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Use of Airborne Digital Imagery to Examine Floodplain Complexity at Varying Discharges

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USE OF AIRBORNE DIGITAL IMAGERY TO EXAMINE FLOODPLAIN COMPLEXITY

AT VARYING DISCHARGES

By

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ABSTRACT

Floodplains are composed of aquatic and terrestrial habitats that are frequently reshaped by
hydrologic processes operating at various spatial and temporal scales. I hypothesized that
floodplain habitat complexity is maximized at intermediate discharges because small changes in
flow result in substantial aquatic habitat changes and extreme discharges are associated with a
decreased habitat heterogeneity. Between April and September 2014, I collected ultra-high
resolution digital multispectral imagery of the Clark Fork River, Montana taken on 6 dates
between early spring and fall. Following image mosaicking into a single image, unsupervised
classification of the spectral reflectance was used to identify and quantify different aquatic
habitats observed in the main channel, parafluvial, and orthofluvial zones of the floodplain.
Through the course of the seasonal flood pulse, I observed significant changes in the spatial
abundance of many habitat cover types (riffles, runs, shallow shorelines, overbank flow), but not
others (backwaters, springbrooks, pools, ponds), suggesting that discharge is only a partial driver
of the abundance of aquatic habitats. Riffles and runs and the most common transitions from one
habitat to another dominated the main channel over the hydrograph changes that occurred
between these habitats. The dominance of these habitats among main channel habitats was
reflected in the low alpha diversity of the main channel, which was least diverse during peak
flow conditions. Additionally, the main channel generally had low beta diversity, indicating that
plots were usually very similar in habitat composition. The parafluvial zone was dominated by
cobbles at low flows, transitioned to isolated parafluvial flood channels at moderate discharges,
and dominated the expanded main channel during peak flow conditions. The parafluvial was the
most diverse zone with peaks in alpha diversity occurring at intermediate flows on both the
rising and falling limbs of the hydrograph. Furthermore, the beta diversity of the parafluvial
zone tended to be high, suggesting that parafluvial plots were often dissimilar from each other.
The orthofluvial zone was dominated by herbaceous habitat; however, I did observe aquatic
habitats in the orthofluvial as well. Orthofluvial springbrooks transitioned to flood channels
during high discharge as their upstream end connected during elevated discharges and then
returned to springbrooks after the flood. The orthofluvial zone had an intermediate level of alpha
diversity with the largest habitat diversity observed during peak flow. The beta diversity values
of this zone indicated that most plots had some habitat cover type in common. I concluded that
there is a relationship between discharge and floodplain habitat complexity, however it is
influenced by an interaction between location on the riverscape and discharge.

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I. Introduction

River corridors are spatially dynamic mosaics of diverse aquatic and terrestrial habitats in various stages of succession, each with various ecological functions (Vannote et al., 1980; Junk et al., 1989; Tockner et al., 2000; Stanford et al. 2005). The physical structure of the river channel and therefore the spatial distribution of habitats are controlled by physical processes, particularly the movement of water and sediment within the channel and between the channel and its floodplain (Junk et al., 1989; Poff et al., 1997; Lorang and Hauer, 2003). The riverscape is a result of several patterns and processes occurring at various scales (Lorang and Hauer, 2006), such as flooding, channel avulsion, cut and fill alluviation, wood recruitment, and regeneration of riparian vegetation (Stanford et al., 2005). Many of these patterns and processes are associated with a river's natural flow regime and are responsible for the distribution of riverine habitats, which are spatially altered through time.

For many systems flooding and flow pulses are part of the natural flow regime (Junk et al. 1989; Tockner et al. 2000), which is critical to sustaining native biodiversity and ecosystem integrity within riverscapes (Stanford, 1996; Poff et al., 1997). Magnitude, frequency, duration, timing, and rate of change of hydrologic conditions are considered critical components of a river system's flow pattern (Poff and Ward, 1989; Poff et al., 1997). The flood pulse, the portion of the flow regime when overbank flow occurs, has been documented as a critical disturbance (Resh et al., 1988) to floodplain ecosystems (Junk et al., 1989; Poff et al., 1997; Stanford et al., 2005). Years of flooding exceeding the threshold entrainment of a river reshape the channel and creates the current morphological condition of the river (Lorang and Hauer, 2003). Not only is the flood pulse important for the creation of new habitats, but it also enables the exchange of matter, nutrients, and energy between the river and its floodplain (Junk et al., 1989; Bayley,

1995). Ward and Stanford (1983) applied the intermediate disturbance hypothesis to running waters, arguing that moderate levels of disturbance caused by flooding are linked to greater levels of biotic diversity. Large, frequent disturbances would exclude species that require more time to establish, but at low levels of disturbance competitive interactions also exclude species (Ward and Stanford, 1983; Resh et al., 1988). Additionally, flow pulses, extremes that occur below bankfull (Tockner, 2000), play a role in the lateral channel migration of the river channel, which shapes the riverscape by structuring topographic features, connecting or disconnecting from floodplain habitats, influencing succession, and determining turnover rates of landscape elements (Ward et al., 2002; Stanford et al., 2005).

Studies have documented that spatial complexity and diversity of aquatic habitats are strongly tied to the geomorphology of the floodplain, with greater aquatic habitat complexity observed in gently sloping, lower, braided reaches with large active floodplains (Arscott et al., 2002, Whited et al., 2013). However, spatial heterogeneity also seems to be related to discharge with changes across scales observed during expansion and contraction events. These changes are controlled by regional processes at the catchment scale and local processes at the floodplain scale (Tockner et al., 2000; Whited et al., 2007).

Connectivity was defined by Amoros and Roux (1988) as the exchange of matter, energy, and biota between different elements of the riverine landscape via the aqueous medium. Minor increases in flow may cause reconnection with some habitats, while others may require large floods to re-establish a connection (Ward and Stanford, 1995; Tockner et al., 2000). The degree of connectivity between habitat types has an influence on floodplain complexity, which is defined as the variation in geomorphic, hydrologic, and biological forms, functions, and linkages that exists among ecologically distinct elements of floodplain landscapes. Amoros and Bornette

(2002) found that complexity resulting from connectivity is highly dependent on the water source and the distance from the main channel. During periods of high flow, the degree of connectivity is high and habitat boundaries are eliminated, resulting in homogenous landscapes and decreased floodplain complexity (Amoros and Bornette, 2002; Thomaz et al., 2007). In periods of connectivity, off channel habitats are reset through scour and the removal of sediments and organic matter (Ward et al., 2002). Within the active channel, higher water velocity, which coincides with elevated discharges, prevents hydrologic, chemical, or biotic divergences that are observed in distinct habitats at decreased flows (Lewis et al., 2000). In addition to the effects of seasonal flooding, hydrologic connectivity and its observed influence on floodplain complexity can vary greatly on shorter temporal scales from flow pulses occurring below bankfull conditions (Tockner et al., 2000).

Tockner et al. (2002) argued that the relationship between riverscape heterogeneity and discharge is an important characteristic of river systems. Numerous previous studies have focused on habitat complexity over long time scales (Arscott et al., 2000; Arscott et al., 2002; van der Nat et al., 2003) or between multiple floodplain systems (Arscott et al., 2000; Arscott et al., 2002; Luck et al., 2010; Whited et al., 2013). At the same time, river systems are notoriously variable across time and factors that drive habitat heterogeneity operate across scales, requiring further research that focuses on different temporal and spatial scales. While the areal proportions of different habitat types has been found to remain fairly constant at the long term or annual scale (Whited et al., 2007), processes occurring at shorter time scales affect the current state of the river and its floodplain (Ward et al., 2002). Previous studies suggest that under natural conditions, aquatic habitats may be highly dynamic over these shorter temporal scales, with small flow pulses creating major habitat changes (Tockner et al., 2000; van der Nat et al., 2003).

At this finer temporal scale, a floodplain habitat may increase or decrease in its areal abundance (Ward et al., 2002).

The seasonal expansion and contraction of channel networks that results from the annual flood pulse and its impact on connectivity and habitat heterogeneity have been less studied (Tockner et al., 2000). Furthermore, few studies have compared changes in spatial heterogeneity over time caused by fluctuating discharges or patterns in landscape heterogeneity occur during flow pulses (Tockner et al., 2000). Whited et al. (2002) showed that habitats in the Lower Yakima River experienced substantial changes with only moderate changes in flow. Depending on the dynamics of a river channel, habitats may be ephemeral or stable for decades (Junk et al., 1989, van der Nat et al., 2003). Different aquatic habitat features are created and maintained by a range of varying discharges (Poff et al., 1997) with some studies suggesting that habitat complexity may be minimized during peak and base flows. Off-channel habitats are less abundant and more isolated during low summer flow conditions (Whited et al., 2007). Alternatively, at high flows, channels become wider, deeper, and faster, frequently merging into a single large channel (Mosley, 1982). During these periods of inundation and isolation, floodplains may experience a homogenizing effect with fewer aquatic habitats observed (Ward et al., 2002).

Previous studies that examined biodiversity in floodplains have determined the importance of different degrees of connectivity and habitat heterogeneity (Ward et al., 1999, Lewis et al., 2000). Understanding how aquatic habitats develop or disappear from the landscape has implications for plant and animal species as well as ecological function and ecosystem productivity (Stanford et al., 2005). Predictable variation in diverse riverine habitats is important for the completion of the life cycle for many riverine species, as well as the survival of

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many organisms, including plants, aquatic insects, and fish (Cummins, 1973; Greenberg et al., 1996; Junk and Piedade, 1997; Humphries, 1999; Sheldon, 2002; Arscott et al., 2003). Species diversity of individual groups is maximized at different points within the gradient of connectivity between a river and its floodplain (Tockner et al., 1999) and the various aquatic and terrestrial floodplain habitats are known to play roles in species development within the riverscape. For example, shallow shorelines, backwaters, and springbrooks provide nurseries to developing fish (Copp, 1988; Kwak, 1988; Rosenfeld et al., 2008). Distinct riverine habitats have unique temperature (Hauer and Hill, 2006) and physico-chemical signatures (Valett et al., 2014), suggesting that different habitat types function differently (Arscott et al., 2000).

Understanding the prominence of specific habitats and the length of time they exist on the landscape has implications for the ecological function of the floodplain. For example, riffles have been suggested to act as biological filters because surface water infiltrates the sediment upstream of a riffle and exfiltration of interstitial waters occurred downstream from the riffle. This means that riffles are fed by surface water that has crossed interstitial habitat, which influences water temperature, nutrient loads, and benthic communities (Claret et al., 1998). Similar to riffles, pools are also tied to specific ecological function. Pool tailouts are more heavily influenced by surface waters, giving rise to a slightly different functional community (Mermillod-Blondin et al., 2000). Springbrooks provide thermal heterogeneity and habitat refugia (Snyder and Stanford, 2000) can promote productivity by providing nutrients in areas of converging flows (Bansak, 1998) or hyporheic return flow into the river channel (Wyatt et al., 2008), or moderate water temperatures for the entire system (Gibert et al., 1994).

Habitat dynamics and their relation to discharge is important in the face of climate change, which has affected and will continue to alter the timing, magnitude, frequency, and

duration of the flood pulse (Poff, 2002; Gibson et al., 2005; Whited et al., 2007; Bryant, 2009).

In addition to climate change, other threats to the natural flow regime include dam regulation and

irrigation diversion (Kingsford, 2000; Tockner and Stanford, 2002). Dams that alter the timing

and magnitude of ecologically critical high and low flows are known to create regionally

homogenous riverscapes (Poff et al., 2007) and diversions are understood to alter the ecology of

floodplains resulting in the death and poor health of aquatic species (Kingsford, 2000).

Understanding the timing of maximum complexity and the discharge associated with it have

ecological and economic implications for regulation by dams and removal of discharge for

irrigation purposes (Barbier and Thompson, 1998). With ample threats to natural flow regimes, it

has become increasingly important to understand the relationship between discharge and

riverscape habitat complexity in every spatial and temporal scale.

Based on these observations, there is a relationship between discharge and floodplain

habitat complexity. However, the specific nature of that complexity across changing flow

regimes is less understood. To better understand this relationship, I proposed the following

hypothesis.

H: Floodplain habitat complexity is maximized during periods of intermediate discharge

of a flooding event because small changes in flow result in substantial aquatic habitat

changes and extreme discharges are associated with decreased habitat heterogeneity.

For the purpose of studying this hypothesis I addressed three questions

Q1: How do the areas of various floodplain habitats change from base flow to peak flow

to base flow?

Q2: What patterns exist in the transitions made by these floodplain habitats throughout the course of a flood event?

Q3: How do fluctuations in discharge influence habitat diversity, as well as dissimilarity in habitat composition?

I predicted that during peak flow conditions complexity is decreased because the floodplain would be dominated by inundation from a single main channel habitat cover type. I also predicted that floodplain complexity would decrease during base flow conditions as the water receded to a single, homogenous channel. Furthermore I expected to observe consistent patterns in transitions made by habitat covers (i.e. cobble to riffles to runs to riffles to cobble). Lastly, I expected that the area occupied by specific aquatic habitats, such as riffles, runs, pools, etc. would change with increased discharge and that certain habitat cover types would become dominant at base and peak flow conditions (Figure 1).
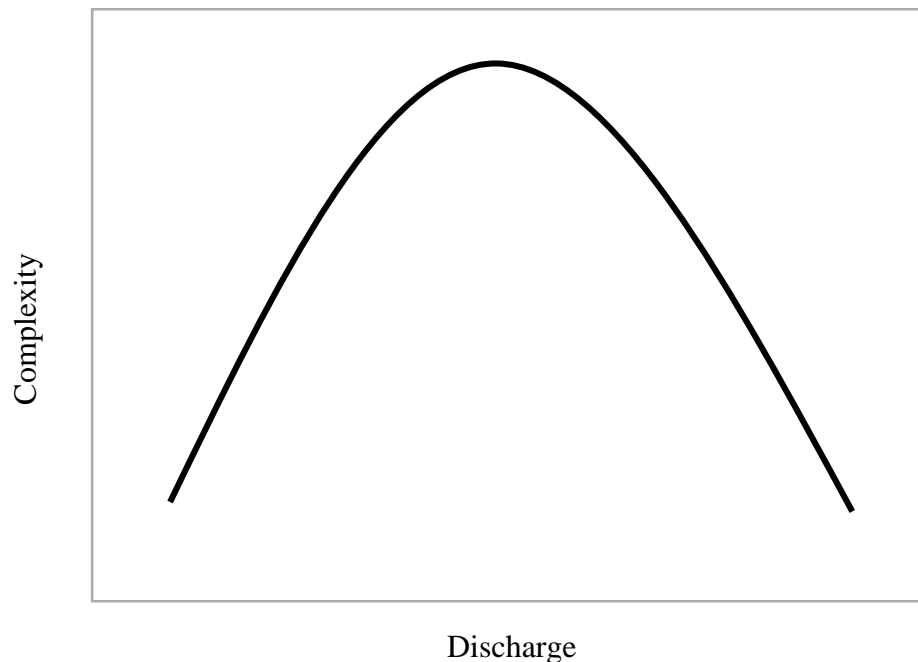
Figure 1. Theoretical relationship between complexity and discharge

II. Study Site

The Clark Fork River is a gravel-bed river located in Western Montana and a tributary to the Columbia River. This study focuses on a reach in the Middle Clark Fork sub-basin of the river as it flows through the Missoula Valley (Figure 2). The drainage area of the Middle Clark Fork sub-basin is 15594 km^2 and receives 76.4 centimeters in annual average precipitation (U.S. Geological Survey, 2014). The average annual flow based on discharge data collected from 1929 to 2013 is 83 m^3 /s, with an average high flow of 434 m^3/s occurring in May and an average low flow of 39 m^3/s in September (Figure 3) (U.S. Geological Survey, 2013). The slope of the main channel is 3.45 meters per kilometer and the mean basin elevation is 5690 feet above sea level (U.S. Geological Survey, 2014). Forty six percent of the basin is above 6000 feet, suggesting a large impact from snowmelt which is reflected in the hydrograph. There are few lakes, ponds, or swamps observed in the basin, with only 0.38% of the basin occupied by these habitats and 75.8 % is forested (U.S. Geological Survey, 2014).

The Clark Fork enters the alluvial Missoula Valley from the confining reach of the Hellgate Canyon, then immediately flowing through a reach that is constrained by the city of Missoula. Further downstream, of the city, the river flows through an unconfined, braided reach 6.5 km to the confluence with the Bitterroot River. My study focused on this unconfined section of the Clark Fork River, which is composed of active and abandoned channels, springbrooks, ponds, and stands of regenerating and mature vegetation (Figure 2). The river is connected to and free to move laterally across its floodplain. The elevation of the valley at the upstream end of the study reach is 963 meters and the elevation at the confluence with the Bitterroot River is 951 meters.
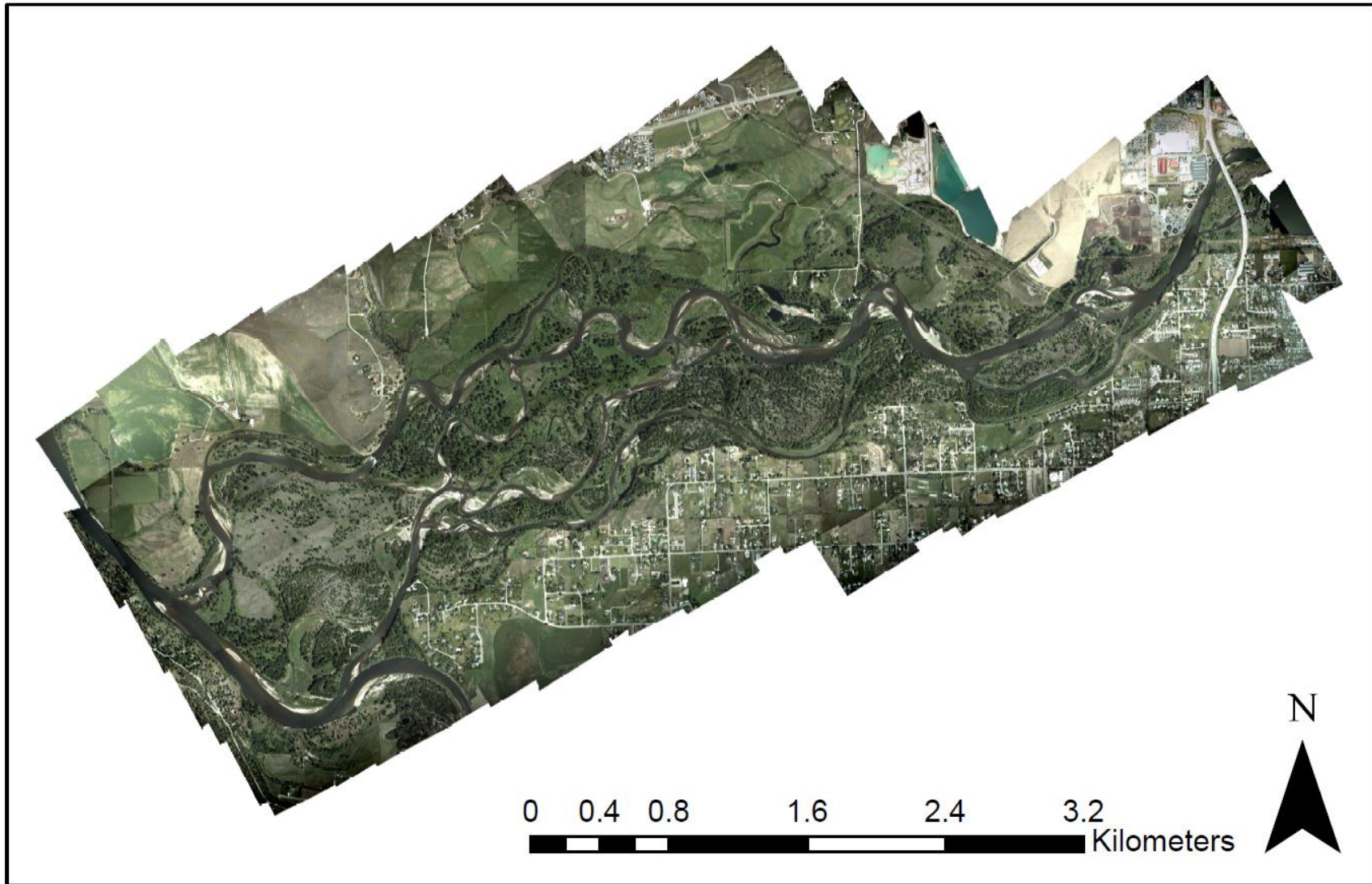
Figure 2. Aerial view of the island braided study reach on the Clark Fork River as it flows through the Missoula valley in western Montana.
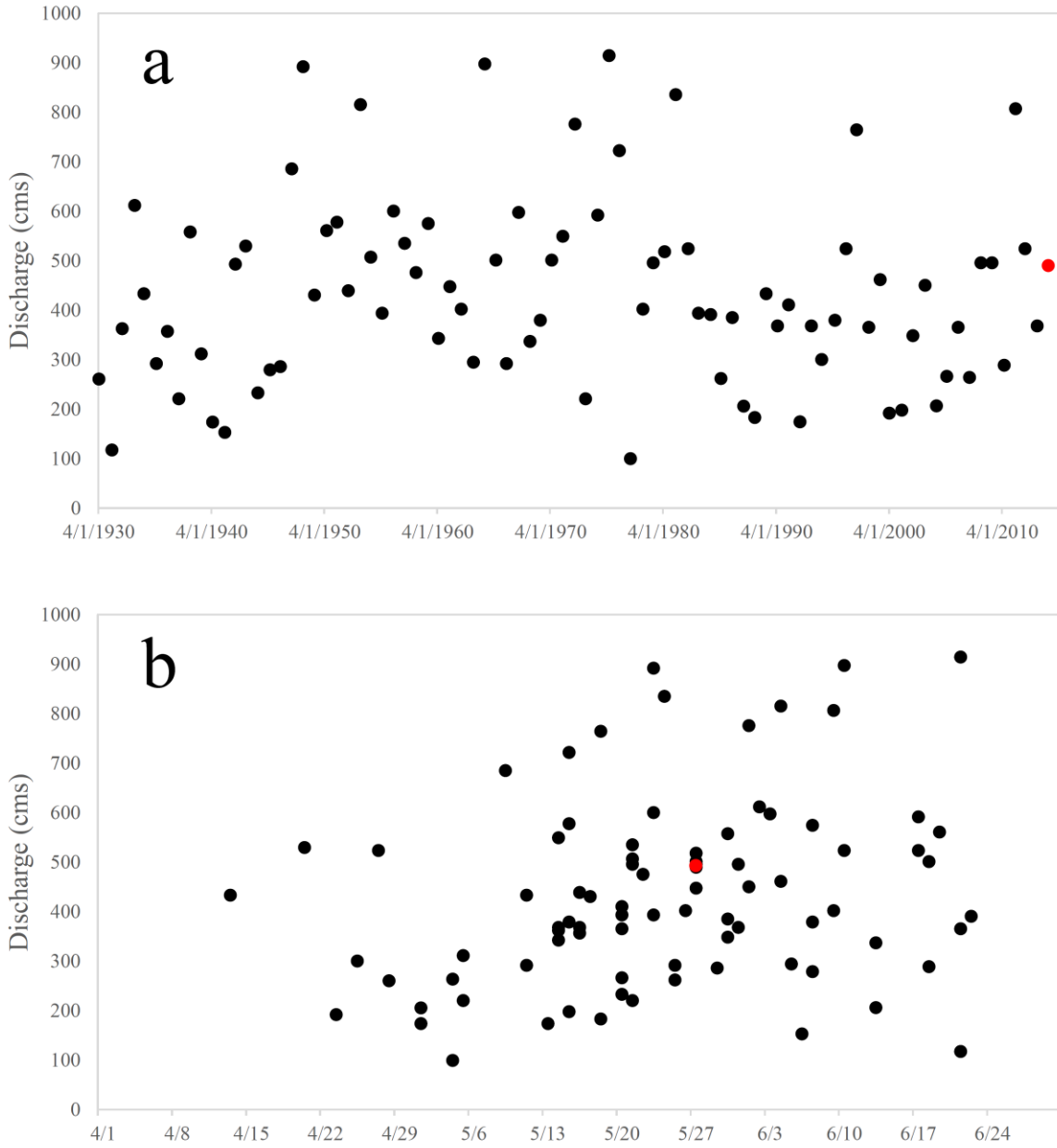
Figure 3 (a) Annual maximum discharge (CMS= cubic meters per second) from 1930-2014 for the study reach on the Clark Fork River (USGS site 12340500). Peak flow for 2014 was 484.23 m^3/s on May 27 and is represented by the red dot. (b) The annual maximum discharge (CMS) distributed by calendar date showing interannual variation in day that maximum discharge occurred each year from 1930-2014.

While this section of the river is more unconfined than the reach immediately upstream, the floodplain remains highly impacted by humans. Missoula's wastewater treatment plant is located at the top of the reach, as is a property owned by a company that has produced several gravel pits and ponds in the process of making concrete and asphalt. The northern bank of the study reach is largely made up of agricultural and grazing land, with a few roads and buildings located with the orthofluvial zone. The southern bank of the study reach is restricted in its movement by a large residential area, some of which is located in the orthofluvial zone.

III. Methods

Photo Collection, Processing, and Mosaicking

I used remotely sensed digital aerial photography to address the relationship between discharge and floodplain habitat complexity. Past studies used airborne imagery to assess riverine habitats (Hauer and Lorang, 2004) and quantify large scale changes in floodplains and river corridors (Arscott et al., 2000; Whited et al., 2002; Whited et al., 2003; Lorang et al., 2005). Substrate and turbidity are important factors that affect the accuracy of image classification because they can alter the spectral reflectance of water as well as influencing depth and velocity estimations (Roberts and Anderson, 1999). Nevertheless, major channel features can be identified by their unique spectral reflectance resulting from different depth and velocity profiles (Whited et al., 2002; Whited et al., 2003).

I acquired aerial photographs using an ultrahigh density multi-spectral imager (Princeton Instruments) on seven dates through the course of the snowmelt flood event in 2014 (Figure 4). The discharge data for the seven dates was collected from USGS stream gage 12340500, which is located on the Clark Fork River above Missoula, MT, three miles downstream from the confluence of the Clark Fork and Blackfoot rivers. The first set of photographs, collected on

April 8 (discharge = $90.05 m^3/s$), was representative of base flow prior to the flood pulse. May

8 ($300.16 m^3/s$) and May 21 ($362.46 m^3/s$) exemplified floodplain structure during the rising

limb of the flood pulse. May 27 ($484.23 m^3/s$) represented conditions at peak flow. According

to USGS discharge data, the peak flow of 2014 did in fact occur on May 27th. July 2

($169.33 m^3/s$) represented the falling limb of the flood pulse. Finally, September 5 ($45.59 m^3/s$)

was representative of base flow conditions after the flood event. I observed slightly larger peak

flow conditions in 2014 when compared to the maximum discharges from 1930-2014 (Figure 3).

The dates of collection were highly dependent on the weather, with photographs being collected

between 10 am and 1 pm on clear sky days. These data were used for image classification of

habitat features on the seven dates during the flood pulse.

I used Erdas Imagine software to georectify the raw remotely sensed data to a 2013

National Agriculture Imagery Program (NAIP) orthorectified photograph of Missoula County

with one meter spatial resolution. All images were rectified in the UTM coordinate system NAD

83 and cast into UTM Zone 11. For each image, I identified nine ground control points (GCP's)

and fit a second order polynomial equation with a root mean square (RMS) error of less than 2

pixels to complete the image to map rectification process. The images were resampled once

using nearest neighbor interpolation to 0.2 X 0.2 meter pixels for consistency across all

photographs. Each corrected photo was viewed in ArcMap to ensure the correct geospatial

location as well as an approximate 30% overlap and alignment with other images.

Upon completion of georectification process, I used the MosaicPro tool in Erdas Imagine

to radiometrically correct and mosaic the photographs from each of the six dates to six separate

digital images. I used automatic color balancing for radiometric adjustments and a weighted

Date	Discharge (cms)
4/8/2014	90.05
5/8/2014	300.16
5/21/2014	362.46
5/27/2014	484.23
7/2/2014	169.33
9/5/2014	45.59
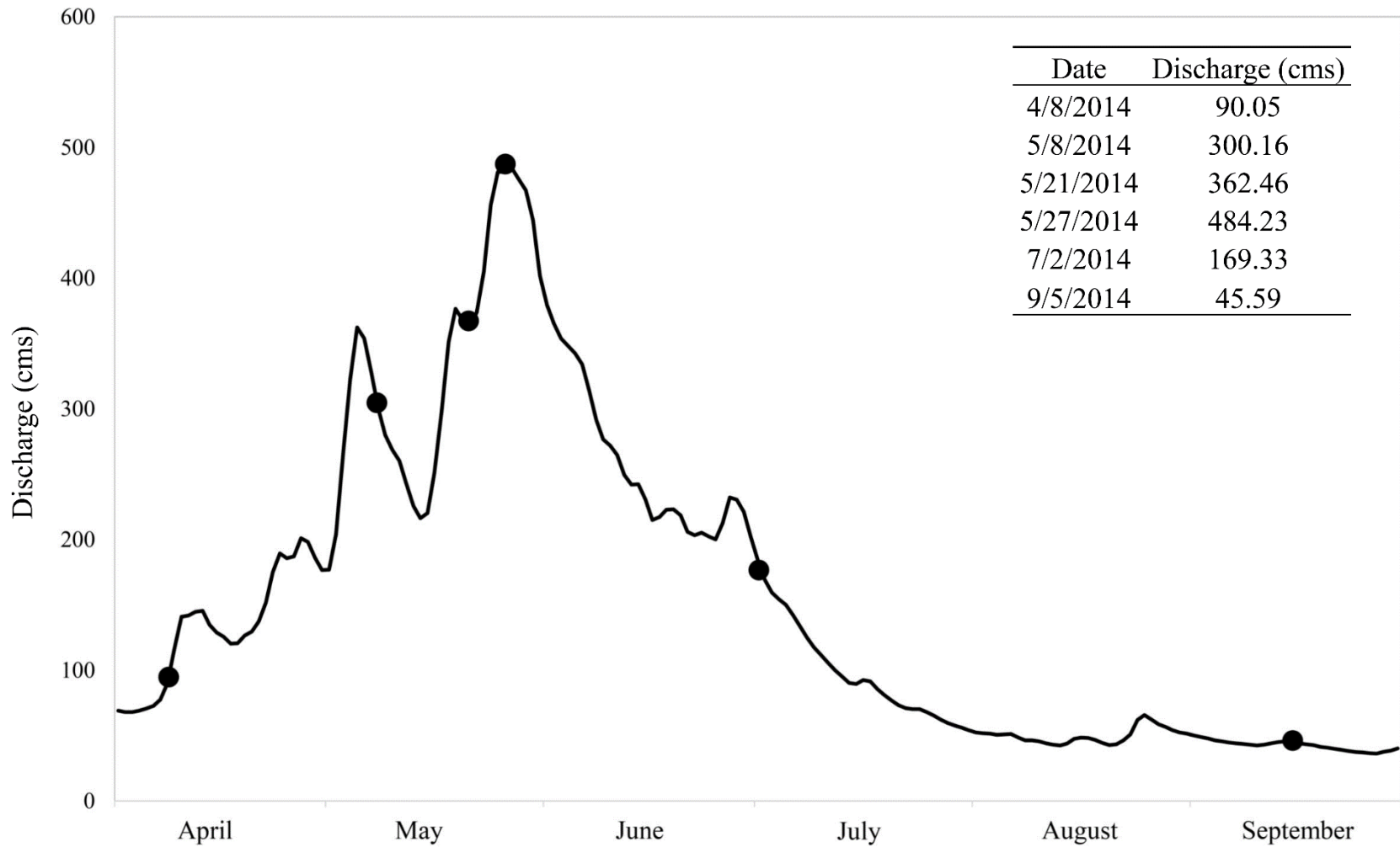
Figure 4. The discharge hydrograph (CMS=cubic meters per second) in the Clark Fork River (USGS Site 12340500) from April 1, 2014 through September 30, 2014. Black dots represent dates of remote sensing data collection.

seamline with a segment length of eight pixels to create virtually seamless mosaics. The weighted seamline generator was chosen per recommendations for mosaicking images of rivers from the Erdas Imagine Field Guide and Jensen (2005).

Plot Selection and Habitat Classification

In ArcMap, I used the imagery from April 8, 2014 to identify three zones within the floodplain: the main channel, parafluvial, and orthofluvial. The main channel was determined by permanently connected primary channels with a thalweg present (Stanford, 2006). The parafluvial zone was identified as areas that experience annual scour and deposition with early successional vegetation (Stanford, 2006). I identified this zone by the presence of exposed cobble, shallow ponds, large woody debris and early stage vegetation (Stanford, 2006; Whited et al., 2007). I identified the orthofluvial zone as the portion of the floodplain that is only reworked by large floods, but frequently experiences inundation by the annual flood pulse. Additionally, mature patches of vegetation are frequently observed in this zone (Stanford, 2006). The orthofluvial zone was clearly identifiable based on the presence of mature cottonwoods, conifers, and evidence of abandoned channels. The boundaries of these zones did not change in their location throughout the study period. This means that when the main channel grew in size and expanded into the parafluvial zone during high flows, I observed main channel habitats in the parafluvial zone. Additionally, the flood pulse caused a shift in the location of the main channel, however the boundaries of the main channel zone did not move. This resulted in parts of the main channel zone transitioning to parafluvial habitat cover types.

I completed a power analysis to determine the number of plots required for each zone to detect the true mean area occupied by each habitat cover type 90% of the time and conservatively selected the largest number of required plots. The result indicated a need for 331

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5x5 meter plots in the main channel, 1160 5x5 meter plots in the parafluvial zone, and 350 50x50 meters plots in the orthofluvial zone. I used Hawth's Analysis tool for ArcGIS (Beyer, 2004) to create and randomly select the appropriate number of plots for each zone to be analyzed for their habitat composition at six various discharges. The same plots within three zones were analyzed on each of the six dates of photo collection, resulting in a stratified random sample with a repeated measures design (Figure 5).

In ArcMap version 10.2.2, I used heads-up digitizing (manually drawing polygons around each habitat feature) to demarcate 21 different habitat cover types observed within the main channel, parafluvial, and orthofluvial plots (Table 1). During this process, channel units were identified as fairly homogenous localized areas that displayed different depth and velocity characteristics from the adjoining areas (Bisson et al., 2006). I then used an unsupervised classification within Erdas Imagine to group pixels with similar spectral characteristics into unique clusters (Jensen, 2005). Lorang et al., (2005) demonstrated that these clusters correctly identified depth and flow conditions of surface water habitats, concluding that the results of unsupervised image classifications were adequate. In a prior study, differences between ground truth measurements and the unsupervised classification were associated with isolated pixels that are insignificant on the large scale of this study (Lorang et al., 2005). In ArcMap, I visually examined the pixel categories, combined, and reclassified each cluster from the unsupervised classification as a specific habitat type including: wood, main channel riffle, main channel run, main channel pool, main channel shallow shoreline, backwater, cobble, early stage vegetation, shadow, residential, pond, springbrook, herbaceous, flood channel riffle, flood channel run, flood channel pool, flood channel shallow shoreline, mature cottonwood, mature willow, conifer, and overbank flow (Figure 5).
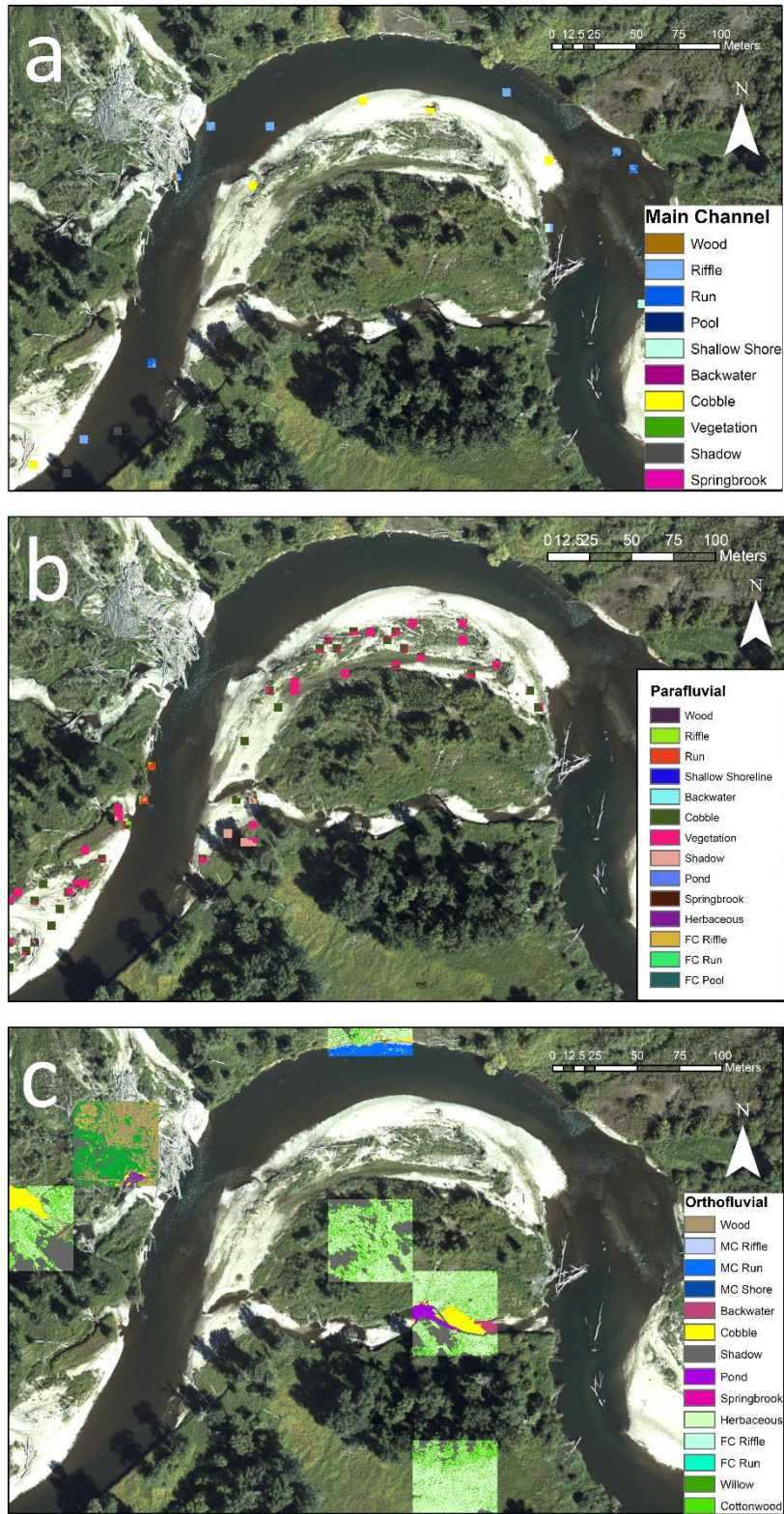
Figure 5. Examples of the sampling method demonstrating main channel (Panel A), parafluvial Panel B), and orthofluvial (Panel C) plots classifications on September 5, 2014. The main channel and parafluvial plots are 5x5 meters and the orthofluvial plots are 50x50 meters.

To map and measure the areas of floodplain habitat cover types, I followed guidelines

established by prior studies in the northern Rocky Mountain ecoregion (Hauer et al., 2002;

Lorang et al., 2005; Whited et al., 2007). As the sampling period is specifically focused on a

flood event, turbidity effected the depth classifications (Whited et al., 2002) of typically deeper

and darker habitats on four of the photograph collection days (April 8, May 8, May 21, and May

27). The roughness of the water surface of riffles allowed them to be distinguished from runs by

their spectral reflectance. Pools were identified as darker areas that occur at the end of turbulent

water runs behind log jams or root wads or at the confluence of two channels. Shallow

shorelines were classified as wetted areas of primary and secondary channels that were adjacent

Table 1. Habitat cover types that could be discriminated in each of the three floodplain zones on
at least one date throughout the study period. FC = Flood Channel; MC = Main Channel

Main Channel	Parafluvial	Orthofluvial
Backwater	Backwater	Backwater
Cobble	Cobble	Cobble
Herbaceous	FC Riffle	Conifer
Pool	FC Run	Cottonwood
Riffle	FC Shallow Shoreline	FC Pool
Run	Herbaceous	FC Riffle
Shadow	MC Pool	FC Run
Shallow Shoreline	MC Riffle	FC Shallow Shoreline
Springbrook	MC Run	Herbaceous
Vegetation	MC Shallow Shoreline	MC Riffle
Wood	Overbank Flow	MC Run
	Pond	MC Shallow Shoreline
	Shadow	Overbank Flow
	Springbrook	Pond
	Vegetation	Residential (houses or street
	Wood	Shadow
		Springbrook
		Willow
		Wood

to the shore. Overbank flow was classified as flow that was above bankfull and outside any channel, abandoned or connected. Lastly, backwaters and springbrooks share the characteristic that they are only connected to the main channel on their downstream end. To distinguish them from each other, I identified areas that were wider than they were long, with no evidence of flowing water as backwaters. Springbrooks were longer than they were wide and showed evidence that water was moving downstream.

Individual Habitat Patterns

To assess how the areal abundance of each habitat type change through the course of a flood event, I created boxplots to display the dependent variable (the area of each habitat type) against the independent variable (discharge) for each of the treatment levels, the six discharges, in the three floodplain zones: main channel, parafluvial, and orthofluvial. Additionally, I removed the zone designations and repeated the same process for the floodplain as a whole. These plots demonstrated all populations were extremely positively skewed. No transformations were able to correct both the non-normality and heterogeneous variance and for this reason I used the Friedman test, a nonparametric equivalent to the repeated measures analysis of variance (Demsar, 2006). If the null hypothesis that there was no difference in the distributions of area values was rejected, I used the Nemenyi post-hoc test in the PMCMR R package (Pohlert, 2014), a nonparametric version of the Tukey test (Demsar, 2006). All plots, data transformations, and statistical tests were completed in R version 3.1.2. Because of the inherent variability of ecological systems, I accepted any p-value < 0.1 as significant.

Habitat Transitions

Specific shifts in floodplain habitat structure were studied by using graphical analysis similar to methods established in Kleindl et al., (2015). To examine the transitions made by habitat types through the course of a flood event, I assigned a single habitat type to each plot based on the dominant cover. I created transition tables to summarize the changes in habitat cover types between each sample date. These transitions tables were used to create alluvial graphs that could be visually examined to understand any patterns in habitat development through the course of the flood event. The tool used to create the alluvial graphs is currently in development in R (https://github.com/mbojan/alluvial). In the alluvial diagram, each black bar is a node that represents a date of data collection beginning April 8 and progressing through the flood pulse to September 5. The height of each bar in the node represents the number of plots dominated by that cover type. The transition tables between each date were combined into three summary tables, one for the main channel, one for the parafluvial zone, and one for the orthofluvial zone. The summary transition tables provide the exact number of plots changing from one habitat type to another through the study period as a whole. These tables were used to understand the most common transitions made by floodplain habitat cover types as the discharge increases from base flow to peak flow and decreases from peak flow to base flow.

Habitat Diversity

To analyze habitat diversity, I calculated alpha and beta diversity indices for each of the three floodplain zones (main channel, parafluvial zone, and orthofluvial zone) on all six dates. For these calculations each habitat type was considered a "species" and the number of pixels classified as each habitat represented the abundance, similar to methods established by Arscott et al. (2000). For the purpose of this study, the alpha diversity was considered the habitat diversity

of the entire floodplain and was quantified using the Shannon Diversity Index (H') applied to the sum total of all pixels classified as each habitat type on one sample date. I evaluated significant differences in the Shannon Diversity values by using a bootstrapping technique in the asbio package in R (Aho, 2015) to obtain the mean Shannon Index value and standard error for each of the three floodplain zones on every date (Arscott et al. 2002).

Beta diversity refers to the level of dissimilarity in habitat structure between two individual plots and was calculated using the vegan package in R (Oksanen, 2015). I used the beta diversity index proposed by Wilson and Shmida (1984), which combines the idea of species turnover by including the gain (g) and loss (l) of species and standardizes by average sample richness, $\bar{\alpha}$.

$$\beta_T = [g(H) + l(\mathrm{H})]/2\bar{\alpha}$$

This index is recommended over other beta diversity indices for use in ecological applications (Wilson and Schmida, 1984; Koleff et al. 2003). Beta diversity values range from 0 (complete similarity in habitat composition between plots) to 1 (complete dissimilarity in habitat composition between plots) (Amoros and Bornette, 2002). Because the beta diversity data was highly positively skewed, I used Kernel Density plots and the Kolmogorov-Smirnov Test to analyze significant differences ($p<0.1$) in the beta diversity distributions of the three floodplain zones on each of the seven dates. The Kernel Density Estimation (KDE) is a non-parametric way to estimate the probability density function of a continuous random variable, in this case beta diversity. The KDE plots were created in R using the ggplot2 package (Wickham, 2009).

Complexity

Theoretically, floodplain complexity would be lowest if the entire riverscape was composed of a single habitat cover type and would be greatest if each habitat cover type was equally represented. Therefore, species evenness is a good measure of complexity. Evenness refers to how similar in numbers of pixels each habitat "species" are, or how equal the abundance of habitats is numerically. It represents the variation in forms, functions, and linkages in floodplain habitats defined by complexity. I used the same method of habitats as "species" and the number of pixels as abundance to determine complexity of the three floodplain zones by calculating the evenness at each discharge. Evenness is determined as the observed level of diversity divided by the maximum diversity (i.e., equal distribution among habitat cover types and maximum complexity) for an observed species richness (McGarigal and Marks, 1994). It is reported as a proportion of maximum evenness, equaling one when habitats are represented equally and zero when a single cover type dominates the landscape (McGarigal and Marks, 1994; Concepcion, 2008).

IV. Results

Areal Abundance of Main Channel Zone Habitats

I observed significant changes throughout the study period in the areal abundance of three habitat cover types in the main channel zone: riffles, runs, and cobble. Despite having observed each during on at least one date, there were no significant changes in the amount of area classified as early stage vegetation, springbrooks, pools, shallow shorelines, backwaters, or wood within the main channel zone. Lastly, the amount of area classified as shadow in the main channel zone remained constant throughout the study period (Table 2).

Riffles and runs dominated the main channel at all discharges. The amount of area classified as riffle increased on the rising limb and decreased on the falling limb, becoming the largest habitat by far at peak flow (Table 2). The distribution of area values classified as riffle during peak flow was highly significantly different ($p < 0.01$) from all other dates. The intermediate discharges on April 8, May 8, May 21, and July 2 had an moderate amounts of area classified as riffle and did not differ significantly from each other, but did ($p < 0.1$) from all other dates. Lastly, September 5 had the least amount of area classified as riffle, both differing significantly ($p < 0.01$) from all other dates. The area classified as run remained constant at all discharges except for peak flow on May 27. On this date, the areal abundance of runs was significantly ($p < 0.01$) lower than all other dates (Table 2). There was no significant difference in the abundance of runs on any other date.

The amount of area classified as cobble followed a predictable pattern, with less area classified as this habitat cover during the elevated discharges on April 8, May 8, May 21, May 27, and July 2, with no significant differences among these dates (Table 2). The areal abundance of cobble was greatest in the main channel zone on September 5, base flow conditions after the flood pulse. The distributions of cobble area values for this date was significantly different ($p < 0.1$) from all other dates.

Areal Abundance of Parafluvial Zone Habitats

The parafluvial zone habitat cover types which experienced a significant change in their area during the flood pulse were cobble, main channel riffle, main channel run, main channel shallow shoreline, flood channel riffle, flood channel run, flood channel shallow shoreline, and overbank flow (Table 3). The parafluvial zone habitat cover types that did not change in their

Table 2. Summary table of multiple comparison tests using Friedman rank sums (alpha=0.1) between the amount of area classified as habitat cover types on the six dates in the main channel zone, with significantly different distributions represented by alphabetical letters.

	8-Apr	8-May	21-May	27-May	2-Jul	5-Sep
Backwater	A	A	A	A	A	A
	3.64E+05	3.24E+05	3.24E+05	3.24E+05	3.24E+05	3.27E+05
Cobble	B	B	B	B	B	A
	3.16E+05	3.07E+05	3.04E+05	3.07E+05	3.34E+05	4.17E+05
Herbaceous	A	A	A	A	A	A
	3.22E+05	3.39E+05	3.54E+05	3.27E+05	3.22E+05	3.22E+05
Pool	A	A	A	A	A	A
	3.67E+05	3.26E+05	3.25E+05	3.26E+05	3.20E+05	3.21E+05
Riffle	B	B	B	A	B	C
	2.63E+05	4.75E+05	2.40E+05	3.55E+05	4.13E+05	2.39E+05
Run	A	A	A	B	A	A
	4.10E+05	2.22E+05	4.56E+05	3.52E+05	2.38E+05	3.07E+05
Shadow	A	A	A	A	A	A
	3.01E+05	3.34E+05	3.35E+05	3.45E+05	3.19E+05	3.52E+05
Shallow Shoreline	A	A	A	A	A	A
	3.08E+05	3.28E+05	3.28E+05	3.23E+05	3.41E+05	3.57E+05
Springbrook	A	A	A	A	A	A
	3.30E+05	3.30E+05	3.30E+05	3.30E+05	3.30E+05	3.33E+05
Vegetation	A	A	A	A	A	A
	3.55E+05	3.16E+05	3.17E+05	3.20E+05	3.36E+05	3.41E+05
Wood	A	A	A	A	A	A
	3.34E+05	3.37E+05	3.31E+05	3.26E+05	3.30E+05	3.29E+05

abundance despite having been observed on at least one date throughout the study period were main channel and flood channel pools, backwaters, springbrooks, ponds, vegetation, and wood (Table 3). Like in the main channel zone, the amount of area classified as shadow remained constant (Table 3).

Because the boundaries of the three zones remained the same throughout the study period, the main channel expanded into the parafluvial zone during high flows. As a result, I observed several main channel habitats in the parafluvial zone. Main channel riffles observed in the parafluvial zone followed an anticipated pattern, steadily increasing in their abundance on the rising limb, becoming the most abundant habitat by far at peak flow (Table 3). At base flows on April 8 and September 5, this habitat cover type nearly disappeared from the parafluvial landscape. The largest area was observed during peak flow, the distribution of which was highly significantly different ($p<0.01$) from all other dates. I identified the second largest amount of main channel riffles in the parafluvial zone on the rising limb. The distributions of riffle area values during these flows differed significantly ($p<0.01$) from all other dates, but not from each other.

The largest amount of main channel run in the parafluvial zone was observed during the two rising limb discharges on May 8 and 21. The distributions of area values observed at these intermediate discharges of 300.16 m^3/s and 362.46 m^3/s significantly differed ($p<0.01$) from all other flows, including each other. Base flow conditions both before and after the flood (April 8 and September 5), peak flow (May 27), and falling limb (July 2) discharges were associated with less area classified as main channel run and their distributions did not significantly differ from each other (Table 3).

Table 3. Summary table of multiple comparison tests using Friedman rank sums (alpha=0.1) between the amount of area classified as habitat cover types on the six dates in the parafluvial zone, with significantly different distributions represented by alphabetical letters.

	8-Apr	8-May	21-May	27-May	2-Jul	5-Sep
Backwater	A 4.08E+06	A 4.01E+06	A 4.02E+06	A 4.02E+06	A 4.08E+06	A 4.02E+06
Cobble	B 4.99E+06	D 3.50E+06	E 3.10E+06	F 2.54E+06	C 4.57E+06	A 5.54E+06
FC Riffle	C 3.93E+06	AB 4.30E+06	C 3.98E+06	BC 4.05E+06	A 4.39E+06	D 3.59E+06
FC Run	B 4.13E+06	A 4.41E+06	B 4.07E+06	B 4.09E+06	B 4.01E+06	C 3.54E+06
FC Shallow Shoreline	B 4.62E+06	A 4.02E+06	B 4.33E+06	B 3.80E+06	B 3.85E+06	B 3.62E+06
Herbaceous	A 4.64E+06	B 4.02E+06	B 4.21E+06	C 3.70E+06	B 4.14E+06	C 3.54E+06
MC Pool	A 4.02E+06	A 4.07E+06	A 4.06E+06	A 4.08E+06	A 4.01E+06	A 4.01E+06
MC Riffle	D 3.16E+06	B 4.22E+06	B 4.53E+06	A 5.55E+06	C 3.58E+06	D 3.21E+06
MC Run	C 3.55E+06	B 4.51E+06	A 5.06E+06	C 3.81E+06	C 3.72E+06	C 3.59E+06
MC Shallow Shoreline	D 4.62E+06	B 4.02E+06	A 4.33E+06	BC 3.80E+06	BC 3.85E+06	C 3.62E+06
Overbank Flow	B 3.96E+06	B 4.02E+06	B 4.02E+06	A 4.31E+06	B 3.97E+06	B 3.96E+06
Pond	A 4.11E+06	A 4.06E+06	A 4.00E+06	A 4.00E+06	A 4.04E+06	A 4.02E+06
Shadow	A 3.78E+06	A 3.98E+06	A 4.29E+06	A 3.67E+06	A 4.12E+06	A 4.38E+06
Springbrook	A 4.10E+06	A 4.08E+06	A 3.97E+06	A 3.91E+06	A 4.08E+06	A 4.10E+06
Vegetation	A 3.93E+06	A 3.37E+06	A 3.33E+06	A 3.90E+06	A 5.01E+06	A 4.71E+06
Wood	A 4.10E+06	A 4.07E+06	A 4.05E+06	A 4.03E+06	A 4.05E+06	A 3.93E+06

Note: Paired letters indicate a distribution of area values that fell between two distributions that differed significantly

The greatest amount of area classified as main channel shallow shoreline in the parafluvial zone was observed at a flow of 362.46 m^3/s on May 21 (Table 3). The distribution of shallow shoreline area values for this intermediate discharge on the rising limb was significantly different (p<0.1) from all dates. I observed the second largest area classified as main channel shallow shoreline in the parafluvial zone during base flow conditions prior to the flood, the distribution of which was significantly different (p<0.1) from all other dates. Intermediate discharges on May 8 and July 2 and peak flow conditions on May 27 were associated with the next largest amount of area classified as shallow shore, differing significantly (p<0.01) from all other dates. I observed the least amount of shallow shore during base flow on September 5, when this habitat cover type disappeared from the parafluvial zone (Table 3).

The amount of cobble area in the parafluvial zone followed a predictable pattern (Table 3). The largest amounts of cobble area were observed during base flow conditions on April 8 and September 5. The area classified as cobble decreased on the rising limb and increased on the falling limb. All distributions of cobble area values were significantly different (p<0.05) (Table 3).

Flood channel riffles were the most common habitat type found in parafluvial secondary channels at all flows. The largest area classified as flood channel riffles was associated with an intermediate discharge of 169.33 m^3/s on the falling limb on July 2, which had a distribution of area values that differed significantly (p<0.1) from every date except a moderate discharge of 300.16 m^3/s on the rising limb of the hydrograph. This discharge, observed on May 8, was linked to the next largest amount of area classified as flood channel riffle and was significantly different (p<0.01) from the other discharges except for peak flow on May 27. The distributions of area values on May 27 were the third largest, but its distribution did not differ significantly

from lower flows observed on April 8 or May 21. These discharges had similar distributions that did not differ significantly from each other. September 5 had the least amount of area classified as flood channel riffle, the distribution of which differed significantly ($p<0.1$) from all other dates (Table 3).

Unlike in the main channel, runs in parafluvial flood channels were always less abundant than riffles. I observed the largest flood channel run areas during the rising limb at a flow of 300.16 m^3/s on May 8, the distribution of which differed significantly ($p<0.1$) from all other flows. Intermediate discharges of 90.05 m^3/s (April 8), 169.33 m^3/s (July 2), and 362.46 m^3/s (May 21), as well as peak flow 484.23 m^3/s (May 27) demonstrated similar distributions of flood channel run area values, which did not differ from each other, but did differ significantly ($p<0.1$) from all other discharges. I observed the least amount of flood channel run area during base flow conditions on September 5, which differed significantly ($p<0.01$) (Table 3).

Flood channel shallow shorelines were most abundant in the parafluvial zone on May 8 during the rising limb discharge of 300.16 m^3/s (Table 3). The distribution of area values during this flow differed significantly ($p<0.01$) from all other dates. The amount of area classified as flood channel shallow shoreline was less for all other discharges, the distributions of which did not differ from each other (Table 3).

I observed the largest amount of area classified as overbank flow during the three largest discharges: 300.16 m^3/s, 362.46 m^3/s, and 484.23 m^3/s. These flows differed significantly ($p<0.05$) from those that were observed on the three other dates, but not from each other (Table 3).

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The habitat cover types that changed significantly through the course of the flood event in the orthofluvial zone were cobble, flood channel riffles, flood channel runs, wood, and overbank flow. Despite having identified these habitats within the orthofluvial zone during at least one flow, I observed no significant changes in the areal abundance of cottonwoods, conifers, backwaters, springbrooks, main channel and flood channel shallow shorelines, flood channel pools, or ponds (Table 4).

Similar to the main channel and parafluvial zones, the orthofluvial zone had the largest area classified as cobble during base flow and the least during high flows (Table 4). The distributions of area values for the three largest flows on May 8, 21, and 27 (300.16 m^3/s, 362.46 m^3/s, and 484.23 m^3/s respecitively) were significantly different from all other dates with the least amount of cobble. Both base flows, 90.05 m^3/s on April 8 and 45.59 m^3/s on September 5, were associated with the most cobble and were significantly different from all the other dates. The moderate flow of 169.33 m^3/s on July 2 had an intermediate amount of cobble causing it not to differ from any other discharge.

The two dominant aquatic habitats found in the orthofluvial zone were flood channel riffles and flood channel runs. Both of these habitat cover types increased in their abundance as the discharge increased and decreased in their abundance as the discharge decreased. Flood channel riffles were most abundant during the highest discharges on May 8, May 21, and May 27. Flows of 90.05 m^3/s on April 8 and 169.33 m^3/s on July 2 were associated with an intermediate amount of flood channel riffles and I observed the least amount of flood channel riffles during the lowest flows on September 5. The flows with the largest amount of flood

Table 4. Summary table of multiple comparison tests with Friedman rank sums (alpha=0.1) between the amount of area classified as habitat cover types on the six dates in the orthofluvial zone.

	8-Apr	8-May	21-May	27-May	2-Jul	5-Sep
Backwater	A	A	A	A	A	A
	4.33E+05	4.33E+05	4.33E+05	4.33E+05	4.33E+05	4.36E+05
Cobble	B	D	E	F	C	A
	4.75E+05	3.89E+05	3.88E+05	3.84E+05	4.32E+05	5.08E+05
Conifer	A	A	A	A	A	A
	4.36E+05	4.34E+05	4.34E+05	4.35E+05	4.34E+05	4.33E+05
Cottonwood	D	C	BC	B	A	CD
	4.04E+05	4.26E+05	4.33E+05	4.46E+05	4.72E+05	4.18E+05
FC Pool	A	A	A	A	A	A
	4.33E+05	4.35E+05	4.35E+05	4.33E+05	4.33E+05	4.33E+05
FC Riffle	BC	AB	AB	A	BC	C
	4.35E+05	4.67E+05	4.56E+05	4.68E+05	4.26E+05	3.94E+05
FC Run	A	A	A	A	AB	B
	4.47E+05	4.61E+05	4.63E+05	4.59E+05	4.23E+05	3.87E+05
FC Shallow Shoreline	A	A	A	A	A	A
	4.22E+05	4.36E+05	4.61E+05	4.44E+05	4.42E+05	4.16E+05
Herbaceous	A	B	D	C	C	B
	5.47E+05	4.75E+05	3.47E+05	3.88E+05	4.14E+05	4.81E+05
MC Riffle	A	A	A	A	A	A
	4.27E+05	4.34E+05	4.33E+05	4.48E+05	4.41E+05	4.28E+05
MC Run	A	A	A	A	A	A
	4.29E+05	4.38E+05	4.35E+05	4.36E+05	4.41E+05	4.31E+05
MC Shallow Shoreline	A	A	A	A	A	A
	4.29E+05	4.31E+05	4.37E+05	4.31E+05	4.36E+05	4.31E+05
Overbank Flow	B	B	BC	A	B	B
	4.05E+05	4.27E+05	4.49E+05	5.32E+05	4.15E+05	4.05E+05
Pond	A	A	A	A	A	A
	4.30E+05	4.45E+05	4.36E+05	4.35E+05	4.44E+05	4.24E+05
Residential	A	A	A	A	A	A
	4.35E+05	4.36E+05	4.36E+05	4.34E+05	4.27E+05	4.37E+05
Shadow	B	B	A	B	B	B
	3.56E+05	3.93E+05	5.23E+05	3.78E+05	3.89E+05	4.46E+05
Springbrook	A	A	A	A	A	A
	4.20E+05	4.38E+05	4.47E+05	4.48E+05	4.31E+05	4.31E+05
Willow	A	A	A	A	A	A
	4.25E+05	4.29E+05	4.35E+05	4.28E+05	4.43E+05	4.39E+05
Wood	A	D	BC	C	C	AB
	4.97E+05	3.14E+05	4.38E+05	4.23E+05	4.20E+05	4.68E+05

 Note: Paired letters indicate a distribution of area values that fell between two distributions that differed significantly.

channel riffles differed significantly (p<0.1) from the discharges with the least amount of riffle, but the distributions of area values for the intermediate flows on April 8 and July 2 did not differ significantly from those associated with the higher or lower flows (Table 4).

Like runs in the main channel, orthofluvial flood channel runs remained fairly constant, with no significant differences observed in the distributions of area values for flows observed on

April 8, May 8, May 21, May 27, or July 2 (Q=90.05 m^3/s, 300.16 m^3/s, 362.46 m^3/s, or 484.23 m^3/s, 169.33 m^3/s respectively). These flows did not differ significantly from each other, but did differ (p<0.1) from base flow conditions on September 5 (45.59 m^3/s), when less orthofluvial flood channels were present (Table 4).

The largest amount of area classified as wood in the orthofluvial zone was observed during base flow conditions both prior to and following the flood pulse (90.05 m^3/s and 45.59 m^3/s). The distributions of area values for these two flows differed significantly (p<0.05) from all other discharges. I identified less wood during elevated discharges of 169.33 m^3/s, 362.46 m^3/s, and 484.23 m^3/s, the distributions of which differed significantly (p<0.01) from all other flows. Finally, the least amount of wood in the orthofluvial zone was observed on May 8 during a discharge of 300.16 m^3/s, which had a distribution of area that was significantly different (p<0.01) from all other dates (Table 4).

The amount of area classified as overbank flow was greatest during peak flow on May 27, which was the only date that differed significantly (p<0.01) from other dates (Table 4). There was no significant difference in the amount of area classified as overbank flow between all other discharges.

Whole Floodplain

When the zone designations were removed and the analysis run for the floodplain as a whole, I observed significant changes in the amount of area at different flows of the following habitat cover types: main channel riffles, main channel runs, main channel shallow shorelines, cobble, herbaceous, flood channel riffles, flood channel runs, flood channel shallow shorelines, overbank flow, and early successional stage vegetation (Table 5). In the floodplain as a whole, there were no changes in the areal abundance of wood, main channel or flood channel pools, backwaters, residential, pond, springbrooks, willows, cottonwoods, or conifers (Table 5).

Even without the zone boundaries, main channel riffles continued to follow the same pattern, increasing in abundance as discharges grew larger (Table 5). Main channel runs however, no longer remained constant. This habitat cover type was most abundant on May 21, followed by May 8, and then July 2, all intermediate discharges. Main Channel runs were least abundant during base flow conditions prior to and after the flood pulse and during peak flow conditions. Main channel shallow shorelines in the floodplain as a whole were most abundant during base flow conditions prior to the flood on April 8, followed by May 21 and May 8, with the least amount of area observed during peak flow conditions, discharges on the falling limb, and base flow conditions after the flood pulse (Table 5).

Flood channel habitats like riffles, runs, and shallow shorelines tended to be most abundant during intermediate discharges (Table 5). I observed the largest amount of area classified as flood channel riffle in the floodplain as a whole on May 8 and July 2 and the least amount during base flow on September 5. Flood channel runs were largest on May 8, followed by May 21 and May 27, and least abundant on September 5. Shallow shorelines in secondary channels peaked in their areal abundance on May 8, trailed by May 21. Predictably, overbank

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Table 5. Summary table of multiple comparison tests using Friedman rank sums (alpha=0.1) between the amount of area classified as habitat cover types on the six dates for the floodplain as a whole.

	8-Apr	8-May	21-May	27-May	2-Jul	5-Sep
Wood	A	A	A	A	A	A
	1.05E+07	9.80E+06	1.03E+07	1.02E+07	1.03E+07	1.02E+07
MC Riffle	D	B	B	A	C	D
	8.68E+06	1.06E+07	1.10E+07	1.30E+07	9.55E+06	8.50E+06
MC Run	CD	B	A	CD	C	D
	9.45E+06	1.13E+07	1.20E+07	9.66E+06	9.80E+06	9.05E+06
MC Pool	A	A	A	A	A	A
	1.02E+07	1.03E+07	1.03E+07	1.03E+07	1.02E+07	1.01E+07
MC Shallow Shoreline	A	BC	B	C	C	C
	1.12E+07	1.01E+07	1.06E+07	9.73E+06	9.94E+06	9.64E+06
Backwater	A	A	A	A	A	A
	1.03E+07	1.02E+07	1.02E+07	1.02E+07	1.03E+07	1.02E+07
Cobble	B	D	E	F	C	A
	1.18E+07	9.00E+06	8.39E+06	7.49E+06	1.12E+07	1.33E+07
Shadow	CD	B	A	C	B	A
	9.71E+06	1.01E+07	1.07E+07	9.75E+06	1.03E+07	1.08E+07
Residential	A	A	A	A	A	A
	1.02E+07	1.02E+07	1.02E+07	1.02E+07	1.02E+07	1.02E+07
Pond	A	A	A	A	A	A
	1.03E+07	1.03E+07	1.01E+07	1.01E+07	1.03E+07	1.01E+07
Springbrook	A	A	A	A	A	A
	1.02E+07	1.03E+07	1.01E+07	1.01E+07	1.03E+07	1.03E+07
Herbaceous	A	B	B	C	B	C
	1.11E+07	1.03E+07	1.05E+07	9.45E+06	1.03E+07	9.60E+06
FC Riffle	B	A	B	AB	A	C
	1.00E+07	1.07E+07	1.02E+07	1.03E+07	1.07E+07	9.27E+06
FC Run	B	A	AB	AB	B	C
	1.04E+07	1.09E+07	1.04E+07	1.04E+07	1.01E+07	9.19E+06
FC Pool	A	A	A	A	A	A
	1.02E+07	1.02E+07	1.02E+07	1.02E+07	1.02E+07	1.02E+07
FC Shallow Shoreline	B	A	AB	B	B	B
	9.93E+06	1.08E+07	1.03E+07	1.01E+07	1.02E+07	9.90E+06
Overbank Flow	B	B	B	A	B	B
	9.93E+06	1.01E+07	1.02E+07	1.11E+07	1.00E+07	9.93E+06
Willow	A	A	A	A	A	A
	1.02E+07	1.02E+07	1.02E+07	1.02E+07	1.02E+07	1.02E+07
Cottonwood	A	A	A	A	A	A
	1.02E+07	1.02E+07	1.02E+07	1.02E+07	1.03E+07	1.02E+07
Conifer	A	A	A	A	A	A
	1.02E+07	1.02E+07	1.02E+07	1.02E+07	1.02E+07	1.02E+07
Early Stage Vegetation	B	C	C	B	A	A
	9.97E+06	9.07E+06	8.99E+06	1.01E+07	1.19E+07	1.13E+07

Note: Paired letters indicate a distribution of area values that fell between two distributions that differed significantly.

flow was largest during peak flow conditions on May 27, which was the only date to significantly differ from the others for the floodplain as a whole (Table 5).

The only vegetative covers that displayed significantly different areas for the floodplain as a whole were the herbaceous and early successional stage vegetation (Table 5). The herbaceous cover type was most abundant on April 8, followed by May 8, May 21, and July 2. High flows on May 27 and increased error from shadows on September 5 decreased the abundance of the herbaceous cover type in the floodplain as a whole. Early stage vegetation was most abundant on July 2 and September 5 as it became established on the post-flood geomorphic template (Table 5).

The amount of error contributed by shadow varied by date, with the most observed on May 21 and September 5. May 8 and July 2 had the next largest amount of shadow, followed by April 8 and May 27 (Table 5).

Habitat Transition Patterns

I observed 1655 total plot transitions in the main channel zone throughout the study period (Table 6). Riffles and runs dominated this zone at all discharges (Figure 6), with the majority of transitions involving these habitat covers. Overwhelmingly, in the main channel zone riffles remained riffles, with 27% of all transitions falling into this group. Additionally runs most commonly remained runs, a pattern followed by 20% of all plots through the study period. The main source of turnover in habitat was riffle becoming run (13%) or run becoming riffle (17%) (Table 6). I did, however, observe transition patterns in other habitat cover types within the main channel zone. Shallow shorelines most commonly transitioned to riffles, with 33% of plots dominated by shallow shorelines becoming riffle (Table 6). Fifty percent of the pool plots

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became runs, making it the most likely transition for pools (Table 6). Riffles and runs were the most common source of pools, with 74% of pool plots coming from these two habitats (Table 6). The most common transition for wood dominated plots was to become riffle, with 40% of wood dominated plots making this transition. Conversions of wood plots to aquatic habitats on the rising limb were expected as the water level increased, however I also observed transitions from aquatic habitats to wood on the rising limb (Figure 6), suggesting an import of wood into the system. Riffles were the largest source of wood, with 30% of the plots that transitioned to wood coming from riffles.

Because the main channel shifted in its location, but the boundaries of the main channel zone did not, I observed the appearance of habitats on the falling limb that are generally considered parafluvial cover types. For example, I identified plots dominated by springbrooks, cobbles, and vegetation as the main channel receded into its newly formed channel (Figure 6). One riffle plot and one cobble plot transitioned to springbrook during base flow conditions after the flood pulse (Figure 6). Overwhelmingly, the largest source of cobble were riffles, with 62% of cobble plots transitioning from riffles and 17% coming from runs. Cobble was abundant in the main channel zone on September 5, becoming the third largest habitat cover type after riffles and runs (Figure 6). Furthermore, I observed early successional stage vegetation in the main channel zone (Figure 6), which came from both aquatic habitats (82%) as well as cobble (12%). Lastly, shadows were a source of error that interfered with identifying some habitats. In the main channel zone, 3% of riffle plots and 4% of run plots were affected by shadow at some point through the study period (Table 6). Some plots remained shadow, with 34% of plots coming from those already dominated by shadow.

Table 6. Summary table of all plot transitions that occurred in the main channel zone throughout the study period.

| | | | | | Transition To: | | | | | |
Cover Type	Cobble	Pool	Riffle	Run	Shadow	Shallow Shore	Springbrook	Vegetation	Wood	Total
Backwater	-	-	1	-	-	-	-	-	-	1
Cobble	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
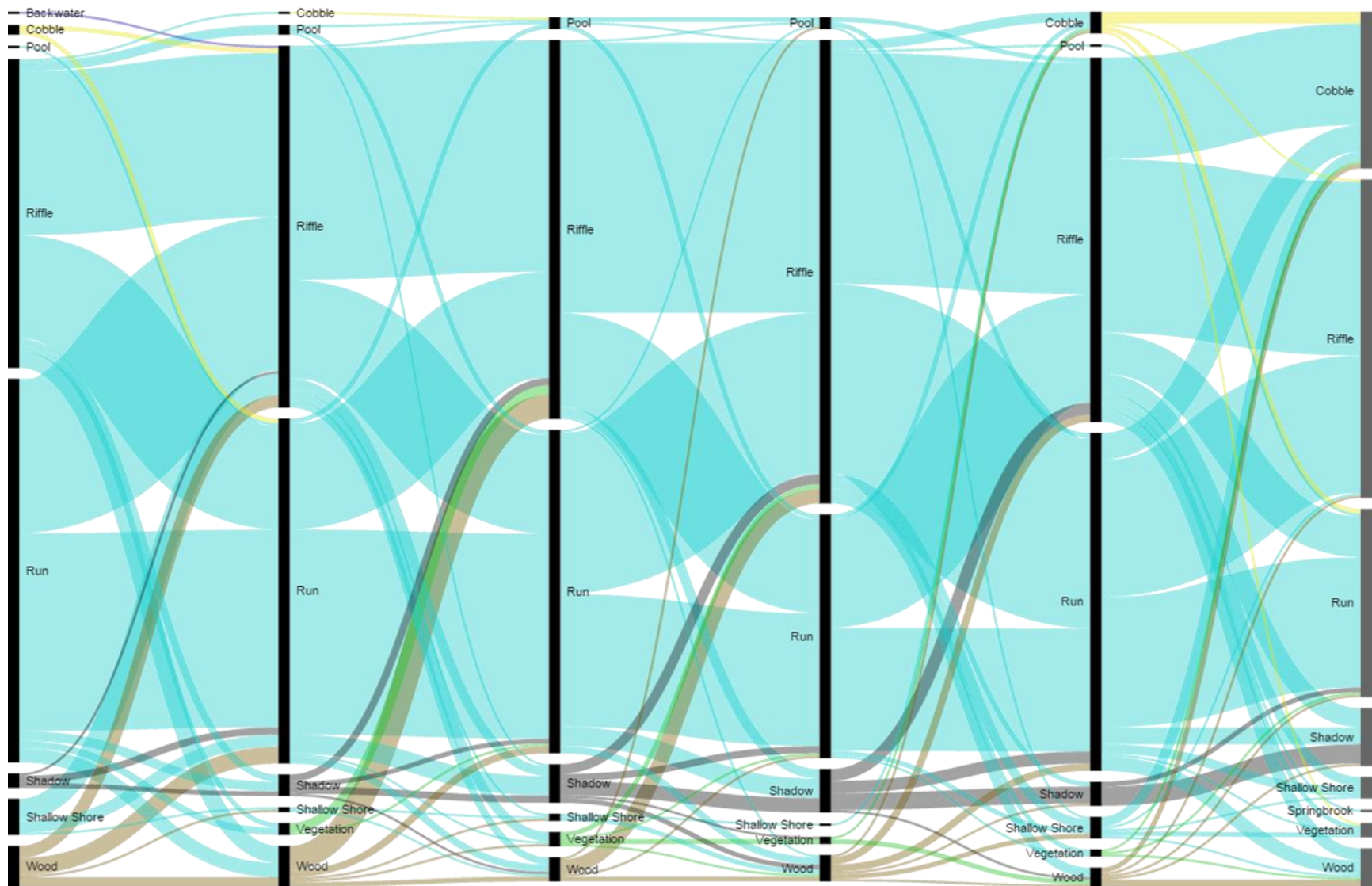
Transition From:

Figure 6. Alluvial diagram showing the transitions made by habitat cover types in the main channel zone of the Clark Fork reach through the course of the 2014 flood event.

In the parafluvial zone, I observed 5800 total plot transitions throughout the study period from April 8 to September 5 (Table 7). Overall, there were more habitat cover types and less domination by a single habitat in the parafluvial zone, particularly at intermediate discharges (Figure 7). Again, because the boundaries of the parafluvial zone remained constant, both main channel and off channel habitat cover types were observed in this zone. At the beginning of the study period the parafluvial zone was mostly cobble. The dominant habitat type then became flood channel riffles on May 8, then main channel runs on May 21. On May 27 an extremely large number of plots transitioned to main channel riffle. During the falling limb, the parafluvial zone returned to being mostly cobble and vegetation (Figure 7).

I observed clear patterns for main channel habitats observed in the parafluvial zone. Twenty-six percent of plots dominated by main channel riffle transitioned to cobble throughout the study period, making it the most likely shift for this habitat cover type (Table 7). Main channel riffles also frequently did not transition (21%) or became flood channel riffles (13%) (Table 7). During peak flow conditions, main channel riffles became the most dominant habitat cover type by far in the parafluvial zone (Figure 7). Runs from the main channel most often became main channel riffles, with 45% of plots following this pattern (Table 7). Main channel runs had a large presence in the parafluvial zone, particularly on the rising limb of the hydrograph. It was the most dominant habitat on May 21 (Figure 7). The largest source for main channel shallow shorelines was cobble, with 34% coming from this habitat cover (Table 7). These transitions generally occurred on the rising limb, while 21% of shallow shorelines originated from main channel riffles on the falling limb (Table 7 & Figure 7).

In addition to main channel aquatic habitats, I also observed patterns in the transitions of off-channel aquatic habitats in the parafluvial zone such as backwaters, springbrooks, and flood

Table 7. Summary table of all plot transitions that occurred in the parafluvial zone throughout the study period. FC = flood channel; MC = main channel

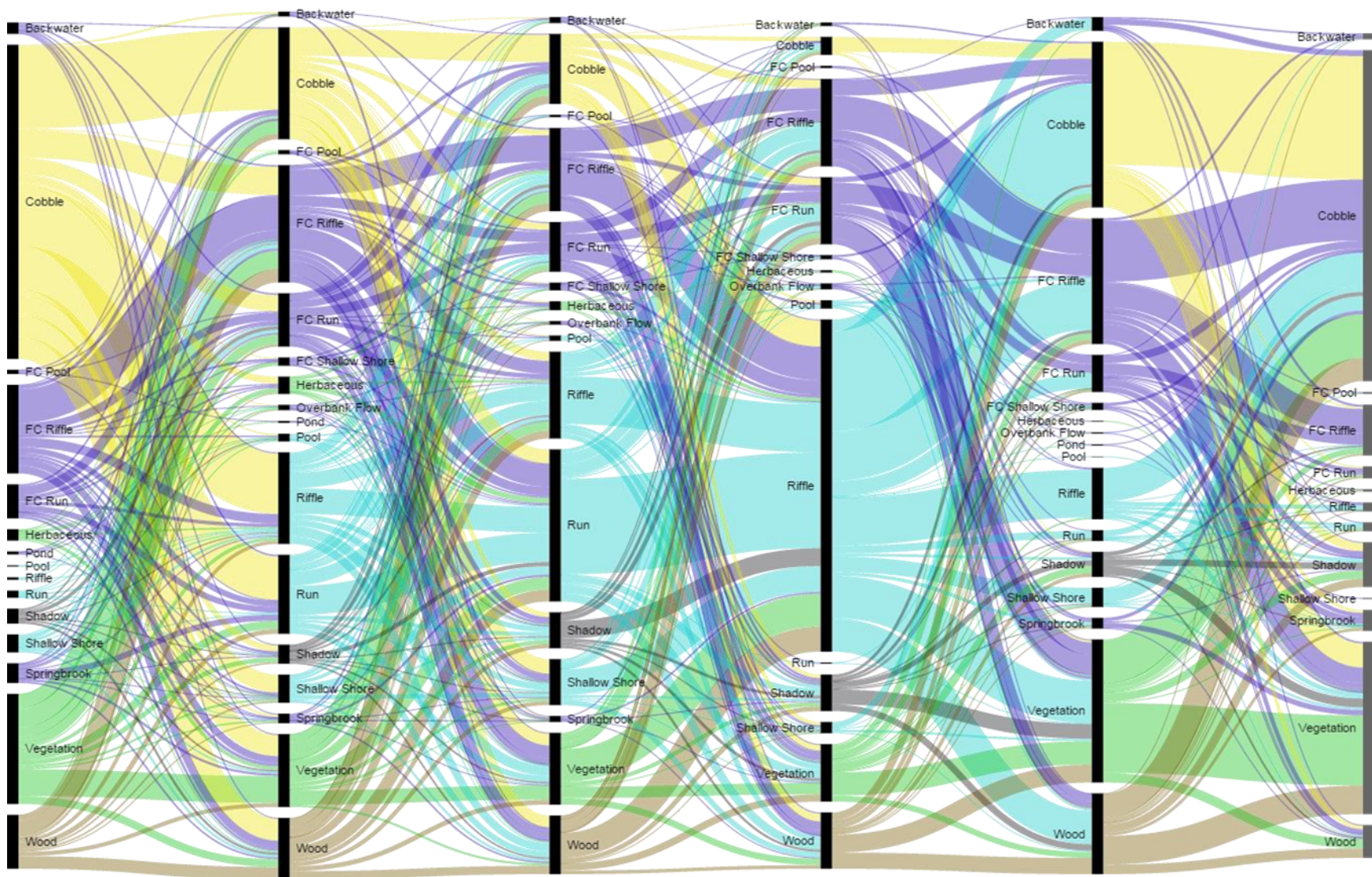|		Transition To:																
Transition From:		Backwater	Cobble	FC Pool	FC Riffle	FC Run	FC Shallow Shore	Herbaceous	MC Pool	MC Riffle	MC Run	MC Shallow Shore	Overbank Flow	Pond	Shadow	Springbrook	Vegetation	Wood	Total
	Backwater	3	16	-	11	7	-	-	-	4	4	-	2	-	2	3	9	5	66
	Cobble	7	420	2	74	53	4	14	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

Figure 7. Alluvial diagram showing the habitat cover transitions throughout the study period in the parafluvial zone. Main channel habitat cover types are represented by light blue. Off channel aquatic habitats are represented by dark blue.

channels. Thirty-nine percent of backwaters came from main channel riffles, by far the largest source of these standing waters. Backwaters then most commonly transitioned to cobble, with 24% of backwater dominated plots following this pattern (Table 7). Springbrooks most commonly came from flood channel habitats, which accounted for 39% of transitions to springbrook plots. Forty-six percent of springbrook dominated plots then transitioned to vegetation, which may represent legitimate transitions or may be a result of the growth of vegetation throughout the study period (Table 7). Overall, transitions to backwaters and springbrooks each only accounted for 1% of total plot transitions, indicating the small number of plots dominated by these habitat cover types (Table 7 & Figure 7).

Flood channel habitats, including riffles, runs, pools, and shallow shorelines, were the more prominent off-channel habitats in the parafluvial zone, accounting for 21% of all transitions (Table 7). Flood channel riffles most commonly experienced no transition, with 30% of this habitat cover type not changing throughout the study period. After secondary channel riffles, main channel riffles were the largest source, accounting for 15% of transitions to flood channel riffles (Table 7). The second most common transition for flood channel riffles, after remaining the same, was to cobble, with 17% of plots dominated by secondary channel riffles making this change (Table 7). Flood channel riffles were a common habitat in the parafluvial zone, becoming the most dominant aquatic cover type on April 8, May 8, July 2, and September 5 (Figure 7). The two dates on which secondary channel riffles were not the most dominant were May 21 and May 27, those with the largest discharges when the main channel expanded into the parafluvial zone (Figure 7). Unlike runs in the main channel, flood channel runs were always less abundant than flood channel riffles. Seventeen percent of flood channel runs came from flood channel riffles, the largest source for secondary channel runs (Table 7). Additionally, flood

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channel runs frequently transitioned flood channel riffles, with 24% of the transitions made by plots dominated by runs in secondary channels following this pattern (Table 7). Pools and shallow shorelines in secondary channels made up a very small proportion of the parafluvial zone, accounting for 0.3% and 1% of all plot transitions, respectively (Table 7 & Figure 7). There did not appear to be any apparent pattern in the source of flood channel pools, but they appear to commonly transition to flood channel runs with 42% of plots dominated by secondary channel pools following this form (Table 7). Secondary shallow shorelines frequently came from flood channel riffles and runs (48%) and most commonly transitioned to cobble (22%) (Table 7).

Like flood channel pools and shallow shorelines, ponds and overbank flow made up a small proportion of plot transitions in the parafluvial zone (Table 7). Transitions to ponds were the least likely pattern, with only 0.1% of all plots making this conversion (Figure 7). With this very small number of plots, there does not appear to be any distinct pattern in cover types that act as a source for ponds; nor is there any common habitat that ponds transition to. Overbank flow accounted for only 0.4% of all plot transitions through the study period in the parafluvial zone (Table 7 & Figure 7). The largest sources of overbank flow was vegetation (19%), which was also the cover type that this habitat transitioned to (30%) (Table 7).

In the orthofluvial zone, I observed 1760 total plot transitions through the study period (Table 8). Overwhelmingly, the orthofluvial zone was dominated by the herbaceous cover type, which generally doesn't transition to any other habitat cover (Figure 8). Forty-nine percent of all the plot transitions that occurred in the orthofluvial zone are accounted for by herbaceous plots remaining herbaceous (Table 8). After remaining the same, herbaceous dominated plots are most likely to transition to plots dominated by shadow (14%), a result of the leaf out and growth of vegetation throughout the study period (Table 8 & Figure 8). The mature vegetation of the

orthofluvial zone, including cottonwoods, willows, and conifers, also underwent few transitions to different cover types. Most plots dominated by cottonwood remained so, with 41% of these plots not undergoing any transition. Cottonwoods were then most likely to transition to shadow (34%) and herbaceous (22%) (Table 8). Similarly, willow plots generally did not change, with 56% remaining the same. These plots also transitioned to being dominated by shadow (18%) and herbaceous (26%) (Table 8). Finally, conifer dominated plots made up a small number of the total plots (0.2%) and these plots generally did not transition (57%) (Table 8).

Aquatic habitats in the orthofluvial zone were a small proportion of the landscape, only representing 7% of all plot transitions, particularly compared to the herbaceous cover type (Table 8). Flood channel riffles and runs were the most dominant aquatic habitat in this zone (Figure 8). These habitats generally did not transition, with 32% of secondary channel run plots and 38% of secondary channel riffles remaining the same throughout the study period (Table 8). If these habitats did transition, it was most commonly to each other. Twenty-four percent of plots dominated by flood channel riffles transitioned to flood channel runs and 18% of flood channel runs plots transitioned to flood channel riffles (Table 8).

Springbrooks, ponds, and overbank flow made up the rest of the aquatic habitats observed in the orthofluvial zone. Plots dominated by springbrooks commonly transitioned from the herbaceous cover type (33%) or remained springbrooks (29%) (Table 8). Additionally, springbrooks commonly transitioned to the herbaceous cover type, with 33% of springbrook dominated plots following this pattern (Table 8). A single orthofluvial plot was dominated by a pond and this plot did not undergo any transitions throughout the study period (Table 8 & Figure 8). Lastly, the largest source of overbank flow in the orthofluvial zone was the herbaceous cover

Table 8. Summary table of all plot transitions that occurred in the orthofluvial zone throughout the study period. FC = flood channel; MC = main channel

| Transition From:	Cobble	Conifer	Cottonwood	FC Riffle	FC Run	Herbaceous	Overbank Flow	Pond	Residential	MC Run	Shadow	Springbrook	Willow	Wood	Total
Cobble	-	-	-	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
MC 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
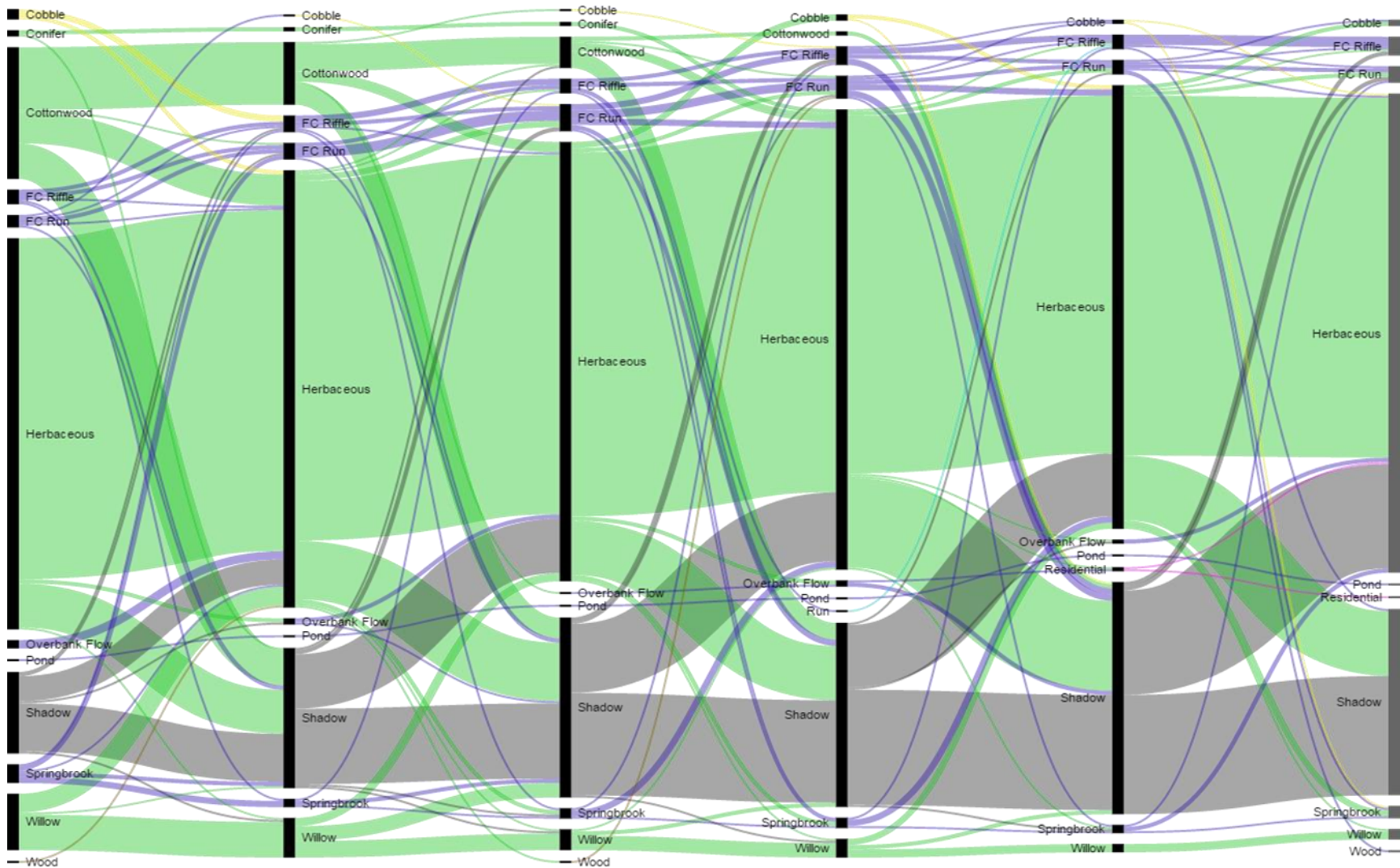
Figure 8. Alluvial diagram showing habitat cover transitions through the study period in the orthofluvial zone. Off channel habitats are represented by dark blue, vegetative habitats are represented by green, cobble is represented by yellow, wood is represented by brown, and shadow is represented by grey.

type, which accounted for 56% of transitions to overbank flow throughout the study period (Table 8). As the water receded on the falling limb of the hydrograph, plots that had become dominated by overbank flow during high discharge returned to the herbaceous cover type, with 62% of overbank flow plots following this pattern (Table 8 and Figure 8).

Habitat Diversity

To address the influence of discharge on habitat diversity, I calculated Shannon's diversity index for each zone and every date. Each habitat type was designated in the model as a species and the number of pixels classified as that habitat type was designated as the species abundance. The main channel had a lower species richness than the other two zones, with 11 habitat species identified in the main channel zone and 17 habitat species in the parafluvial and orthofluvial zones (Figure 9). Because I used a sum total of all the plots, the results represent the alpha diversity of the floodplain on a given date. The parafluvial zone generally had the largest habitat diversity of the three zones (Average H'=1.90) with peaks in diversity during intermediate discharges: 169.33 m^3/s (H'=2.04), 300.16 m^3/s (H'=2.25), and 362.46 m^3/s (H'=2.23) (Figure 9). The orthofluvial zone was less diverse than the parafluvial zone, but more diverse than the main channel (Average H'=1.63), with a peak in habitat diversity (H'=1.81) occurring during peak flow conditions of 484.23 m^3/s (Figure 9). The main channel had the lowest level of habitat diversity of the three floodplain zones (Average H'=1.19). Shannon diversity was greatest during base flows both prior to (H'=1.21) and after the flood pulse (H'=1.28). The main channel experienced the lowest Shannon diversity during peak flow (H'=1.01) (Figure 9). Despite the appearance of these patterns, I observed no significant differences in alpha diversity between dates for any of the zones (main channel (p=0.99), parafluvial zone (p=0.17), or the orthofluvial zone (p=0.99)).
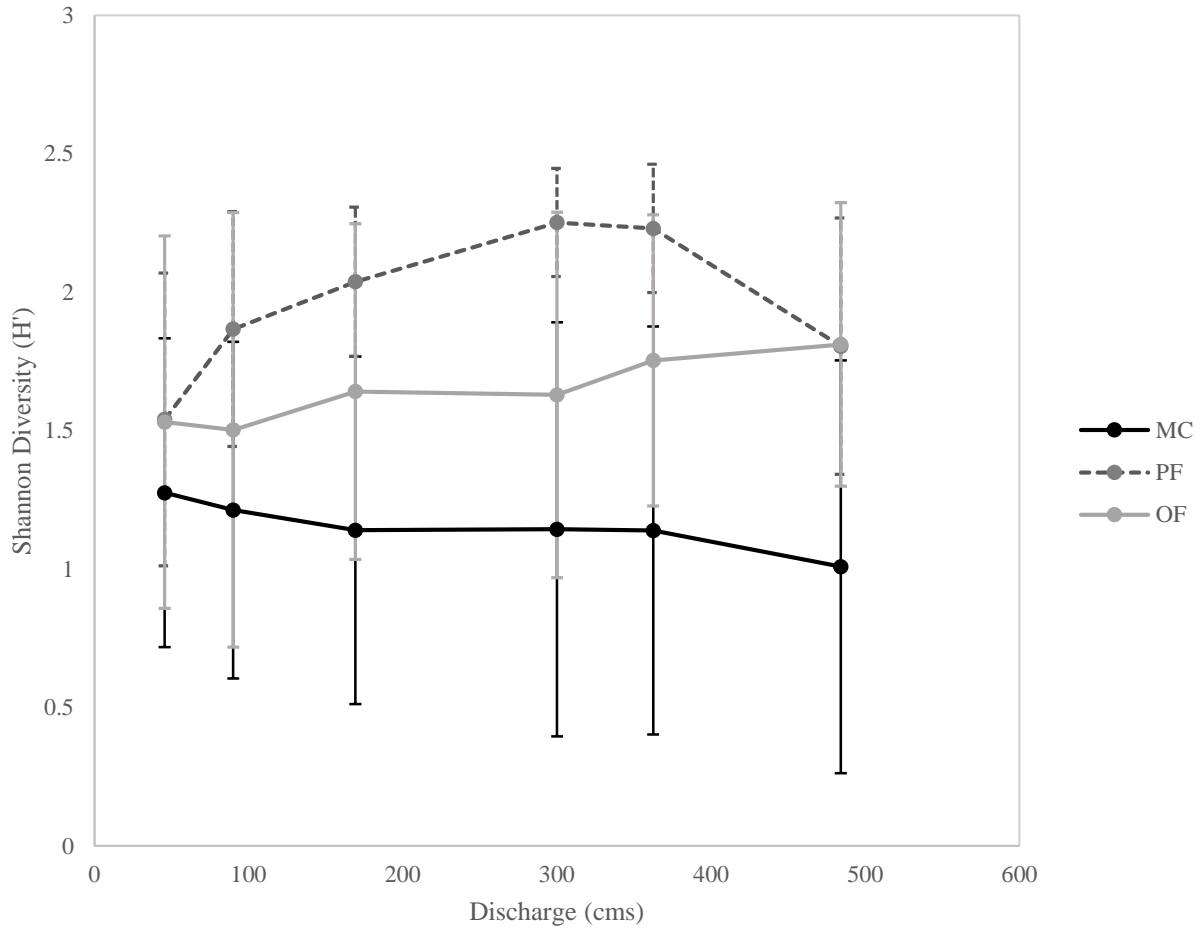
Figure 9. Shannon alpha diversity of habitat in the main channel (MC), parafluvial (PF), and orthofluvial (OF) zones at the six discharges (cubic meters per second) on the sample dates of the study. Error bars display 90% confidence intervals around the bootstrapped mean diversity value for each zone at each discharge.

I followed the same method of designating habitats as species and their pixel counts as abundance in the model to address changes in beta diversity, a measure of the dissimilarity in habitat structure between two plots. The results are presented in non-parametric Kernel Density Plots because of extremely skewed populations. Generally, beta diversity was lowest in the main channel, intermediate in the orthofluvial zone, and greatest in the parafluvial zone. On most dates there was an elevated probability of there being no difference between plots (beta=0) and

thereby a low beta diversity in the main channel (Figure 10a). This was especially true during periods of intermediate discharge ($300.16 m^3/s$ and $362.46\ m^3/s$) on the rising limb of the flood pulse. Peak flow conditions ($484.23\ m^3/s$) show an elevated frequency of beta values of approximately 0.3. Base flow conditions after the flood pulse ($45.59\ m^3/s$) was associated with the greatest probability of two plots having entirely different compositions in the main channel (Figure 10a). The distributions of beta diversity in the main channel were all significantly different ($p<0.01$) from each other.

The beta diversity in the parafluvial zone was generally greater than the main channel for all dates, with an increased likelihood that the composition of two plots was entirely different (beta=1) (Figure 10b). This probability was greatest during intermediate discharges on the rising limb ($300.16 m^3/s$ and $362.46\ m^3/s$). These were the same flows associated with the highest probability of the lowest beta diversity in the main channel, meaning as the main channel plots become more similar in their composition, parafluvial plots become increasingly dissimilar. The lowest parafluvial beta diversity was observed at a flow of $45.59\ m^3/s$, a discharge when the water had receded into the main channel and most parafluvial plots had some cobble cover present (Figure 10b). The beta diversity distributions for each flow differ significantly ($p<0.01$) from all other discharges.

In the orthofluvial zone, all dates followed a similar distribution pattern with a high probability of beta diversity values ~ 0.5 (Figure 10c). This value indicates that two plots are likely to have some habitat composition in common, but it was rare to find plots that are entirely different or entirely similar. There was a slightly increased probability of a beta diversity value equal to one during peak flow conditions and a slightly increased likelihood of a beta diversity value equal to zero during the lowest discharges (Figure 10c). Like the main channel and
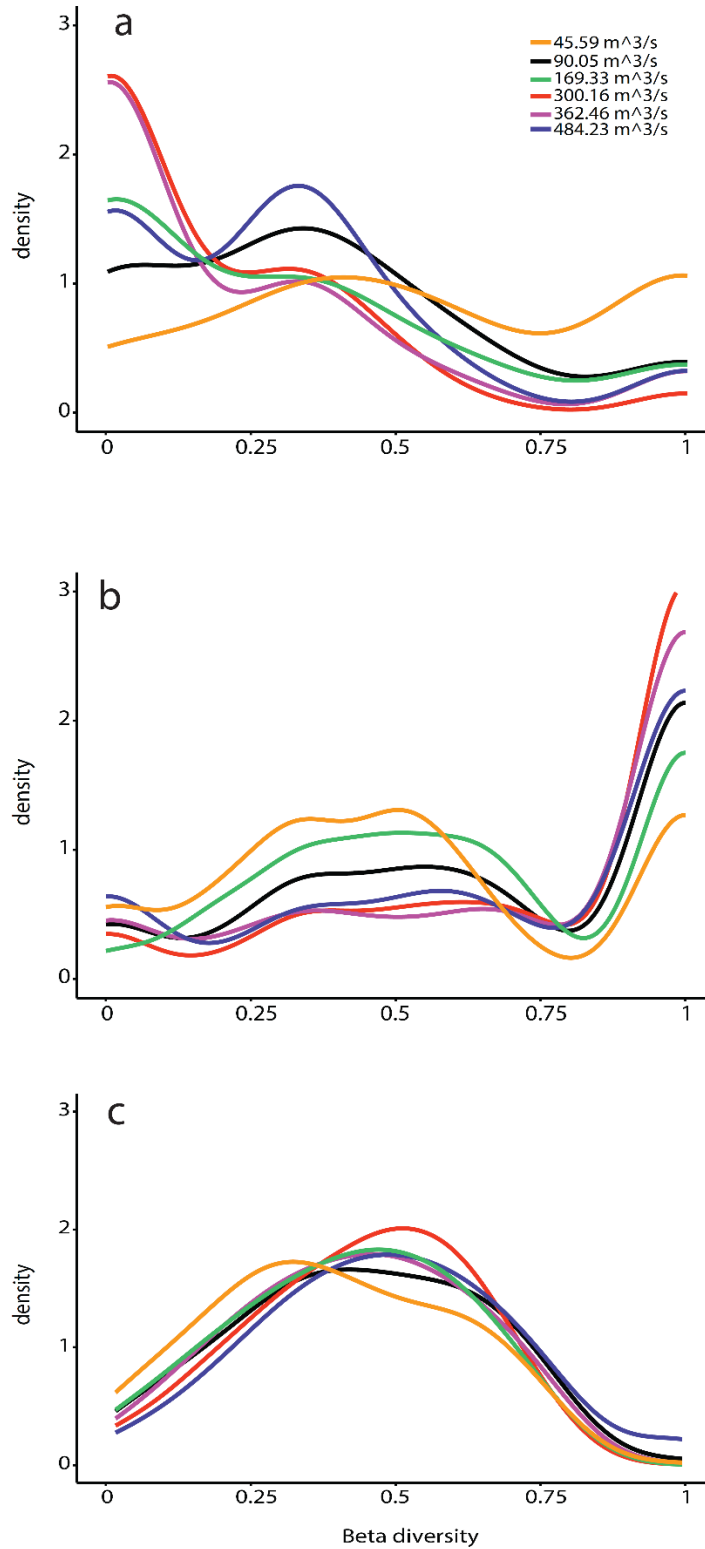
Figure 10. Kernel density plots of the (a) main channel zone, (b) parafluvial zone, and (c) orthofluvial zone beta diversity distributions for the seven dates during the study period. Each discharge distribution in all three zones were significantly different (p<0.01).

parafluvial zone, the distributions for each flow differ significantly (p<0.01) from all other discharges.

Complexity

Complexity in the main channel, parafluvial, and orthofluvial zones was measured in species evenness (E) to represent variation in the forms, functions, and linkages of the floodplain habitat cover types. The main channel zone was the most complex of the three floodplain zones during base flow conditions, with E=0.38 and E=0.29 at the two lowest discharges (45.59 m^3/s and 90.05 m^3/s respectively). As discharge increased, the complexity of the main channel decreased becoming the least complex of the three zones during high flow conditions, with E=0.18 at the two largest discharges (362.46 m^3/s and 484.23 m^3/s respectively) (Figure 11).

The orthofluvial zone followed the opposite pattern of the main channel zone, with low complexity at base flow and high complexity at peak flow (Figure 11). At low flows (45.59 m^3/s and 90.05 m^3/s) the orthofluvial zone was the least complex of the three floodplain zones (E=0.18 and E=0.15). The orthofluvial zone then increased in its complexity as discharge increased. The greatest complexity (E=0.23) in the orthofluvial zone was observed during peak flow conditions of 484.23 m^3/s. At this high discharge, the orthofluvial zone was just as complex as the parafluvial zone (Figure 11).

The parafluvial zone followed the hypothesized pattern, with low complexity observed during base and peak flow and maximum complexity during intermediate discharges (Figure 11). At low flows (45.59 m^3/s and 90.05 m^3/s), the parafluvial zone was less complex than the main channel, but more complex than the orthofluvial zone (E=0.23 and E=0.26, respectively). At the intermediate discharges of 169.33 m^3/s, 300.16 m^3/s, and 362.46 m^3/s, the parafluvial
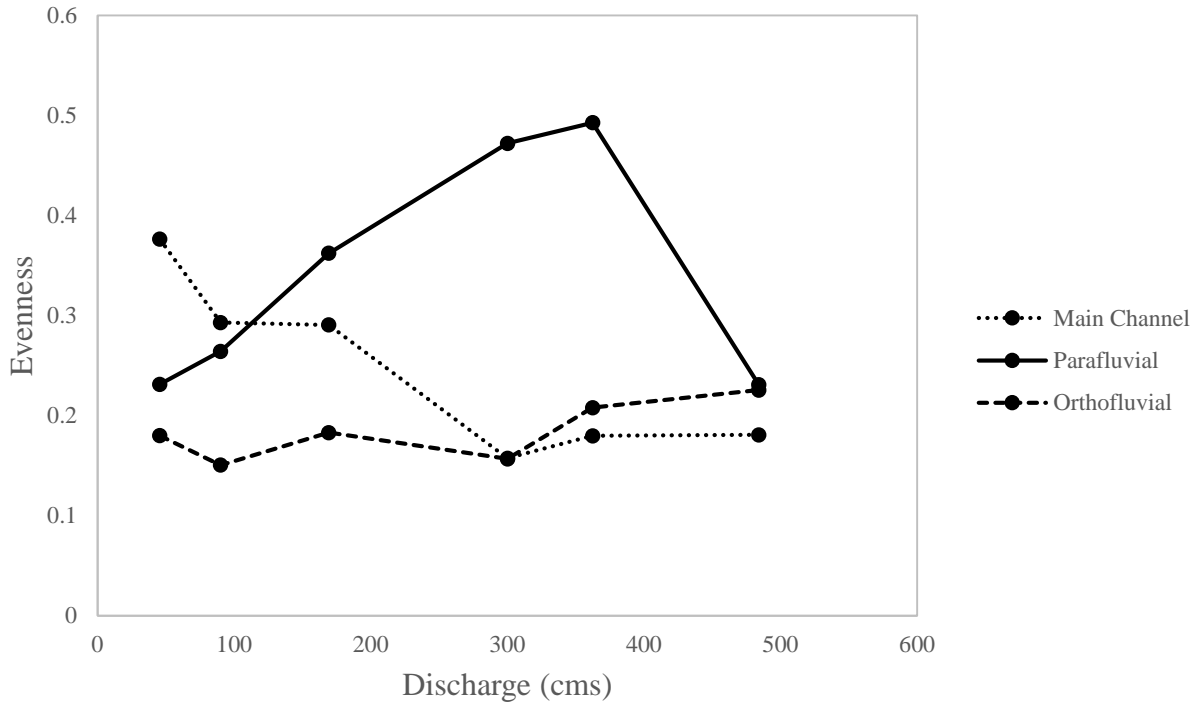
Figure 11. Complexity as represented by evenness for the three floodplain zones at the six discharges (CMS=cubic meters per second) on the sample dates of the study.

was the most complex zone, peaking on May 21 (E=0.36, E=0.47, and E=0.49, respectively). During high flows on May 27, the complexity of the parafluvial zone was equal to that of the orthofluvial (E=0.23) (Figure 11).

V. Discussion

I hypothesized that floodplain complexity is maximized at the intermediate discharge of a flooding event because small changes in flow result in substantial aquatic habitat changes (Tockner et al., 2000; Arscott et al., 2002; van der Nat et al., 2002; van der Nat et al., 2003; Whited et al., 2007)) and because extreme discharges are associated with a decrease in habitat heterogeneity (Mosley, 1982; Ward et al., 2002, Thomaz et al., 2007). While several other studies have focused on changes in floodplain habitat that result from a flood event, few have

focused on the temporal changes in habitat heterogeneity that occur in response to fluctuating discharges throughout the course of a flood event. The combination of larger than average flows and the island braided study reach on the Clark Fork River resulted in an ideal situation to study the influence of the flood pulse on aquatic habitat complexity.

Overall, I observed patterns in the abundance of several habitat cover types in the main channel, parafluvial, and orthofluvial zones. I also observed patterns in the habitats that did not change in their abundance through the course of the flood event, the results of which also have important implications for this study. Additionally, many patterns were observed in the timing and the types of transitions that occurred between floodplain habitat cover types during the flood pulse. Finally, the habitat alpha and beta diversity of the three zones on each date provide insight into the influence of discharge on the structure of the riverscape, both on the floodplain and individual habitat scale.

Peak flow in 2014 was only slightly larger than average for the Clark Fork reach (Figure 2). The average annual peak flow from 1930 to 2014 was 434.44 m^3/s occurring at the end of May. The peak flow observed during the study period was $484 m^s/s$ on May 27. This means the 2014 hydrograph was near the typical flood pulse conditions for the study reach and truly represents the typical development and destruction of floodplain habitats, the transitions they make, and floodplain habitat diversity. We could expect to observe similar results as long as the flood waters continue to achieve at least the discharges observed in this study.

Several previous studies (Whited et al., 2002; Hauer and Lorang, 2004 Lorang et al., 2005; Whited et al., 2007; Whited et al., 2013) have used aerial photography and unsupervised classifications to identify the spatial distribution of floodplain habitats. I used these methods to identify patterns in various aquatic habitat abundances on several dates representative of discrete

discharges during a flooding event. These methods do, however, have some limitations. Whited et al. (2002) concluded that the most important factors affecting the accuracy of the image classification were turbidity and substratum conditions. The spectral reflectance of water and therefore depth estimations are altered by changes in substrate and turbidity, which inhibit detailed depth classifications (Whited et al., 2002).

The only turbidity data for the Clark Fork River was collected during the 2007 water year, with no information available for the study period in 2014. In 2007, peak flow ($368\ m^3/s$) and the most turbid water (44 NTUs) both occurred on May 4. The turbidity during peak flow conditions ranged from 36 to 44 NTUs. Turbidity measurements on the rising limb during 2007 ranged from 7.5 to 30 NTUs. During the falling limb turbidity measurements ranged from 4 to 27 NTUs. The aerial photographs used for this study show evidence of increased turbidity on the dates associated with the rising limb and peak flow of the flood pulse: April 8, May 8, May 21, and May 27. Presumably, turbidity in 2014 followed a similar pattern to 2007, with the elevated turbidity measurements observed on the rising limb and maximum turbid conditions corresponding with maximum peak flow on May 27. Turbidity on these dates, particularly May 27, inhibited more thorough depth classifications of aquatic habitats by degrading the ability of the sensor to distinguish variations in water depth.

In addition to errors that may have resulted from turbidity, Whited et al. (2002) documented the negative effect of spectral reflectance variations among adjacent remote sensing image scenes on classification accuracy. There was at least one noticeable seam line in each map of the study reach that likely contributed to some classification errors. These variations have been attributed to differences in bidirectional reflectance (Lillesand et al., 2008) levels between individual image scenes and were partially accounted for through pre-processing of the imagery.

In addition to turbidity and seam lines, the growth of vegetation and the shadows associated with it also influence the measurements of floodplain habitat areas. The study period captured the growing period for vegetation, starting with bare trees and shrubs, progressing through leaf out, growth, and finally the changing colors of autumn foliage. As various vegetation types grew, some habitat cover types, particularly those located in the orthofluvial zone, were effectively hidden. Like vegetation, shadows also hide other floodplain habitats. Photos were collected as close to solar noon as possible to minimize their presence, resulting in no significant difference between dates in the amount of area classified as shadow in the main channel and parafluvial zones. On May 21, photos were collected about an hour earlier, resulting in a slightly larger shadow area in the orthofluvial zone. These shadows affected the classification of various vegetation cover types as well as aquatic habitats like flood channel riffles and runs, springbrooks, and overbank flow (Figure 8). Additionally, the growth of vegetation in the orthofluvial zone accounted for some error in the observed transitions. As cottonwoods and willows leafed out and the amount of shadow from their foliage increased, the number of pixels in a plot that had assigned to one type are split between vegetative and shadow covers and the dominant habitat tends to become herbaceous (Figure 8).

It was necessary to use a unique unsupervised classification for each date. Because the study period began in April, prior to vegetation leaf-out, and progressed through the growing season to September when the vegetation was senesced or losing leaves, a supervised classification or spectral library would have increased classification errors. This would also be true of aquatic classifications, as the level of turbidity was so variable throughout the flood pulse. This means the depth classifications are only based on pixel clusters of a single date, a benefit of

using separate classifications. For example, had the same classifications been used for all dates, a run on September 5 may have been classified as a riffle simply because it was shallower.

Riffles and runs were the most prominent floodplain habitats in both the main and flood channels. Main channel riffles dominated both the main channel and parafluvial zones during peak flow, which is consistent with the findings of Whited et al. (2002) that concluded not only that riffle habitats were greater under higher flows, but that the deep and fast riffle category increased its surface area by 62% during high flow conditions. Presumably the riffles observed during peak flow were also deep and fast, but the increased turbidity observed during elevated discharges affected accurate depth classifications.

In both the main channel and parafluvial zone, the area classified as riffles increased with increasing discharge, peaked during maximum flow, and decreased with decreasing discharge, highlighting how highly influenced the parafluvial zone is by its connections and close location to the main channel (Amoros and Bornette, 2002). During low flow conditions in the parafluvial zone, I observed point bars, vegetated islands, and cobble bars which created separate secondary channels, ponds, and springbrooks. However, at peak flow these distinct habitats became inundated creating a single channel of turbulent, fast, and deep water. Many previous studies report similar observations of a single, large, fast, and deep channel at high flows (Mosley, 1982; Thomaz et al., 2007) further confirming that despite turbid conditions we can conclude riffles observed during peak flow conditions were fast and deep. Main channel riffles and runs were not observed in the orthofluvial zone and flood channel riffles and runs were not found in the main channel zone.

In the main channel zone, the amount of area classified as run did not statistically change between all discharges except peak flow. Because the amount of run area remained constant in

this zone and the amount of riffle grew and then decreased, this study suggests that as discharge increases, the new habitat that forms in the main channel is most often riffle. Similarly, Mosley (1982) concluded that increases of water surface area tend to come from the addition of fast deep, turbulent water to a constant area of shallow, slow water, the location of which changes. Additionally, as the discharge decreases and aquatic habitats disappear from the riverscape, riffles experience the greatest loss in area. At high discharge, main channel runs disappeared from the main channel and the parafluvial zone and at base flows on either end of the flood pulse runs became the dominant aquatic habitat in the main channel. These findings are similar to the results reported by Whited et al. (2002), which concluded that both shallow and slow and shallow, fast non-riffle habitats increased in their surface area during base flow. The disappearance of runs on May 27 may be explained by the extreme turbid conditions that likely affected the classification of these typically deeper, darker waters. Once again highlighting the connection of the parafluvial zone to the main channel, main channel runs observed in the parafluvial zone followed a similar pattern to runs observed in the main channel zone. Main channel runs in the parafluvial zone disappeared at base flow conditions because the main channel had receded from the parafluvial zone, however they also disappeared at peak flow, confirming the results observed in the main channel.

Like the main channel, runs and riffles at all discharges also dominated secondary channels. However, patterns in the abundances of these habitats were slightly different based on the location of the channel. Amoros and Bornette (2002) argued that the water source and location of a habitat in regards to the main channel influence patterns in habitat heterogeneity, which is supported by my results. Four permanent parafluvial flood channels were observed at all discharges. These were generally observed cutting off point bars from the orthofluvial zone,

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creating cobble islands. Parafluvial flood channels were dominated by riffles at all flows, probably because flood channels tend to be shallower than the main channel. Secondary channel riffles even became the most dominant habitat in the parafluvial zone during periods of intermediate discharge. Most secondary channels in the parafluvial zone were an ephemeral habitat type which were only observed on the rising and falling limbs of the flood pulse becoming inundated at peak flow and disappearing from the landscape at base flow. The short residence time of parafluvial flood channels also influenced the presence of secondary channel runs, which only appeared during periods of elevated discharge.

Orthofluvial flood channels were more permanent features than the secondary channels of the parafluvial zone. There were two permanent secondary channels observed in the orthofluvial zones at all discharges, one orthofluvial springbrook that transitioned to a flood channel during periods of high flow, and five orthofluvial flood channels that were only observed during high flows. The permanently connected orthofluvial flood channels displayed a similar pattern in the development of riffles and runs to the main channel, with more run observed than riffle during base flows. The increases in riffle habitat again suggest that in orthofluvial secondary channels the habitat that is most commonly formed and destroyed during elevated discharge are riffles. Based on the observed patterns in riffle and run dynamics we can conclude that the areal abundance of riffles is related to discharge, while the abundance of runs is not.

While riffles and runs were by far the largest habitats observed in all zones, there were other habitats whose distributions were related to discharge. One example is shallow shorelines observed in both primary and secondary channels. Significant changes in shallow shorelines for both channels were observed only in the parafluvial zone. Main channel shallow shorelines were

pushed into the parafluvial zone as discharge increased. Additionally, as parafluvial secondary channels formed new shallow shoreline was created at intermediate flows. Overhanging vegetation in the orthofluvial zone and the shadows associated with the vegetation likely impacted the classification of flood channel shallow shorelines, causing no significant difference in the amount of flood channel shallow shoreline observed. However, there may be increased secondary channel shallow shorelines in the orthofluvial zone during periods of elevated discharge.

The last habitat cover type that experienced changes in its abundance as a result of changing discharge was overbank flow, which was only observed in the parafluvial and orthofluvial zones. In both zones, this habitat cover type was only observed on May 8, May 21, and May 27, the dates with the largest discharges. While overbank flow itself does not necessarily provide quality habitat, it does supply water to newly forming habitats (Amoros and Bornette, 2002). Overbank flow is also important because its presence increases habitat heterogeneity at later dates on the falling limb of the flood pulse and base flow conditions (Thomaz et al., 2007). This was particularly evident in the orthofluvial zone. Overbank flow in the orthofluvial zone connected at least one channel which otherwise would not have experienced flow and left behind a few ponds observed on later dates. Additionally, overbank flow is important to the function of the ecosystem (Junk et al., 1989; Tockner et al., 2000). These flows connect the floodplain to its river, affecting the exchange of nutrients, organic matter, and living organisms (Junk et al., 1989; Bayley, 1995). Lastly, the presence of overbank flow during periods of high discharge impacts the succession and regeneration of certain vegetation and fish reproduction (Junk et al., 1989; Amoros and Bornette, 2002). However, at

high flows, overbank flow decreases habitat heterogeneity by increasing connectivity between previously distinct habitats (Mosley, 1982; Thomaz et al., 2007).

The abundance of some habitat cover types did not significantly change in any of the three riverscape zones during the flood pulse, suggesting that their presence and area are not affected by fluctuations in discharge. These habitat cover types were backwaters, main channel and flood channel pools, springbrooks and ponds. The areal abundance of wood only changed significantly in the orthofluvial zone.

Backwaters were most commonly observed in the parafluvial zone and were observed at all discharges. They were only observed in the main channel during base flow conditions after the flood pulse, reflecting shifts that occurred in the location of the main channel. These shifts resulted in parts of the original main channel zone becoming more parafluvial in nature during base flow conditions after the flood pulse. It is possible that I observed no changes in their areal abundance because backwaters tend not to survive floods and decay faster than all other habitat cover types (van der Nat et al., 2003). It is believed that their short lifespan is related to flow pulses that occur below bankfull and the continuous cut and fill processes that affect attached channels (Tockner et al., 2000; van der Nat et al., 2003).

It is likely that no significant differences were observed in the areal abundance of pools for two reasons: (1) they represent a very small proportion of the landscape area at all discharges and (2) the process of how and where they form results in a constant abundance. In braided channels, like the study reach, pools are commonly formed at the confluence of two braids (Bisson et al. 2006). In addition to confluence zones, pools were identified as deep waters with smooth surfaces at the end of turbulent water runs behind log jams and root wads. While pools that were behind log jams and root wads may have been washed out or inundated at high flows,

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the formation of new channels that were only connected at high flows possibly caused more pools to form in the confluence zones. Pool abundance was also likely influenced by the lack of changes in the structure of wood in the parafluvial and orthofluvial zones.

While the distributions of springbrook area did not differ significantly in the main channel, there was a pattern observed. Springbrooks were only observed in the main channel zone after the flooding event. This was another indication of a channel shift that resulted in portions of the main channel zone becoming more like the parafluvial zone. Similarly, I observed a pattern in the areal abundance of parafluvial springbrooks with the largest area occurring during base flow and the least observed during peak flow. However, this pattern did not produce significantly different distributions of springbrook area. Orthofluvial springbrooks were frequently observed, with three large examples present at all flows. While these did expand in size at high flows, there was not a significant difference in the distributions of springbrook area among dates. Two of these large springbrooks transitioned to flood channels at high flows, but new springbrooks formed causing no significant differences in the amount of orthofluvial springbrook area observed through time. In the parafluvial and orthofluvial zone, this habitat type was particularly affected by the growth of vegetation during the study period, which effectively hid springbrooks from view on later dates. In particularly braided sections of river, springbrooks appear to be a fairly permanent habitat cover type (Arscott et al., 2000; van der Nat et al., 2003). Vegetated islands provide stability and cause less turnover in habitat patches like springbrooks and ponds (van der Nat et al., 2003).

It appears that fewer parafluvial ponds were observed during peak and base flows, nonetheless the areal abundance of parafluvial ponds did not differ significantly. Like pools, parafluvial ponds occupied a very small portion of the landscape, which likely influenced the

insignificant changes in their distributions. Like backwaters, parafluvial ponds are very short-lived as a result of their shallow depths (van der Nat et al., 2003) and may have disappeared from the landscape between the photographs collected on May 27 and July 2. There were also no significant differences in the abundance of orthofluvial ponds; however, this was not because they were absent from the landscape. Two oxbow ponds were observed in abandoned channels; but, the water in these areas did not come from any connection to the main channel during high flow and did dry out by the end of the study period suggesting a groundwater source. Additionally, during intermediate flow conditions, two ponds were observed in secondary channels that had been connected to the main channel during high flow and these ponds also disappeared during base flow conditions.

Despite the natural ponds that were observed in the orthofluvial zone, a majority of the ponds observed in the study were permanent man-made structures with depths extending below the alluvial water table and that maintain a fairly stable water level throughout the year. They are the result of agricultural and grazing lands within the floodplain, as well as former commercial gravel pits. Despite these more permanent ponds, the natural orthofluvial ponds in this study may not experience significant change because ponds that occur in island braided reaches tend to experience less turnover in habitat type (van der Nat et al., 2003). According to van der Nat et al. (2003), orthofluvial ponds can be some of the oldest habitat patches in island braided reaches, a result of the stability provided by vegetated islands.

The patterns I observed in the development of vegetation within the three floodplain zones were expected, with low areal abundances on April 8 and increasing abundance through the growing season. Vegetation in the main channel and parafluvial zones was generally in early life stages, making it difficult to distinguish between types. The increased presence of vegetation

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in the main channel and parafluvial zones on the falling limb and during autumn base flow conditions is suggestive of regeneration and succession. In the orthofluvial zone, it was possible to distinguish deciduous vegetation that was mainly cottonwood and willows from coniferous vegetation. The abundances of these cover types did not undergo any changes during the study period, highlighting the stability of vegetated islands.

The amount of wood in the main channel and parafluvial zones did not change, however, some turnover did occur. In the main channel, many wood plots predictably transitioned to riffles or runs as discharge increased. This wood was either exported from the system or submerged. On the falling limb, I observed riffles and runs that transitioned back to wood plots. However, I observed interesting transitions from riffle and run plots to wood on the rising limb, suggesting an import of new wood into the system. Because there were no significant changes in the amount of wood observed by date, this means that the amount of wood exported from the system was approximately the same as the amount that entered the system during the flood pulse.

In the parafluvial zone, wood plots most commonly transitioned to vegetation plots. This is most likely a result of the growth of vegetation through the study period; as willows in the parafluvial zone leafed out, wood was hidden by vegetation. After transitions to vegetation, plots dominated by wood were most likely to remain wood. Cobble transitioned to wood and wood transitions to cobble frequently occur. This is likely a result of the similarities in the spectral reflectances of wood and cobble and do not reflect legitimate transitions. I observed one large log jam in the main channel and another in the parafluvial zone. Neither showed any major changes throughout the flood event apart from becoming submerged at high flows.

The abundance of wood in the orthofluvial zone did change significantly with the largest amount of area identified during base flow conditions. Numerous prior studies have shown that

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wood has little hydraulic influence, but is extremely influential on the aquatic and terrestrial habitat diversity of riverscapes (Abbe and Montgomery, 1996; Piegay and Gurnell, 1997 Shields and Smith, 2006).

When I removed the zone designations and repeated the analysis of habitat abundance for the floodplain as a whole, many of the patterns observed within the zones were reinforced. For example, the same habitats (wood, backwaters, springbrooks, ponds, main channel and flood channel pools, willows, cottonwoods, and conifers) did not experience changes in their areas throughout the study period, again indicating that fluctuations in discharges do not affect the abundance of these cover types. Furthermore, main channel and flood channel riffles, main channel and flood channel shallow shorelines, overbank flow, early stage vegetation and cobble followed similar patterns as what I observed when the zone boundaries were present. The major difference that I observed without the zone boundaries, was the pattern followed by runs both in the main channel and flood channels. In both primary and secondary channels, runs were most abundant during intermediate discharges on the rising limb, meaning their abundance did not remain constant throughout the study period. This is the same pattern that was observed in the parafluvial zone, but not the main channel or orthofluvial zones, meaning that the area classified as runs in the floodplain as a whole is highly influenced by water filling the active channel. This highlights complexity at intermediate discharges and how the development of complexity is linked to water expanding into the parafluvial zone.

While some changes in the area of some habitats may have been insignificant because they occupy such a small amount of space on the floodplain, this study shows that these habitats do contribute to the habitat diversity within the floodplain. I calculated both alpha and beta habitat diversity values for the three floodplain zones on each of the seven dates. Previous

studies have indicated that habitat diversity assessed using Shannon's H' does not correlate with water level, but is associated with distributaries, confluences, floodplain perimeter, and aquatic area (Arscott et al., 2000). The diversity of habitats also has a strong link to the geomorphology of the entire floodplain, with the greatest complexity observed in gently sloping, island braided reaches similar to the study site (Arscott et al., 2002; Ward et al., 2002). Increases in habitat diversity are observed through a combination of various forms of hydrological connectivity including permanent connections to the main channel on both the upstream and downstream ends, permanent connection to the main channel on the downstream end, temporary connections occurring during high flow, or groundwater infiltration (Amoros and Bornette, 2002). A variety of these connections were observed in the parafluvial zone, giving it the greatest habitat diversity of the three zones. Some of these connections were observed in the orthofluvial zone, creating an intermediate level of habitat diversity. The main channel, by definition, has one water source and in general had very few connections observed. For these reasons it had the lowest habitat diversity.

Shannon's Diversity index is affected by species richness and evenness. Therefore, the disappearance of some habitat cover types from the three zones at various discharges has an influence on the Shannon value. In the main channel, backwaters and springbrooks were only observed at a flow of 45.59 m^3/s, increasing the number of species and thereby increasing alpha diversity. In the parafluvial zone, flood channel shallow shorelines and overbank flow were not observed during the two lowest discharges (45.59 m^3/s and 90.05 m^3/s), decreasing the number of species and the associated Shannon Diversity value. Therefore on April 8, the number of habitat species observed in the parafluvial zone was sixteen. Additionally, no main channel pools were observed in the parafluvial zone during the lowest discharge, further decreasing the

number of habitat species on September 5 to fifteen. There were no parafluvial springbrooks

observed during peak flow conditions of 484.23 m^3/s, resulting in only 16 habitat species at this

discharge. During the three intermediate flows, all 17 parafluvial habitat cover types were

observed. In the orthofluvial zone, overbank flow was not present during the two lowest flows

(45.59 m^3/s and 90.05 m^3/s). Additionally, flood channel pools were only observed during the

intermediate discharges on the rising limb, contributing to a greater number of habitat species on

these dates. Flood channel shallow shorelines disappeared during the lowest discharge (45.59

m^3/s), further decreasing the number of habitat species on September 5. Therefore the final

count for orthofluvial habitat species was as follows: sixteen species on April 8; eighteen on May

8; eighteen on May 21; seventeen on May 27; seventeen on July 2; and fifteen on September 5.

Despite there being no significant differences in alpha diversity between discharges, the

Shannon's values of the parafluvial zone appeared to follow the hypothesized pattern of

maximized diversity at intermediate discharges and decreased diversity at both base and peak

flows. Additionally, the parafluvial zone was generally the most diverse of the three zones. It is

unsurprising that the parafluvial zone would exhibit the most habitat diversity. At the floodplain

scale habitat diversity depends on the distance to the main channel and the existence of

permanent versus temporary connections to the main channel (Amoros and Bornette, 2002). The

parafluvial zone had the most direct contact with the main channel as well as three permanent

connections that maintained parafluvial flood channels throughout the entire study period. I

observed both main channel and off channel habitats in the parafluvial zone, which influenced

greater habitat diversity by having an increased number of "species".

The discharges that were associated with the largest alpha diversity in the parafluvial

zone were 300.16 m^3/s and 362.46 m^3/s, which were also the dates with the largest frequency

of two plots being entirely dissimilar (beta=1). Base flow conditions of 45.59 m^3/s on

September 5 produced the least diverse parafluvial zone conditions, both in alpha and beta

diversity. The beta diversity values on this date most frequently ranged from 0.25 to 0.6,

indicating that most plots had some habitat type in common. This is likely explained by the large

abundance of cobble during this low discharge, a habitat cover type that was observed in most

plots during base flow conditions. While the alpha diversity values were not significantly

different, each of the beta diversity distributions were, suggesting that discharge does influence

habitat dissimilarity in the parafluvial zone.

The orthofluvial zone experienced its greatest alpha habitat diversity at peak flow

because the zone actually had water in it. At high flows, the orthofluvial zone showed evidence

of many groundwater seeps appearing in springbrooks and ponds and otherwise disconnected

flood channels filled. The greater number of habitats observed during peak flow is likely what

increased the Shannon diversity value. Overall the orthofluvial zone was generally less diverse

in both alpha and beta diversity than the parafluvial zone, but more diverse than the main

channel. The orthofluvial beta diversity of all dates show similar-shaped distributions, with

increased probability of intermediate beta diversity values. This suggests that on all dates in the

orthofluvial zones, most plots had some habitat cover in common, likely an effect of the high

abundance of the herbaceous cover type. While the distributions show similar patterns, each was

significantly different, indicating discharge influences beta diversity in the orthofluvial zone. The

increased diversity at peak flow is reflected in the slightly elevated frequency of beta diversity

values equal to one during peak flow. The lowest beta diversity values, frequently ranging from

approximately 0.2 to 0.3, were observed during base flow conditions on April 8 and September

5. On these dates, plots are slightly more likely to be more similar in their habitat composition.

Dates associated with intermediate discharges, particularly 300.16 m^3/s, have the largest

frequency of beta diversity values equal to about 0.5, suggesting that as discharge increased and

the water entered the orthofluvial zone, floodplain habitats become more dissimilar.

Overall, the main channel was generally the least diverse of the three floodplain zones,

both in alpha and beta diversity. These results support the findings of Ward et al. (2002) who

concluded that the main channel exhibited low spatial heterogeneity. The main channel

experienced its greatest alpha habitat diversity during base flow conditions after the flood pulse

on September 5. Similarly, on this date there was an increased likelihood of observing larger

beta diversity values. These elevated values are indicative of the shifts in the channel that

occurred during flooding. This discharge was more diverse because portions of the main channel

have become more parafluvial in nature. For example, there were springbrooks and backwaters

observed on this date in the main channel zone and although they did not differ in their area from

other dates, they do increase the habitat diversity at this low flow. This underlines the

importance of outlying observations and provides an argument for why these data points should

not be removed from the data set. While the area occupied by these habitats may be statistically

insignificant, their importance is reflected by the habitat diversity calculations.

These results, as well as the transitions observed in the main channel and parafluvial

zone, show evidence of succession. It is during base flow conditions that habitat change occurs

through successional rebuilding (Stanford et al., 2005; Thomaz et al., 2007). I observed

transitions of cobble plots transforming to vegetation after the flood pulse, indicating the

regeneration of willow and cottonwood species in these zones. The higher observed beta

diversity between plots during base flow conditions may represent this succession occurring in

main channel and parafluvial zone.

Opposite from the parafluvial zone, which showed that the beta diversity values were greatest on the rising limb, I observed the lowest beta diversity values in the main channel during the 300.16 m^3/s and 362.46 m^3/s discharges. This suggests that plots became increasingly similar as discharge increased, which was expected based on the development patterns of riffle habitats in the main channel. Similar to the parafluvial and orthofluvial zones, the pattern observed in alpha diversity in the main channel was not significant, but the beta diversity distributions were all significantly different from each other. Again, this suggests that floodplain habitat diversity may not be related to discharge, but that the dissimilarity between plots was influenced by discharge.

Arscott et al. (2002) concluded that aquatic habitat diversity did not correlate with water level, which is partially supported by this study. Despite the appearance of patterns in alpha diversity in all three floodplain zones, there were no significant differences between dates. However, when the diversity of the three floodplain zones are compared for the same discharge, there appears to be a pattern in habitat development. At base flow the three zones all display the same level of habitat diversity. At intermediate discharges the parafluvial zone provides habitat that has disappeared in the main channel, likely providing refugia for aquatic species that need to move out of the main channel as it becomes dominated by turbid, turbulent, fast, deep water. When the parafluvial zone is overtaken by the main channel and becomes turbulent riffle habitat at peak flow, the orthofluvial zone has peaked in its diversity. At this high discharge aquatic species can find diverse habitats in the flood channels and springbrooks of the orthofluvial zone. As the discharge falls, the parafluvial zone once again peaks in complexity and gives a final refuge as the main channel continues to recover from the flood pulse and rise in complexity. Previous studies that have focused on landscape-level habitat diversity concluded that island

braided reaches are most diverse at intermediate discharges (Ward et al., 2002). The current

study suggests that this pattern in landscape level diversity is manifested in the parafluvial zone,

which is consistent with the findings of Whited et al. (2013) that concluded that the complexity

of a river channel corresponds with shallow shore and parafluvial habitats because they represent

recent fluvial activity. Previous studies have not examined the alpha diversity of the three-

floodplain zones, nor the beta diversity that represents habitat turnover.

Overall, complexity of the main channel zone decreased with increased discharge,

complexity in the orthofluvial zone increased with increased discharge, and the parafluvial zone

followed the hypothesized pattern of maximized complexity at intermediate discharges.

Discharge influences complexity of a floodplain, and the role of flow is particularly evident in

creating diverse forms, functions, and linkages of habitats in the parafluvial and orthofluvial

zones. The intermediate disturbance hypothesis applied to streams by Ward and Stanford (1993)

indicates that biodiversity of floodplains is maximized by moderate levels of disturbance from

flooding. This study suggests that the disturbance created by flooding influences complexity

differently based on the distance to the main channel, but that patterns in maximized complexity

at intermediate discharges is manifested in the parafluvial zone.

V. Conclusion

In conclusion, I observed a relationship between discharge and floodplain complexity

during the flood pulse. The areal abundance of aquatic habitats and the habitat diversity of three

floodplain zones appear to correspond with changes in flow. Fluctuations in discharge were tied

to predictable habitat transition patterns and river flow did influence areal abundance of some

aquatic habitats, but not all. On a finer temporal scale, aquatic habitats developed and

disappeared from the riverscape.

There was a relationship between discharge and the habitat diversity of floodplain zones, but not necessarily in the same zone through time. Different levels of discharge were associated with significant differences between the habitat diversity of the three floodplain zones. During base flow conditions, the three zones had the same level of habitat diversity, but higher levels of habitat diversity in the parafluvial and orthofluvial zones were linked with greater discharge. In the main channel, however, decreased habitat diversity was associated with increased discharge. River flow influenced beta diversity representative of habitat dissimilarity between plots. The beta diversity of the main channel was generally low, but plots were most likely to be the same during the rising limb of the hydrograph. Shifts in the location of the channel gave rise to a greater beta diversity in the main channel later in the study period. The shifts made parts of the main channel more parafluvial in nature. The parafluvial zone had the greatest likelihood of two plots being entirely different, while in the orthofluvial zone plots generally had some habitat composition in common. The location on the floodplain (main channel, parafluvial, or orthofluvial zones) corresponded with both alpha and beta habitat diversity. Lastly, habitats that occupied small areas were important to habitat diversity, which explained why changes in alpha diversity are not significant but the beta diversity distributions do differ significantly.

Overall, diverse habitats that differ in their geomorphology were created and destroyed throughout a flooding event, directly affecting the habitat heterogeneity at different flows. This study underscores the importance of natural flow regimes and how the timing, magnitude, and duration of a flooding event impacts the floodplain complexity. The three-floodplain zones evolve, providing different habitat cover types at each discharge, which is important for the ecological function of the floodplain and the life cycles of many plant and animal species. Understanding how hydrology shapes the structure of the floodplain and the impacts it has on

ecological function is critical as natural flow regimes are increasingly threatened by diversions,

regulation, and climate change.

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