Temporal variability in hydrology modifies the influence of geomorphology on wetland distribution along a desert stream

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Summary

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 5 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 analyse 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.

Key-words: aquatic plant ecology, Bayesian modelling, environmental gradient, hierarchical, hydrological variability, plant community structure, plant–climate interactions, 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

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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–for example, 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 & Patten 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. This 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
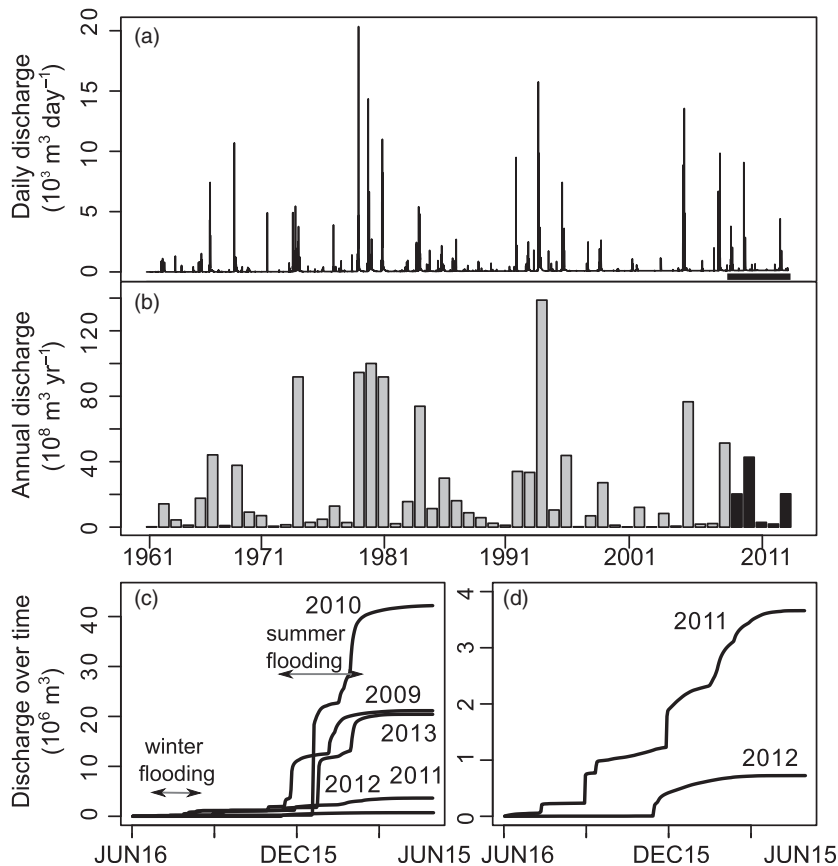
Fig. 1. Hydrological conditions at Sycamore Creek, Arizona during the study period, including (a) daily discharge (the study period is indicated with a horizontal bar on the *x*-axis), (b) annual discharge (the study period is denoted by black bars) and cumulative daily discharge during (c) the survey 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.

change in response to fluctuations in the environmental setting. To address these questions, we conducted a 5-year (2009–2013) survey of the dominant wetland species to quantify the presence/absence and abundance along a 12-km section of the stream. The 5 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). 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 north-east 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) and 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. 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 instream 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: that is, 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 5 years (2009–2013) 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). 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 12-month period was 9.9 million m^3. The years 2009 (21.2 million m^3) and 2013 (20.4 million m^3) were two average years, at the 68th percentile within the 53-years record (calculated for the same 12-month interval across the entire record). These 2 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 1 month later in 2013 compared with 2009 (Fig. 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-years record. The largest peak discharge during June 2011 and June 2012 was only 2.4 m^3 s^{-1} in December 2011 (Fig. 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 (15 June 2009, 14 June 2010, 13–14 June 2011, 16 June 2012 and 14 June 2013), 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 subdominant (< 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. percentage 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 1990s (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, …, 5) at sampling point i (i = 1, 2, …, 440) in year t (t = 1, 2, …, 5 for 2009, 2010, …, 2013). The likelihood for $y_{i,k,t}$ is defined by Bernoulli distribution:

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

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:

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

The coefficients, β, vary by species (k) and year (t), and β_1–β_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
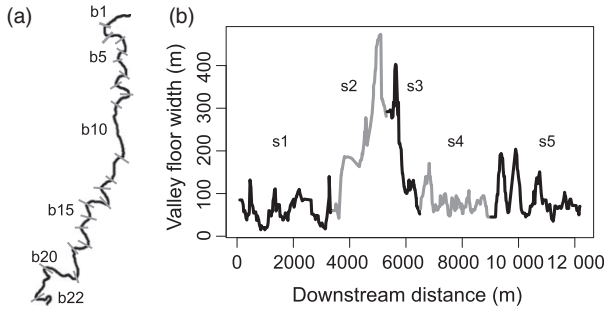
Fig. 2. Schematic for the two spatial scales in the models: (a) fine-resolution band scale and (b) coarse-resolution segment scale.

at point i (e.g. via competition or facilitation). That is, $\alpha_{kj,t}$ 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. 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. 2a). Secondly, the coarser segment (s) scale captures the alteration of constrained and unconstrained channels (Fig. 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 main stem of the stream into five 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. 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 ($i = 1, 2, \ldots, 120$) and time t ($t = 1, 2, \ldots, 5$ years for 2009, 2010, $\ldots$, 2013), we assumed logit(c) followed a normal distribution:

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

We defined the logit-scale mean (μ) 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 analyse 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 (μ):

$$\mu_{i,t} = b_{0,t} + L_t c_{i,t-1} + \varepsilon''_{b(i),t} + \gamma''_{s(b(i)),t}$$

$c_{i,t-1}$ is the wetland cover in the previous year ($t = 2, \ldots, 5$ for 2010, 2011, $\ldots$, 2013). And L_t is the legacy effect of the previous year's cover at stream unit i ($i = 1, 2, \ldots, 120$). 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 modelling 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 β, b, α, λ, λ', and L terms), we specified vague priors via normal distributions with large variances. Secondly, for the spatial random effects (i.e. the ε, ε', ε'', γ, γ', and γ'' terms), we assumed zero-centred normal priors with unknown variances such as *Normal*(0, σ^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. $\sigma_{\varepsilon,t}$, $\sigma_{\varepsilon',t}$, $\sigma_{\varepsilon'',t}$, $\sigma_{\gamma,t}$, $\sigma_{\gamma',t}$, $\sigma_{\gamma'',t}$). Thirdly, 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 > 3000 independent samples (for details on MCMC procedures, see Gamerman & 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 vs. the average predicted probability of occurrence for each species. For the patch data, we compared the predicted vs. observed percentage 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 trade-off 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 5-year study period. The stream channel between 3000 and 5000 m had almost no wetland establishment (Figs 3 and 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. 4). Despite the high variability in wetland spatial

distribution both in space and time, locations of some wetland patches have been stable (Fig. 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), although the previous year's cover was still a significant factor. We also analysed 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. 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. 3). After the large flood in January 2010, wetland cover decreased dramatically (Fig. 3d), reaching the lowest of the 5 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. 3d). There were only two small flood events in 2011 and no floods in 2012 between January and June (Fig. 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*.

Fig. 3. Changes in wetland cover and spatial distribution between 2009 and 2013 along the 12-km main stem 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 2 for species codes.
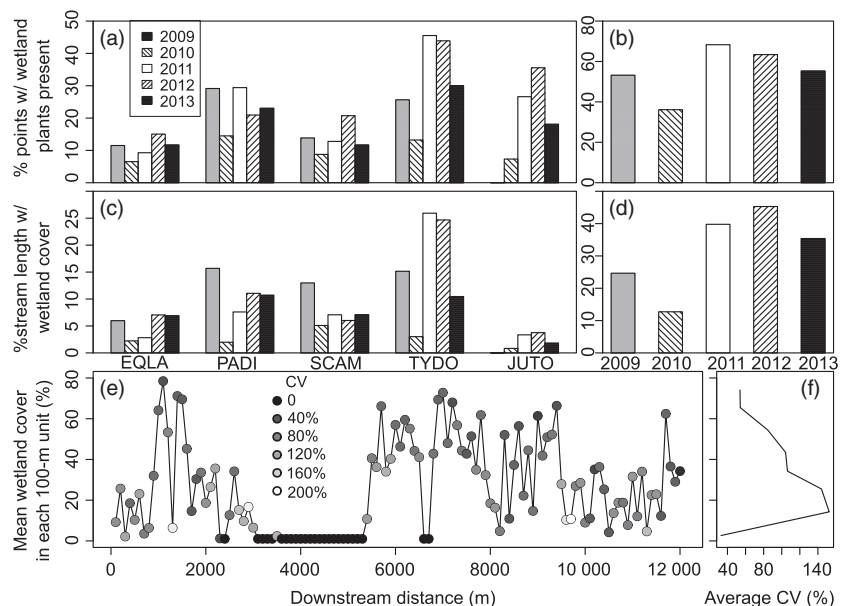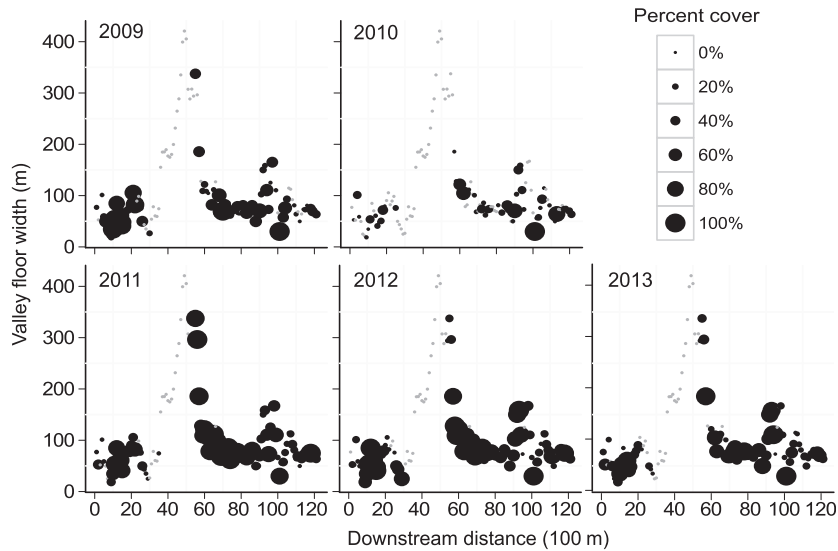
Fig. 4. Spatial distribution of wetland patches along the channel in relation to valley floor width. The channel is divided evenly into 100-m units. The size of each point is proportional to the percentage of channel length covered by wetlands within each unit. The small grey points represent segments without wetland cover.

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. 1c) except that floods in 2013 were 1 month later than those in 2009, the patch cover of *T. domingensis* in 2013 was only 70% of that in 2009 (Fig. 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. 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 favourable 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. 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). 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,

Table 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 the 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
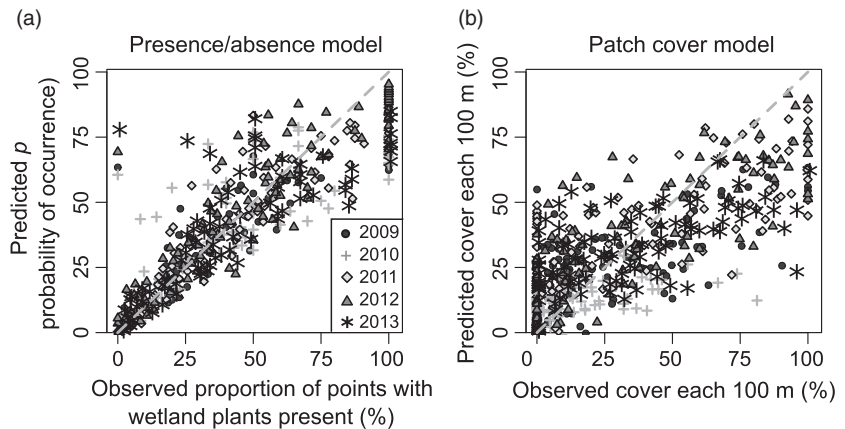
Fig. 5. Observed vs. predicted response variables for (a) the presence/absence point model and (b) the patch cover model. For the wetland cover model, the model fit was better in dry years (2011 and 2012) than in average years (2009 and 2013). The model goodness-of-fit was poorest for wetland cover in 2010. Dashed diagonal line is the 1:1 line.

we used the coefficient of determination (R^2) from a regression of the observed fraction vs. 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), with observed vs. predicted values falling around the 1:1 line (Fig. 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).

Both the direction and magnitude of the geomorphic effects varied among species and changed over time (years) (Table 2 and Fig. 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 5 years (Table 2). Elevation (E) was not a significant predictor of the presence of wetland plants overall, although the presence of *P. distichum* and *S. americanus* was significantly correlated (negatively and positively, respectively) with elevation. Water permanence (W) had a significant positive effect on species occurrence in all 5 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 2). The magnitude of the effect of water permanence (W) varied significantly among the five wetland species (Fig. 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. 7). Significant species associations can be attributed to two factors: the shared or opposite requirement for a particular physical environment (i.e. coexistence) 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. 7).

Table 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 five species. Species codes are as follows: 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.

The spatial random effects indicated significant unexplained spatial variability at multiple spatial scales that varied among years (Table 1; Fig. 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. 8). Significant
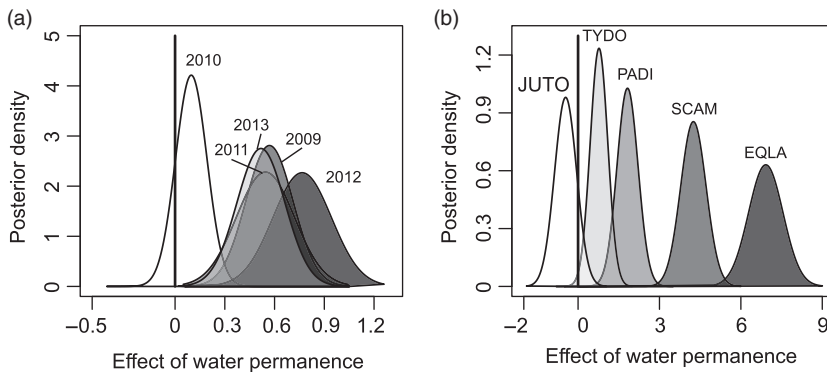
Fig. 6. Posterior distributions for the effect of water permanence (a) in different years (results from patch cover model) and (b) for different species (results from presence/absence point model). See Table 2 for species codes. The vertical line at zero indicates the lack of an effect of water permanence.
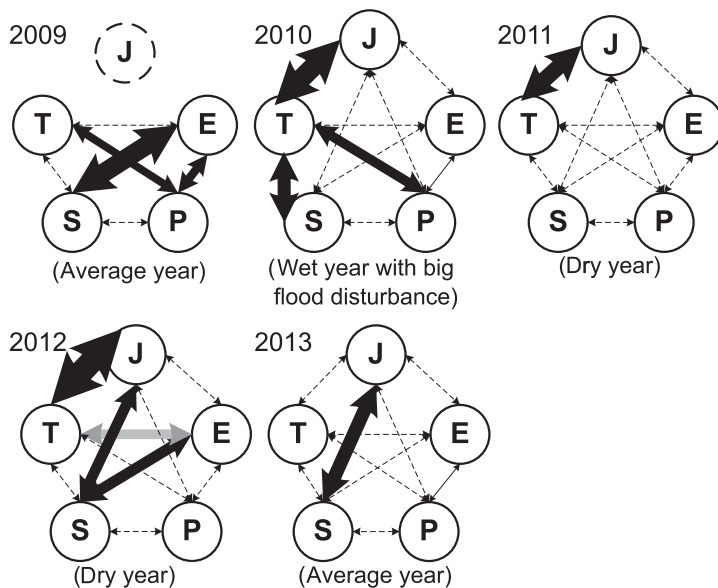

Fig. 7. Species interaction effects changed among years. Dashed arrows indicate that the corresponding species-species effect was not significant, and solid arrows denote significant species associations. The black arrows represent a significant positive effect, and the grey arrows represent a significant negative effect; arrow width is proportional to the effect size (i.e. the strength of the species associations). Species codes are as follows: P = *Paspalum distichum*, S = *Schoenoplectus americanus*, E = *Equisetum laevigatum*, J = *Juncus torreyi* and T = *Typha domingensis*.

segment-level spatial random effects still emerged after accounting for the geomorphic, biotic and fine-scale band effects (Fig. 8), with least variation among segments (σ_s) occurring in 2010 and greatest occurring in the two dry years (2011 and 2012) (Table 1). Segment 2, which was the part of the stream where the valley floor widened in a downstream direction (Fig. 2b), had significantly lower probability of wetland occurrence across all 5 years. Conversely, segments 3 and 4, which are located in the part of the stream where the valley is narrowing downstream (Fig. 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).

Elevation (*E*), channel slope (*S*) and valley floor width (*V*) had no significant effect on the distribution of wetland cover

(Table 2). Water permanence (*W*) explained most of the variance in wetland cover across all years except for 2010 (Table 2), although effect size varied among years, with the largest effect occurring in the driest year (2012) (Fig. 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. 8). Greater values for σ_b and σ_s in dry years also indicated more evident spatial random effects (Table 1). In dry years, segment 3, where the valley floor narrowed sharply (Fig. 2b), had higher wetland abundance than expected (i.e. given the effects of the covariates included in the model) compared with the other segments (Fig. 8). The spatial effect at band scale was also most significant in the driest year, 2012 (Fig. 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
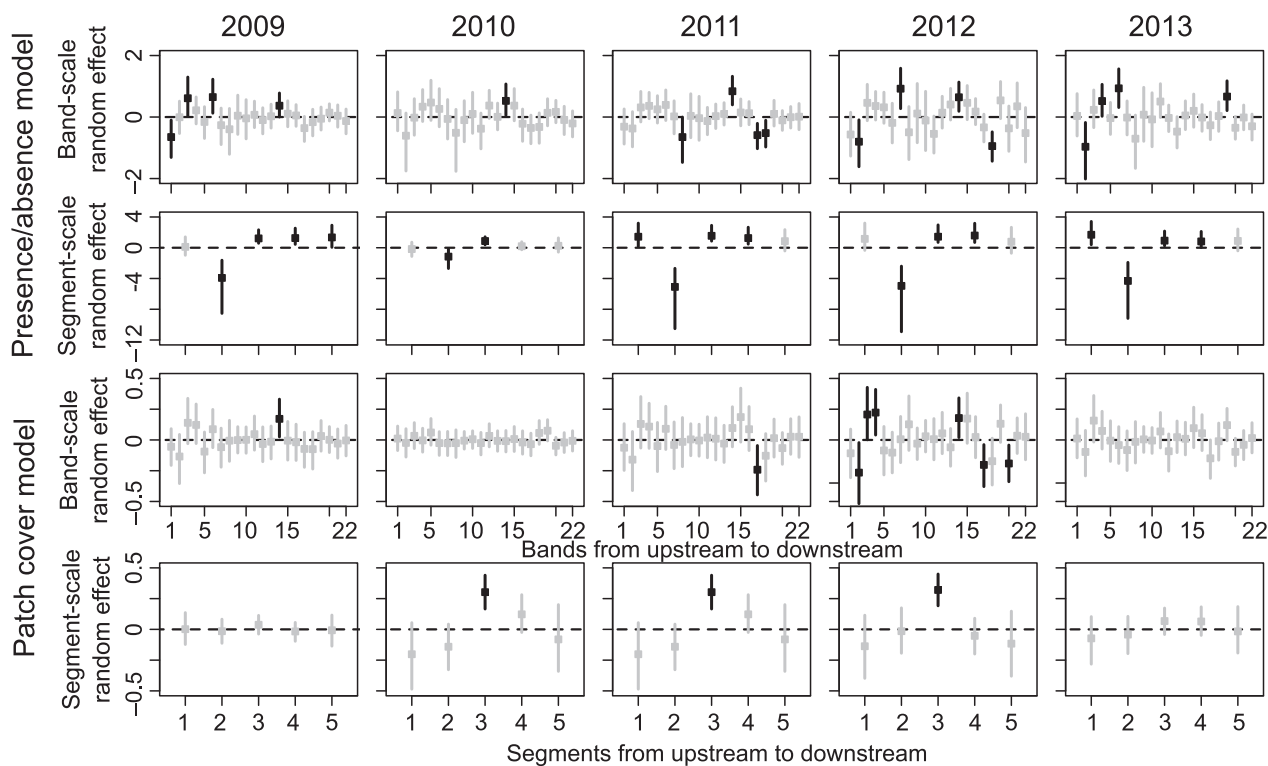
Fig. 8. The posterior mean and 95% credible interval (CI) for the spatial random effects at fine-resolution band scale and coarse-resolution segment scale in presence/absence point model (upper two rows) and patch cover model (lower two rows) in different years. Significant random effects (95% credible interval does not contain 0) are marked as black, and non-significant effects are in grey.

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). 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; Fig. 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 with the average years or the single wet year (Table 1; Fig. 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. 3b,d). The band-scale spatial effects capture the interactions between morphodynamics and hydrology in meandering rivers (Fig. 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 the 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. 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. 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 data set 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 4 years. Similar long-term consequences of large disturbances have been observed in other studies. For example, Stromberg, Fry & Patten (1997) found that in the 3 years following a 25-year

flood in the Hassayampa River, north-west 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 aridland 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. 7). This could have resulted from the changed relative abundance of different species in different years (Fig. 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 *et al.* 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. 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 5 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.

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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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