ARTICLE

Trajectories and state changes of a grassland stream and riparian zone after a decade of woody vegetation removal

Walter K. Dodds[1] | Zak Ratajczak[1] | Rachel M. Keen[1] |
Jesse B. Nippert[1] | Bartosz Grudzinski[2] | Allison Veach[3] |
Jeffery H. Taylor[1] | Amanda Kuhl[1]

[1]Division of Biology, Kansas State University, Manhattan, Kansas, USA

[2]Department of Geography, Miami University, Oxford, Ohio, USA

[3]Department of Integrative Biology, University of Texas at San Antonio, San Antonio, Texas, USA

Correspondence
Walter K. Dodds
Email: wkdodds@ksu.edu

Abstract

Riparian zones and the streams they border provide vital habitat for organisms, water quality protection, and other important ecosystem services. These areas are under pressure from local (land use/land cover change) to global (climate change) processes. Woody vegetation is expanding in grassland riparian zones worldwide. Here we report on a decade-long watershed-scale mechanical removal of woody riparian vegetation along 4.5 km of stream channel in a before–after control impact experiment. Prior to this removal, woody plants had expanded into grassy riparian areas, associated with a decline in streamflow, loss of grassy plant species, and other ecosystem-scale impacts. We confirmed some expected responses, including rapid increases in stream nutrients and sediments, disappearance of stream mosses, and decreased organic inputs to streams via riparian leaves. We were surprised that nutrient and sediment increases were transient for 3 years, that there was no recovery of stream discharge, and that areas with woody removal did not shift back to a grassland state, even when reseeded with grassland species. Rapid expansion of shrubs (*Cornus drummondii*, *Prunus americana*) in the areas where trees were removed allowed woody vegetation to remain dominant despite repeating the cutting every 2 years. Our results suggest woody expansion can fundamentally alter terrestrial and aquatic habitat connections in grasslands, resulting in inexorable movement toward a new ecosystem state. Human pressures, such as climate change, atmospheric CO_2 increases, and elevated atmospheric nitrogen deposition, could continue to push the ecosystem along a trajectory that is difficult to change. Our results suggest that predicting relationships between riparian zones and the streams they border could be difficult in the face of global change in all biomes, even in well-studied sites.

KEYWORDS
alternative states, nutrients, riparian zone, stream discharge, thresholds, water quality, woody vegetation

INTRODUCTION

Riparian zones are key control points in material transfer between terrestrial and aquatic habitats due to high biogeochemical activity (McClain et al., 2003). The riparian zone mediates water flow into stream channels, where moisture may select for woody plant growth due to increased water availability relative to other upslope terrestrial landscapes (Rood et al., 2003). Riparian vegetation can exert controls on stream channel morphology (Sweeney et al., 2004), strongly affect water quality (Banner et al., 2009; Dodds & Oakes, 2006; Dosskey et al., 2010; Grudzinski et al., 2016), and alter energy flow and food webs in streams (Baxter et al., 2005; Vandermyde & Whiles, 2015). Deforestation in temperate forested watersheds can strongly increase movement of nutrients and sediments to streams without intact riparian zones (Hobbie & Likens, 1973). However, the role of riparian zones in controlling the movement of nutrients (e.g., Herndon et al., 2015; Van Meerveld et al., 2019) and water (Tabacchi et al., 2000) to streams is complex and context dependent. Thus, the implications of large directional changes in species cover or composition in riparian zones (e.g., invasive species, turnover in plant functional groups) may be difficult to predict, particularly under a changing climate.

Woody expansion in grasslands is common globally (Briggs et al., 2005; Naito & Cairns, 2011; Scholes & Archer, 1997) and occurs over decades (Silva et al., 2009; Veach et al., 2014; Veach, Dodds, & Skibbe, 2015). This expansion has implications for stream ecosystem function (Larson et al., 2018; Reisinger et al., 2013; Riley & Dodds, 2012) and terrestrial plant diversity (Ratajczak et al., 2012). Woody expansion is likely due to a combination of local and regional factors for grasslands. Riparian zones have greater soil moisture than the remainder of the terrestrial landscape and are typically subject to reduced fire intensity, allowing trees and woody shrubs to proliferate while avoiding the competitive edge of C_4 grasses for water uptake from surface soils (Bond & Midgley, 2000). Locally, fire suppression is a common contributor to woody plant expansion (Briggs et al., 2005; Scholes & Archer, 1997). Even in frequently burned areas, elevated CO_2 may allow tree saplings to reach disturbance-resistant heights faster or conserve more carbon belowground, facilitating resprouting after fire (Kgope et al., 2010).

Positive feedbacks and shifts in competitive hierarchies can accelerate and then cement transitions from grassland to woodland. For example, when woody plants displace grasses, it reduces fire fuel load, which lowers woody plant mortality and increases woody recruitment at the grass–woody plant ecotone (Anderies et al., 2002;

Ratajczak et al., 2011). Mature woody plants develop a deeper root system and avoid belowground competition with grasses (Anderies et al., 2002; O'Keefe et al., 2019; Ratajczak et al., 2011). These functional vegetative properties suggest the possibility of hysteresis, where transitions to an alternative riparian woody state are difficult to reverse (Collins et al., 2021). However, traditional models of alternative stable states do not necessarily consider changes under shifting baselines (Frelich & Reich, 1999; Ritchie et al., 2021) as are occurring with human-induced climate change, propagule pressure of newly dominant species, and broad-scale atmospheric nitrogen deposition.

Kings Creek on Konza Prairie Biological Station (KPBS) is one grassland area experiencing the expansion of woody riparian vegetation (Veach et al., 2014; Veach, Dodds, & Skibbe, 2015). Earlier hectometer-scale manipulative experiments at Kings Creek removed woody riparian vegetation on either side of stream channels. These experiments compared woody removal areas to naturally grassy and forested areas above and below the removal zones. The researchers documented that, in woody removal zones, (1) stream communities shifted to filamentous green algae from a thin diatom-dominated biofilm cover (Riley & Dodds, 2012) and toward a higher proportion of grazing invertebrates (Vandermyde & Whiles, 2015), (2) removals increased the rates of stream gross primary production by increasing light (Riley & Dodds, 2012), and (3) removals increased benthic stream and riparian soil denitrification rates (Reisinger et al., 2013) and marginally influenced soil microbial communities with stronger shifts in bacterial compared with fungal components (Veach, Dodds, & Jumpponen, 2015). Thus, woody expansion and subsequent removal on Kings Creek can have strong effects on local stream and riparian soil properties.

Many ecological responses are sensitive to scale (Levin, 1992). Therefore, large-scale experiments that capture ecosystem and meta-community responses are required to match the minimum scale at which management and biodiversity conservation occurs (Schindler, 1998). In 2010, we performed a large-scale manipulation that cut all woody riparian vegetation in a 119-ha watershed on Kings Creek along 4.8 km of stream channel to assess the cumulative influences of woody riparian vegetation on stream and riparian ecosystem structure and function. We hypothesized that nutrients, sediment, and water transport would all increase once woody vegetation was no longer intercepting these materials. We physically removed trees and shrubs biannually for the duration of the experiment and tested statistical differences related to the removal using a before–after control impact (BACI) approach. We also established vegetation transects in the removal area under three conditions:

woody, grassland, and woody replanted with grassland seeds. Stream data for 3 years before and 3 years after the removal showed significant water chemistry responses (Larson et al., 2018). Removal resulted in 10- to 100-fold increases in stream water nitrate and two- to 25-fold increases in total and soluble reactive phosphorus and suspended solids. Long-term stream monitoring before the experiment indicated declines in discharge and an increased number of no-flow days, which did not correlate with precipitation or temperature trends (Dodds et al., 2012), but Larson et al. (2018) found no significant hydrologic changes over 3 years after woody removal.

The expansion of woody vegetation is generally expected to have the greatest hydrologic impact in mesic grasslands, where precipitation exceeds evapotranspiration (Huxman et al., 2005), with woody removal potentially facilitating streamflow recovery. On average, precipitation at KPBS roughly equals evapotranspiration (Keen et al., 2022), except during drought years in woody encroached watersheds, when increased transpiration by woody vegetation causes evapotranspiration to outpace precipitation (Logan & Brunsell, 2015). Woody removal studies in other grassland ecosystems have mixed effects on hydrology. Removal has led to increases in streamflow or groundwater recharge in some cases (Bosch & Hewlett, 1982), but this trend is not universal (Dugas et al., 1998; Wilcox, 2002; Wilcox et al., 2006). When no detectable recovery in streamflow was observed 3 years after removal, Larson et al. (2018) left the question open as to whether the stream ecosystem state was in a new configuration or if the changes were temporary and more time was necessary to detect recovery. This is an important question, because the influence of woody riparian vegetation on grassland streamflow is controversial and there are few direct whole-watershed manipulative experiments testing the effects of woody removal in grassland ecosystems (Brown et al., 2005).

Ten years after removal, we can now assess the decade-long changes of key populations, communities, and functions in this experiment in addition to shorter-term changes in stream water quality. We now test whether riparian vegetation shifted with the removal in formerly forested areas, and whether cut riparian areas replanted with grassland forb and grass seeds became similar to nearby natural grassy riparian areas. We also analyzed longer-term records of stream hydrology, stream chemistry, organic matter deposition, and responses of stream mosses to canopy opening. Finally, we conducted surveys of channel morphology before and 10 years after woody removal. We hypothesized that removal of woody vegetation followed by regular cutting of woody vegetative regrowth and replanting areas with grassland seed would (1) cause terrestrial plant communities to move to a state

more similar to open riparian areas, with more rapid shifts in areas that were replanted, (2) shift hydrology to more water yield and fewer zero-flow days, resulting in stream water isotopic signatures approaching those of water sources previously exploited by woody species with deeper roots, (3) have modest effects on stream chemistry, (4) widen stream channels and have modest effects on the concentration of suspended sediments in the stream water, (5) decrease allochthonous detrital inputs to streams, and (6) cause stream channel moss cover to become more similar to areas with more open canopy. We then used these data to address directional changes and alterations of stream and riparian ecosystem states in the region, with implications for riparian functions in other biomes as well.

METHODS

Site description, removal, and general experimental design

We used a BACI design. We provide timelines, major sample types, and sampling dates in Table 1. Trees and shrubs were expanding in the riparian zone and some upland areas for decades prior to removal (Veach et al., 2014; Weihs et al., 2016). Upland and some riparian area flora were predominantly grass (*Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium*, and *Sorghastrum nutans*). Dominant tree species in the woody riparian zone prior to removal included *Celtis occidentalis* (Hackberry), *Cercis canadensis* (redbud), *Gleditsia triacanthos* (honey locust), *Quercus macrocarpa* (bur oak), *Quercus muehlenbergii* (chinquapin oak), and *Ulmus americana* (American elm). The common shrub species were *Cornus drummondii* (roughleaf dogwood), *P. americana* (American plum), and *Rhus glabra* (smooth sumac) and were generally more abundant in areas with more moisture (e.g., seeps on the hillslopes and riparian zones furthest upstream).

The geology of the site is characterized by 1- to 2-m-thick limestone units alternating with 2- to 4-m-thick mudstone layers. Soils in uplands are shallow and those in the lowland are silty-clay loams up to 2 m thick. Soils are fine, smectitic, mesic Udertic Paleustolls. Most streamflow is dominated by shallow groundwater pathways through the limestone, with very modest contributions by surface sheet flow, even during strong rainstorms (Hatley et al., 2023).

We have one treatment and two control watersheds on KPBS (Figure 1a,b). The treatment watershed was N2B (39.08995 N, 96.58900 W), and the control watersheds were N4D (39.087356 N 96.584417 W) and N1B (39.08656 N,

TABLE 1 Sample types and activities with locations and dates (NA, not applicable).

| Sample type/activity	Locations	Dates/frequency
Initial cutting	Whole watershed riparian	November 2010–February 2011
Follow-up cutting	Half watershed every other year	2011–2020
Watershed burning	Entire watershed, biannually	2009, 2011, 2013, 2015, 2017, 2019, 2021
Discharge measurements	Weirs at N2B treatment and two control watersheds	1986–2020 every 5 min
Water chemistry samples	Weirs at N2B treatment and two control watersheds, N4D, N1B	1986–2020 three times per week when flowing
Water isotopes	Weirs at N2B treatment and two control watersheds, N4D, N1B	2010–2020 three times per week when flowing
channel morphology	Upstream from weirs at N2B, N1B	2010, 2011, 2013, 2019 (N1B, N2B), 2010, 2011, 2013 (N4D)
Moss surveys	Transects up from N2B and N4D weirs	2011 and 2020
Leaf surveys, long term	Mainstem transects (AL) collected year round	1980–2020
Leaf material in stream channel	Mainstem stream, immediately below cut area on N2B, in cut area N2B, in control watershed N1B	2020
Plant surveys	Four transects of 10 m, with four plots in open grassland, four plots in cut riparian forest with supplemental seed, and four plots in cut riparian forest without supplemental seed	2010, 2011, 2020
Remotely sensed plant cover	Mainstem stream, from headwaters to terminus in N1B, N2B, and N4D	1978, 2002, 2003, 2010, 2012, 2014, 2016, 2018, 2020

96.57703 W). We picked two control watersheds that bracketed the burn frequency of the treatment watershed, and bison have been present on all watersheds since 1992 at ~0.21 animal units (AU)/ha. Watershed N2B has an area of 119 ha and is burned every 2 years. The control watershed N1B had an area 120 ha and was burned every year, and the other control watershed, N4D, had an area of 135 ha and was burned every 3 to 4 years. We cleared the entire stream drainage (4.8 km stream length) of watershed N2B of woody riparian vegetation (trees and shrubs) within 30 m of each side of the main channel, and side channels were cleared to 10 m on either side during winter 2010–2011 (Figure 1b–e). We used chainsaws, a walk-behind field and brush mower (DR power equipment), and Stihl 450 brush cutters to cut the vegetation. Wherever possible we cut woody material to less than 15 cm in height. Trees whose trunk diameter was >50 cm were girdled and left standing. All cut material was removed to outside the stream channel, and materials except for large tree trunks and branches were either removed from the 30-m boundary or piled for burning inside of the 30-m boundary. Woody stumps and stems were not treated with herbicide; therefore, we recut a third to half of the stream riparian each year during the winters of 2011–2020. We rotated to any area uncut the previous year or where woody regrowth was the thickest.

Mapping historic trends and removal areas

We tracked changes in overstory woody plant cover, within and outside of riparian areas, for the control and treatment watersheds using remote sensed aerial imagery (following the same approach and images as Keen et al. [2022]). We combined images from several sources (see Appendix S1: Table S1 in Keen et al. [2022] for the source of each image and related details) to identify comparable true color aerial images (red, green, and blue wavelengths) with a resolution of at least 1 m. This search yielded color images from 2002, 2003, 2010, 2012, 2014, 2016, 2018, 2019, and 2020 and a black-and-white image from 1978. In our experience, grassy areas are easier to differentiate from shrubs, appearing as a homogeneous green to beige in true-color images and white to light gray in black-and-white images. Further, grasses were probably dominant in the 1978 image (Ratajczak et al., 2014). Therefore, this image was still included in analyses (Appendix S1: Table S1 in Keen et al. [2022]).
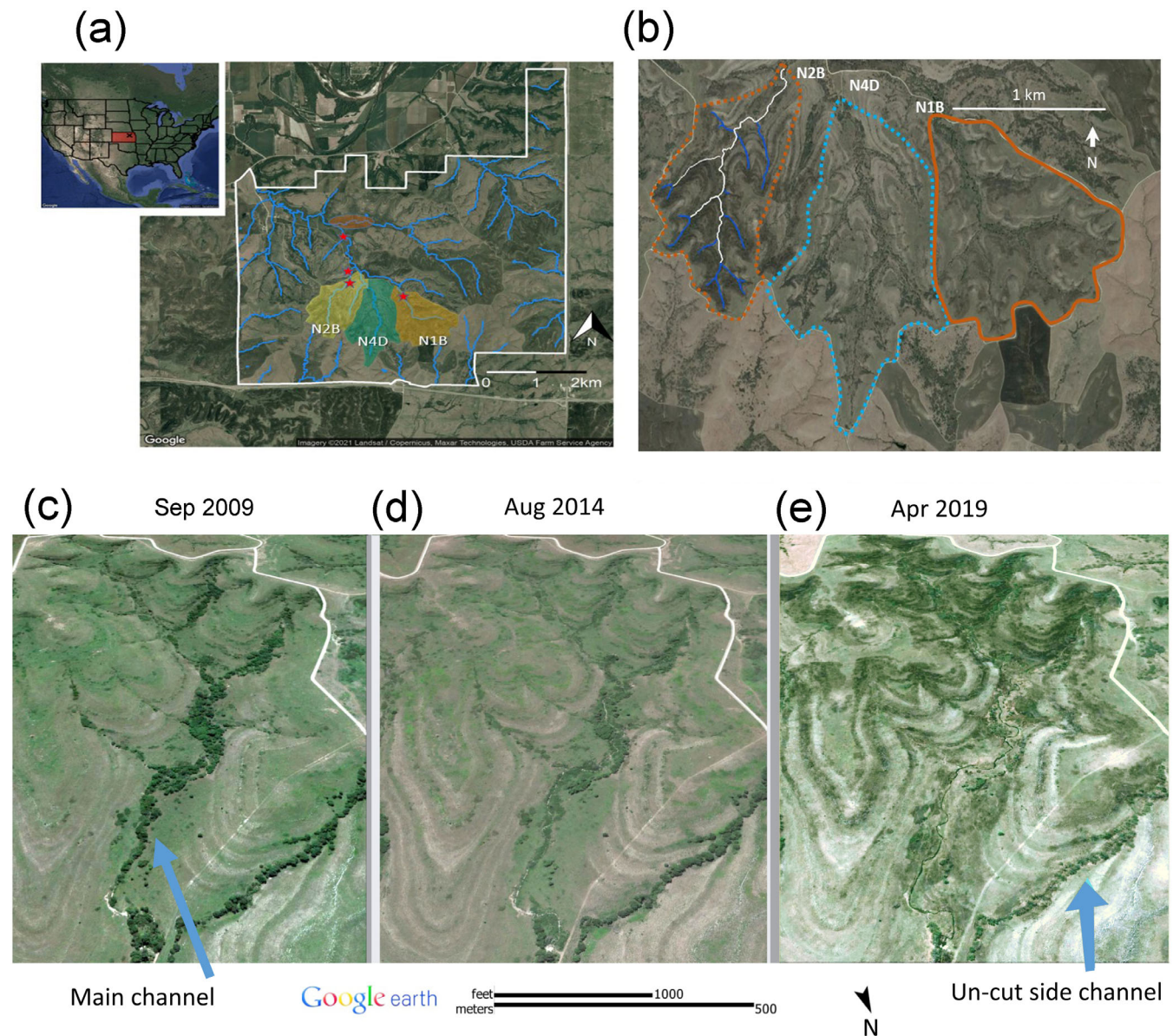
FIGURE 1 Location of experimental and control watersheds at Konza Prairie Biological Station, moss and organic material sampling locations (red stars), and litterfall sampling locations (red ellipse) (a), experimental and control watersheds with woody removal areas indicated by white lines (30 m on each side of channel) and blue lines (10 m on each side of channel). Weirs near watershed labels (b). Aerial imagery of treatment watershed before (c), 4 years after (d), and 9 years after (e) woody removal. Note the side channel in the uncut adjacent watershed retained canopy cover, but the main channel has no canopy cover over stream.

Within each watershed, we established a network of permanent plots for photo interpretation of vegetation types. Each circular plot was 1256 m^2 (20-m radius), with 38 plots in the nonriparian zone and 29 plots in the riparian area. This level of replication allowed for ~50 m between plots. We could obtain larger sample size for the nonriparian zone because the riparian zone only occupies approximately one fifth of the watershed. We placed plots within the riparian zone at regular intervals with randomization (10–20 m). Our plots in the broader watershed were at similar intervals but skipped over semiriparian side channels.

We used photo interpretation to outline woody vegetation for each combination of image and plot. Polygons were drawn around all distinguishable trees, shrubs, and areas that were indistinguishable from woody vegetation (this category comprises <5% of woody plant coverage overall but most coverage in the 1978 image) at a submeter resolution. Two users (Brynn Ritchey and Zak Ratajczak) interpreted each image to increase accuracy, both of whom have experience working with ground-truthing and aerial surveys of vegetation on site (Keen et al., 2022).

Plant community sampling and postcut reseeding

In fall 2010, we established plant community plots to assess the potential ability of the riparian zone to shift to a grassland state based on cutting alone and cutting with replanting. The three treatments were (1) naturally open riparian grassland before the removal, (2) areas cleared of woody vegetation, and (3) areas cleared of woody vegetation and seeded with prairie plant species. The addition of the seeded treatment was designed to determine whether recovery of grassland vegetation was hindered by propagule limitation. The seeded and nonseeded removal plots were adjacent to each other and randomly assigned. Each community type had four plots, each of which was 10 m parallel along and 3 m perpendicular to the stream channel. Each plot had four plant composition transects along which we sampled four 1-m^2 subplots along each transect. Vegetative cover of vascular plant species was determined using a modified Daubenmire scale (Gibson & Hulbert, 1987).

We planted plots with seed collected from nearby species in fall 2010. Seeds were collected from 70 species, with six species (listed by mass), *S. nutans*, *A. gerardii*, *Antenneria neglecta*, *Elymus canadensis*, *Silphium laciniatum*, and *Silphium integrifolium*, making up more than half of the total seed mass added. The seeding rate was relatively high (~38 kg/ha). This was about twice the recommended rate for grassland restoration, since we did not clean or test seeds for viability. While we did not clean seed (e.g., no pappus removed, seeds like those of purple prairie clover not removed from pods, wild coffee seeds not removed from fruits), *Echinacea* seeds were separated from the capitulum. Seed for each species was stored in paper bags at room temperature until time of seeding. Seeds were sown onto each plot and gently raked in on 28 December 2010 shortly after woody cutting. A paper bag was prepared for seed addition in each treatment plot, with all species mixed. Seed was hand broadcast, passing over the treatment plot at least three times in the process of emptying each bag to ensure even spread and that any smaller seeds settling to the bottom would be spread throughout.

Hydrology and water chemistry

Hydrology and water chemistry were measured at weirs N2B, N4D, and N1B. Weirs are of a v-notch design with water height measured using Druck pressure transducers from 1987 to 2013 and YSI WaterLOG Bubbler/Pressure Sensors H-3553 from 2013 to the present. Sensors measure and log depth every 5 min, and the sensors are calibrated against manual height measurements approximately every 3 days during flow and converted to discharge with a rating curve.

Water chemistry and suspended sediment samples were also taken at weirs three times per week during flow, but the frequency was decreased to once per week in 2020 because of the COVID-19 restrictions. Samples were collected using acid-washed containers and kept on ice until being returned to the laboratory, where they were processed the same day.

Dissolved inorganic and total N and P were subsampled and stored frozen for analyses using standard methods on an OI Analytical Flow Solution IV analyzer. Samples for dissolved materials were filtered through a 0.4-μm filter (glass fiber filter, GF/F, Cytiva Whatman) and analyzed for dissolved inorganic N (NO_3^-–N + NO_2^-–N, NH_4^+–N), orthophosphate (PO_4^{3-}), and dissolved organic carbon. Total N and P samples were not filtered. Laboratory N and P analyses were verified biannually via shared sample analysis of US Geological Survey Standard Reference Sample (http://bqs.usgs.gov/srs/). Dissolved organic C samples were filtered, acidified, and analyzed using a Schimadzu TOC-L.

Weekly stream water isotopic samples (during periods of flow) were collected from the treatment watershed (N2B) and two adjacent watershed streams for comparison (N1B and N4D). Stream water samples were analyzed for $\delta^{18}O$ using a Picarro WS-CRDS isotopic water analyzer at the Stable Isotope Mass Spectrometry Laboratory at Kansas State University. Isotopic ratios are expressed in delta notation relative to Vienna Standard Mean Ocean Water. The long-term within-run precision was <0.15‰ for $\delta^{18}O$.

Channel morphology and stream sediments

Channel morphology transects were surveyed in 2011 and resurveyed in 2019 in watersheds N2B (seven transects) and N1B (eight transects) as in Grudzinski and Daniels (2018). Briefly, we established permanent cross sections in each watershed, spaced at about 20-m intervals. We surveyed each cross section with a surveyor's level and leveling rod at a 15.2-cm spatial resolution. Bank-full width (w) was measured for each transect, and cross-sectional depth (d) was calculated by averaging all depth measurements across the bank-full width. The $w{:}d$ ratio was determined by dividing the bank-full width by the average cross-sectional depth, and channel area was determined by multiplying bank-full width by average cross-sectional depth.

We determined volatile and total suspended solid concentrations with water samples collected as

previously outlined. Measured samples (50–4000 mL) were filtered onto prepared and preweighed Whatman 934 AH 1.5-μm retention glass microfiber filters (precombusted in a muffle furnace at 500°C and weighed). Sample filters were then oven dried at 100–105°C, weighed, combusted at 500°C, and reweighed (to the nearest 0.1 mg). We calculated total suspended sediment concentrations as follows: total suspended solids/L = (total mass − filter mass)/volume filtered. We calculated volatile suspended solids (ash-free mass) concentrations as follows: volatile mass/L = (dry filter sample − combusted mass)/volume filtered.

Periodically, we subjected a batch of filters to a second drying and weighing to check for problems associated with water of rehydration. Rewetting and redrying of roughly one in 20 samples over the few hundred taken yielded less than 1% change in measured weights.

Stream moss, organic material, and litter deposition

Organic material in the stream channel was surveyed in four locations on 8 January 2021 in dry channels that had not flowed since woody leaf senescence (Figure 1a). The four sites were (1) upstream of the weir in the removal area watershed N2B (39.08995 N, 96.58900 W), (2) downstream of removal area in watershed N2B in a channel with intact riparian forest (39.08994 N, 96.58859 W), (3) further downstream of the previous point, in mature gallery forest and at one of the long-term litter deposition sites (39.09867 N, 96.88967 W), and (4) in the control watershed N1B, in an area of younger riparian forest with small trees (39.08656 N, 96.57703 W). Each site had ten 0.25-m² quadrats spaced over a few 100 m. We took 10–20 paces upstream and blindly cast the quadrats into the channel. All leaves, small wood, and seed parts were collected from inside the quadrats and weighed in the field. For large samples, the entire damp sample was weighed and an ~30-g subsample was placed in a paper bag to assess damp mass to dry mass. The entire sample was taken and weighed for smaller samples. The subsamples were weighed again and then the bag alone after 3 days of drying at 60°C. The proportion of damp to wet mass for each sample was used to correct the dry mass of the entire sample. A subset of 18 samples of collected leaves was ashed at 450°C to determine the ratios of ash-free dry mass (AFDM) to dry mass. This factor was 0.74 with a SD of 0.07.

We assessed long-term litter collection data to understand how litter deposition changes with forest development. We used the Gallery Forest Litterfall data (Table 1), which is a series of 32 permanently located, 50 × 50 × 50-cm³ "deep-dish" litterfall collectors (open top wire mesh boxes). The boxes are arranged along five transects on the north fork of Kings Creek in areas with riparian forest outside the bison grazed area (Figure 1a). Each transect had two to 11 boxes depending on the width of the riparian area of a given transect. Samples were collected monthly, March to December, weather permitting. Samples were dried for a minimum of 3 days at 60°C. Finally, samples were sorted into woody, seed/reproductive, and leaf categories and weighed.

We surveyed in-stream moss cover upstream of the weirs on watersheds N2B and N4D in May 2011 (immediately after the cutting treatment) during baseflow and on 8 January 2021 under dry conditions. Briefly, a 0.25-m² quadrat was randomly placed within the active stream channel every 6 m along the stream channel until 10 transects in the main channel of N2B and N4D were sampled. The square quadrat had a grid with 50 equally sized subquadrats and proportion of moss cover was estimated for each subquadrat. The data are represented as the proportion of moss cover.

Statistical methods

Detailed results and platforms for statistical tests are available in Appendix S1 and S2. For each seeded and nonseeded plot, we used transect as the unit of replication by averaging all four subplots within each transect and calculated the species richness and Shannon's index, grass cover, forb cover, and woody plant cover. Shannon's index (H) was expressed as e^H, which is interpreted as the estimated number of species with equivalent abundance.

For all univariate plant community response variables, we performed an ANOVA with treatment (open grassland, seeded riparian removal, and unseeded riparian removal), year, and their interactions as main effects, with a random effect for plot. Transect was included as a random effect, and the model was implemented using the "lmer" function from the lme4 packages (Bates et al., 2015). All variables met assumptions of normality of residuals and homogeneity of variance of residuals, so no transformations were needed. Pairwise contrasts were performed for response variables with significant interaction terms using estimated marginal means (using the emmeans package and "emmeans" function in R [Lenth et al. 2019]) contrasts with a Tukey honest squares difference (HSD) adjustment to p-values.

We also calculated changes in plant community composition as a function of treatment and time. Zero saturation can distort multivariate composition, so we only used species that were found in at least 20% of all combinations of treatment, plot, and sampling year, which yielded a

matrix with 41 species. Composition was measured using nonmetric dimensional scaling, which identified two axes of composition. We used Bray–Curtis as our distance metric and the Wisconsin double transformation for scaling, where each unit step indicates an ~50% turnover in composition. This approach resulted in a stress value of 0.146. To determine whether differences in non metric multi dimensional scaling (NMDS) space were significant, we performed a permutational multivariate ANOVA with treatment, year, and their interactions as factors (Appendix S1: Table S11). We used Bray–Curtis as the distance metrics and with 1000 permutations. We used the vegan package in R for composition analyses (Oksanen et al., 2020).

We tested for temporal trends and differences by watersheds in stream water ^{18}O with analysis of covariance (ANCOVA) using year as the continuous and watershed as the categorical variable using Statistica 13 (Dell Statsoft). Stream chemistry and hydrology were aggregated at 3-month intervals or greater. This was because streamflow was autocorrelated at shorter time windows (data not shown). Autocorrelation was determined using nonparametric ranked correlation and offsetting the mean daily discharge by sequentially increasing time steps.

Proportion of moss cover data was highly zero-inflated; therefore, we used a negative binomial generalized linear regression model using the "glm.nb" function in the MASS R package (Venables & Ripley, 2002). The watershed (treatment watershed N2B vs. control watershed N4D), time of sampling, and their interaction were fixed independent variables in the model. Comparisons were calculated using the estimated marginal means ("emmeans" in emmeans package [Lenth et al., 2019]) contrasts that use a Tukey HSD to p-values to determine statistical differences for the interaction term in pairwise comparisons.

We used ANCOVA (general linear model in Statistica) to test for changes in channel morphology over time and to compare watersheds N1B and N2B. This analysis used year as the continuous and watershed as the categorical variable, with depth, width, width:depth or width × depth (area) as the response variable.

RESULTS

Vegetative cover

We removed woody vegetation (trees and shrubs) such that the channel was no longer shaded along much of its length over the period of study. Spatial imagery of the stream channel before and after the onset of woody removal shows that trees were removed effectively along the entire length of the channel and that vegetation did not cover the channel (Figure 1c–e). A more detailed analysis of vegetative cover revealed that shrub cover replaced tree cover in the riparian zone despite repeated cutting of resprouting trees and shrubs (Figure 2). However, the shrubs were not tall enough to obscure the channel.

Starting in the 1980s, woody cover was <50% in the riparian zone and barely detectable outside the riparian zone (Figure 2). By 2010, just before cutting occurred, total woody cover in general was greater in the riparian zones of all the watersheds than outside of the riparian zone. Total cover increased both inside and outside of the riparian zone in all watersheds, but potentially less in the annually burned watershed (N1B) than in the biannually (N2B) and quadrennially burned (N4D) watersheds.

Proportional tree cover was near zero outside the riparian zones in all three watersheds throughout the experiments. Riparian tree cover in the two control watersheds increased from 1980 through 2020. Riparian tree cover in the removal watershed increased to ~45% by 2010 and then dropped to less than 10% after removal. The residual tree cover reflects that our plots for remote sensing were slightly wider than the corridor of riparian tree removal.

The proportion of shrub cover increased in all watersheds both inside and outside of the riparian zone. Proportional shrub cover was greater in the riparian zones than outside. Shrub cover increased the most in the riparian zone of the treatment watershed following woody removal. This occurred despite repeated cutting of resprouting or newly recruiting shrubs and trees in the riparian zone and explains why total woody riparian cover did not change in the woody removal treatment.

Plant community trends

All but one univariate plant community response variable were significantly different in riparian versus open communities (Figure 3, Appendix S1: Tables S1 and S2). For all treatments, there was no significant difference between the seeded and unseeded treatments for any of the response variables. Species richness had a significant treatment by year interaction ($p < 0.05$). Richness was greater in open prairie relative to riparian with or without seed in 2010 and 2020, but similar in 2011. The Shannon index (e^H) was not significantly different among treatments ($p = 0.08$) but did significantly decrease over time by a similar magnitude across treatments ($p < 0.001$ for year and $p = 0.18$ for the interaction term).

Treatment, year, and their interaction were both significant ($p < 0.001$) for grass cover and woody cover
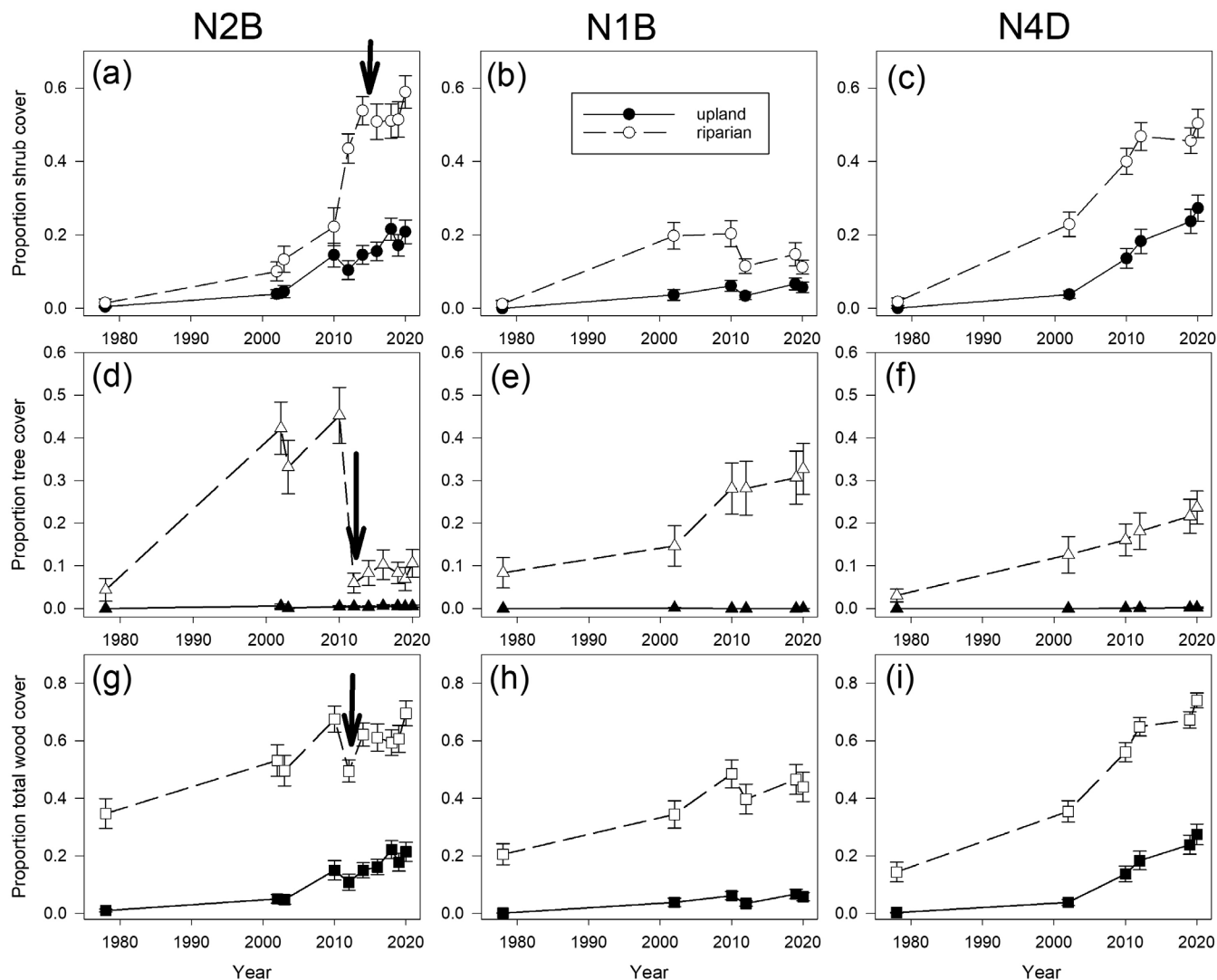
FIGURE 2 Proportion of shrub (a–c), tree (d–f), and total woody (g–i) cover in riparian zones and upland areas of treatment watershed (N2B) (a, d, g), and the two control watersheds, N1B (b, e, h) and N4D (d, f, i). Error bars = 1 SE. Arrow indicates beginning of woody removal.

(Appendix S1: Tables S4 and S6) but followed opposite patterns: In open prairie, grass cover was higher and increased over time, compared to lower cover in the riparian treatments and a decrease over time. Woody plant cover was higher in the riparian treatments, with a decrease in cover after cutting, followed by an increase. Woody plant cover was lower in open prairie and changed little over time. Treatment and year were both significant for forb cover ($p < 0.05$), with lower cover in the riparian treatments and a decrease over time across treatments.

Two NMDS axes explained a large proportion of community composition (Appendix S2: Figure S1). A clear separation of species typical of open prairie versus those typical of forest, wetland, shrub thicket, and early succession forest was apparent on the first axis.

Seeding had no apparent influence on community structure. Among open prairie species there was little separation of species along the second axis, with many plots centered near dominant prairie grasses (e.g., big bluestem *A. gerardii*, little bluestem *S. scoparium*) and common forbs (e.g., stiff-leaved goldenrod, *Solidago rigida*). In contrast, the second axis spans several different woody plant subcommunities (Appendix S2: Figure S1).

Before and just after tree removal, riparian composition reflected forest species, such as the overstory tree species *U. americana*, understory shrubs such as poison ivy (*Toxicodendron radicans*) and coral berry (*Symphoricarpos orbiculatus*), and vines (e.g., common moonseed, *Menispermum canadense*). Just after tree removal, the riparian community included some species more common in
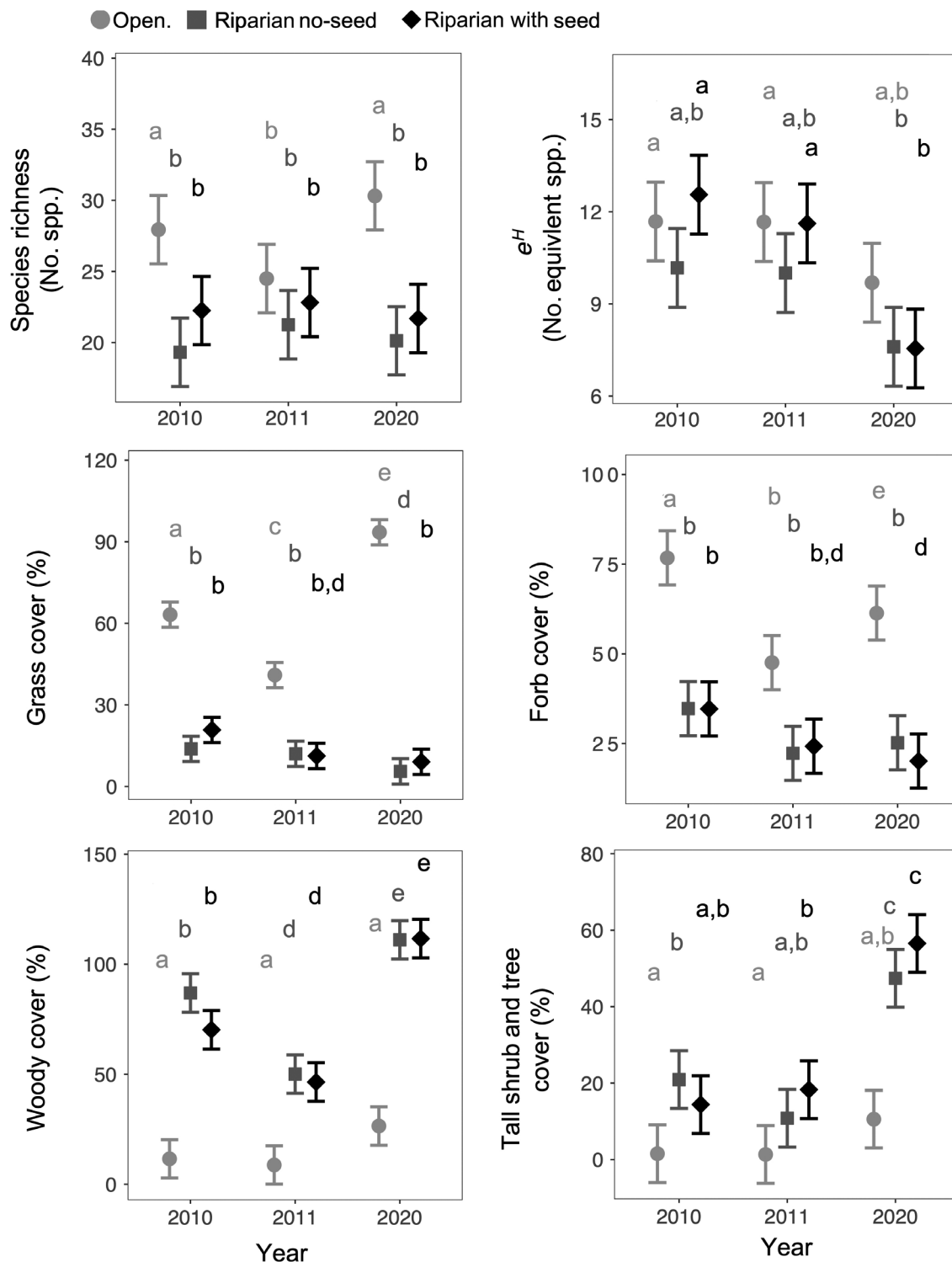
FIGURE 3 Univariate changes in species richness (top left), eveness (top right), grass cover (middle left), forb cover (middle right), woody cover (bottom left), and tall shrub and tree cover (bottom right). Circles stand for open grassland, squares for riparian areas without seed, and diamonds for riparian areas with added seed. Letters within each panel denote statistically significant differences between groups.

open habitats, such as the grasses *Poa pratensis* and *Elymus virginicus* (Appendix S2: Figure S2). As of 2020, the riparian community now resembles a shrub thicket, with abundant roughleaf dogwood (*C. drummondii*), which is the most

common encroaching shrub in open tallgrass prairies on site (Ratajczak et al., 2011, 2014). Other thicket-forming shrubs were also common in riparian plots (e.g., prickly ash, *Zanthoxylum americanum*), along with marshlike

herbaceous species, such as Marsh Muhly (*Muhlenbergia racemosa*).

Hydrology

We saw no clear response of hydrology to woody removal. However, these streams are highly variable with respect to discharge and intermittent conditions (Figure 4). ANCOVA using hydrologic data from N2B, N1B, and N4D indicated that year had no significant effect on mean discharge or the proportion of days in a year with flow, but that watershed was significant ($p = 0.009$) with respect to mean discharge but not proportion of days with flow. This relationship corresponds to the slightly larger watershed size and greater discharge rates in N4D compared to the other two watersheds (Appendix S1: Tables S11 and S12).

Stream water $\delta^{18}O$ decreased significantly by year ($p = 0.02$; Figure 5), and there was a marginal difference by watershed ($p = 0.08$, ANCOVA; Appendix S1: Table S13). Errors within years were highly correlated across watersheds (e.g., years with high $\delta^{18}O$ variability occurred in all watersheds simultaneously). Unfortunately, we did not have ample prevegetation removal data to test for changes specific to the vegetation removal in watershed N2B against the other two watersheds. However, all watersheds behaved very similarly regardless of vegetation cutting or burn frequency.
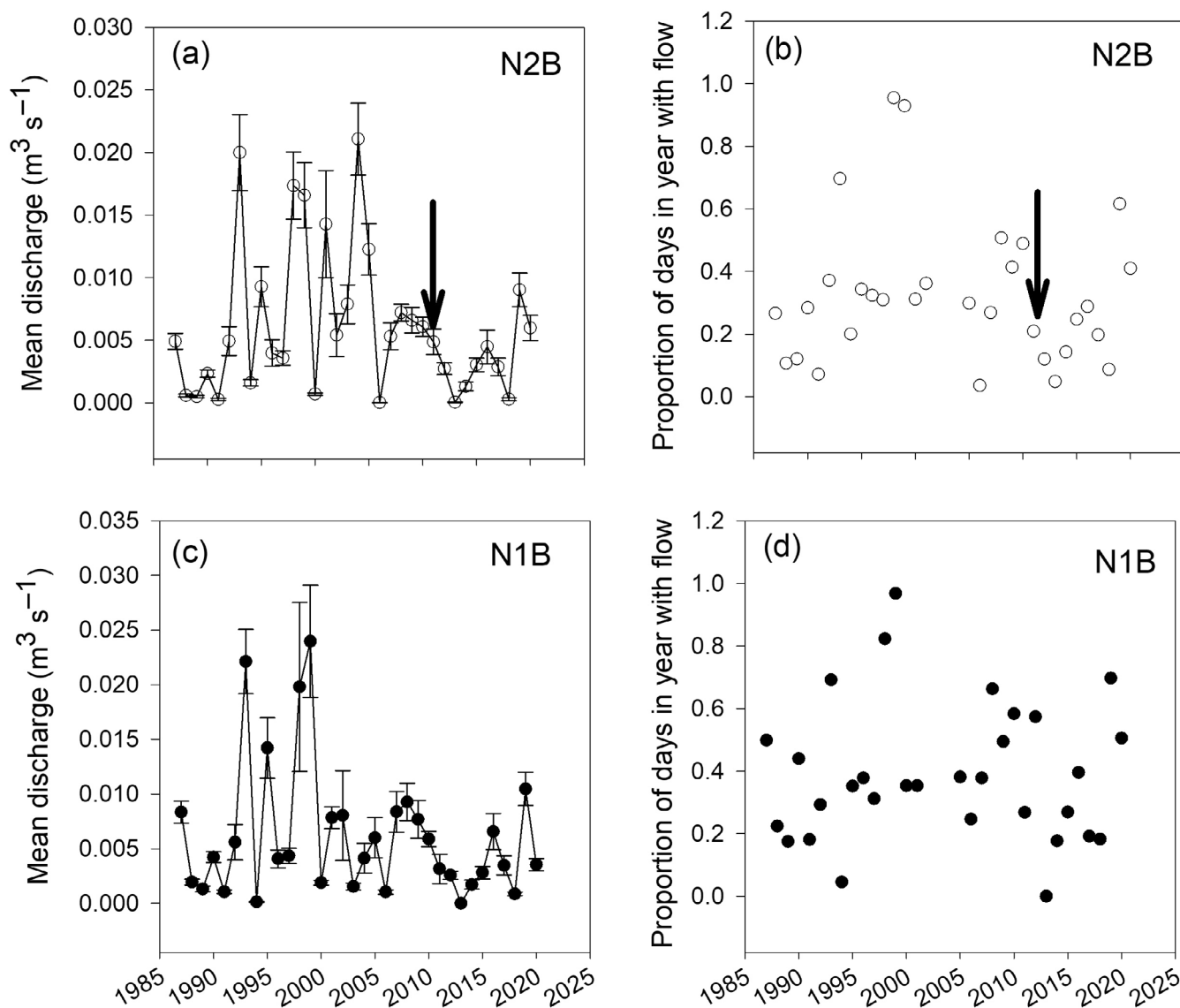
FIGURE 4 Mean daily discharge in each year and total proportion of days with flow in each year from watersheds N2B (open symbols) and N1B (closed symbols). Error bars = 1 SE. Arrow indicates start of woody removal in treatment watershed.
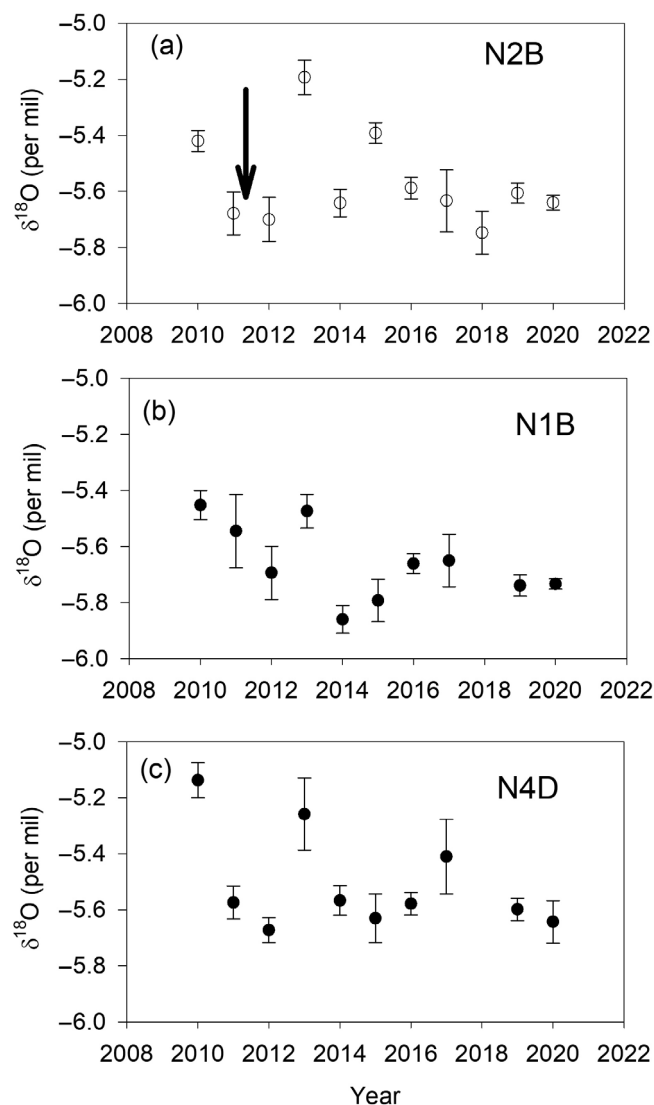
FIGURE 5 Trends in average yearly stream water $\delta^{18}O$ in treatment (open symbols) and two control watersheds (closed symbols). Error bars = 1 SE. Arrow indicates start of woody removal on treatment watershed.

Nutrient dynamics

Nutrient chemistry varied by analyte and by treatment (Figure 6). Nitrate exhibited almost a 100-fold increase in the treatment watershed (N2B) and then dropped close to pretreatment levels. This was significant by year and comparing before and after cutting (Appendix S1: Table S23), indicating that the cutting did cause a large spike in nitrate. The control watersheds did not have an overall increase over time, nor did they have a strong increase in the years immediately after cutting. In contrast, dissolved organic carbon did not respond to the cutting or watershed, but it did increase in all watersheds over the period of record. Total phosphorus increased to a peak in the early 2000s and then decreased, with

significant differences by year and before and after cutting (Appendix S1: Table S19). The peak in 2000 was before removal, and there was a subsequent decline following that peak, with a brief peak in total P immediately following cutting, with concentrations moving back to the long-term trend of decline in the years following the cutting. We analyzed other nutrients (e.g., ammonium, soluble reactive P) and did not see differences related to the removal (Appendix S1: Tables S19 and S22).

Channel morphology and sediment transport

We found that the removal of woody riparian vegetation led to more than a doubling of suspended sediment concentrations during the 3 years immediately following the cutting in the treatment watershed (Figure 7). After this initial increase, we observed a decrease in sediment concentration approaching that observed prior to the woody vegetation removal. The control watershed had substantially greater and more variable sediment concentrations but did not exhibit the peak we saw following cutting of the treatment watershed. Volatile sediments mirrored total suspended sediments in the treatment watershed, but they were less tightly coupled in the control watersheds. Given the apparent nonlinear response to cutting, we elected not to analyze these trends statistically.

We saw no significant effect of year on depth or width, width × depth (area), or width:depth of the stream channel (Appendix S1: Tables S14, S15, S17, and S18). However, N2B had greater width:depth than N1B (13.3 and 10.3, respectively, $p = 0.007$; Appendix S1: Table S16), indicating differences were not due to treatment. Had differences been due to treatment, then year should have been significant.

Stream channel moss and organic material, temporal trends of riparian leaf deposition

The proportion of moss differed by watershed ($t = 1.97$, $p = 0.05$; Appendix S1: Table S24) and sampling period ($t = 4.17$, $p < 0.001$) and had a significant watershed-by-sampling-period interaction ($t = -4.27$, $p < 0.001$). Specifically, moss represented a greater proportion of active stream channel in the treatment watershed N2B relative to control treatment N4D in 2011 (immediately after the removal, $z = 4.16$, $p = 0.002$) but became significantly lower in N2B 10 years after removal ($z = -4.17$, $p = 0.0002$), so that it was similar
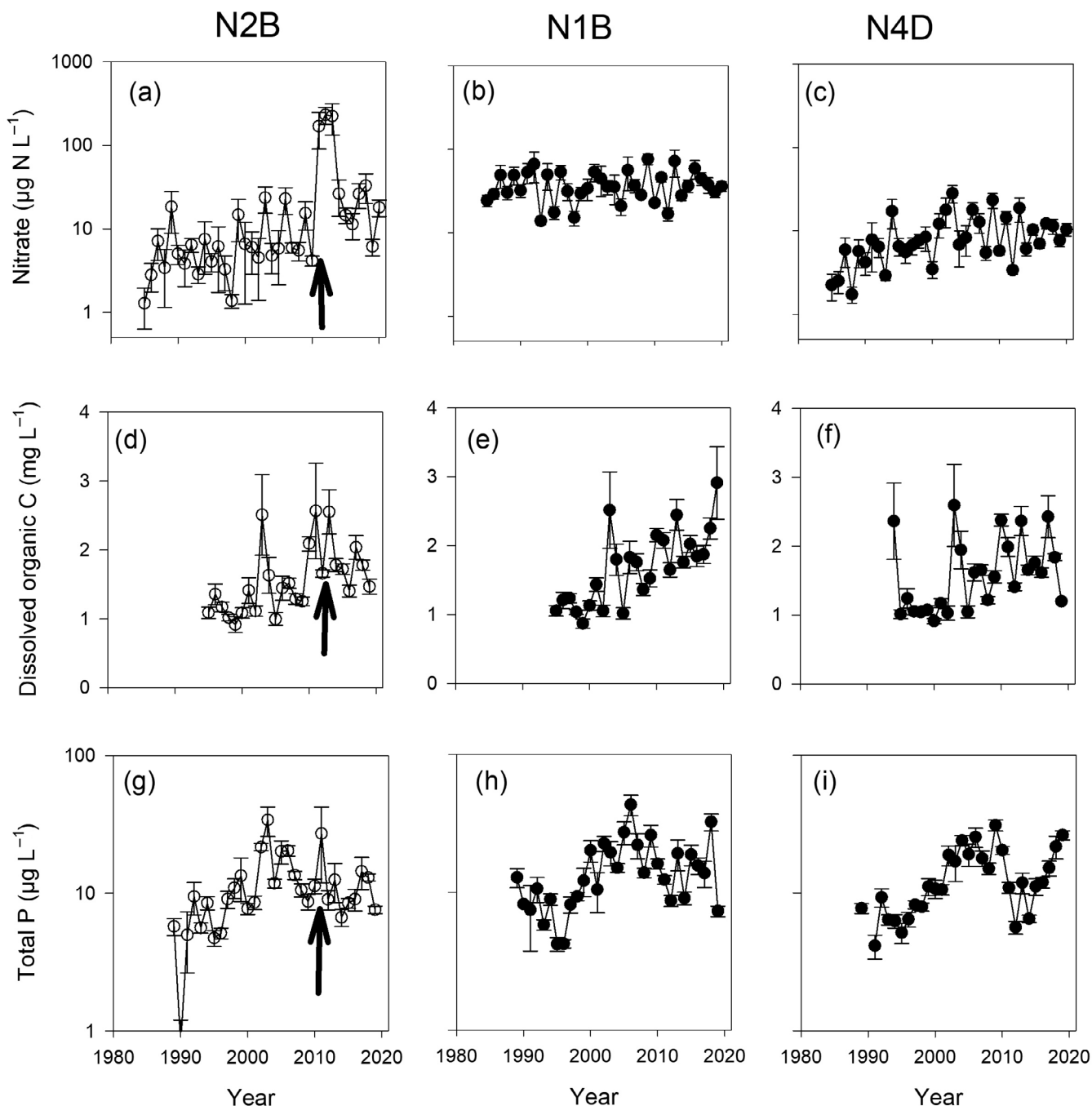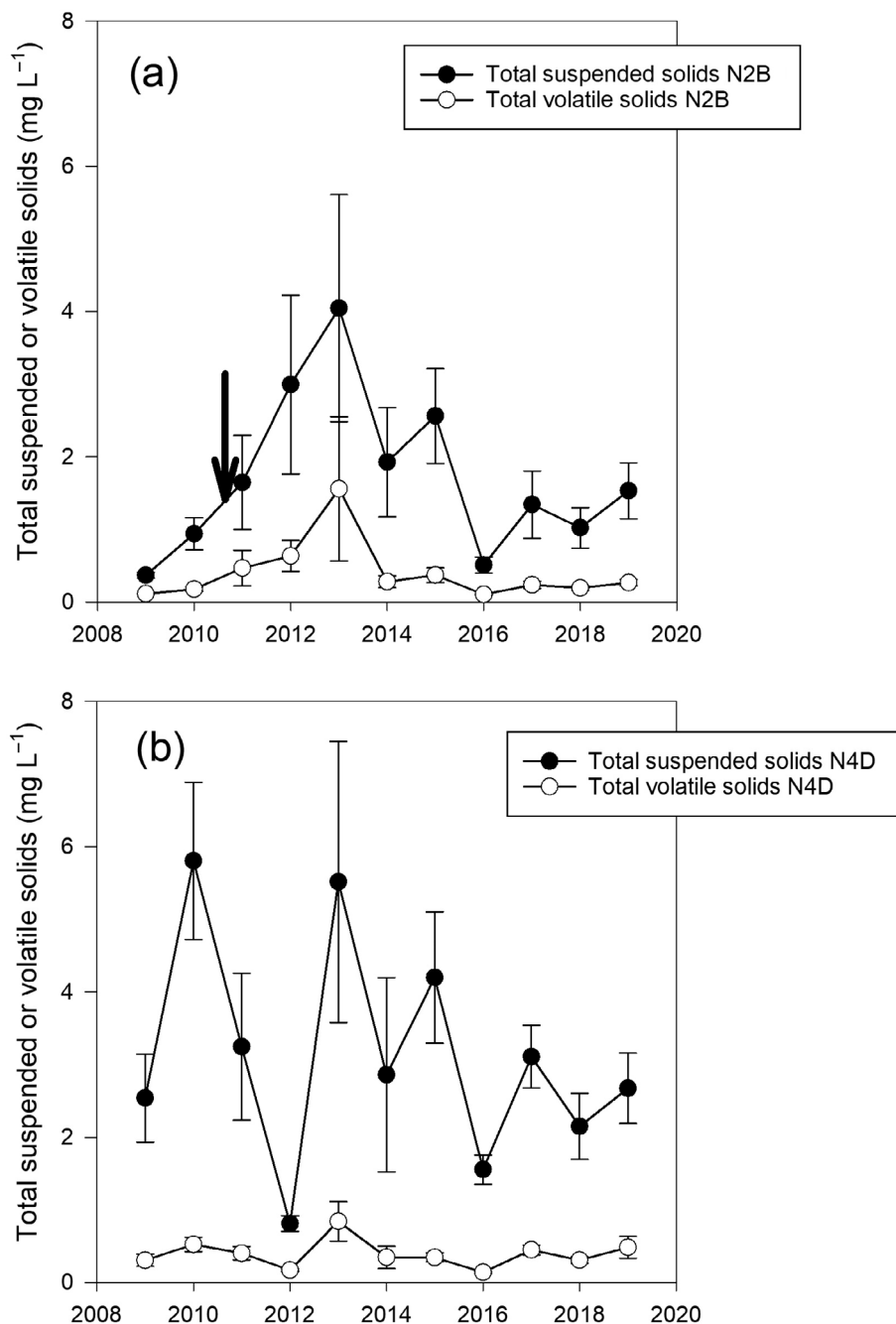
FIGURE 6 Trends in annual mean concentrations of nitrate, dissolved organic carbon, and total phosphorus by year for treatment (N2B, open symbols) and two control (N1B, N4D, closed symbols) watersheds. Note that nitrate and total P are on a log scale, but dissolved organic C is not. Error bars = 1 SE. Arrows indicate start of woody removal on treatment watershed.

in proportion to N4D in 2020 (Figure 8) indicating that long-term removal lowered the coverage of moss within streams.

Organic matter deposition in Konza riparian forests increased from 1981 to 2019 (Figure 9a Appendix S1: Table S25), with an increase of about 7 g m^{-2} year^{-1} per decade. The highest rate of deposition was about 110 g m^{-2} year^{-1}. The instream channel surveys

(Figure 9b, Appendix S1: Table S26) revealed the lowest mass of leaves in the woody removal area, intermediate levels in the young riparian forest of N1B, and the highest masses in the intact riparian forest of N1B and further down in Kings Creek. Maximum deposition in stream channels was fivefold or more than maximum from long-term litter collections. However, litter collections are made with everything that falls

FIGURE 7   Annual mean concentrations of suspended total and volatile sediments in treatment (N2B) and control (N4D) as function of year. Error bars = 1 SE. Arrow indicates start of woody removal on treatment watershed.

directly into the collector boxes, and stream channels also include lateral litter transport from adjacent terrestrial habitats.

DISCUSSION

Long-term research is full of "ecological surprises" (Dodds et al., 2012; Paine et al., 1998) and, increasingly, allows for the detection of novel ecosystems (Hobbs et al., 2009).

Predictive ecology strives to anticipate these events such that they are not surprises (Dodds, 2009). The unpredictability of ecology may in part be based on the fundamental results of evolutionary processes, the inability of reductionism to predict emergent properties (Mayr, 2004), and the complexity of systems composed of neither very large nor very small numbers of total individual components, also referred to as middle-number systems (Newman et al., 2019). Further complicating prediction is the fact that we are in a no-analog world, and the idea of ecological
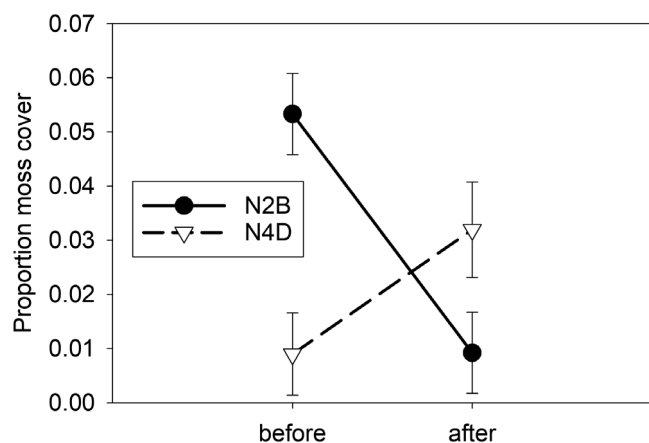
FIGURE 8 Proportions of moss in treatment (N2B) and control (N4D) watersheds. Error bars = 1 SE.

equilibrium may be an outdated construct, especially as many ecological drivers change rapidly (Hughes et al., 2013; Svenning & Sandel, 2013; Williams & Jackson, 2007). Ecological surprises can be most evident and transformational when systems cross thresholds and enter alternative ecological states, and now some tools may be able to predict the onset of such system shifts (Bestelmeyer et al., 2011; Dudney et al., 2018; Scheffer & Carpenter, 2003).

Konza Prairie Biological Station is an area with an extraordinary number of ecological publications. A search of the "Web of Science core collection" in 2021 finds 584 papers using the term "Konza Prairie," with about 33 new publications per year over the last decade. These papers include those using the words "plant physiology" (11 papers), "evapotranspiration" (25), "hydrology" (25), "discharge" (20), "riparian" (20), "woody expansion" (15), "stream" (81), and "water chemistry" (22). Thus, we expect fewer ecological surprises at this site than other less studied areas. Yet, we found several responses that followed expected trajectories based on past work on site, and several others that diverged from our expectations.

Results that matched predictions

Some of the responses were relatively easy to predict. For example, many species of stream bryophytes adapt well to low light, and some species (but not all) may not tolerate higher temperatures and desiccation associated with open canopy and dry stream beds (Marschall & Proctor, 2004; Stream_Bryophyte_Group, 1999). Our general observations in Konza streams suggest that stream-associated mosses are more abundant in shaded areas, and our survey results were consistent with this view as moss cover decreased in the removal over a decade and
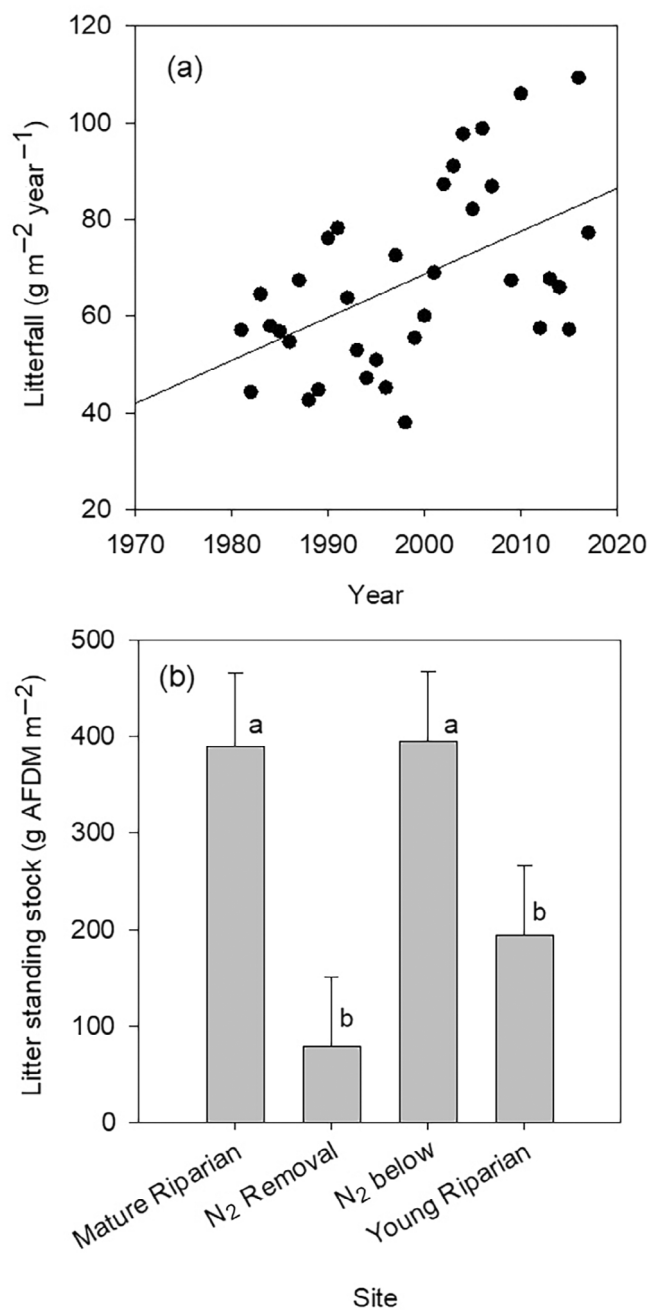
FIGURE 9 Mean annual litter deposition rates (a). Each year's mean litterfall represents 200–600 individual measurements of annual litterfall in riparian zone of Kings Creek. Ash-free dry mass (AFDM) of leaf litter collected in stream channels (b). Different letters by bars denote $p < 0.05$ post hoc ANOVA.

increased in the control watershed where riparian canopy cover was steadily increasing. Mosses are slow growing, and their responses to ecological disturbances can be evident on a decadal scale (Slavik et al., 2004), which was the timeframe over which we observed a response.

The fact that leaf deposition rates strongly decreased was also logical given that we removed riparian trees, and this had been predicted based on prior smaller-scale

research (Vandermyde & Whiles, 2015). However, shrub cover increased, and this did not result in corresponding increases in dead leaf standing stocks in the stream channels. While shrubs produce leaf area similar to deciduous forests (Ratajczak et al., 2011), the shrubs are not as tall and their leaves are smaller, so they are less likely to be transported into the channel and will degrade more quickly. Our prior observations were that large amounts of shrub leaves were rarely found in stream channels, even when they dominated riparian vegetation. Our results matched prior estimates of leaf input into the streams, which found annual inputs of 482 g AFDM m^{-2} total organic material in the same reach as our downstream reach and 118 g AFDM m^{-2} in upstream reaches without canopy cover (Gurtz et al., 1988). Assuming a 74% AFDM/DM conversion based on prior measurements (95% CI $\pm$ 4%), our values were 388 and 79 g AFDM m^{-2} in the same downstream reach and the woody removal reaches, respectively. Dodds et al. (1996) measured annual inputs of 89 and 26 g AFDM m^{-2} at the same downstream location and an upland grassy area, respectively, using litter trap methods to account for vertical and lateral inputs. While these numbers were obtained with different methods, years, and sampling areas, they all point to substantially greater allochthonous carbon influx rates in areas with closed canopy riparian vegetation. These results all point to food web shifts in the stream of the removal area as we expect greater primary production with more light (Riley & Dodds, 2012) and shifts to organisms less dependent upon allochthonous leaf material in open areas (Stagliano & Whiles, 2002; Vandermyde & Whiles, 2015), as shown from prior experiments.

Unanticipated responses

Rapid shrub replacement and lack of seeding effect

Our observed responses of shrubby riparian woody vegetation differed from those observed by O'Connor et al. (2020) manipulating upland shrubs with cutting. They found substantial reductions in shrub density after removing half of the aboveground biomass (simulated browsing) in shrub islands of the dominant shrub *C. drummondii* repeated five times every year for 3 years. Both "browsed" and "nonbrowsed" shrubs were burned in the third year. After the simulated browsing and burning treatment, shrub cover decreased by 90% and physiological indicators of shrub health declined substantially. These areas were mostly upland (not riparian), so it could be that the differential responses to cutting were due to lower moisture availability or more intense

biomass removal. Also, we removed all aboveground biomass in the winter when nutrients would have been translocated to roots, and O'Connor et al. (2020) removed biomass repeatedly during the growing season. Like this browsing study, we expected the woody removal treatments to decrease total cover with repeated cutting. However, in our study shrub cover increased dramatically, essentially replacing trees as the dominant cover in riparian zones. Shrub cover also increased in nonriparian zones, but at a much lower rate. Removal of tree canopies likely resulted in an increase in light availability in the riparian zone, which could have contributed to the rapid expansion of resprouting shrub species (Briggs et al., 2005; Heisler et al., 2004) as well as decreased competition for nutrients and water below ground.

The dramatic increase in shrub cover in the woody removal treatments is consistent with increases in shrubs often observed from single top kills from fire or cutting (Heisler et al., 2004). All the dominant woody species that occur at KPBS, except *Juniperus virginiana*, are capable of resprouting. Top kill of resprouting shrubs often has the unintended consequence of increasing stem and canopy density in the long term (Heisler et al., 2004). Lasting reductions typically depend on chemical treatment coupled with prescribed fire (Brock & Brock, 2004; Engle et al., 2006; Nelson et al., 2006; Stubbendieck & Kottas, 2005) or other interventions, like burning under extreme drought conditions (Twidwell et al., 2016). While our intervention of repeated cutting of shrubs coupled with biannual burning was extreme, it was insufficient to stop the trajectory of increased woody riparian cover.

Standard management practice in grazed pastures in the region is cutting trees with stumps treated with herbicide and aerial spraying to kill shrubs. However, given the research goal of Konza, these treatments were not allowable under management restrictions. It is possible others in the region would also avoid herbicides (e.g., producers of organic beef). Our data illustrate the challenges to woody removal without chemical applications to reinforce the physical removal treatment over time.

Seeding grassland species in addition to cutting also did not restore conditions similar to those in naturally grassland riparian areas. However, establishment of seeded species was poor, for several possible reasons. Dry weather could have prevented reestablishment of grassland species, as 2012 was an exceptionally dry year (569 mm, the driest since 1988). Additionally, bison and other grazers could have consumed existing grassland species or newly sprouted seeds and trampled sprouting seeds in the riparian zone, leading to poor recruitment of seedlings. We noted heavy bison use of the newly cleared riparian areas, and Knapp et al. (1998) documented that

bison prefer nitrogen-rich regrowth. It is also likely that other herbivores (e.g., browsing deer, grasshoppers) prefer new growth that is most nutritious. Our stream data suggest high nitrogen availability following cutting that could have led to high nitrogen in regrowth. Increased grazing could have also decreased fire intensity and moderated its influence on controlling woody vegetation.

Lack of a hydrology effect

We also expected that cutting woody vegetation would alter stream hydrology prior to our study. Evapotranspiration often increases following woody encroachment in grasslands (Acharya et al., 2017; O'Keefe et al., 2020), particularly in more humid areas (Huxman et al., 2005). Shrubs typically have higher transpiration rates than grasses (O'Keefe et al., 2020; Scott et al., 2006; Wang et al., 2018). In addition, the deeper root systems of shrubs provide access to less variable water sources compared to shallow-rooted grasses (Nippert & Knapp, 2007), allowing shrub transpiration to occur at consistently high rates throughout the growing season (O'Keefe et al., 2020). This is compounded by the near doubling of leaf area that occurs with woody encroachment on site, leading to higher rates of watershed-scale water loss via transpiration (Keen et al., 2022; Ratajczak et al., 2011). Thus, we initially hypothesized that low flow conditions in Kings Creek were a result of woody expansion in the riparian zone (Dodds et al., 2012) and that removing woody riparian vegetation would decrease evapotranspiration and restore stream flow.

Instead, there has been no rebound in streamflow after a decade of riparian tree removal. This is likely a result of (1) the continued expansion of woody cover outside of the riparian zone, which is estimated to have increased watershed-scale transpirative water loss by roughly 25% since 1978 (Keen et al., 2022), and (2) the rapid replacement of cut trees with resprouting shrubs in the riparian zone (Figure 2), which could have canceled out the expected reduction in tree water use after removal. The overall increase in woody cover within and outside the riparian zone (Figure 2g) and the associated increase in transpirative water loss make it likely that expansion of woody cover has decreased the amount of water making it into the stream/groundwater system, despite a decade of riparian tree cutting (Keen et al., 2022).

In addition to increasing evapotranspiration, woody encroachment has the potential to impact belowground movement of water by altering soil structure and increasing soil macroporosity and preferential flow paths (Sullivan et al., 2019; Vero et al., 2018; Wilcox et al., 2022). Successful removal of established woody vegetation may effectively alleviate the increase in transpirative water loss, but the impacts of woody root systems on soil structure and infiltration pathways likely leave legacies that last for years to decades in the system as roots decay (Lu et al., 2020). In this way, removing aboveground woody vegetation—even when fully successful—only addresses part of the problem of woody encroachment with regard to grassland ecohydrology and water yield.

Konza Prairie has an underlying merokarst geology, where water moves through complex systems of perched limestone aquifers, and stream discharge is primarily fed by groundwater (Costigan et al., 2015; Hatley et al., 2023; Macpherson, 1996). Groundwater levels respond rapidly to precipitation inputs, indicating a high degree of connectivity between surface and subsurface water pools (Brookfield et al., 2017; Vero et al., 2018). Alterations to the connectivity of this system caused by above- and belowground effects of woody encroachment could result in longer-term changes in stream discharge that cannot be reversed with a decade of woody vegetation removal. This is particularly true in a system encroached by clonal, resprouting shrubs that are exceedingly difficult to remove once established, as was found in this study.

Unpredictable and decoupled stream nutrient influences

Woody removal in riparian corridors was expected to decrease leaf inputs and, consequently, decrease dissolved organic carbon exports in the streams. Although we did see decreased leaf inputs, dissolved organic carbon concentrations were not impacted by woody removal. Rüegg et al. (2015) hypothesized that greater concentrations of organic carbon in upland streams were related to more algal productivity. We would expect more algal productivity in open channels than in closed ones based on logic and prior experiments, but the removal did not influence dissolved organic carbon concentrations relative to control watersheds. As all watersheds that we analyzed had increases in riparian woody vegetation, this could be driving the increases in dissolved organic C over time. Some carbon forms (dissolved black carbon) in Kings Creek are relatively unresponsive to decadal patterns of fire history (Ding et al., 2013). However, Pisani et al. (2016) did find that stream sediment carbon matched terrestrial carbon sources (C_4 grasses, woody vegetation, algal producers), indicating shorter-term linkages with terrestrial carbon.

We were surprised initially at the dramatic increases in nitrate concentrations given that prior research reported nitrate increases with forest removal, but not necessarily with just riparian removal (see *Discussion* in

Larson et al., 2018). Prior research indicated that woody removal could increase NO_3^- content in riparian soils, leading to increased rates of denitrification (Reisinger et al., 2013). However, denitrification removes NO_3^-, so we could not be certain of the cumulative effects of whole-watershed influences on stream water chemistry.

Channel morphology stasis

We anticipated increases in channel width, width:depth, and channel area following the removal of riparian vegetation, as losses in riparian vegetation can increase erosion (e.g., Abernethy & Rutherfurd, 2000; Prosser et al., 2001), including within our study area (Grudzinski et al., 2016). However, rapid replacement of trees with shrubs (Figure 2) could have minimized the period of higher sediment mobility, explaining the lack of significant changes in channel morphology after removal (Figure 7). Despite cutting at the surface, subsurface tree roots can remain intact for several years, while new shrub roots begin to establish. These new root systems and the rapid replacement of surface cover are likely effective at preventing meaningful amounts of stream bank widening (e.g., Polvi et al., 2014) and, thus, changes to channel morphology within the study area.

Moving baselines and decoupled drivers of ecosystem indicators

Paine et al. (1998) hypothesized that ecological surprises (novel state change shifts) were most likely to happen under compound perturbations. Resilience science also suggests that extreme reductions in the dominant organism (woody plants) and with no recovery by the opposing dominant organisms (grasses and herbaceous species) means it is likely the novel system state is now entrenched/resilient. Our data suggest that under compound perturbations (CO_2 and atmospheric N fertilization, climate change, and riparian woody expansion), our site is subject to state shifts in several fundamental ecological characteristics at the terrestrial–aquatic interface. Perhaps the most unexpected finding was that compounded disturbance failed to revert the ecosystem to a grass-dominated ecosystem, even with reseeding.

The most striking response to the woody removal manipulation was the increase in nitrate concentrations by almost two orders of magnitude and sediments by 10-fold in the first 3 years of the experiment, followed by a rapid fall to previous levels. However, this is not a return of nitrate concentrations to a stable state, as they have been consistently increasing in the treatment

watershed (N2B) and one of the control watersheds (N4D) since the 1970s. What is driving these increases is not well understood. Similarly, there are long-term increases in dissolved organic carbon, total phosphorus, and water $\delta^{18}O$ across watersheds. The increase in dissolved organic carbon could be tied to expansion of woody vegetation, but the exact mechanisms of this are not known, other than the fact that woody riparian vegetation directly input more coarse organic materials into the stream channels (O'Keefe & Nippert, 2017; Ratajczak et al., 2011). However, if the carbon trend were a short-term response, we would expect the dissolved organic carbon in the treatment watershed to decrease since we clearly lowered the amount of coarse organic material entering the stream channel.

The transition of riparian zones in this watershed to a woody vegetative state seems inexorable without very strong management strategies. In the short term, we were successful at removing aboveground tree biomass, but we stimulated riparian shrub growth in our experimental watershed. If we were to continue the frequent burning but remove the pressure of continued tree removal, we would expect trees to eventually recover. This is because recent data on site suggest these tree species can sprout underneath shrubs and use them as shield against fires (Nippert et al., 2021). The dominant encroaching shrubs at our study site (*C. drummondii, P. americana*, and *R. glabra*) are not common under the oak gallery forest that eventually establishes in riparian zones. Thus, we believe that shrub-dominated riparian zones are transitional. Aerial imagery for the Kings Creek watershed from 1939 indicates very little tree cover in the riparian zones of our study watersheds and less shrub cover (Briggs et al., 2005). Our data on shrub and tree cover support the idea of transition to gallery forest through a shrub state (Figure 2). Here we see in the watershed in which trees have most recently expanded (N1B) that there is a corresponding decrease in shrub cover. Similarly, in watershed N4D, riparian tree cover is increasing more rapidly than shrub cover, though not causing riparian shrub cover to decrease. Finally, our treatment of removing trees seemed to result in explosive increases in shrub cover, suggesting that tree growth suppresses shrub growth.

Our results have different implications for management depending upon the specific goals. Maintaining grassy riparian zones is the goal of ranchers in the region and could be the goal of those trying to "restore" native grassland streams by managing their riparian zones. Our data suggest that herbicide treatments or potentially more frequent cutting or browsing (e.g., goats or elk) during the growing season are the only approaches likely to achieve those goals. Our data do not support the idea that woody removal could increase discharge in these systems, though given the large

hydrologic variability, even larger-scale and longer-term experiments may be necessary to achieve this goal. If conservation goals are to shift stream food webs to those found in streams with more grassy riparian cover (less coarse organic carbon input, more algal production), then the removal approach we took here could work.

We have a system that appears to be moving into a new stable ecosystem state, streams dominated by tree-covered riparian zones. Prior regional research of mostly forested areas based on oak tree burn scars from Oklahoma indicated a median fire interval of every 3 years prior to European settlement (DeSantis et al., 2010). A similar study of oak trees in Arkansas indicated a mean fire interval of 4.6–16 years (Guyette & Spetich, 2003). Mean fire return intervals in northeast Oklahoma determined from pine tree burn scars were 7.5 years prior to settlement (Stambaugh et al., 2013). Mean fire intervals for trees in grass-dominated Tallgrass Prairie Preserve in the southern part of the Flint Hills indicated mean fire return intervals prior to European settlement of 3.4 years (Allen & Palmer, 2011). These data indicate that areas with tallgrass prairie (e.g., Tallgrass Prairie Preserve) could be maintained historically with fire frequencies less than 3 years. Our treatment watershed was burned every 2 years, but tree cover continued to increase for decades in this watershed (and those burned annually and every 4 years) during the study. Riparian tree cover increased in spite of this burning, consistent with the analysis of Veach, Dodds, and Skibbe (2015). As we documented in this paper, the shifts in riparian vegetation have cascading effects on the stream ecosystems they border, ultimately leading to streams more similar to those in deciduous forest systems further to the east in more mesic regions.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data are available in the Environmental Data Initiative (EDI) Data Portal as follows: watershed burning from Blair and O'Neal (2021) at https://doi.org/10.6073/pasta/213f54ba6ce198ee51f5931fe66faad1; discharge measurements from Dodds (2021a) at https://doi.org/10.6073/pasta/14bad446298b9892f27ab9fc1b1dfd55, Dodds (2021c) at https://doi.org/10.6073/pasta/4e1b5546c7441c0a843d8194dc14a2be, and Dodds (2021b) at https://doi.org/10.6073/pasta/2c832e5ed96b2a203a0df79aac5bd6b3; water chemistry samples from Dodds (2020) at https://doi.org/10.6073/pasta/bb6b065e5b25234dd1bb80ff476933e0 and Dodds (2021d) at https://doi.org/10.6073/pasta/a18e25742ac8ff40321d753f61048fe8; water isotopes from Nippert (2022) at https://doi.org/10.6073/pasta/c42752bdcd4c5a7455e3505a96d7e457; channel morphology from Grudzinski (2022) at https://doi.org/10.6073/pasta/58d0d84aa5a60203295a6e26739e4754; moss surveys from Dodds (2022b) at https://doi.org/10.6073/pasta/c22f8685ab249cd073e9cc7da2db542e; leaf surveys long term from Nippert (2021) at http://doi.org/10.6073/pasta/6c27e23f7b47624602afc64402197979; leaf material in stream channel from Dodds (2022c) at https://doi.org/10.6073/pasta/538d07d7c143ac72105c34a3c9d935c5; plant surveys from Dodds (2022a) at https://doi.org/10.6073/pasta/7860c438e56ab6cf04acbd7f5c4c27a7; remotely sensed plant cover from Ratajczak (2022) at https://doi.org/10.6073/pasta/682b8d7a78aa814e96dba672cdabd34c; and seedling rates from Dodds (2022d) at https://doi.org/10.6073/pasta/7ffd75d9ad801d280b5957b05f20168d.

ORCID
Walter K. Dodds https://orcid.org/0000-0002-6666-8930
Zak Ratajczak https://orcid.org/0000-0002-4675-5738
Rachel M. Keen https://orcid.org/0000-0002-5270-1381
Jesse B. Nippert https://orcid.org/0000-0002-7939-342X
Allison Veach https://orcid.org/0000-0001-9845-3558
Jeffery H. Taylor https://orcid.org/0000-0003-1636-9569

REFERENCES
Abernethy, B., and I. D. Rutherfurd. 2000. "The Effect of Riparian Tree Roots on the Mass-Stability of Riverbanks." *Earth Surface Processes and Landforms* 25: 921–37.

Acharya, B. S., Y. Hao, T. E. Ochsner, and C. B. Zou. 2017. "Woody Plant Encroachment Alters Soil Hydrological Properties and Reduces Downward Flux of Water in Tallgrass Prairie." *Plant and Soil* 414: 379–91.

Allen, M. S., and M. W. Palmer. 2011. "Fire History of a Prairie/Forest Boundary: More than 250 Years of Frequent Fire in a North American Tallgrass Prairie." *Journal of Vegetation Science* 22: 436–44.

Anderies, J. M., M. A. Janssen, and B. H. Walker. 2002. "Grazing Management, Resilience, and the Dynamics of a Fire-Driven Rangeland System." *Ecosystems* 5: 23–44.

Banner, E., A. Stahl, and W. Dodds. 2009. "Stream Discharge and Riparian Land Use Influence In-Stream Concentrations and Loads of Phosphorus from Central Plains Watersheds." *Environmental Management* 44: 552–65.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.

Baxter, C. V., K. D. Fausch, and W. Carl Saunders. 2005. "Tangled Webs: Reciprocal Flows of Invertebrate Prey Link Streams and Riparian Zones." *Freshwater Biology* 50: 201–20.

Bestelmeyer, B. T., A. M. Ellison, W. R. Fraser, K. B. Gorman, S. J. Holbrook, C. M. Laney, M. D. Ohman, et al. 2011. "Analysis of Abrupt Transitions in Ecological Systems." *Ecosphere* 2: art129.

Blair, J., and P. O'Neal. 2021. "KFH01 Konza Prairie Fire History ver 13." Environmental Data Initiative. https://doi.org/10.6073/pasta/213f54ba6ce198ee51f5931fe66faad1.

Bond, W. J., and G. F. Midgley. 2000. "A Proposed CO_2-Controlled Mechanism of Woody Plant Invasion in Grasslands and Savannas." *Global Change Biology* 6: 865–9.

Bosch, J. M., and J. Hewlett. 1982. "A Review of Catchment Experiments to Determine the Effect of Vegetation Changes on Water Yield and Evapotranspiration." *Journal of Hydrology* 55: 3–23.

Briggs, J., A. Knapp, J. Blair, J. Heisler, G. Hoch, M. Lett, and J. McCarron. 2005. "An Ecosystem in Transition: Woody Plant Expansion into Mesic Grassland." *Bioscience* 55: 2245–57.

Brock, T. D., and K. M. Brock. 2004. "Oak Savanna Restoration: A Case Study." In *Proceedings of the North American Prairie Conferences*. Lincoln, NE: University of Nebraska.

Brookfield, A., G. Macpherson, and M. Covington. 2017. "Effects of Changing Meteoric Precipitation Patterns on Groundwater Temperature in Karst Environments." *Groundwater* 55: 227–36.

Brown, A. E., L. Zhang, T. A. McMahon, A. W. Western, and R. A. Vertessy. 2005. "A Review of Paired Catchment Studies for Determining Changes in Water Yield Resulting from Alterations in Vegetation." *Journal of Hydrology* 310: 28–61.

Collins, S. L., J. B. Nippert, J. M. Blair, J. M. Briggs, P. Blackmore, and Z. Ratajczak. 2021. "Fire Frequency, State Change and Hysteresis in Tallgrass Prairie." *Ecology Letters* 24: 636–47.

Costigan, K. H., M. D. Daniels, and W. K. Dodds. 2015. "Fundamental Spatial and Temporal Disconnections in the Hydrology of an Intermittent Prairie Headwater Network." *Journal of Hydrology* 522: 305–16.

DeSantis, R. D., S. W. Hallgren, and D. W. Stahle. 2010. "Historic Fire Regime of an Upland Oak Forest in South-Central North America." *Fire Ecology* 6: 45–61.

Ding, Y., Y. Yamashita, W. K. Dodds, and R. Jaffé. 2013. "Dissolved Black Carbon in Grassland Streams: Is there an Effect of Recent Fire History?" *Chemosphere* 90: 2557–62.

Dodds, W. 2020. "NWC01 Stream Water Chemistry for the King's Creek Drainage Basin on Konza Prarie ver 13." Environmental Data Initiative. https://doi.org/10.6073/pasta/bb6b065e5b25234dd1bb80ff476933e0.

Dodds, W. 2021a. "ASD02 Stream Discharge Measured at the Flumes on Watershed N04D at Konza Prairie ver 14."

Environmental Data Initiative. https://doi.org/10.6073/pasta/14bad446298b9892f27ab9fc1b1dfd55.

Dodds, W. 2021b. "ASD05 Stream Discharge Measured at the Flumes on Watershed N01B at Konza Prairie ver 15." Environmental Data Initiative. https://doi.org/10.6073/pasta/4e1b5546c7441c0a843d8194dc14a2be.

Dodds, W. 2021c. "ASD06 Stream Discharge Measured at the Flumes on Watershed N02B at Konza Prairie ver 14." Environmental Data Initiative. https://doi.org/10.6073/pasta/2c832e5ed96b2a203a0df79aac5bd6b3.

Dodds, W. 2021d. "ASS01 Suspended Sediments in Streams Impacted by Prescribed Buring, Grazing and Woody Vegetation Removal at Konza Prairie ver 8." Environmental Data Initiative. https://doi.org/10.6073/pasta/a18e25742ac8ff40321d753f61048fe8.

Dodds, W. 2022a. "RIV02 Plant Transect Data for the N2B Experiment at Konza Prairie ver 1." Environmental Data Initiative. https://doi.org/10.6073/pasta/7860c438e56ab6cf04acbd7f5c4c27a7.

Dodds, W. 2022b. "RIV04 Moss Cover in Streams in Wooded Riparian Areas and Areas where Canopy Had Been Cut at Konza Prairie ver 1." Environmental Data Initiative. https://doi.org/10.6073/pasta/c22f8685ab249cd073e9cc7da2db542e.

Dodds, W. 2022c. "RIV05 Leaf Mass in Streams in Wooded Riparian Areas and Areas where Canopy Had Been Cut at Konza Prairie ver 1." Environmental Data Initiative. https://doi.org/10.6073/pasta/538d07d7c143ac72105c34a3c9d935c5.

Dodds, W. 2022d. "RIV07 Seeding Rates Woody Removal of a Tallgrass Prairie Stream and Riparian Zone after a Decade of Woody Vegetation Removal ver 1." Environmental Data Initiative. https://doi.org/10.6073/pasta/7ffd75d9ad801d280b5957b05f20168d.

Dodds, W., and R. M. Oakes. 2006. "Controls on Nutrients across a Prairie Stream Watershed: Land Use and Riparian Cover Effects." *Environmental Management* 37: 634–46.

Dodds, W. K. 2009. *Laws, Theories, and Patterns in Ecology*. Berkeley: University of California Press.

Dodds, W. K., R. E. Hutson, A. C. Eichem, M. A. Evans, D. A. Gudder, K. M. Fritz, and L. Gray. 1996. "The Relationship of Floods, Drying, Flow and Light to Primary Production and Producer Biomass in a Prairie Stream." *Hydrobiologia* 333(3): 151–9.

Dodds, W. K., C. T. Robinson, E. E. Gaiser, G. J. Hansen, H. Powell, J. M. Smith, N. B. Morse, S. L. Johnson, S. V. Gregory, and T. Bell. 2012. "Surprises and Insights from Long-Term Aquatic Data Sets and Experiments." *Bioscience* 62: 709–21.

Dosskey, M. G., P. Vidon, N. P. Gurwick, C. J. Allan, T. P. Duval, and R. Lowrance. 2010. "The Role of Riparian Vegetation in Protecting and Improving Chemical Water Quality in Streams 1." *JAWRA Journal of the American Water Resources Association* 46: 261–77.

Dudney, J., R. J. Hobbs, R. Heilmayr, J. J. Battles, and K. N. Suding. 2018. "Navigating Novelty and Risk in Resilience Management." *Trends in Ecology & Evolution* 33: 863–73.

Dugas, W., R. Hicks, and P. Wright. 1998. "Effect of Removal of Juniperus Ashei on Evapotranspiration and Runoff in the Seco Creek Watershed." *Water Resources Research* 34: 1499–506.

Engle, D. M., T. N. Bodine, and J. F. Stritzke. 2006. "Woody Plant Community in the Cross Timbers over Two Decades of Brush Treatments." *Rangeland Ecology & Management* 59: 153–62.

Frelich, L. E., and P. B. Reich. 1999. "Minireviews: Neighborhood Effects, Disturbance Severity, and Community Stability in Forests." *Ecosystems* 2: 151–66.

Gibson, D. J., and L. C. Hulbert. 1987. "Effects of Fire, Topography and Year-to-Year Climatic Variation on Species Composition in Tallgrass Prairie." *Vegetatio* 72: 175–85.

Grudzinski, B. 2022. "RIV03 Channel Morphology in Streams in Wooded Riparian Areas and Areas before and after Canopy Cutting at Konza Prairie ver 1." Environmental Data Initiative. https://doi.org/10.6073/pasta/58d0d84aa5a60203295a6e26739e4754.

Grudzinski, B. P., and M. D. Daniels. 2018. "Bison and Cattle Grazing Impacts on Grassland Stream Morphology in the Flint Hills of Kansas." *Rangeland Ecology & Management* 71: 783–91.

Grudzinski, B. P., M. D. Daniels, K. Anibas, and D. Spencer. 2016. "Bison and Cattle Grazing Management, Bare Ground Coverage, and Links to Suspended Sediment Concentrations in Grassland Streams." *JAWRA Journal of the American Water Resources Association* 52: 16–30.

Gurtz, M. E., G. R. Marzolf, K. T. Killingbeck, D. L. Smith, and J. V. McArthur. 1988. "Hydrologic and Riparian Influences on the Import and Storage of Coarse Particulate Organic Matter in a Prairie Stream." *Canadian Journal of Fisheries and Aquatic Sciences* 44: 655–65.

Guyette, R. P., and M. A. Spetich. 2003. "Fire History of Oak–Pine Forests in the Lower Boston Mountains, Arkansas, USA." *Forest Ecology and Management* 180: 463–74.

Hatley, C. M., B. Armijo, K. Andrews, C. Anhold, J. B. Nippert, and M. F. Kirk. 2023. "Intermittent Streamflow Generation in a Merokarst Headwater Catchment." *Environmental Science: Advances* 2: 115–31.

Heisler, J., J. Briggs, A. Knapp, J. Blair, and A. Seery. 2004. "Direct and Indirect Effects of Fire on Shrub Density and Aboveground Productivity in a Mesic Grassland." *Ecology* 85: 2245–57.

Herndon, E. M., A. L. Dere, P. L. Sullivan, D. Norris, B. Reynolds, and S. L. Brantley. 2015. "Landscape Heterogeneity Drives Contrasting Concentration–Discharge Relationships in Shale Headwater Catchments." *Hydrology and Earth System Sciences* 19: 3333–47.

Hobbie, J. E., and G. E. Likens. 1973. "Output of Phosphorus, Dissolved Organic Carbon, and Fine Particulate Carbon from Hubbard Brook Watersheds." *Limnology and Oceanography* 18: 734–42.

Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. "Novel Ecosystems: Implications for Conservation and Restoration." *Trends in Ecology & Evolution* 24: 599–605.

Hughes, T. P., C. Linares, V. Dakos, I. A. van be Leemput, and E. H. van Nes. 2013. "Living Dangerously on Borrowed Time during Slow, Unrecognized Regime Shifts." *Trends in Ecology & Evolution* 28: 149–55.

Huxman, T. E., B. P. Wilcox, D. D. Breshears, R. L. Scott, K. A. Snyder, E. E. Small, K. Hultine, W. T. Pockman, and R. B. Jackson. 2005. "Ecohydrological Implications of Woody Plant Encroachment." *Ecology* 86: 308–19.

Keen, R. M., J. B. Nippert, P. L. Sullivan, Z. Ratajczak, B. Ritchey, K. O'Keefe, and W. K. Dodds. 2022. "Impacts of Riparian and Non-riparian Woody Encroachment on Tallgrass Prairie

Ecohydrology." *Ecosystems.* https://doi.org/10.1007/s10021-022-00756-7.

Kgope, B. S., W. J. Bond, and G. F. Midgley. 2010. "Growth Responses of African Savanna Trees Implicate Atmospheric [CO_2] as a Driver of Past and Current Changes in Savanna Tree Cover." *Austral Ecology* 35: 451–63.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1998. "The Keystone Role of Bison in North American Tallgrass Prairie." *Bioscience* 49: 39–50.

Larson, D. M., W. K. Dodds, and A. M. Veach. 2018. "Removal of Woody Riparian Vegetation Substantially Altered a Stream Ecosystem in an Otherwise Undisturbed Grassland Watershed." *Ecosystems* 22: 64–76.

Lenth, R., H. Singmann, J. Love, P. Buerkner, and M. Herve. 2019. "Package 'emmeans' R Package Version 1.4.2. 2019." https://CRAN.R-project.org/package=emmeans.

Levin, S. 1992. "The Problem of Pattern and Scale in Ecology: The Robert H MacArthur Award Lecture." *Ecology* 73: 1943–67.

Logan, K., and N. Brunsell. 2015. "Influence of Drought on Growing Season Carbon and Water Cycling with Changing Land Cover." *Agricultural and Forest Meteorology* 213: 217–25.

Lu, J., Q. Zhang, A. D. Werner, S. Li, S. Jiang, and Z. Tan. 2020. "Root-Induced Changes of Soil Hydraulic Properties–A Review." *Journal of Hydrology* 589: 125203.

Macpherson, G. L. 1996. "Hydrogeology of Thin Limestones: The Konza Prairie Long-Term Ecological Research Site, Northeastern Kansas." *Journal of Hydrology* 186: 191–228.

Marschall, M., and M. C. F. Proctor. 2004. "Are Bryophytes Shade Plants? Photosynthetic Light Responses and Proportions of Chlorophyll a, Chlorophyll b and Total Carotenoids." *Annals of Botany* 94: 593–603.

Mayr, E. 2004. *What Makes Biology Unique?: Considerations on the Autonomy of a Scientific Discipline.* Cambridge, UK: Cambridge University Press.

McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. A. Johnston, and E. Mayorga. 2003. "Biogeochemical Hot Spots and Hot Moments at the Interface of Terrestrial and Aquatic Ecosystems." *Ecosystems* 6: 301–12.

Naito, A. T., and D. M. Cairns. 2011. "Patterns and Processes of Global Shrub Expansion." *Progress in Physical Geography* 35: 423–42.

Nelson, L. R., A. W. Ezell, and J. L. Yeiser. 2006. "Imazapyr and Triclopyr Tank Mixtures for Basal Bark Control of Woody Brush in the Southeastern United States." *New Forests* 31: 173–83.

Newman, E. A., M. C. Kennedy, D. A. Falk, and D. McKenzie. 2019. "Scaling and Complexity in Landscape Ecology." *Frontiers in Ecology and Evolution* 7: 293.

Nippert, J. 2021. "PGL01 Litterfall Collection in Riparian Gallery Forest at Konza Prairie ver 12." Environmental Data Initiative. https://doi.org/10.6073/pasta/6c27e23f7b47624602afc64402197979.

Nippert, J. 2022. "RIV01 Stream Water Isotopes in Wooded Riparian Areas and Areas where Canopy Had Been Cut at Konza Prairie ver 1." Environmental Data Initiative. https://doi.org/10.6073/pasta/c42752bdcd4c5a7455e3505a96d7e457.

Nippert, J. B., and A. K. Knapp. 2007. "Soil Water Partitioning Contributes to Species Coexistence in Tallgrass Prairie." *Oikos* 116: 1017–29.

Nippert, J. B., L. Telleria, P. Blackmore, J. H. Taylor, and R. C. O'Connor. 2021. "Is a Prescribed Fire Sufficient to Slow the Spread of Woody Plants in an Infrequently Burned Grassland? A Case Study in Tallgrass Prairie." *Rangeland Ecology & Management* 78: 79–89.

O'Connor, R. C., J. H. Taylor, and J. B. Nippert. 2020. "Browsing and Fire Decreases Dominance of a Resprouting Shrub in Woody Encroached Grassland." *Ecology* 101: e02935.

O'Keefe, K., D. M. Bell, K. A. McCulloh, and J. B. Nippert. 2020. "Bridging the Flux Gap: Sap Flow Measurements Reveal Species-Specific Patterns of Water Use in a Tallgrass Prairie." *Journal of Geophysical Research: Biogeosciences* 125: e2019JG005446.

O'Keefe, K., and J. B. Nippert. 2017. "Grazing by Bison Is a Stronger Driver of Plant Ecohydrology in Tallgrass Prairie than Fire History." *Plant and Soil* 411: 423–36.

O'Keefe, K., J. B. Nippert, and K. A. McCulloh. 2019. "Plant Water Uptake along a Diversity Gradient Provides Evidence for Complementarity in Hydrological Niches." *Oikos* 128: 1748–60.

Oksanen, J., F. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. Minchin, R. O'Hara, G. Simpson, and P. Solymos. 2020. "Vegan: Community Ecology Package." R Package Version 2.5-7; 2019. https://cran.r-project.org/web/packages/vegan/vegan.pdf.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. "Compounded Perturbation Yield Ecological Surprises." *Ecosystems* 1: 535–45.

Pisani, O., W. K. Dodds, and R. Jaffé. 2016. "Characterizing Organic Matter Inputs to Sediments of Small, Intermittent, Prairie Streams: A Molecular Marker and Stable Isotope Approach." *Aquatic Sciences* 78: 343–54.

Polvi, L. E., E. Wohl, and D. M. Merritt. 2014. "Modeling the Functional Influence of Vegetation Type on Streambank Cohesion." *Earth Surface Processes and Landforms* 39: 1245–58.

Prosser, I. P., I. D. Rutherfurd, J. M. Olley, W. J. Young, P. J. Wallbrink, and C. J. Moran. 2001. "Large-Scale Patterns of Erosion and Sediment Transport in River Networks, with Examples from Australia." *Marine and Freshwater Research* 52: 81–99.

Ratajczak, Z. 2022. "RIV06 Remote Sensing in and around Riparian Zones at Konza Prairie ver 1." Environmental Data Initiative. https://doi.org/10.6073/pasta/682b8d7a78aa814e96dba672cdabd34c.

Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. "Woody Encroachment Decreases Diversity across North American Grasslands and Savannas." *Ecology* 93: 697–703.

Ratajczak, Z., J. B. Nippert, J. C. Hartman, and T. W. Ocheltree. 2011. "Positive Feedbacks Amplify Rates of Woody Encroachment in Mesic Tallgrass Prairie." *Ecosphere* 2: 1–14.

Ratajczak, Z., J. B. Nippert, and T. W. Ocheltree. 2014. "Abrupt Transition of Mesic Grassland to Shrubland: Evidence for Thresholds, Alternative Attractors, and Regime Shifts." *Ecology* 95: 2633–45.

Reisinger, A. J., J. M. Blair, C. W. Rice, and W. K. Dodds. 2013. "Woody Vegetation Removal Stimulates Riparian and Benthic Denitrification in Tallgrass Prairie." *Ecosystems* 16: 1–14.

Riley, A. J., and W. K. Dodds. 2012. "The Expansion of Woody Riparian Vegetation, and Subsequent Stream Restoration, Influences the Metabolism of Prairie Streams." *Freshwater Biology* 57: 1138–50.

Ritchie, P. D. L., J. J. Clarke, P. M. Cox, and C. Huntingford. 2021. "Overshooting Tipping Point Thresholds in a Changing Climate." *Nature* 592: 517–23.

Rood, S. B., J. H. Braatne, and F. M. Hughes. 2003. "Ecophysiology of Riparian Cottonwoods: Stream Flow Dependency, Water Relations and Restoration." *Tree Physiology* 23: 1113–24.

Rüegg, J., J. J. Eichmiller, N. Mladenov, and W. K. Dodds. 2015. "Dissolved Organic Carbon Concentration and Flux in a Grassland Stream: Spatial and Temporal Patterns and Processes from Long-Term Data." *Biogeochemistry* 125: 393–408.

Scheffer, M., and S. R. Carpenter. 2003. "Catastrophic Regime Shifts in Ecosystems: Linking Theory to Observation." *Trends in Ecology & Evolution* 18: 648–56.

Schindler, D. W. 1998. "Replication Versus Realism: The Need for Ecosystem-Scale Experiments." *Ecosystems* 1: 323–34.

Scholes, R., and S. Archer. 1997. "Tree-Grass Interactions in Savannas." *Annual Review of Ecology and Systematics* 28: 517–44.

Scott, R. L., T. E. Huxman, D. G. Williams, and D. C. Goodrich. 2006. "Ecohydrological Impacts of Woody-Plant Encroachment: Seasonal Patterns of Water and Carbon Dioxide Exchange within a Semiarid Riparian Environment." *Global Change Biology* 12: 311–24.

Silva, L. C., M. Anand, J. M. Oliveira, and V. D. Pillar. 2009. "Past Century Changes in Araucaria Angustifolia (Bertol.) Kuntze Water Use Efficiency and Growth in Forest and Grassland Ecosystems of Southern Brazil: Implications for Forest Expansion." *Global Change Biology* 15: 2387–96.

Slavik, K., B. Peterson, L. Deegan, W. Bowden, A. Hershey, and J. Hobbie. 2004. "Long-Term Responses of the Kuparuk River Ecosystem to Phosphorus Fertilization." *Ecology* 85: 939–54.

Stagliano, D. M., and M. R. Whiles. 2002. "Macroinvertebrate Production and Trophic Structure in a Tallgrass Prairie Headwater Stream." *Journal of the North American Benthological Society* 21: 97–113.

Stambaugh, M. C., R. P. Guyette, and J. Marschall. 2013. "Fire History in the Cherokee Nation of Oklahoma." *Human Ecology* 41: 749–58.

Stream_Bryophyte_Group. 1999. "Roles of Bryophytes in Stream Ecosystems." *Journal of the North American Benthological Society* 18: 151–84.

Stubbendieck, J., and K. L. Kottas. 2005. *Maintaining Grassland Biodiversity while Controlling the Shrub Rhus glabra.* Hohhot, China: XXI International Grassland Congress.

Sullivan, P. L., M. W. Stops, G. L. Macpherson, L. Li, D. R. Hirmas, and W. K. Dodds. 2019. "How Landscape Heterogeneity Governs Stream Water Concentration-Discharge Behavior in Carbonate Terrains (Konza Prairie, USA)." *Chemical Geology* 527: 118989.

Svenning, J. C., and B. Sandel. 2013. "Disequilibrium Vegetation Dynamics under Future Climate Change." *American Journal of Botany* 100: 1266–86.

Sweeney, B. W., T. L. Bott, J. K. Jackson, L. A. Kaplan, J. D. Newbold, L. J. Standley, W. C. Hession, and R. J. Horwitz. 2004. "Riparian Deforestation, Stream Narrowing, and Loss of Stream Ecosystem Services." *Proceedings of the National Academy of Sciences* 101: 14132–7.

Tabacchi, E., L. Lambs, H. Guilloy, A. M. Planty-Tabacchi, E. Muller, and H. Decamps. 2000. "Impacts of Riparian Vegetation on Hydrological Processes." *Hydrological Processes* 14: 2959–76.

Twidwell, D., W. E. Rogers, C. L. Wonkka, C. A. Taylor, Jr., and U. P. Kreuter. 2016. "Extreme Prescribed Fire during Drought Reduces Survival and Density of Woody Resprouters." *Journal of Applied Ecology* 53: 1585–96.

Van Meerveld, H., J. W. Kirchner, M. J. Vis, R. S. Assendelft, and J. Seibert. 2019. "Expansion and Contraction of the Flowing Stream Network Alter Hillslope Flowpath Lengths and the Shape of the Travel Time Distribution." *Hydrology and Earth System Sciences* 23: 4825–34.

Vandermyde, J. M., and M. R. Whiles. 2015. "Effects of Experimental Forest Removal on Macroinvertebrate Production and Functional Structure in Tallgrass Prairie Streams." *Freshwater Science* 34: 519–34.

Veach, A. M., W. K. Dodds, and A. Jumpponen. 2015. "Woody Plant Encroachment, and its Removal, Impact Bacterial and Fungal Communities across Stream and Terrestrial Habitats in a Tallgrass Prairie Ecosystem." *FEMS Microbiology Ecology* 91: fiv109.

Veach, A. M., W. K. Dodds, and A. Skibbe. 2014. "Fire and Grazing Influences on Rates of Riparian Woody Plant Expansion along Grassland Streams." *PLoS One* 9: e106922.

Veach, A. M., W. K. Dodds, and A. Skibbe. 2015. "Correction: Fire and Grazing Influences on Rates of Riparian Woody Plant Expansion along Grassland Streams (vol 9, e106922, 2014)." *PLoS One* 10: e0129409.

Venables, W., and B. D. Ripley. 2002. *Statistics Complements to Modern Applied Statistics with S-Plus*, 4th ed. Berlin, Germany: Springer.

Vero, S., G. Macpherson, P. Sullivan, A. Brookfield, J. Nippert, M. Kirk, S. Datta, and P. Kempton. 2018. "Developing a Conceptual Framework of Landscape and Hydrology on Tallgrass Prairie: A Critical Zone Approach." *Vadose Zone Journal* 17: 1–11.

Wang, J., X. Xiao, Y. Zhang, Y. Qin, R. B. Doughty, X. Wu, R. Bajgain, and L. Du. 2018. "Enhanced Gross Primary Production and Evapotranspiration in Juniper-Encroached Grasslands." *Global Change Biology* 24: 5655–67.

Weihs, B., R. Bergstrom, C. Ruffing, and K. McLauchlan. 2016. "Woody Encroachment of a Riparian Corridor in a Tallgrass Prairie: Dendrochronological Evidence from Kansas." *Papers in Applied Geography* 2: 1–8.

Wilcox, B. P. 2002. "Shrub Control and Streamflow on Rangelands: A Process Based Viewpoint." *Rangeland Ecology & Management/Journal of Range Management Archives* 55: 318–26.

Wilcox, B. P., S. Basant, H. Olariu, and P. A. M. Leite. 2022. "Ecohydrological Connectivity: A Unifying Framework for Understanding How Woody Plant Encroachment Alters the Water Cycle in Drylands." *Frontiers in Environmental Science* 10: 934535.

Wilcox, B. P., M. K. Owens, W. A. Dugas, D. N. Ueckert, and C. R. Hart. 2006. "Shrubs, Streamflow, and the Paradox of Scale." *Hydrological Processes* 20: 3245–59.

Williams, J. W., and S. T. Jackson. 2007. "Novel Climates, No-Analog Communities, and Ecological Surprises." *Frontiers in Ecology and the Environment* 5: 475–82.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.