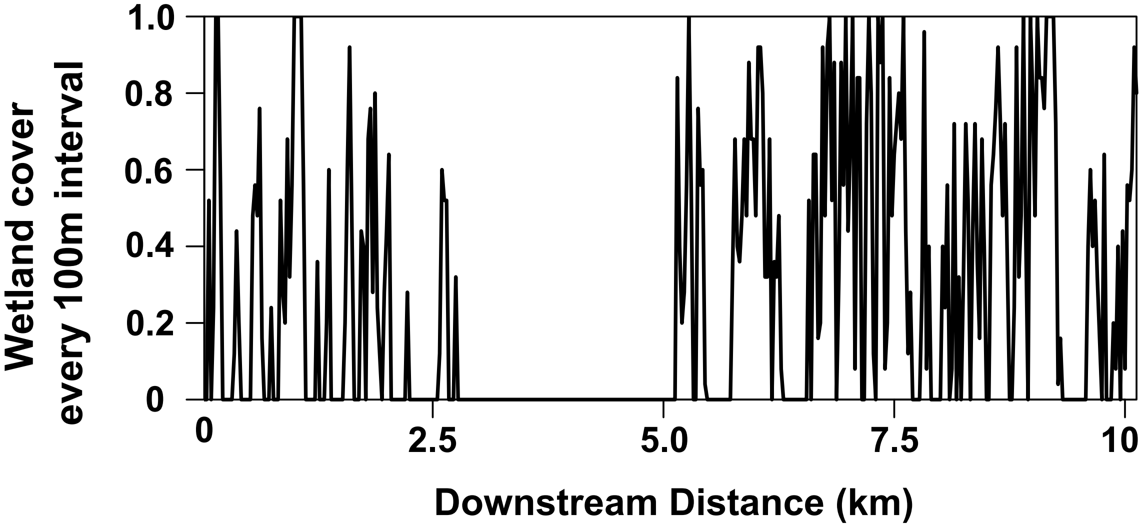
	ML.Est	**Std.Err**	**low.CI**	**up.CI**	**ML.Est**	**Std.Err**	**low.CI**	**up.CI**	**ML.Est**	**Std.Err**	**low.CI**	**up.CI**
	s1 (“*subset*”)				*s2* (“*subset*”)				“*connected-pseudo-complete*”			
R_N	0.384	0.0444	0.316	0.490	0.225	0.020	0.192	0.269	0.262	0.0181	0.225	0.297
R_P	0.184	0.0211	0.144	0.228	0.224	0.020	0.185	0.269	0.181	0.0126	0.156	0.206
R_C	0.162	0.019	0.130	0.205	0.122	0.010	0.106	0.144	0.0634	0.00451	0.0551	0.0727
B_{NN}	**0.866**	**0.0669**	**0.689**	**0.954**	**0.891**	**0.035**	**0.800**	**0.942**	**0.881**	**0.0298**	**0.796**	**0.914**
B_{NP}	0.0172	0.0663	-0.0896	0.171	0.048	0.051	-0.054	0.151	0.0245	0.0303	-0.0305	0.0879
B_{PN}	0.0323	0.0537	-0.0712	0.146	**0.094**	**0.036**	**0.034**	**0.177**	**0.0797**	**0.0294**	**0.0253**	**0.148**
B_{PP}	**0.916**	**0.0638**	**0.712**	**0.964**	**0.904**	**0.060**	**0.735**	**0.973**	**0.943**	**0.0351**	**0.833**	**0.968**
B_{CC}	**0.839**	**0.0499**	**0.715**	**0.902**	0.996	0.022	0.920	1.007	**0.963**	**0.0182**	**0.906**	**0.975**
Q_N	0.0560	0.0278	0.000244	0.0972	0.020	0.008	0.000479	0.0316	0.0475	0.0116	0.0229	0.0672
Q_P	0.0756	0.0227	0.0230	0.111	0.046	0.016	0.0125	0.0753	0.0552	0.0116	0.0327	0.0767
Q_C	0.0519	0.017	0.0119	0.0805	0.009	0.00371	0.000166	0.0146	0.0207	0.00392	0.0124	0.0275
UPW_N	**0.726**	**0.188**	**0.357**	**1.114**	**1.25**	**0.167**	**0.921**	**1.592**	**0.818**	**0.119**	**0.591**	**1.066**
UPW_P	0.0781	0.175	-0.246	0.436	0.057	0.188	-0.341	0.427	0.0297	0.114	-0.192	0.249
UPW_C	-0.205	0.14	-0.492	0.0415	-0.11	0.113	-0.343	0.0919	-0.0285	0.0663	-0.174	0.0946
WTP_N	-0.00559	0.0354	-0.0893	0.0527	0.0123	0.0162	-0.0224	0.0424	-0.0000498	0.0162	-0.0339	0.0298

WTP_P	0.0112	0.0408	-0.0700	0.0871	**-0.0408**	**0.0249**	**-0.0987**	**-0.000986**	-0.00293	0.0191	-0.0433	0.0344
WTP_C	**0.109**	**0.0407**	**0.0519**	**0.211**	0.0123	0.0118	-0.00738	0.0421	**0.0310**	**0.0105**	**0.0145**	**0.0554**
RCH_N	-0.0336	0.0565	-0.135	0.0815	-0.0160	0.0199	-0.0529	0.0268	0.0173	0.0378	-0.0462	0.0994
RCH_P	-0.00314	0.0639	-0.141	0.122	-0.000502	0.0341	-0.0597	0.0775	-0.0303	0.0410	-0.112	0.0453
RCH_C	-0.0213	0.0481	-0.126	0.0575	0.0122	0.0222	-0.0481	0.0406	0.0198	0.0223	-0.0244	0.0617
CYN_N	-0.00234	0.0812	-0.169	0.148	-0.05.53	0.0476	-0.156	0.0279	-0.0435	0.0422	-0.132	0.0338
CYN_P	0.0881	0.0802	-0.0367	0.289	-0.0162	0.0684	-0.142	0.130	0.0482	0.0445	-0.0342	0.139
CYN_C	0.0967	0.0672	-0.00706	0.248	0.00385	0.0311	-0.0532	0.0659	0.0177	0.0263	-0.023	0.0800
ALG_N	-0.0999	0.248	-0.592	0.371	**-0.332**	**0.213**	**-0.452**	**-0.202**	**-0.298**	**0.133**	**-0.544**	**-0.0342**
ALG_P	-0.168	0.219	-0.617	0.230	0.22	0.184	-0.107	0.609	0.0110	0.131	-0.235	0.271
ALG_C	-0.0156	0.187	-0.399	0.348	0.0503	0.0957	-0.115	0.259	0.0423	0.0779	-0.110	0.194
WET_N	-0.0654	0.0328	-0.128	0.000537	0.00462	0.0154	-0.0244	0.0346	-0.0239	0.0176	-0.0583	0.0111
WET_P	-0.0579	0.035	-0.130	0.00706	-0.00269	0.0214	-0.0446	0.0380	-0.00599	0.0176	-0.0415	0.0279
WET_C	-0.0144	0.0283	-0.0735	0.0374	0.0000325	0.00924	-0.0173	0.0188	0.00219	0.0105	-0.0197	0.0214
DRY_N									-0.0390	0.0389	-0.122	0.0281
DRY_P									0.0348	0.0455	-0.0427	0.137

APPENDIX E

SUPPLEMENTARY FIGURE 1

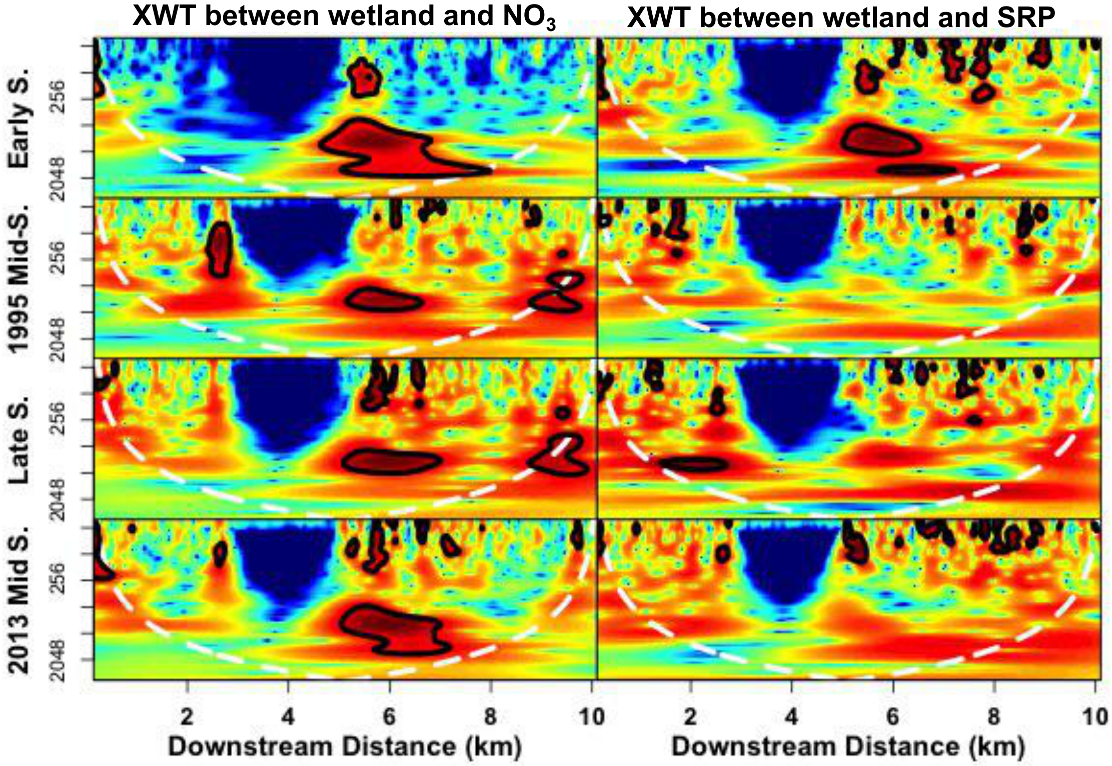
FIGURE 1. Wetland abundance distribution along 10-km main stem of Sycamore Creek two weeks after water chemistry survey in 2013.



APPENDIX F

SUPPLEMENTARY FIGURE 2

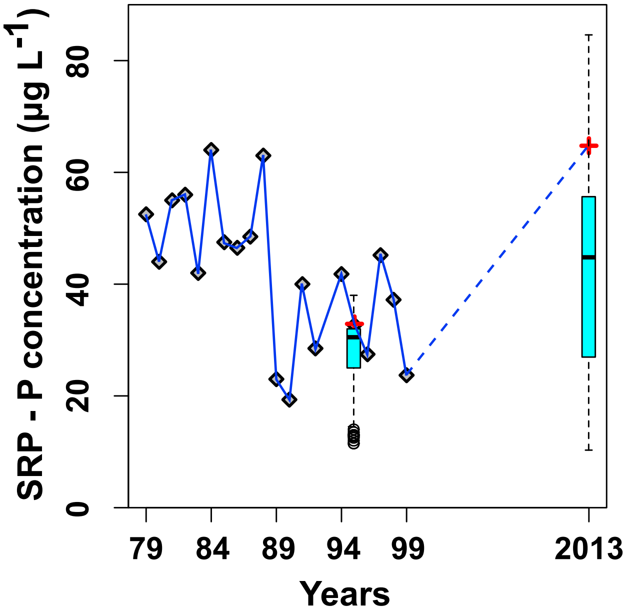
FIGURE 2. Cross wavelet analysis (XWT) between wetland abundance and spatial patterns of NO_3 concentration and SRP concentration in four surveys (different rows). See Figure 3.6 caption for detailed description of the wavelet plots.



APPENDIX G

SUPPLEMENTARY FIGURE 3

FIGURE 3. The long-term (1970 to 1999) SRP concentration (mean SRP concentration in the May of each year) variability in Sycamore Creek. For the long-term data, the data were collected from the same monitoring site (about 6 km downstream distance). For 1995 and 2013 when the May spatial survey was conducted, box plots are shown to represent the spatial variability in concentration over the 10-km surveying range. The red "+" labels the concentration of SRP at the long-term monitoring site.



APPENDIX H

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