Seasonal flooding affects habitat and landscape dynamics of a gravel-bed river floodplain

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Abstract: Floodplains are comprised of aquatic and terrestrial habitats that are reshaped frequently by hydrologic processes that operate at multiple spatial and temporal scales. It is well established that hydrologic and geomorphic dynamics are the primary drivers of habitat change in river floodplains over extended time periods. However, the effect of fluctuating discharge on floodplain habitat structure during seasonal flooding is less well understood. We collected ultra-high resolution digital multispectral imagery of a gravel-bed river floodplain in western Montana on 6 dates during a typical seasonal flood pulse and used it to quantify changes in habitat abundance and diversity associated with annual flooding. We observed significant changes in areal abundance of many habitat types, such as riffles, runs, shallow shorelines, and overbank flow. However, the relative abundance of some habitats, such as backwaters, springbrooks, pools, and ponds, changed very little. We also examined habitat transition patterns throughout the flood pulse. Few habitat transitions occurred in the main channel, which was dominated by riffle and run habitat. In contrast, in the near-channel, scoured habitats of the floodplain were dominated by cobble bars at low flows but transitioned to isolated flood channels at moderate discharge. The areal abundance of habitat types in near-channel floodplain areas varied as discharge fluctuated. These areas were most diverse and dissimilar in habitat composition at intermediate flows during both the rising and falling limbs of the hydrograph. The geomorphically stable areas of the floodplain were dominated by herbaceous habitat, and we observed fewer transitions from one habitat type to another during the seasonal flood pulse. However, the largest habitat diversity occurred during peak flow, which highlights the influence of flooding on the development and expansion of a broad array of aquatic habitats during the annual cycle of flooding. We conclude that the response of floodplain habitat abundance and diversity is strongly influenced by location on the riverscape.
Key words: floodplains, gravel-bed river, habitat diversity, flooding disturbance

The shifting mosaic model proposed by Bormann and Likens (1979b) identifies 4 phases of development in forested ecosystems. The final stage is the shifting mosaic steady-state, in which the proportion of habitats with different sizes, ages, and compositions remains relatively constant over time, but the location of individual habitat patches change. Several studies have suggested that the shifting mosaic steady-state concept may describe large-river floodplains as well as the forested ecosystems for which this concept was first described and proposed as a functional model (Arscott et al. 2002, van der Nat et al. 2003, Hohensinner et al. 2005, Latterell et al. 2006). Floodplain habitats are constructed by many processes that interact across space and time, including flooding, channel avulsion, cut and fill alluviation, recruitment of large wood, and regeneration of riparian vegetation (Stanford et al. 2005). These processes shift the location of diverse aquatic and terrestrial patches across the floodplain, but the habitat types and their relative abundance remain in a dynamic equilibrium (Salo et al. 1986, Ward et al. 2002). Stanford et al. (2005) called this phenomenon the shifting habitat mosaic and determined it to be a critical process in riverine ecosystems.

The driving force behind the dynamics of shifting habitat mosaics is disturbance (Bormann and Likens 1979a, b, Mooney and Godron 1983, Sousa 1984, Sprugel 1985), which is a discrete event that disrupts ecosystem, community, or

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population structures by changing resource availability or the physical environment (Pickett and White 1985). Disturbance events occur on a continuum of severity and can be described by their size, magnitude, frequency, and predictability (Resh et al. 1988). Variation in these characteristics among disturbance events can influence the consequent reorganization and successional patterns of the system (Sousa 1984). Catastrophic disturbances can initiate reorganization and the development of a new ecosystem, whereas more mild or localized disturbances can create new habitat patches (Bormann and Likens 1979a, b).

For floodplain ecosystems, flooding is a common natural disturbance (Resh et al. 1988) that drives the distribution of habitat patches over decades to centuries (Stanford et al. 2005, Whited et al. 2007). Flooding can be described by its regime, which includes magnitude, frequency, duration, rate of change, and timing (Poff et al. 1997). Extremely large floods are infrequent but generate major geomorphological change across the floodplain by channel avulsion as well as cut and fill alluviation (Hauer and Lorang 2004). In contrast, seasonal floods that reach bankfull—the river stage where water just begins to spill out of the channel on to the floodplain—build and maintain active channels by transport and deposition of sediment that cause channel migration (Junk et al. 1989, Tockner et al. 2000, Lorang and Hauer 2003, 2017, Whited et al. 2007). Bankfull flooding disturbances generally have a 1.5 y return interval and are considered the critical discharge level at which threshold entrainment of unconsolidated substrates occurs (Wolman and Leopold 1957, Leopold et al. 1964). These disturbances enable the exchange of matter, nutrients, and energy between the river and its floodplain (Junk et al. 1989, Poole et al. 2006). In addition, bankfull disturbances disrupt riparian and benthic communities (Hart and Finelli 1999, Bendix and Hupp 2000) and ultimately set the stage for succession as flow recedes (Nanson and Beach 1977, Mahoney and Rood 1998).

It is important to understand the patterns and processes that contribute to the long-term shifting mosaic of floodplain ecosystems during flood disturbance. Heterogeneous and continuously dynamic floodplains are more resistant to environmental variation and resilient to perturbation (McCluney et al. 2014), support greater biodiversity (Ward et al. 1999, Hauer et al. 2016), and are more productive (Junk et al. 1989, Thoms 2003) than simplified riverine landscapes with reduced complexity and integrity (Peipoch et al. 2015). The total area of aquatic and terrestrial habitats before flooding is usually similar to the total area after flooding (Ward et al. 2002, Stanford et al. 2005), even though individual patches regularly transition into different habitat types (Arscott et al. 2002, van der Nat et al. 2003, Hauer and Lorang 2004). Few studies have described habitat dynamics during a flood pulse. Understanding the link between changes in discharge and the landscape patterns during a seasonal flood will provide insight into the annual flux and spatial change in habitats, as well as the long-term structure and function of floodplains. In this study, we addressed the following questions: 1) How does a bankfull flood disturbance affect the spatial and temporal dynamics of aquatic and terrestrial floodplain habitats? and 2) How does seasonal flooding disturbance affect the spatial and temporal composition of the floodplain landscape?

METHODS

Study site

This study was conducted on a 6.5-km braided section of the Clark Fork River, which is a gravel-bed river in western Montana, USA and a major tributary of the Columbia River. The study reach includes a broad, active floodplain with paleo channels, springbrooks, ponds, and stands of regenerating and mature vegetation. The annual average discharge (1929–2013), average maximum flow in May, and average minimum flow in September are 83, 434, and 39 m^3/s, respectively. Throughout this paper, we refer to the recently scoured and redeposited cobble bars and sites of early vegetation regeneration as the parafluvial zone. We refer to areas of gallery forest, old channels, and herbaceous surfaces as the orthofluvial zone (see Stanford et al. 2005).

Remote sensing data acquisition and sampling design

We collected aerial imagery (RGB bands, 16 bit) of the study reach with an ultrahigh density multi-spectral imager (Princeton Instruments, Trenton, New Jersey). Raw images were collected at a data density of 80–90 MB per image and flash downloaded to an onboard computer with a solid state hard drive. Images were captured at 3 s intervals from an altitude of 1000 m above the floodplain surface along 12 flight lines generally oriented northeast to southwest 250 m apart. These images provided data with 30% overlap laterally and longitudinally across and along the floodplain. We collected image data that spanned the seasonal flood hydrograph on 6 dates in 2014. Hydrographic data from the US Geological Survey (USGS) stream gage 12340500, located on the Clark Fork River above Missoula, Montana is a very close approximation of the river flow through the study reach because only a few small streams enter the river between the gauging site and our study segment. We selected the collection dates by closely following river discharge reported by this stream gage and monitoring for clear weather conditions. This information allowed us to obtain the best possible imagery while simultaneously capturing imagery coincident with base, rising limb, maximum annual, and falling limb discharges. We also restricted our image data collection to 1.5 h before or after local solar noon to minimize shadow effects. We collected the first imagery data on April 8 during baseflow conditions prior to the seasonal flood pulse. We collected imagery data during the rising limb of the hydrograph on May 8 and May 21. On May 27, we collected data near the 2014 peak flow. On July 2, we collected imag-

ery data that characterized the falling limb of the hydrograph following the flood pulse. Finally, on September 5 we collected imagery data at late summer base flow conditions (Fig. 1).

We used 9 ground control points and a 2nd-order polynomial equation with a root mean square error of <2 pixels to georectify the raw, remotely-sensed data to a 2013 National Agriculture Imagery Program orthorectified photograph. The images were resampled once with nearest neighbor interpolation to transform uncorrected to geometrically corrected images (0.2- × 0.2-m pixels). Each corrected photo was viewed in ArcMap version 10.2.2 (ESRI, Redlands, California) to ensure correct geospatial location. Upon completion of the georectification process, we used the MosaicPro tool in Erdas Imagine version 15.1 (Hexagon Geospatial, Atlanta, Georgia) to radiometrically correct and create a nearly seamless digital image mosaic for each sample date. In ArcMap, we designated the April 8 imagery as our baseline data, and used it to identify the main channel, parafluvial, and orthofluvial zones (Fig. 2). The boundaries of these zones were held constant throughout the study across the flood cycle. For example, the April 8 parafluvial zone became main channel habitat types during high discharge in late May, but was still considered part of the parafluvial zone.

To determine the response of specific habitats to flooding disturbance, we used a randomized plot design and sampled the same plot within the imagery on each date. The plot locations were selected randomly from the April 8 digital image mosaic of each zone with Hawth's analysis tool for ArcGIS (Beyer 2004). We applied a power analysis to a subset of plots to determine the number of plots required for 90% confidence that the estimated mean area would be within 0.25 m^2 of the true mean in each zone. We conservatively selected the largest number of plots required for 90% confidence: 331 (5 × 5 m) main channel plots, 1160 (5 × 5 m) parafluvial plots, and 352 (50 × 50 m) orthofluvial plots (Fig. 3A). We report the total number of potential transitions that occurred throughout the season, whether or not the plots changed from 1 type to another. Thus, there were 1655 potential transitions in the main channel, 5800 in the parafluvial channel, and 1760 in the orthofluvial channel.

We followed guidelines established by prior studies in the northern Rocky Mountain ecoregion to map and measure floodplain habitats within plots across dates (Hauer and Lorang 2004, Lorang et al. 2005, Whited et al. 2007). Our image classifications were developed with a method that combines visual examination with expert knowledge of a site and its conditions through different flows (following Lorang et al. 2005). This method has been used to correctly identify depth and flow conditions of surface-water habitats (Lorang et al. 2005, 2013, Stanford et al. 2017). We manually drew polygons around features in ArcMap to reduce potential misclassification by demarcating cover categories including wood, main channel water, flood channel water, springbrooks, backwater, pond, cobble bar, vegetation, and shadow (Fig. 3B). For each cover category (e.g., flood channel water), we used unsupervised classification within Erdas Imagine to group

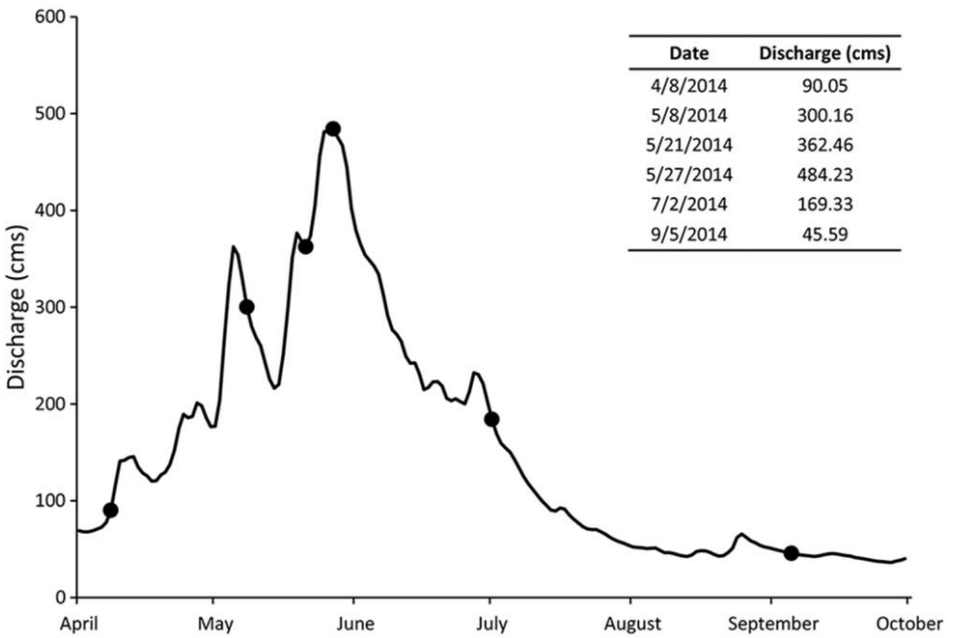

Figure 1. The discharge hydrograph (cms = m^3/s) in the Clark Fork River (US Geological Survey site 12340500) from 1 April to 30 September, 2014. Black dots represent dates of remote sensing data collection.

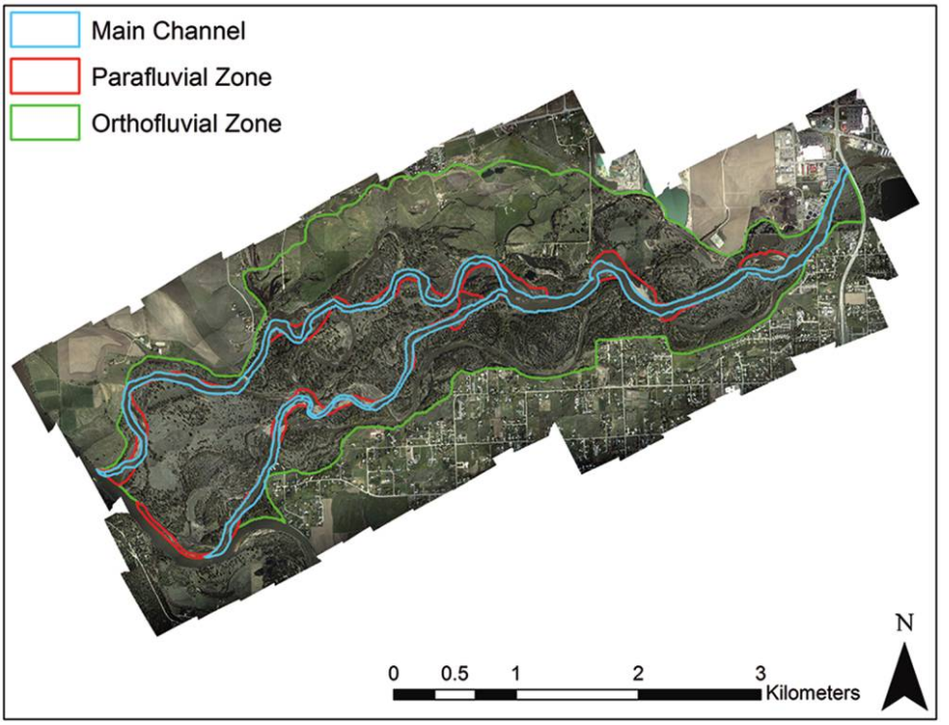

Figure 2. Aerial view of the island braided study reach on the Clark Fork River as it flows through the Missoula valley in western Montana. The 3 floodplain zones are outlined, and these boundaries were held constant throughout the study.

the pixels within each plot into unique clusters based on similar spectral reflectance (Fig. 3C; Jensen 2015). Finally, we visually examined the unsupervised results for each cover category and combined classifications for the same habitat types (Fig. 3D). All pixels were reclassified as one of the following floodplain habitats: wood, riffle, run, pool, shallow shoreline, backwater, pond, springbrook, overbank flow, cobble bar, early successional vegetation, shadow, residential, herbaceous, cottonwood, willow, or conifer. All reclassified pixels were merged into a single mosaic for each sample date (Fig. 3E).

Habitat response to flooding disturbance

We calculated the area of every habitat type within each plot to assess the spatial and temporal dynamics of individual habitat types during flooding disturbance. We analyzed the same plots from the 3 floodplain zones on each sample date, which resulted in a stratified random sample within a repeated measures design. The distributions of habitat area values within each plot were extremely positively skewed, and we were unable to correct for either non-normality or heterogeneous variance with transformations. We, therefore, applied the nonparametric Friedman test (Demsar 2006) to every habitat type to determine whether the distribution of area values significantly differed on at least 1 sampling date. These tests yielded 1 p-value for each habitat-cover type, and we considered test results to be significant at $\alpha = 0.1$.

If the p-value from the Friedman Test was significant ($p < 0.1$), we used the Nemenyi post-hoc test in the *PMCMR* package in R (Pohlert 2014) to test for significant differences ($p < 0.1$) in the distributions of areas of each habitat type across sample dates. This test is a nonparametric version of the Tukey Test (Demsar 2006). Each post-hoc test yielded 1 p-value for each pairwise comparison between sample dates, resulting in 15 p-values per habitat type. The Nemenyi post-hoc test is conservative and accounts for family-wise error, so we did not correct for multiple comparisons (Pohlert 2014). We completed this analysis for the whole floodplain and for each of the 3 floodplain zones. All statistical analyses were done with R version 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria). We used a significance level of $\alpha = 0.1$ because of the inherently high natural variation in ecological systems.

To understand patterns in the development of individual floodplain habitats during flood disturbance, we assigned 1 habitat type to each plot based on the dominant cover. We built transition tables to summarize changes in habitat cover types between each sample date, and we used these tables to create alluvial diagrams in RAWGraphs version 1.2.0 (DensityDesigns, Milan, Italy; Kleindl et al. 2015, Mauri et al. 2017). The transition tables for each date were combined

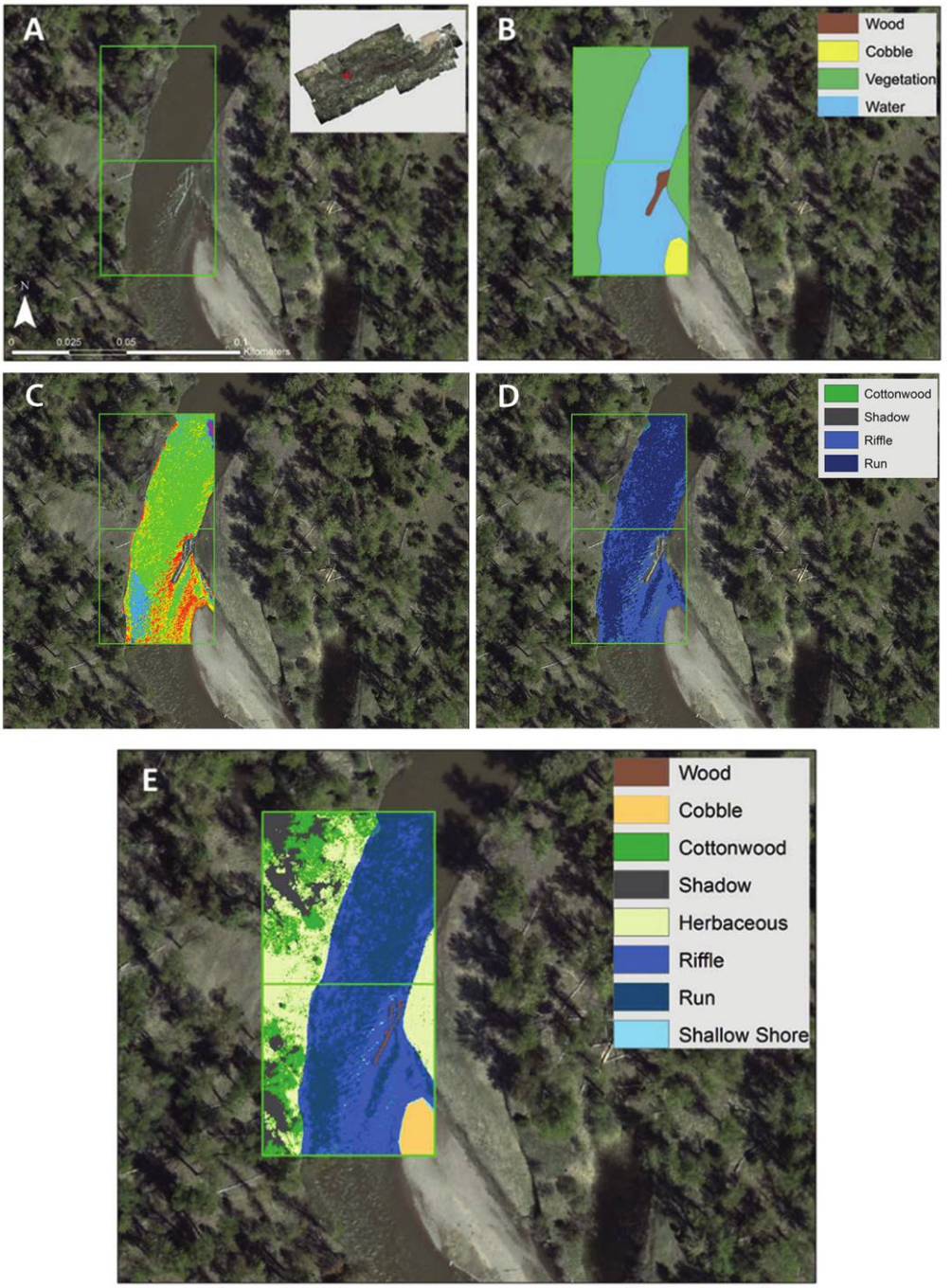

Figure 3. An example of the process used to classify pixels as floodplain habitat types applied to 2 orthofluvial plots with imagery from May 8. This process was repeated in the 3 floodplain zones on each sample date for all plots. A.—An example of 2 orthofluvial plots that were sampled on each date. B.—The results of the heads-up digitizing process that demarcated cover categories within all plots. C.— The output of the unsupervised image classification resulted in 10 classes (each represented by a different color for the digitized water category). D.—The results of visual examination and reclassification of the unsupervised output for the digitized water category. E.—An example of the final classification raster for 2 orthofluvial plots on May 8.

into a summary table for each floodplain zone. These tables show the number of plots that changed from 1 habitat to another throughout the study period. We used these tables and alluvial diagrams to quantify and visualize the most common transitions made by floodplain habitats during the seasonal flood disturbance.

Floodplain response to flooding disturbance

To assess spatial and temporal dynamics of the floodplain landscape during disturbance, we calculated both α and β habitat diversity. Alpha diversity is the mean habitat diversity within a floodplain zone, and was quantified with the Shannon diversity index (H′), which captures both habitat richness (R, number of habitats) and evenness,

$$H' = \sum_{i=1}^{R} p_i \ln(p_i) \quad \text{(Eq. 1)}$$

where p_i is the proportion of pixels belonging to the i^{th} habitat (Arscott et al. 2000). We used this index to calculate α diversity of each floodplain zone on each sample date. We tested for differences in the mean Shannon diversity values of each date with the bootstrap function in the *asbio* package in R (Aho 2015), which we used to obtain the mean and standard error (SE) for each of the floodplain zones on every sample date (Arscott et al. 2002).

Beta diversity is the dissimilarity in habitat composition between 2 plots, and we calculated it with the *vegan* package in R (Oksanen et al. 2015). We used the β-diversity turnover index (β_T) proposed by Wilson and Shmida (1984). This analysis compared the abundance (number of pixels) and richness (number of habitat types) of 2 plots, generating 1 β_T value for every pair of plots within a floodplain zone. The β_T index considers the number of pixels in the 2nd plot that are habitat types not present in the 1st plot (G) and the number of pixels in the 1st plot that are habitat types not present in the 2nd plot (L). It then standardizes by average plot richness, $\bar{\alpha}$.

$$\beta_T = [G + L]/2\bar{\alpha} \quad \text{(Eq. 2)}$$

This analysis compared every pair of plots within a zone on each sample date and yielded a distribution of values for each zone that ranged from 0 (complete similarity in habitat composition of 2 plots) to 1 (complete dissimilarity in habitat composition of 2 plots) (Amoros and Bornette 2002). These results were highly skewed, so we used Kernel Density Estimation (KDE), a nonparametric estimate of the probability density function of a continuous random variable, to generate β-diversity distributions for each zone on each sample date. We used the Kolmogorov–Smirnov test to test for significant differences ($p < 0.1$) in the β-diversity distributions of each sample date within each of the 3 floodplain zones. We made the KDE plots in R with the *ggplot2* package (Wickham 2009).

RESULTS

Habitat identification and interference of spectral reflectance

Image classification identified 17 aquatic and terrestrial habitat types that represented homogenous patches within the landscape. Terrestrial habitats had distinct vegetation characteristics, and aquatic habitats had distinct depth and velocity characteristics. We were able to use the classification results to quantify the area occupied by each habitat type on every date and to calculate α- and β-diversity indices.

The final identification of some habitat types was affected by error associated with turbidity, vegetation, and shadow. Turbidity influences the spectral signature of light reflected by the water column, which can diminish the ability of the sensor to distinguish variations in water depth (Whited et al. 2002, Pan et al. 2015). We observed increased turbidity on the rising limb of the hydrograph and during peak flow (May 8, 21, 27). However, visual examination helped reduce error during the reclassification process by differentiating aquatic habitats with spectral signatures altered by turbidity. In addition to turbidity, vegetation growth contributed to classification error because shadows from tall vegetation, especially cottonwood trees, obscured some non-gallery habitat types from view of the airborne imager. The classified % shadow ranged from 4.4 to 5.0% of total classified pixels across all data collection dates of the study. In the main channel, 33 of 1655 potential plot transitions from shadow to legitimate floodplain habitat occurred, and 51 floodplain habitat to shadow transitions occurred (Table 1). In the parafluvial zone, 191 of 5800 total plot transitions from floodplain habitat to shadow occurred, and 241 transitions from floodplain habitat to shadow occurred (Table 2). Error from shadows occurred most often in the orthofluvial zone, where of 1760 total plot transitions, 171 were floodplain habitat to shadow and 221 were shadow to floodplain habitat (Table 3).

Spatial and temporal habitat dynamics

During the flooding cycle we observed significant differences ($p < 0.1$) in the areal abundance of habitats at the whole-floodplain scale and within each zone. At the whole-floodplain scale, the areal abundance of riffles, runs, shallow shores, cobble bars, herbaceous cover, overbank flow, and early successional vegetation was significantly different on at least 1 sample date (Table S1). In contrast, we found no changes in the total area classified as wood, pools, backwater, ponds, springbrooks, willows, cottonwoods, or conifers at the whole-floodplain scale.

In the main channel zone, the total area of riffles, runs, and cobble bars was significantly different ($p < 0.1$) on at least 1 date (Table S2). There were no significant differences between sample dates in the areas of early stage vegetation, springbrooks, pools, shallow shores, backwaters, shadow, or wood in the main channel, even though we observed these

Table 1. Summary table of all plot transitions that occurred in the main channel zone throughout the study period.

		Transition to:									
		Cobble bar	Pool	Riffle	Run	Shadow	Shallow shore	Springbrook	Vegetation	Wood	Total
Transition from:	Backwater	–	–	1	–	–	–	–	–	–	1
	Cobble bar	5	1	3	4	–	–	–	1	–	14
	Pool	–	3	3	8	1	1	–	–	–	16
	Riffle	47	7	444	219	21	9	1	10	20	778
	Run	13	3	277	327	27	6	–	6	18	677
	Shadow	–	–	13	15	26	–	–	1	4	59
	Shallow shore	5	–	10	5	–	4	–	2	4	30
	Vegetation	2	–	6	3	–	–	–	2	4	17
	Wood	3	1	25	15	2	4	–	1	12	63
	Total	75	15	782	596	77	24	1	23	62	1655

habitats on at least 1 date. Riffles and runs were the most abundant habitats on every sample date in the main channel (Fig. 4), and often did not exhibit habitat transitions during the flooding cycle (Table 1). A total of 1655 potential plot transitions occurred in the main channel throughout the study period. Of these, 771 riffle and run plots did not transition between any sample dates, with 444 were riffle plots remaining riffles and 327 were run plots remaining runs throughout the study. The most common transition was from a riffle to a run during the rising limb of the flood, and from a run to a riffle on the falling limb. In the main channel large and exposed woody debris generally became riffles or runs on the rising limb, and a similar number of riffle and run plots returned to wood accumulation sites on the falling limb. MC pools tended to transition to runs as flooding increased, and eventually returned to pools as flows receded. Cobble bars overwhelmingly originated from riffle. Shallow shores generally transitioned *to* riffles or runs during the rising limb of the hydrograph, and an approximately equivalent amount of shallow shore originated from riffles and runs as discharge decreased. One springbrook appeared at the end of the flooding cycle in the main channel zone. The dominant habitat of this 1 plot began as a cobble bar, transitioned to riffle, and became a continuous flow springbrook at base flow.

In the parafluvial zone we observed significant changes in the total area of cobble bars, overbank flow, main channel (MC) and flood channel (FC) riffles, MC and FC runs, and MC and FC shallow shores (Table S3). We observed MC and FC pools, backwaters, springbrooks, ponds, shadows, and wood in the parafluvial zone on at least 1 date during the flood disturbance, but the total areas of these habitats did not change significantly during the flood cycle. No single habitat type was dominant in the parafluvial zone (Fig. 5). Some plots maintained a consistent classification of MC or FC riffle, cobble bar, or vegetation throughout the flooding disturbance. However, some habitat types transitioned to specific other habitat types in the parafluvial zone (Table 2). For example, MC shallow shores frequently transitioned to MC riffles, which commonly transitioned to cobble bars. Prior to seasonal flooding, the parafluvial zone was nearly 50% cobble bars, with some FC riffle and FC run habitat, vegetation, and large woody debris. During the rising limb of the flood cycle, FC riffles became the most dominant habitat on May 8, and MC runs became the most dominant habitat on May 21. On May 27, our sampling date during the maximum annual discharge, many plots in the parafluvial zone transitioned to MC riffle. During the falling limb of the flood cycle, much of the parafluvial zone returned to cobble bars and early successional vegetation. MC shallow shores appeared in the parafluvial zone during the flooding disturbance. Flood channels generally became riffles on the rising limb and cobble bars on the falling limb. Between July 2 and September 5 there was a clear pattern of parafluvial springbrooks transitioning to early regenerating vegetation as flows receded.

In the orthofluvial zone we observed significant differences in the areas of shadow, cobble bar, FC riffles, FC runs, wood, and overbank flow (Table S4). We observed no significant changes in the distributions of the area values for cottonwoods, conifers, backwaters, orthofluvial springbrooks, MC or FC shallow shores, FC pools, or ponds in the orthofluvial zone, even though we observed each of these habitat types on at least 1 date. In the orthofluvial zone, herbaceous habitat plots were dominant throughout the flood cycle, and 852 of the 1760 plots remained the same habitat type throughout the study period (Table 3). We did observe a loss in the number of plots dominated by cottonwood and willow, which was caused by increases in shadow from the growth of vegetation during the flooding cycle (Fig. 6). Generally, FC riffles and FC runs did not transition to other habitat types, but when they did it was often from a riffle to a run. The overbank flow habitat type most commonly appeared in herbaceous plots on the rising limb of the flood, and these plots transitioned back to herbaceous cover as discharge decreased. We observed 1 pond plot in the orthofluvial zone

Table 2. Summary table of all plot transitions that occurred in the parafluvial zone throughout the flooding disturbance. FC = flood channel; MC = main channel.

		Transition To:																	
		Backwater	Cobble bar	FC pool	FC riffle	FC run	FC shallow shore	Herbaceous	MC pool	MC riffle	MC run	MC shallow shore	Overbank flow	Pond	Shadow	Spring-brook	Vegetation	Wood	Total
Transition from:	Backwater	3	16	–	11	7	–	–	–	4	4	–	2	–	2	3	9	5	66
	Cobble bar	7	420	2	74	53	4	14	8	160	97	61	3	–	39	10	108	76	1136
	FC pool	–	1	–	5	7	1	–	–	1	2	1	–	1	–	–	2	1	22
	FC riffle	7	142	4	236	62	11	11	9	97	49	15	2	1	31	15	88	59	839
	FC run	2	37	1	101	58	5	5	1	41	26	6	1	–	12	16	60	31	403
	FC shallow shore	–	10	–	3	6	2	–	–	7	3	–	–	–	1	–	8	6	46
	Herbaceous	–	3	–	8	3	–	3	1	13	9	2	2	2	3	1	12	6	68
	MC pool	–	2	–	10	1	1	–	1	8	2	1	1	–	1	1	6	4	39
	MC riffle	22	242	1	116	39	3	–	6	194	61	38	3	1	25	7	105	80	943
	MC Run	3	19	1	31	28	3	2	4	188	55	7	2	–	21	1	28	25	418
	MC shallow shore	1	39	2	15	18	2	–	2	53	16	13	–	–	8	2	15	19	205
	Overbank Flow	–	2	–	2	–	–	–	–	3	2	2	2	–	5	–	8	1	27
	Pond	–	2	–	1	1	–	2	–	–	2	–	–	–	–	1	1	–	10
	Shadow	1	17	2	21	15	1	1	2	37	8	6	1	–	29	3	51	25	220
	Springbrook	1	10	–	6	5	1	–	–	6	14	2	–	–	6	2	15	9	77
	Vegetation	6	122	4	81	38	7	11	2	80	39	11	5	–	49	8	244	54	761
	Wood	4	80	1	55	25	5	4	1	62	32	12	3	–	38	9	105	84	520
	Total	57	1164	18	776	366	46	53	37	954	421	177	27	5	270	79	865	485	5800

Table 3. Summary table of all plot transitions that occurred in the orthofluvial zone throughout the flood disturbance.

		Transition To:														
		Cobble bar	Conifer	Cottonwood	FC riffle	FC run	Herbaceous	Overbank flow	Pond	Residential	Run	Shadow	Springbrook	Willow	Wood	Total
Transition from:	Cobble bar	–	–	–	4	1	5	–	–	–	–	1	1	–	–	12
	Conifer	–	4	–	–	–	2	–	–	–	–	1	–	–	–	7
	Cottonwood	1	–	45	–	2	24	1	–	–	–	37	–	–	–	110
	FC riffle	1	–	–	15	9	2	–	–	–	1	7	3	–	–	38
	FC run	3	–	–	8	15	8	–	–	–	–	7	3	–	1	45
	Herbaceous	5	–	1	3	9	852	5	–	1	–	149	8	4	1	1038
	Overbank flow	–	–	–	–	–	8	1	–	1	–	3	–	–	–	13
	Pond	–	–	–	–	–	–	–	5	–	–	–	–	–	–	5
	Residential	–	–	–	–	–	1	–	–	1	–	–	–	–	–	2
	Run	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
	Shadow	–	–	1	5	7	151	2	–	–	–	220	2	3	–	391
	Springbrook	–	–	–	4	3	9	–	–	–	–	4	7	–	–	27
	Willow	–	–	–	–	–	17	–	–	–	–	12	–	40	–	69
	Wood	–	–	–	–	1	1	–	–	–	–	–	–	–	–	2
	Total	10	4	47	40	47	1080	9	5	3	1	441	24	47	2	1760

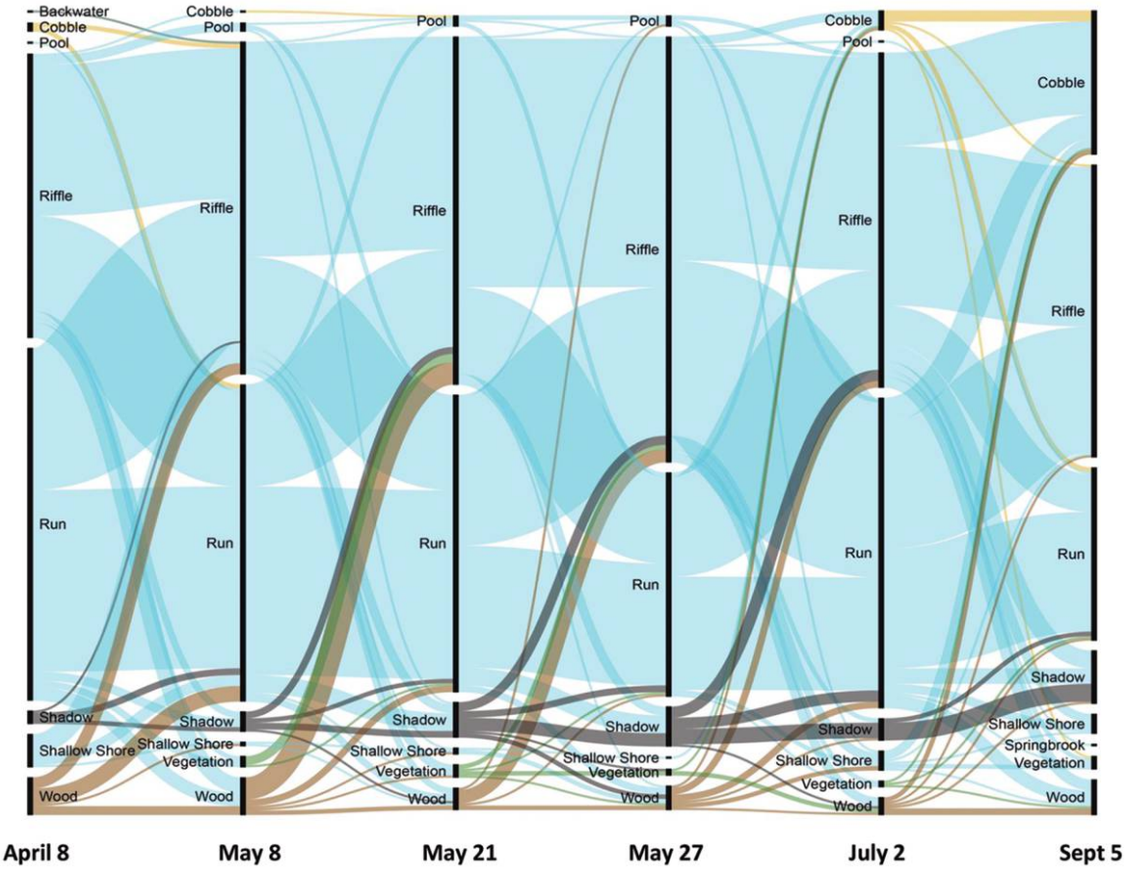

Figure 4. Alluvial diagram that shows transitions (%) between habitat types in the main channel zone throughout the course of the flood pulse cycle. Each black vertical node represents a sample date, and each colored line represents the transition in habitat type made by a single plot between sampling dates.

that did not undergo any transitions during the flooding disturbance. Finally, orthofluvial springbrooks did not usually transition to another habitat type.

Spatial and temporal dynamics of the floodplain

Main channel zone Alpha diversity in the main channel zone was consistent throughout the flooding disturbance, with no significant differences in mean H′ among sample dates ($p = 0.99$; Fig. 7). The average α-diversity (mean H′ = 1.19) was the lowest of the 3 floodplain zones and the main channel had significantly lower α habitat diversity (H′ = 1.01) than either the parafluvial or orthofluvial zones during peak flow. We observed 10 habitat types in the main channel zone on April 8. Habitat richness decreased (R = 9) during the rising limb and peak flow on May 8, 21, and 27. The fewest number of habitats (R = 8) were present during the falling limb, and we observed the highest habitat richness (R = 11) on September 5 at base flow.

Beta diversity of the main channel changed over time, and the β-diversity distribution of each sample date were all significantly different ($p < 0.01$) from each other. The main channel generally had the lowest beta diversity of the 3 floodplain zones. The probability of having similar habitat composition between 2 plots ($\beta_t = 0$) was highest during the rising limb of the hydrograph (May 8 and May 21; Fig. 8A). The greatest probability of 2 plots having entirely different compositions ($\beta_t = 1$) occurred at base flow on September 5.

Parafluvial zone Alpha habitat diversity of the parafluvial zone did not change during the flood cycle, and we found no significant differences in mean H′ by sample date ($p = 0.17$; Fig. 7). The average alpha diversity (mean H′ = 1.90) was higher than it was in the other 2 zones. Additionally, during the rising limb of the flood pulse on May 8 (H′ = 2.25) and May 21 (H′ = 2.23), average alpha diversity was significantly higher than it was in the other zones on those dates. We observed 17 habitat types in the parafluvial zone from April 8 through May 21. Habitat richness in the parafluvial zone was reduced (R = 16) during peak flow on May 27, but increased during the falling limb (R = 17). The lowest habitat richness occurred during base flow on September 5 (R = 14).

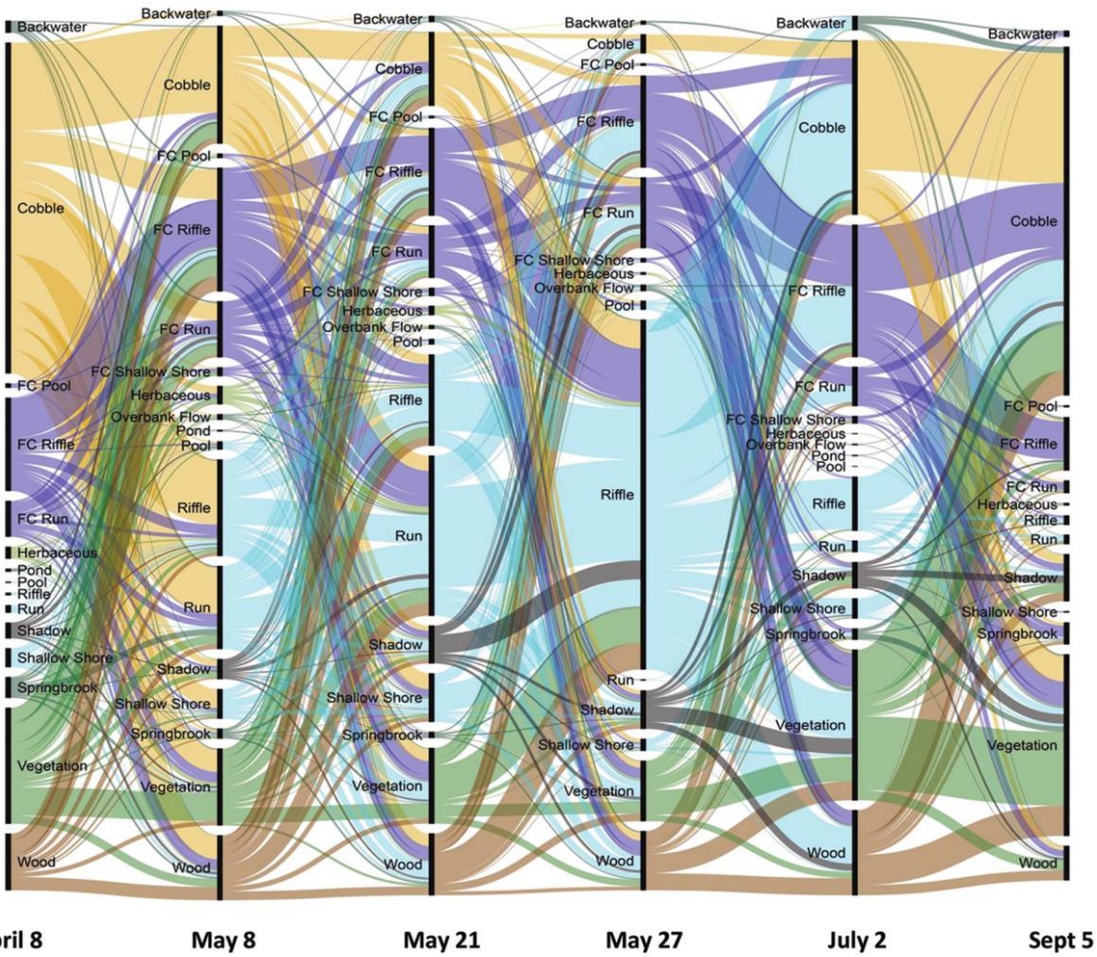

Figure 5. Alluvial diagram that shows transitions (%) between habitat types in the parafluvial zone throughout the course of the flood pulse cycle. Each black vertical node represents a sample date, and each colored line represents the transition in habitat type made by a single plot between sampling dates. Main-channel habitats are shown in light blue, and off-channel habitats are shown in dark blue.

Beta diversity was highest in the parafluvial zone and changed significantly over time, such that the β-diversity distributions of each sample date were all significantly different ($p < 0.01$) from each other. Further, there was a high probability of 2 parafluvial plots being entirely different on the same date ($\beta_t = 1$), especially during the rising limb on May 8 and May 21 (Fig. 8B). The lowest beta diversity in the parafluvial zone occurred during low flows after disturbance, but beta diversity was still likely to be intermediate ($0.25 < \beta_t < 0.75$), indicating some dissimilarity between plots.

Orthofluvial zone Alpha habitat diversity in the orthofluvial zone was consistent throughout the flooding disturbance with no significant differences in mean H′ by sample date ($p = 0.99$; Fig. 7). The average alpha diversity of the orthofluvial zone (mean H′ = 1.63) was intermediate relative to the main channel and parafluvial zone. The orthofluvial zone had significantly higher alpha habitat diversity (H′ = 1.81) than the main channel during peak flow on May 27. Habitat richness in the orthofluvial zone was lowest on April 8 and September 5 (R = 16), intermediate (R = 18) during peak flow on May 27 and on the falling limb on July 2, and highest during the rising limb on May 8 and May 21 (R = 19).

Beta diversity was also intermediate and changed significantly over time, with the beta diversity distributions of each sample date all differing significantly ($p < 0.01$) from each other. All dates had a high probability of $\beta_t \sim 0.5$, so 2 plots were likely to have some habitat in common but were unlikely to be entirely similar or different (Fig. 8C). We observed a slightly increased probability of $\beta_t = 1$ on May 27 and a slightly increased probability of $\beta_t = 0$ on September 5.

DISCUSSION

The shifting habitat mosaic concept states that the relative abundance of diverse floodplain habitats is more or less constant long-term (Stanford et al. 2005). However, little is known about changes in habitat dynamics during a

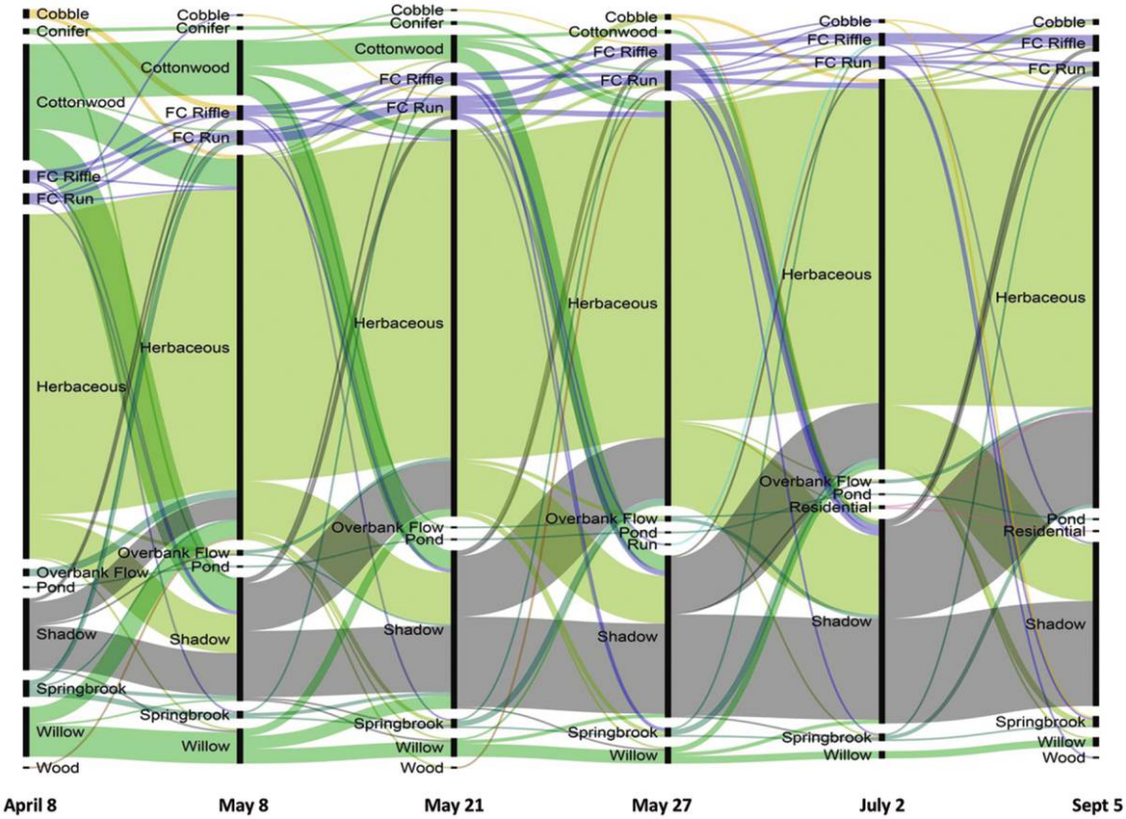

Figure 6. Alluvial diagram that shows transitions (%) made between habitat types in the orthofluvial zone throughout the course of the flood pulse cycle. Each black node represents a sample date, and each colored line represents the transition in habitat type made by a single plot between sampling dates. Main-channel habitats are shown in light blue, and off-channel habitats are shown in dark blue.

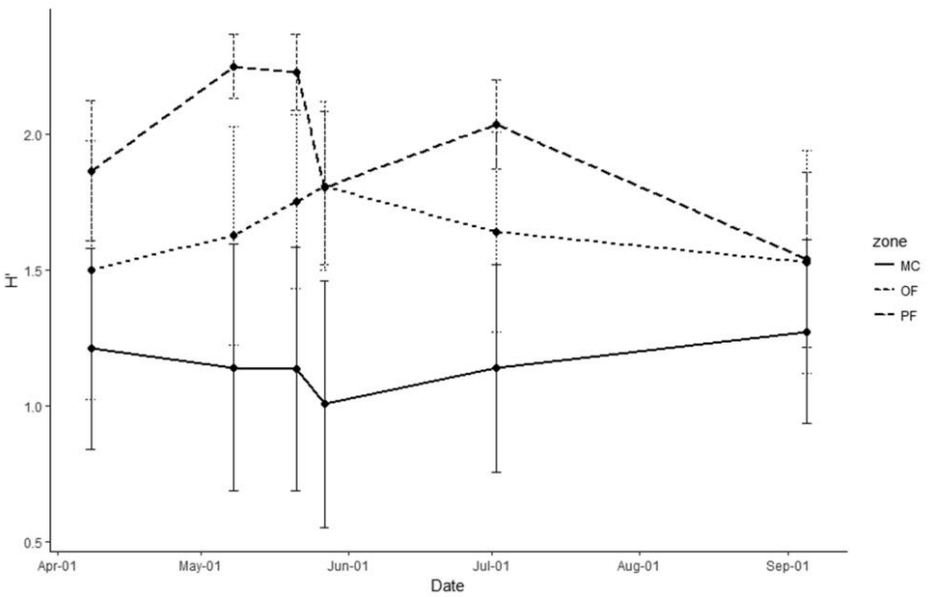

Figure 7. Bootstrapped average (±90% CI) Shannon α habitat diversity (H′) in the main channel (MC), parafluvial (PF), and orthofluvial (OF) zones on each sample date during the flood pulse cycle.

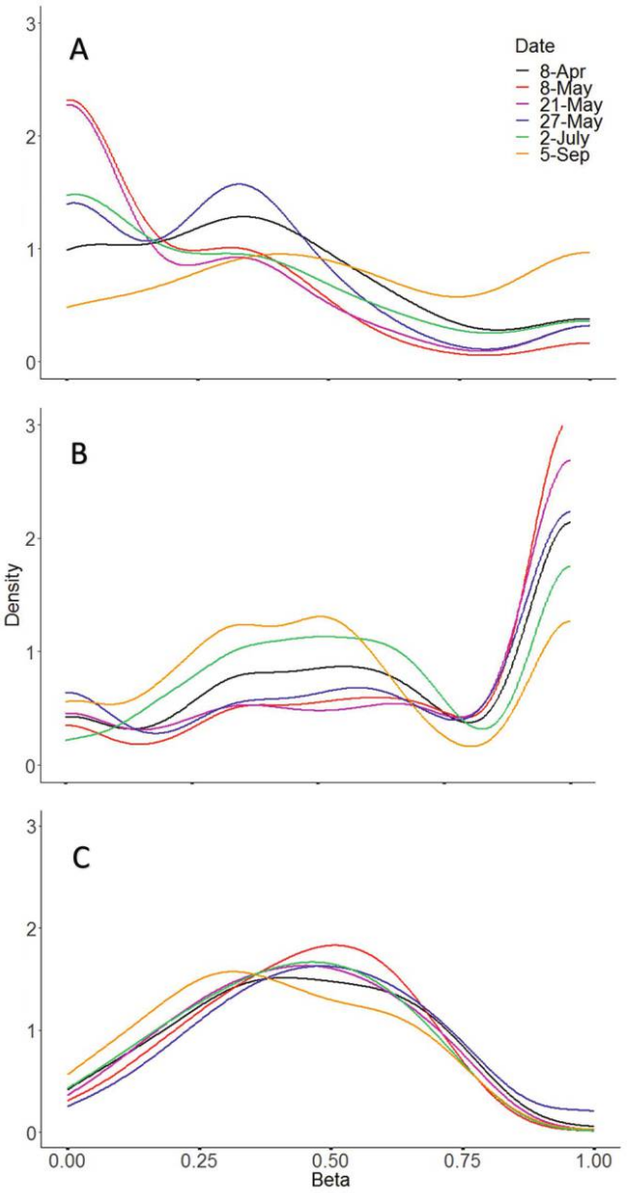

Figure 8. Kernel density plots of the main channel (A), parafluvial (B), and orthofluvial (C) zones β habitat diversity distributions for each sample date over the flood pulse cycle. The density distributions on each date were significantly different ($p < 0.01$) in each of the 3 zones.

flooding event that affects seasonal habitat distribution and abundance and ultimately succession. We found that total area of different habitat types varied across the rising limb, bankfull, and falling limb phases of a flooding disturbance. We also found that the location of habitat types within the floodplain affected their response to seasonal flooding. The spatial distribution of some habitat types changed during the flooding event, but did not increase or decrease in total abundance, whereas both the total abundance and spatial distribution of other habitat types changed during the flooding event.

Habitat response to disturbance

In this study, the total area of channel pools, orthofluvial ponds, orthofluvial springbrooks, large woody debris, and mature vegetation remained constant throughout the flood cycle (Tables S1–S4). However, the distribution of these habitats across the floodplain changed (Figs 4–6). Pools and aggregated wood jams were highly resilient to bankfull flooding disturbance. Pools are formed either downstream of log jams and root wads or at the confluence of 2 braids (Bisson et al. 1982, 2017). We observed that, as high water inundated pools behind snags, flood channels filled and formed new pools at their confluence (Table 2). Likewise, we observed patterns that indicated wood was exported from the system, but a similar amount was generated or recaptured (Tables 1–3). In these instances, bankfull flooding simultaneously created and destroyed habitat, leading to relatively stable abundance throughout the flooding cycle. The persistence of pools and wood throughout the flooding disturbance suggests that the shifting habitat mosaic model can apply to some habitat types on shorter temporal scales.

There were no significant changes in the abundance of mature vegetation, orthofluvial ponds, or orthofluvial springbrooks. These habitats are particularly resistant to flooding disturbance because of their location in the orthofluvial zone. Permanent orthofluvial springbrooks that do not transition to other habitat types during flooding are commonly observed in braided sections of river throughout the world (Arscott et al. 2000, van der Nat et al. 2003), and orthofluvial ponds in island braided reaches tend to experience less turnover. Thus, orthofluvial springbrooks and ponds tend to be some of the oldest habitat patches in a system (van der Nat et al. 2003).

These types of relatively stable and consistently abundant features that remain present during bankfull flooding disturbance can influence ecosystem function by retaining organic matter (Bilby and Likens 1980) and providing important refugia for aquatic species (Sedell et al. 1990, Pearsons et al. 1992, Rempel et al. 2000). Vegetated islands, like those in the orthofluvial zone of our study reach, dissipate energy of floodwaters and provide stability to aquatic habitats located on the island (van der Nat et al. 2003). Additionally, these flood-resilient features often develop and sustain high variation in thermal regimes and bioavailable nutrients that can foster algal growth and high densities of macroinvertebrates (Pepin and Hauer 2002, Wyatt et al. 2008).

In contrast to habitats that remained relatively stable during the flooding event, habitat types that had highly variable areas included shallow shores, riffles, runs, overbank flow, cobble bars, and early successional stages of vegetation (Tables S1–S4). The yearly development patterns of

habitats that do not follow the shifting habitat mosaic during bankfull flooding can influence the long-term structure and function of floodplain systems. Changes in the area and location of shallow shores are important because these patches represent the dynamic edge of the river where active construction and destruction of habitats occurs (Junk et al. 1989). In our study, as shorelines expanded across the active channel and into the parafluvial and orthofluvial zones, new riffle and run habitats developed and the abundance of riffles and runs increased substantially.

Riffles were the habitat most influenced by the flood cycle. Plot transitions in both the main channel and parafluvial zone indicated that as discharge increased and waters spread through the floodplain, cobble bars generally transitioned to riffles (Tables 1, 2). The seasonal expansion of riffle habitat into the parafluvial zone is important because fish often spawn among riffles that are also proximal to high-quality rearing habitats (Beschta and Platts 1986). On the falling limb of the flood cycle, the total area of riffle habitats decreased as they transitioned into bare cobble bars (Figs 4–6). The transition from riffle to cobble bar is important because sediment transport and deposition often occurs at turbulent riffles, which creates bare substrate during the falling limb of the hydrograph. This bare substrate is essential for the regeneration of plant species like cottonwoods and willows (Blom and Voesenek 1996, Mahoney and Rood 1998). In this study, we observed increases in the abundance of cobble bar and early successional vegetation at the falling limb of the hydrograph (Table S3), as well as the transition from riffle to cobble to vegetation between May 27 and September 5 (Table 2) as a major mechanism that leads to succession on floodplains, as proposed by Mahoney and Rood (1998).

In addition to shallow shores, riffles, runs, cobble bars, and early successional vegetation, the abundance of overbank flow was also variable throughout the flood cycle. As discharge increased and flows topped bankfull, the area of overbank flow that extended across most floodplain surfaces significantly increased. This flooding temporarily reduces habitat heterogeneity by connecting previously distinct orthofluvial habitats such as flood channels to the main channel, resulting in a single large channel at high flows (Mosley 1982, Thomaz et al. 2007). However, habitat heterogeneity increases again during the falling limb and baseflow phases (Thomaz et al. 2007). In the present study, overbank flow connected side channels that would not otherwise have experienced flow during the study period. These connections created ponds as floodwaters receded on later dates of the flood cycle.

We also observed highly transient habitats throughout the study period, which included backwaters, parafluvial ponds, and parafluvial springbrooks. These habitat types occupied small areas and rarely lasted more than a few weeks and, thus, often appeared on one sampling date and had disappeared by the next. Backwaters appeared and disappeared faster than all other habitats following peak annual flow. The short timespan of this habitat type was related to flow pulses below bankfull and processes of cut and fill alluviation, as also observed by Tockner et al. (2000) and van der Nat et al. (2003). Similarly, parafluvial ponds are short-lived because they are often shallow (van der Nat et al. 2003). Thus, the density, area, and perimeter of these ponds are highly responsive to changes in the hydrograph (Crete 2012). Despite their short residence times, parafluvial ponds and backwaters provide high-quality nursery habitat for fishes (Crete 2012), and amphibians often select for these types of ephemeral habitats to avoid predation (Hauer et al. 2016).

Our results indicated that habitat change across a typical snowmelt flood cycle is highly influenced by the location of the habitat on the floodplain. For example, we observed areal abundance of runs in the main channel to be fairly constant. In contrast, runs in the parafluvial zone were highly dynamic and increased in abundance during the rising limb of the flood cycle and disappeared rapidly with the falling limb. Shallow shores were also dynamic in the parafluvial zone, but did not change in the main channel or the orthofluvial zones. However, in the analysis of the whole floodplain, the areal abundance of shallow shores and runs increased significantly. These observations indicate runs and shallow shores were strongly influenced by water filling the active channel, and that changes in their area were large enough to influence the pattern for the whole floodplain. Similarly, springbrooks and ponds were either resistant to disturbance or extremely sensitive, depending on their location in the orthofluvial or parafluvial zone. Overall, as demonstrated by the alluvial diagrams (Figs 4–6), habitats in the parafluvial zone were the most dynamic. These habitats changed from 1 habitat to another, and we observed more habitat types and transitions between them during the bankfull flooding disturbance than we did in the other floodplain zones.

Floodplain response to disturbance

Habitat types that experienced increases and decreases in total area during bankfull flooding drove differentiation in α habitat diversity between zones. The creation and increase in abundance of new habitat types in the parafluvial zone during intermediate flows on both the rising and falling limb of the hydrograph generated significantly higher α habitat diversity than the main channel or orthofluvial zones. Similarly, increased habitat richness and abundance in the orthofluvial zone during peak flow resulted in significantly higher α habitat diversity than the main channel on May 27. Shannon index values on September 5 indicated that the loss or decrease in abundance of habitat types caused there to be no difference in habitat heterogeneity between floodplain zones during base flow conditions after the flood.

β habitat diversity among the 3 zones was significantly different, and the β diversity distributions within each zone changed throughout the flooding disturbance. The main channel had the lowest β habitat diversity on the rising limb of the hydrograph, indicating that plots in the main channel became more similar in their habitat composition as discharge started to increase. The main channel exhibited the highest β habitat diversity values on September 5. This occurred because of a shift in the location of the channel and the appearance of parafluvial habitats in the main channel zone, including creation of a new springbrook. Generally, β habitat diversity of the orthofluvial zone was ~0.5, indicating all plots had some habitat in common. However, β habitat diversity in the orthofluvial zone was slightly higher during peak flow and slightly lower during base flow conditions post-flood. The magnitude of the 2014 seasonal flood was average, and the flood only generated slight changes in orthofluvial β habitat diversity. This observation suggests that only very large floods will generate increased dissimilarity in habitat cover within the orthofluvial zone.

The floodplain shifting habitat mosaic (Stanford et al. 2005) contends that habitat diversity is constant over the long-term, but this model is based on measurements taken during base flow across years, decades, or centuries. Our results indicate that habitat diversity is highly variable within the annual flood pulse cycle. This pattern is not just the result of water inundation or fluvial processes causing sediment transport and deposition. Instead, flooding forces differentiation in α and β habitat diversity between the parafluvial, orthofluvial, and main channel zones. The higher α habitat diversity in the parafluvial and orthofluvial zones indicates that the flood pulse resulted in greater habitat richness. The β habitat diversity patterns highlight small and temporary habitats that have little effect on α habitat diversity, but significantly contribute to dissimilarity in habitat composition. When the diversity of the main channel is low during flooding, particularly during the rising limb, the increased number of habitats in the parafluvial and orthofluvial zones, including those that are small, short-lived, or both, can provide critical habitat with different water temperatures, velocities, organic matter retention, nutrient processing, or sedimentation rates (Steiger et al. 2005, Valett et al. 2014, Hauer et al. 2016, Jones et al. 2017). These habitats promote high biological diversity by preventing competitive exclusion (Salo et al. 1986). They also have the potential to leave a legacy of patches with different substrates, organic matter, nutrient availability, and depths to the water table that could influence successional trajectories and the long-term structure and function of the ecosystem.

Conclusions

Our study provides new and additional insight into the spatial and temporal dynamics of floodplain habitats during a typical flood pulse cycle. The results indicate that floodplain habitat composition and abundance are influenced not only by simple inundation, but also by the creation of new and different habitats and zones that differ in whether they follow the shifting habitat mosaic. This range in habitat response to the annual flooding cycle in the snowmelt-dominated, gravel-bed rivers of montane landscapes highlights the variability in habitat response to disturbance and demonstrates the need for studies across different temporal scales. The shifting mosaic steady state model can be applied to floodplains for long periods, but our results suggest that floodplains may not be in a state of dynamic equilibrium on a shorter time scale while a seasonal flood disturbance is ongoing. Some individual habitats, such as pools and wood, follow the shifting mosaic steady state model even during flooding. However, habitat types such as shallow shores and riffles experience significant increases or decreases in their relative abundance during the flood pulse event. As river discharge fills and overflows the channel, habitats lost in one location are often not replaced elsewhere. These patterns result in the differentiation in habitat diversity among floodplain zones, with the parafluvial and orthofluvial zones experiencing greater habitat diversity during the flooding event.

The patterns and processes we observed were influenced by natural flow regimes and the connection between the river and its floodplain. Alterations to the timing, frequency, duration, and magnitude of floods may be associated with changes in the spatial abundance and timing of availability of sensitive habitats, as well as reduced habitat diversity across the floodplain. Furthermore, the spatial and temporal patterns of habitat composition we observed would be significantly affected by channel confinement or downcutting and incision. Both altered flow regimes and disconnection from the floodplain would probably result in the loss of both parafluvial and orthofluvial habitat diversity and complexity, especially during flooding. Habitat diversity and complexity is critical to the life history of many species, and contributes to the high biodiversity and productivity of gravel-bed river floodplains (Hauer et al. 2016). Reduced habitat diversity across the floodplain could lead to additional long-term impacts by disrupting the natural successional trajectories set in motion during the flood pulse disturbance.

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Author contributions: KPD designed the project, conducted the GIS and statistical analyses, and drafted the manuscript. FRH advised KPD on project design and analyses, facilitated acquisition of remotely-sensed data, was mission engineer and pilot, and contributed to the writing of the manuscript.

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