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COUPLING BIOPHYSICAL COMPLEXITY AND FOREST METABOLISM IN A
FLOODPLAIN LANDSCAPE

By

PETER BOOTH DAVIS

Bachelor of Arts, Warren Wilson College, Swannanoa, NC, 2011

Thesis

presented in partial fulfillment of the requirements
for the degree of

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in Systems Ecology

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Approved by:

Scott Whittenburg, Dean of The Graduate School
Graduate School

H. Maurice Valett, Chair
Division of Biological Sciences

Lloyd Queen
College of Forestry and Conservation

Anna Klene
Department of Geography

Marc Peipoch
Division of Biological Sciences

Coupling Biophysical Complexity and Forest Metabolism in Floodplain Landscapes

Chairperson: H. Maurice Valett

Floodplains are biophysically complex systems that are considered among the most productive and biodiverse ecosystems on Earth. Until recently, quantitative assessment of the relationship between complexity and terrestrial production has been constrained by technological limitation. To address how floodplain biophysical complexity and ecosystem function are related, I employed remote sensing, GIS, and spatial analyses to quantify and couple metrics of complexity and terrestrial production, as well as explore the relationship among complexity, vegetation structural diversity, and terrestrial primary productivity. The study site is a 6.75-km by 1.75-km portion of the Bitterroot River floodplain near Carlton, MT upon which 551 sample plots were delimited via segmentation classification. Biophysical complexity, characterized by topographic heterogeneity, structural heterogeneity, and hydrologic connectivity was represented in each sample plot by mean standard deviation ground height, vegetative structural diversity index, mean flow length, mean flow accumulation, mean percent inundation, and gamma index metrics computed from Light Detection and Ranging (LiDAR) data, HEC-RAS inundation modeling, and ArcGIS Arc Hydro derived metrics. Potential primary production was represented by Normalized Difference Vegetation Index (NDVI) values generated from aerial 4-band multispectral imagery. Two questions were addressed in the analyses: 1) What is the causal relationship among floodplain physical complexity, vegetation structural diversity, and terrestrial productivity, and 2) How does floodplain biophysical complexity influence terrestrial primary production. Through these efforts, my goal was to explain how the dynamic nature of riverscapes translates to fundamental measures of ecological form and function. NDVI values ranged from -0.27 to 0.43, and were robustly related to biophysical complexity in which the explanatory variables together accounted for 58% of variation in NDVI ($p < 0.001$). In investigating the relationship between biophysical complexity, vegetation structural diversity, and NDVI, biophysical complexity was positively correlated to NDVI ($r^2 = 0.25$, $p < 0.001$), and structural diversity was positively related to NDVI ($r^2 = 0.51$, $p < 0.001$). These results suggest a causal relationship and support the complexity diversity hypothesis, and the diversity-productivity hypothesis. Structural diversity and connectivity variables accounted for the most explanatory power in all analyses, and overall results indicate that areas of the floodplain with greater biophysical complexity exhibited greater productivity.

Acknowledgments

First, I would like to extend my utmost gratitude to my major advisor, Dr. Maury Valett, for going above and beyond the call of duty in passing on his knowledge, being a mentor, and giving me the chance. I would also like to acknowledge Dr. Marc Peipoch, who made this project possible in every respect by devoting an abundant amount of time and effort to instructing me, and fixing my mistakes. I'm sure it wasn't easy. The contributions of committee members Dr. LLoyd Queen and Dr. Anna Klene, with their remote sensing expertise and guidance, proved to be invaluable. Thank you both very much. I would also like to recognize the remaining members of the Valett Lab for their comradery, encouragement, and creating a fun and "interesting" work environment. Financial support was provided by the MPG Ranch, an outstanding research facility, which made this work possible. Finally, I would like to thank my family, for their continued love, support, and encouragement through all my endeavors.

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Introduction

Investigations into the role of biocomplexity in organizing ecosystem structure and function has long been at the forefront of ecological theory and research (Hutchinson 1957). Studies began with the realization that complex systems exhibit greater ecological niche variability than non-complex systems, and are thereby able to support a diverse range of species (Hutchinson 1961, Croker 1967). MacArthur and MacArthur (1961) explored the role of environmental complexity in organizing species diversity by quantifying the relationship between foliage height diversity and bird diversity in forested landscapes. Complexity theory later came to be a fundamental concept in the field of ecology when it was formally introduced by the National Science Foundation (NSF; Colwell 1998). Michener et al. (2001) defined biocomplexity a few years later as “Properties emerging from the interplay of behavioral, biological, chemical, physical, and social interaction that affect, sustain, or are modified by living organisms, including humans,” but it wasn’t until Cadenasso et al. (2006) that a suitable framework was developed for quantification.

Ecosystem biocomplexity can be quantified along the dimensions of spatial heterogeneity, connectivity, and legacy (Cadenasso et al. 2006). Ecologists have traditionally derived spatial complexity metrics from landscape patches, or spatially defined areas that are compositionally different from their surroundings (Forman and Godron 1986, Pickett and Rogers 1997). Spatial heterogeneity reflects landscape patch dynamics (Pickett et al. 2005), with temporal variation resulting in what has been described as a shifting mosaic of habitat patches (Borman and Likens 1979, Stanford et al. 2005). Connectivity is determined by the spatial organization, and resultant interactions within and among these patches across the landscape (Ward et al. 1999). Legacy, the final dimension of biocomplexity, is dependent upon historical

states of the system that form temporally dependent relationships, which influence the landscapes' current state.

Complexity theory has been applied to a range of disciplines in an effort to better understand properties that emerge due to intricate interactions among and within the components of a system including landscapes, patches, coupled human-natural systems, communities, species, and organisms (Levin 1998, Auyang 1999, Green and Sadedin 2005, Pickett et al. 2005, Amoros and Bornette 2002, Cottingham 2002, Peipoch et al. 2015). Floodplains, due to their extremely dynamic nature, have been shown to be model systems for investigating the complex relationships among ecosystem structure and function (Tockner et al. 2010).

Floodplains, heterogeneity, and the flood-pulse

Riverine floodplains are biophysically complex systems whose spatio-temporal heterogeneity has earned them the reputation of being among the most biodiverse and productive ecosystems on earth (Ward et al. 1999, Tockner and Stanford 2002). Heterogeneity in floodplain structure can be attributed to long-term hydrologic and geomorphic influence on the landscape. In the glaciated Rocky Mountain regions of North America, annual spring snowmelt drives predictable and distinct flood events, known as the flood-pulse, that define riverine systems, and support dependent ecosystem processes (Junk et al. 1989, Bayley 1995, Valett et al. 2005, Caldwell et al. 2015).

During the flood-pulse, off-channel terrestrial habitats are inundated with water sourced laterally from the main channel, while the fluvial process of cut-and-fill alluviation alters floodplain and channel structure over varying temporal and spatial scales (Hauer and Lorang 2004). Patch diversity is thereby established as new distinct surfaces form and evolve over time

into a complex mosaic of habitats across the landscape (Ward et al. 2002, Stanford et al. 2005).

Mosaics manifest as new terrestrial and aquatic habitat types, represented by a diverse range in vegetation and successional stages extending across a lateral gradient from the parafluvial zone (areas adjacent to the main channel that are subjected to annual scour, erosion, and deposition during flood events), to the orthofluvial zone (portions of the floodplain reworked by only the largest flood events, and characterized by mid- to late- successional stage vegetation) (Hauer and Lamberti 2011, Valett et al. 2014, Hauer et al. 2016).

Connectivity and function

Connectivity is a concept that addresses ecosystem function. Ward et al. (1999) defined connectivity as, “The ease with which organisms, matter, or energy traverse the ecotones between adjacent ecological units.” Connectivity has played an important role in both terrestrial and aquatic ecological research. Landscape ecologists have traditionally used connectivity to explain the spatial distribution of abiotic and biotic elements including plants, animals, energy, and matter across a landscape (Forman and Godron 1986, Turner et al. 2001). Dependent on the degree of connectivity, the flow of elements may be inhibited or enhanced, with significant effects on ecosystem structure and function (Turner 2001). Many metrics exist for quantifying connectivity, one of which is the Gamma Index (GI) used to represent network connectivity. Networks are corridors connected by nodes, and GI is calculated as the ratio of the number of links present over the maximum number of possible links in a network (Forman and Godron 1986).

Flood-pulse regimes are responsible not only for establishing floodplain spatio-temporal heterogeneity, but hydrologic connectivity as well (Ward et al. 2002). During periods of

inundation, subsidies sourced from the main-channel are dispersed and retained in off-channel habitats due to interconnectedness and retentive mechanisms that, in part, reflect floodplain topography (Junk et al. 1989). Energy and matter are deposited in the floodplain (Junk et al. 1989, Tockner et al. 2000), replenishing nutrient-limited habitats with nitrogen (N) and phosphorus (P; Valett et al. 2005, Noe and Hupp 2005). Hence, hydrologic connectivity has been shown to play an important role in ecosystem function, including nutrient cycling (Wolf et al. 2013), as well as enhancing biodiversity in both floodplain and main-channel habitats (Salo et al. 1986, Naiman et al. 1993, Tabacchi et al. 1996, Pollock et al. 1998, Johnson et al. 2016).

Floodplains are characterized as being among the most species-rich environments on earth (Ward et al. 1999). Hydrologic connectivity maintains biodiversity in part by inhibiting competitive exclusion through seasonal patterns of inundation (Salo et al. 1986). Systems that exhibit this inundation behavior have been shown to support enhanced plant diversity (Bornette et al. 1998, Pollock et al. 1998, Johnson et al. 2016). This phenomenon is consistent with the intermediate disturbance hypothesis (Ward and Stanford 1983, Junk et al. 1989), which postulates that species richness is most abundant in systems that experience disturbance patterns that are neither too infrequent nor too frequent (Connell 1978). Flood-pulse connectivity thereby acts as a disturbance that maintains a non-equilibrium state in species composition by preventing highly competitive species from dominating, while disturbance events are infrequent enough to allow for re-establishment of numerous viable populations.

Diversity and production

Plant productivity has historically been treated as a dependent function of the abiotic conditions of an ecosystem (Connell and Orias 1964, Rosenzweig and Abramsky 1993). Over

the past twenty years however, an increasing amount of research has begun to support a positive relationship between vegetative structure and function (Loreau et al. 2002, Hooper et al. 2005, Balvanera et al. 2006). One such relationship that has garnered much attention is the association between richness and gross primary production (GPP, Naeem et al. 1994, 1996, Tilman et al. 1996, 1997). In this sense, species richness has been shown to correlate with carbon dioxide (CO₂) consumption, photosynthetically active radiation (PAR) interception, and nutrient utilization (Tilman et al. 1996; Naeem et al. 1994). These findings led to the development of the diversity-production hypothesis, which suggests that communities characterized by high species richness exhibit greater overall rates of productivity due to interspecific differences in plant species augmenting the collective capacity to more effectively incorporate available resources (Cardinale et al. 2006).

Far fewer studies have explored the link between species evenness and ecosystem function. Among the research that has occurred, a dichotomy in quantitative results have emerged (Hillebrand et al. 2008). While some studies suggest that the highest rates in GPP are observed in systems dominated by the most productive species (Norberg et al. 2001, Mulder et al. 2004), others have found that productivity increases along with evenness (Nijs and Roy 2000, Wilsey and Potvin 2000).

Despite the uncertainty surrounding the relationship between diversity and production, much of the research suggests a positive correlation. Since complexity may drive patterns of diversity, it may directly or indirectly be responsible for amplified rates of GPP observed in floodplain systems. Because of the high degrees of spatio-temporal heterogeneity and connectivity driven by the flood-pulse, complexity on floodplains has been associated with enhanced plant diversity (Salo et al. 1986, Bornette et al. 1998, Johnson et al. 2016). This

increase in diversity, according to the diversity-production hypothesis, could be responsible for amplified rates of GPP observed across floodplains. This would suggest a causal association in which complexity drives diversity, which then drives productivity. While a viable explanation for the high production characteristic of floodplains, this relationship has yet to be quantitatively explored.

Quantifying complexity and productivity

Although many studies have related complexity to biodiversity and production, fewer have been able to translate the notion of complexity to a measurable metric. Modern advancements in geographic information systems (GIS), remote sensing methods such as light detection and ranging (LiDAR), and multispectral imaging allow us to quantify ecosystem structure and function at high resolution, and over a range of temporal and spatial scales (Mertes 2002, Papadimitriou 2002, Lorang et al. 2005, Luck et al. 2010, Whited et al. 2007).

Papadimitriou (2002) developed a general approach, applicable across multiple landscapes, using patch metrics to compute complexity, while demonstrating the efficacy of using GIS for processing and analysis. Later, Luck et al. (2010) employed Landsat data to calculate riverine physical complexity metrics, and attempted to correlate complexity to salmon diversity and productivity. Most recently, Scown et al. (2016) used high resolution LiDAR data to quantify a floodplain surface complexity index, and emphasized the importance of incorporating both spatial heterogeneity and connectivity components. Although several studies have quantified complexity, the relationship between landscape biophysical complexity and terrestrial primary production has yet to be explored.

Vegetation structure has been identified as an important aspect of landscape complexity and focuses both on how biomass is distributed as habitat (MacArthur and MacArthur 1961, McDonnell and Stiles 1983) and its contribution to metabolic activity (Díaz and Cabido 1997, Hornung and Foote 2006, Randlkofer et al. 2010). Listopad et al. (2015) developed a repeatable method to quantify vegetation structural biodiversity using LiDAR, based on a modified Shannon-Wiener Index (H'). To compute H' conventionally, the following formula is presented as Equation (1):

$$H' = - \sum_{i=1}^S p_i \log_e p_i, \quad \text{Eq. (1)}$$

where p_i is the proportion of the i^{th} species, and S is the total number of species. Listopad's Lidar Height Diversity Index (LHDI) replaced S with 0.5-m height intervals, and p_i was represented as LiDAR point density, computed as the proportion of total points recorded within each height class. As the distribution of LiDAR point density becomes more evenly distributed across the four height classes, LHDI increases. Listopad et al. determined the LHDI to be an effective method for quantifying vegetation structure, and found a strong correlation between structural diversity and fire disturbance intervals in a forested landscape.

Research presented herein quantifies floodplain biophysical complexity using metrics of topographic heterogeneity, structural diversity, and connectivity, and couples these metrics of complexity to terrestrial primary production. In doing so, I explored the relationship between complexity and productivity by quantifying the association among complexity, diversity, and production. While not represented by its own metrics, the legacy component of complexity identified by Cadenasso et al. (2006) is argued to be embedded in the character of the riverscape's heterogeneity and connectivity. Floodplains, due to the influence of the flood-pulse regime, are extremely dynamic systems, and both the spatial heterogeneity and connectivity

dimensions included in the analyses are representative of the historical influences of flood disturbances and successional responses.

To investigate the relationships among complexity, diversity, and productivity, I addressed two conceptual models that differed in the way that they treat these ecological features in terms of their relationships (Fig. 1). With the first conceptual model (Fig. 1A), I explored how topographic heterogeneity and connectivity metrics together were related to an index of vegetation structural distribution to address links between complexity and diversity, and then extended this line of causality to address the relationship between structural diversity and primary productivity. Results from the first conceptual model address how well the floodplain acts to support both the complexity-diversity and the diversity-production hypotheses, and the extent to which causal association follows a predictable sequence from complexity to diversity and production. Second, I investigated the influence of treating vegetation structural diversity as a measure of floodplain biophysical complexity and how the collection of complexity metrics (i.e., topographic heterogeneity, structural diversity, and connectivity) interactively influence floodplain productivity (Fig. 1B). Together, these efforts address direct and indirect linkages among these entities directed at explaining how the dynamic nature of riverscapes may be quantitatively captured and translated to fundamental and predictable measures of ecological form and function.

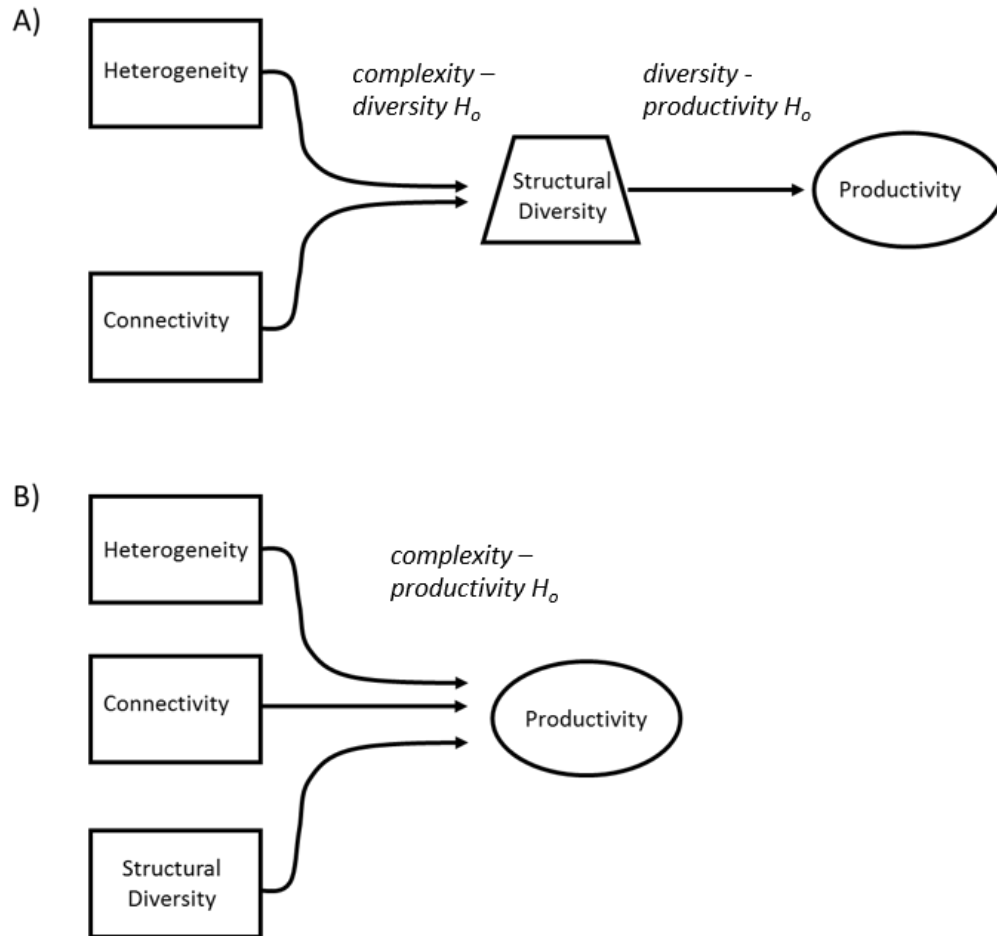


Figure 1. Conceptual models relating measures of complexity (rectangles) to measures of diversity (trapezoid) and productivity (oval). A) Conceptual model one addresses the causal chain linking complexity to diversity and, subsequently, to primary production addressing both the complexity-diversity and diversity-productivity hypotheses. B) Conceptual model two incorporates vegetative structural diversity as one of three measures of complexity that collectively influence primary production.

Methods

Study site and dates

The study site was a 6.75×1.75-km reach of the Bitterroot River and floodplain near Carlton, MT (46°41' N 114°02' W; Fig. 2), hereafter referred to as the riverscape. The eastern portion of the riverscape lies within the property boundaries of the MPG Ranch—a 20,000-acre research ranch with a focus on restoration, conservation, and ecology (MPG Ranch 2017). The Bitterroot River is an unregulated, snowmelt dominated, gravel-bed river (Bywater-Reyes et al. 2015), with significant interaction between the main-channel and off-channel habitats. While many rivers in this region have experienced ecological simplification resulting from anthropogenic development effectively severing main-channel/floodplain connections (Bayley 1995, Ward and Stanford 1995, Poff et al. 1997, Peipoch et al. 2015), this reach of the Bitterroot has predominately avoided such degradation. Spring snowmelt continues to drive an annual flood-pulse regime that inundates the floodplain and fuels ecosystem processes.

Deriving sample plots

TerrSet Geospatial Monitoring and Modeling Software's segmentation classification program was used to develop sample plots across the floodplain (*TerrSet* 2016). Segmentation classification, otherwise known as object-oriented segmentation classification, is a remote sensing method meant to classify land-cover and land-use types of remotely-sensed imagery through statistical pattern recognition of spectral and spatial information (Jensen 2004). For this study, National Agricultural Imagery Program (NAIP) imagery collected between June 15- Sept 11, 2013 was employed in the segmentation classification. NAIP imagery acquired in 2015 was

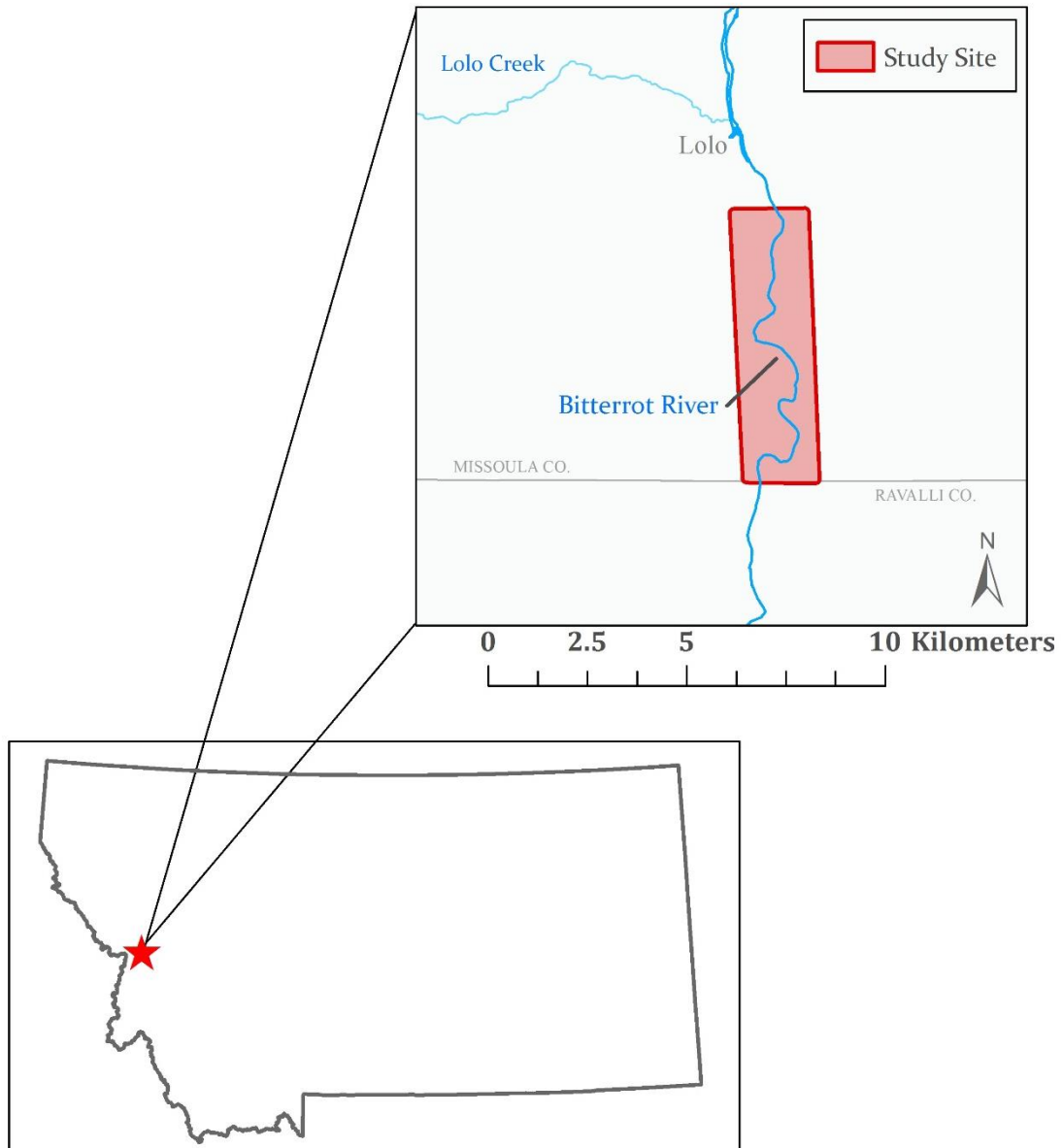


Figure 2. The study included a 1,193 ha portion of the floodplain along a free-flowing reach of the Bitterroot River adjacent to the MPG Ranch. The riverscape is dominated by cottonwood, ponderosa pine, and aspen forests, with a variety of small trees and shrubs including alder, juneberry, woodrose, and currants, and a number of native and non-native grasses.

not available for the study site due to environmental conditions precluding acquisition. Four bands were included in the 2013 imagery (red, green, blue, and near-infrared), and it was orthorectified by the vendor at 1-m resolution. In deriving the sample plots, all four bands were included, and weighted equally in processing. Segmentation classification generates a single layer composed of varying sized, and highly complex polygons characterized by spectral and spatial homogeneity (Jensen 2004), and thus considered patches across the landscape (Turner et al. 2001). Segmentation classification was performed several times on the NAIP imagery in order to achieve a classification scale that generated a computationally tractable number of segments, and neither under-simplified nor oversimplified the landscape.

Ultimately, a classification containing 1311 patches was selected. Plots that were either outside of the floodplain, intersecting water, or containing parafluvial gravel beds were removed. Constraining the analysis to this spatial extent ensured that only vegetated and bare-earth plots were included, and productivity analysis would not be influenced by water or gravel-bed reflectance values. With these restrictions, segmentation classification identified and delineated 551 segments (i.e., $n = 551$ sample plots) for quantitative analysis (Fig. 3). Sample plot size and shape varied considerably across the riverscape. Median plot area was 1.03 ha (0.12 - 8.36 ha), with a median perimeter of 1,860 m (161 - 19,020 m). Half of the plots have an area ≥ 1.82 ha, and 95% of the plots have an area $\geq .51$ ha.

Floodplain biophysical complexity, structural diversity, and primary production

Measures of floodplain complexity, structural diversity, and terrestrial productivity were derived from a collection of data sources and represented by a range of quantitative metrics (Table 1). All data sets were derived from remote sensing platforms and used to

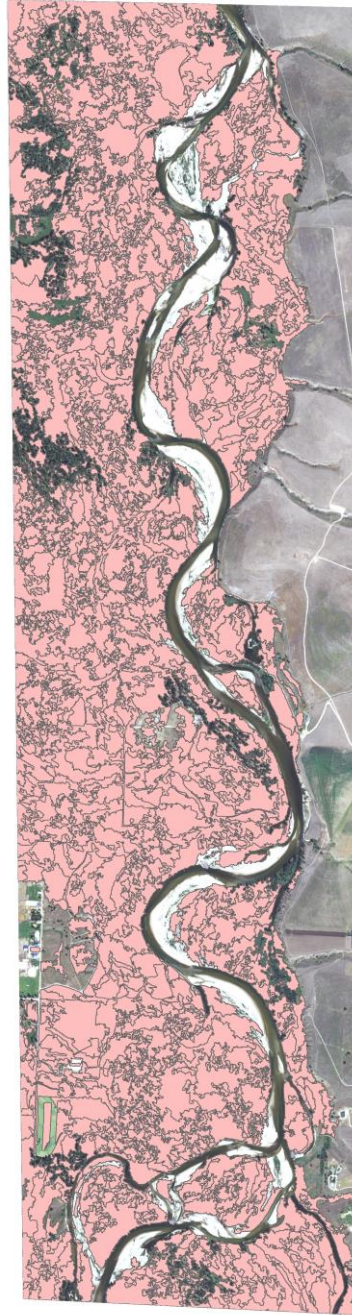


Figure 3. Map of sample plots (pink shaded polygons) developed using a segmentation classification of 2013 NAIP 4-band aerial imagery. Plots containing water or parafluvial gravel bed were removed in order to constrain the analysis to the floodplain, and avoid reflectance values of non-vegetated plots from influencing productivity analysis. 551 sample plots were retained and used in quantitative analysis.

Table 1. Summary of metrics used to represent floodplain biophysical complexity, diversity, and productivity. Complexity variables (left column) were calculated for 551 sample plots across the floodplain. Entity/dimension indicates the dimension of complexity represented by the variable. Data source column specifies the remotely sensed data origin used for calculation, and Method designates the software or formula used to perform calculations.

| Metric | Entity/ Dimension | Data Source | Method |
|---|---|-----------------------|--|
| Ground elevation standard deviation (GESD) | Complexity/ Heterogeneity | LiDAR DEM | ArcGIS |
| Vegetation structural diversity index (VSDI) | Complexity/ Heterogeneity/ Diversity | LiDAR point cloud | Modified Shannon-Wiener Diversity Index, Listopad et. Al. 2015 |
| Percent inundation (PI) | Complexity/ Connectivity – river floodplain interaction | LiDAR DEM | HEC-RAS, HEC-geoRAS |
| Flow accumulation (FA) | Complexity/ Connectivity – within and among plot interaction | LiDAR DEM | Arc Hydro |
| Flow length (FL) | Complexity/ Connectivity – within and among plot interaction | LiDAR DEM | Arc Hydro |
| Gamma index (GI) | Complexity/ Connectivity– within plot interaction | LiDAR DEM | Arc Hydro, ArcGIS, Formon and Godron 1986, Eq. 2 |
| Normalized difference vegetation index (NDVI) | Productivity | Multispectral Imagery | ArcGIS |

address relationships among sample plots at the floodplain scale.

Floodplain biophysical complexity was quantified within each plot using spatial heterogeneity and connectivity metrics generated from aerial LiDAR data. LiDAR data was acquired over the study site on September 9, 2016. Upon receipt of the LiDAR deliverables from the vendor, the quality of the dataset was assessed using LAStools software (Isenburg 2016), and confirmed to meet all contractual specifications, as well as American Society for Photogrammetry and Remote Sensing (ASPRS) standards (ASPRS 2014) version 1.3.

Topographic heterogeneity, represented by sample plot mean standard deviation ground elevation (GESD), was extracted in ArcGIS (*ArcGIS* 2016) from a 0.4-m digital elevation model (DEM) generated from the LiDAR ground points using LAStools. The DEM was detrended, a process that removes the longitudinal gradient driven by downstream changes in elevation before GESD analysis occurred. Detrending was necessary to prevent the natural slope of the reach from influencing topographic complexity metrics. Following Whited et al. (2007), a detrended model was achieved by interpolating a new slope from elevation points extracted at 100-meter intervals along a vector digitized over the main water channel and contours across the riverscape. A final detrended DEM was computed by subtracting the interpolated raster from the original DEM, and adding the minimum ground elevation of the original DEM. GESD was calculated from the DEM for each sample plot in the floodplain using ArcGIS.

Vegetative structural diversity (VSDI) was quantified using a modified Shannon-Wiener Diversity Index using the method developed by Listopad et al. (2015). Quantification was performed on elevation data derived from LiDAR non-ground points after normalizing ground heights. Four vertical height layers: 0 to 0.5 m, 0.5 to 2.5 m, 2.5 to 5 m, and > 5 m were used as a surrogate for species richness (i.e., $S = 4$). LiDAR point density proportions for each height

class, quantified using the LAStools lasheight program, represented the proportional abundance of vegetative biomass within each height class (p_i). VSDI was calculated for each sample plot across the floodplain using a combination of LAStools and ArcGIS.

Floodplain connectivity metrics were quantified using the Hydrologic Engineering Center's River Analysis System (HEC-RAS), the HEC-GeoRAS ArcGIS extension, and the ArcGIS Arc Hydro package (*HEC-GeoRAS* 2012, *HEC-RAS* 2016, *Arc Hydro* 2015). HEC-RAS, developed by the Army Corps of Engineers, is an inundation modeling software that allows for one-dimensional and two-dimensional steady and unsteady flow modeling. HEC-GeoRAS is an ArcGIS extension of HEC-RAS used primarily to geoprocess HEC-RAS model outputs. Arc Hydro is a toolkit package for ArcGIS that contains a number of models and tools for geospatial hydrologic analysis.

Percent inundation (PI) represents the spatial extent of flooding within any given plot as the percent of area covered by water and was computed for each sample plot from an inundation raster generated with HEC-RAS using the 0.4-m DEM created from the LiDAR data. One-dimensional steady-flow modeling used to calculate PI employed a runoff magnitude ($93.98 \text{ m}^3/\text{s}$) determined using daily historical United States Geological Survey (USGS) data on the Bitterroot River. To characterize mean hydrologic flow during the spring flood-pulse, I used historic discharge measurements from the months of March 1 – August 1 for 25 years (1990 to 2015). Since a USGS Streamflow station is not located on the study site, discharge was estimated by adjusting data from USGS station number 12352500, located just downstream of the riverscape near Missoula, MT. Lolo Creek, historically monitored by the now retired streamflow station number 12351500, is the only major tributary between the study site and the Bitterroot gauge (USGS 12352500). A linear regression fit between the Missoula and Lolo stations

($r^2=0.83$, $n=153$, slope = 0.093) was used to derive Bitterroot discharge on the riverscape as: Riverscape Q = Missoula Q – (0.093176* Missoula Q). HEC-RAS inundation model results were exported to ArcGIS as an inundation raster for geospatial analysis using HEC-GeoRAS (Appendix A). PI was computed in ArcGIS for each sample plot as the percentage of the area of the sample plot covered by the inundation raster.

ArcGIS's Arc Hydro package contains functions required to extract topographic and hydrologic information such as watershed area and flow paths from a DEM in accordance with methods established by Jenson and Domingue (1988), and Tarboton et al. (1991). Two measures of hydrologic connectivity employed here address the potential for linkage when flow is derived from upgradient portions of the floodplain. These Arc Hydro-derived metrics of connectivity included mean flow length (FL), and mean flow accumulation (FA), computed using a flow direction grid generated from the 0.4-m LiDAR derived DEM. FA computes for each cell the cumulative number of all cells (i.e., total area) on a downgradient flow path ending at that cell. FL computes for each cell the length of flow along an upgradient flow path from that cell to the point of origin. FA and FL values were computed for each sample plot in ArcGIS.

Gamma Index values across the riverscape were computed using the Arc Hydro-derived flow direction grid. Flow vectors represented links, either between stream nodes or leading to a node; junctions, where two links connected, represented flow nodes. ArcGIS was used to identify, and subsequently quantify the number of links and nodes within each sample plot, from which the GI was then calculated in Excel using a modified form of the GI equation provided by Forman and Gordon (1986) as Equation (2):

$$GI = \frac{Links+10}{3*(nodes+10-2)}. \quad \text{Eq. (2)}$$

Due to the low numbers of links and nodes present in some sample plots, a value of ten was added to all node and link records to avoid the problem of dividing by zero, and to ensure positive GI values.

Connectivity metrics, having been quantified using differing methods, represent multiple forms of hydrologic connectivity. PI represents a sample plots connectedness to the main channel due to its being computed from an inundation model in which flow originates at the main channel. PI also represents lateral inundation as a result of overbank flow during the spring flood-pulse regime. FL and FA are overland flow metrics that are indicative of flow length, time, and distance traveled over land, and therefore reflect within and among plot connectivity. GI is computed within each plot, and is thereby a useful metric to characterize within plot connectivity.

Riverscape terrestrial primary production was represented by normalized difference vegetation index (NDVI) values generated from the 2013 NAIP four-band imagery used in the segmentation classification. NDVI is a widely used remotely sensed vegetation index that has been shown to correlate well with biomass production, absorbed photosynthetically active radiation (APAR), leaf area index (LAI), percent canopy cover, and leaf chlorophyll levels (Tucker 1979, Huete et al. 2002, Zhang et al. 2003, Lillesand et al. 2015). NDVI values are computed using reflectance values in the near-infrared and red bands detected by a sensor following (Lillesand et al. 2015) as Equation (3)

$$NDVI = \frac{\rho_{NIR} - \rho_{RED}}{\rho_{NIR} + \rho_{RED}} \quad \text{Eq. (3)}$$

where: ρ_{NIR} is the proportion of reflectance absorbed in the near-infrared (NIR) region of the electromagnetic spectrum, ρ_{RED} is the proportion of reflectance absorbed in the red region of the electromagnetic spectrum. Riverscape NDVI output values range is between -1 and 1, with

greater values representing greater biomass production. Riverscape NDVI values were computed per pixel in ArcGIS, and aggregated to achieve mean NDVI values for each sample plot.

Data analysis

Two analyses were performed to address the causal sequence suggested by the first conceptual model proposing sequential linkage among complexity, diversity, and productivity (Fig. 1A). First, a multiple regression was used to calculate the relationship between topographic heterogeneity (GESD), connectivity metrics (PI, FA, FL, GI), and VSDI. Second-order Akaike Information Criterion (AICc) scores were generated from a series of candidate models using the MuMIn package in RStudio (Bartoń 2016), and the lowest scored model was selected as the model of best fit. The relationship between structural diversity and productivity was then explored, using a bi-variate linear regression to calculate the relationship between VSDI and NDVI.

To address the second conceptual model in which vegetation structural diversity was included as a complexity metric, I calculated the correlation between floodplain biophysical complexity and productivity using a multivariate approach. I first executed a principal component analysis (PCA) to address associations among complexity metrics (GESD, PI, FA, FL, and VSDI) collectively, and then assessed correlation between PCA scores and NDVI values. Finally, I used a multiple regression to test the relationship between the complexity metrics and NDVI. AICc scores were generated from a series of candidate models, and the lowest scored model was selected as the model of best fit.

Results

Floodplain elevation decreased 8.5 m over 6.7 km of river length, reflecting a landscape gradient of 0.13%. Following detrending, GESD averaged 0.46 and varied by 0.02 m (mean \pm standard error; Fig. 4a; Appendix B). Plots exhibiting the highest GESD (as much as 5.07 m) were located adjacent to the valley wall, while the remaining portion of the floodplain appeared to have an equal distribution of relatively low to moderate GESD values (Fig.4a). Variation in riverscape plot elevation was not related to sample plot area ($r^2 = -0.002$, $p = 0.9$) or to plot perimeter ($r^2 = -0.002$, $p = 0.9$).

The riverscape exhibited a wide range in VSDI values (Appendix C). Mean VSDI across the floodplain was 0.68 ± 0.01 (min – max = 0 - 1.35; Fig. 4b). Several plots exhibited very low VSDI values (equal to or very near zero); these plots were predominately grasslands, and therefore most LiDAR point densities were in the lowest height class. Higher VSDI values were found in the more densely forested areas, characterized by late successional stage vegetation, with an established understory. Half of all sample plots had a $VSDI \geq 0.82$, while 95% of plots had a $VSDI \geq 0.38$. While a significant relationship existed between VSDI and sample plot area ($r^2 = 0.01$, $p = 0.02$), and perimeter ($r^2 = 0.05$, $p < 0.001$), explanatory power was weak. VSDI was not related to the shortest distance from a sample plot to the main channel ($r^2 = 0.005$, $p = 0.09$).

HEC-RAS inundation modeling results indicated great variability and a wide range of PI values among plots across the floodplain (Appendix D). Mean plot PI was 15 ± 0.78 % (0 - 97.5%; Fig. 5a). Half of the sample plots were $\geq 35.7\%$ inundated, while 95% of the sample plots were $\geq 6.6\%$ inundated. While some plots in the riverscape were nearly flooded in their entirety, 195 sample plots (35%) experienced no inundation at all. PI was significantly, but poorly

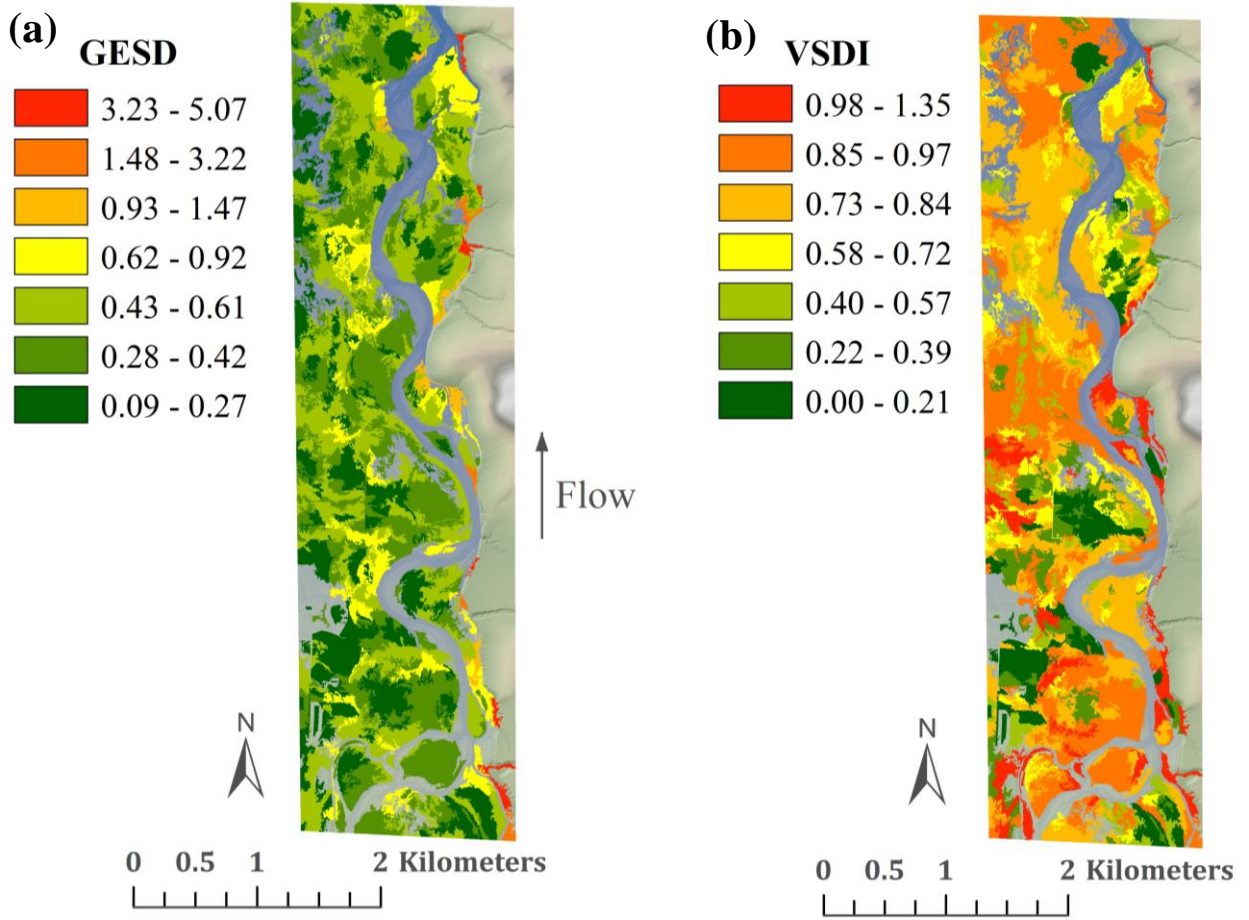


Figure 4. Maps showing the distribution of a) GESD, a topographic heterogeneity metric, for each sample plot across the floodplain, and b) Vegetation structural diversity (VSDI) values for each sample plot across the floodplain. For both maps, color ranges represent mean values for each plot, and metrics are overlain on the LiDAR derived DEM.

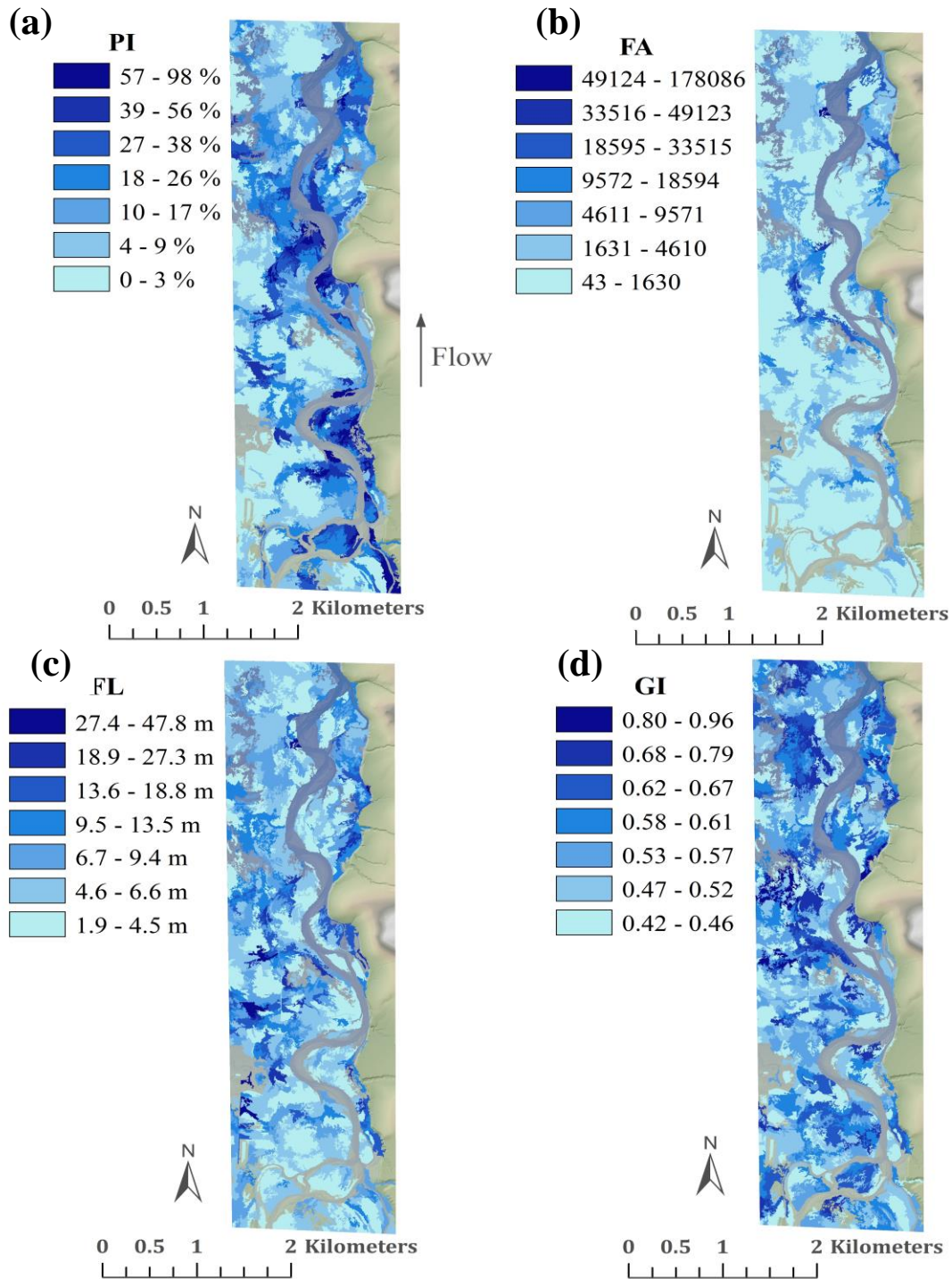


Figure 5. Maps showing the distribution of connectivity metrics including (a) mean PI values (HEC-RAS inundation modeling), (b) mean FA values from (Arc Hydro), (c) mean FL (Arc Hydro) and, (d) GI (Arc Hydro grid in ArcGIS). Values were generated for each sample plot, quantified as indicated in parentheses, and presented overlain on the LiDAR-derived DEM. All color ranges represent mean metric value for each sample plot across the floodplain.

correlated to the shortest distance from the plot to the main channel ($r^2=0.1$, $p < 0.001$). This result suggests that the importance of a plot's location in the riverscape was not determined by direct lateral connection to the main channel.

Among and within plot connectivity, as represented by FA, varied greatly across the floodplain (42.56 - 178,100 cells; Fig. 5b; Appendix E). A mean value of $2,899 \pm 393$ cells corresponded to 463.84 ± 63 m² of upslope contributing area (cell size = 0.4 m²). Flow length also varied considerably among floodplain sample plots with a mean of 7.25 ± 0.23 m (1.91 – 47.82 m; Fig. 5c; Appendix F). The relationship between FL and FA was significant, and had moderate explanatory power ($r^2= 0.37$, $p < 0.001$). FL and PI were also significantly, but poorly related ($r^2= 0.08$, $p < 0.001$), as were FA and PI ($r^2= 0.05$, $p < 0.001$), suggesting that among plot connectivity and plot connectivity to the main channel were not related. No relationship was detected between FA ($r^2= -0.002$, $p < 0.9$) or FL ($r^2= -0.002$, $p < 0.7$) and sample plot area.

Mean GI values for all sample plots was 0.51 ± 0.003 (0.42 - 0.95; Fig. 5d; Appendix G). GI increased with increasing plot area ($r^2=0.37$, $p < 0.001$), and this result is intuitive, suggesting that greater sample plot area provides opportunity for a larger stream network to be contained within the plot. A significant, but weak relationship was detected between GI and PI ($r^2= 0.08$, $p < 0.001$), suggesting a poor correlation between within plot connectivity (i.e., GI) and linkage to the main channel (i.e., PI). Similar results were obtained when the relationship between GI and FA was explored ($r^2= 0.02$, $p < 0.001$), as well as GI and FL ($r^2= 0.08$, $p < 0.001$).

Across the floodplain, NDVI values varied from those indicative of bare earth (≤ 0), to grass and sparse vegetation (0.0 – 0.3), and dense vegetation (0.3 – 0.5). Values for NDVI < 0 were observed for 155 (28%) sample plots, most likely reflecting plots predominately characterized by bare earth or rock. Mean NDVI value among sample plots was 0.09 ± 0.01

(-0.27 - 0.43; Fig. 6), reflecting a riverscape that is productive, and mostly dominated by grass or sparse vegetation. At the same time, half of the sample plot NDVI values were > 0.11 , and 77% of the floodplain plots were productive exhibiting NDVI values ≥ 0 .

Metrics representing both the heterogeneity and connectivity dimensions of complexity were related to vegetation structural diversity; GESD, PI, and GI were included in the model of best fit as defined by the lowest multiple regression AICc score (Table 2). This model showed a significant relationship between predictors and response variable ($p < 0.001$; Table 3).

Together the complexity metrics explained 25% of the observed variation in VSDI (multiple $r^2 = 0.25$, $p < 0.001$; Table 3). PI accounted for just over half of the variance explained by the model (partial $r^2 = 0.14$), while GESD (partial $r^2 = 0.08$), and GI (partial $r^2 = 0.02$) provided the remaining explanatory power (Table 3).

The employed measure of vegetation diversity (VSDI) was significantly and robustly related to log-transformed NDVI ($r^2 = 0.51$, $p < 0.001$; Fig. 7) suggesting exponential increases in productivity associated with increased vegetation complexity. Values for VSDI and NDVI were well distributed across both axes, illustrating broad and congruent variation in vegetation structure and productivity (Fig. 7). A large number of plots (i.e., 55%) were found with VSDI values > 0.7 but < 1.0 with corresponding NDVI scores between 0.16 and 0.2 (Fig. 7). Virtually no plots were characterized by high VSDI (i.e., > 0.8) and low rates of productivity (i.e., < 0 ; Fig. 7). In contrast, a number of plots had very low structural diversity (i.e., < 0.3), but exceptionally high values for NDVI (Fig. 7). Assessment of the VSDI-NDVI regression revealed that around a dozen plots had high residuals (i.e., high NDVI for relatively low VSDI). These plots were examined in ArcGIS, and all but two were found to be in agricultural areas subject to

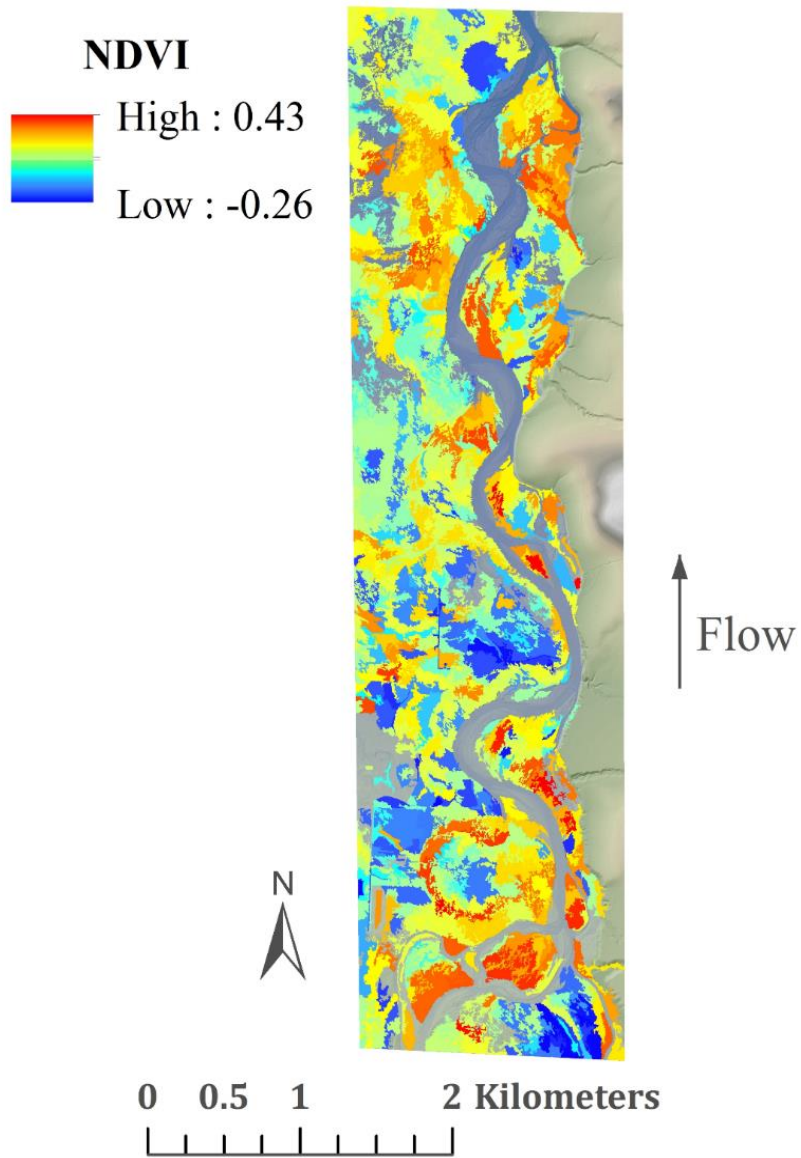


Figure 6. Mean NDVI for each sample plot in the study site, computed from 2013 NAIP imagery.

Table 2. Results of AICc model of best-fit selections used to determine the relationship among VSDI and topographic heterogeneity and connectivity metrics. The best-supported model is highlighted in bold.

| Fixed | AICc | Δ AICc |
|--------------------------|---------------|---------------|
| GI + PI + GESD | -10.35 | 0 |
| GI + PI + FL + GESD | -8.98 | 1.36 |
| GI + PI + FA + GESD | -8.44 | 1.91 |
| PI + GESD | -7.82 | 2.53 |
| GI + PI + FL + FA + GESD | -7.14 | 3.21 |
| PI + FA + GESD | -6.31 | 4.03 |

Table 3. Results of multiple regression analysis used to determine the relationship among VSDI and AICc selected GESD, PI, and GI metrics.

| Parameter | Estimate | SE | P | Partial r ² |
|-----------|----------|-------|--------|------------------------|
| PI | 0.070 | 0.009 | <0.001 | 0.14 |
| GESD | 0.082 | 0.022 | <0.001 | 0.08 |
| GI | 0.158 | 0.074 | 0.03 | 0.03 |

Multiple R-squared: 0.25, Adjusted R-squared: 0.25
F-statistic: 61.88 on 3 and 547 DF, p-value: < 0.001

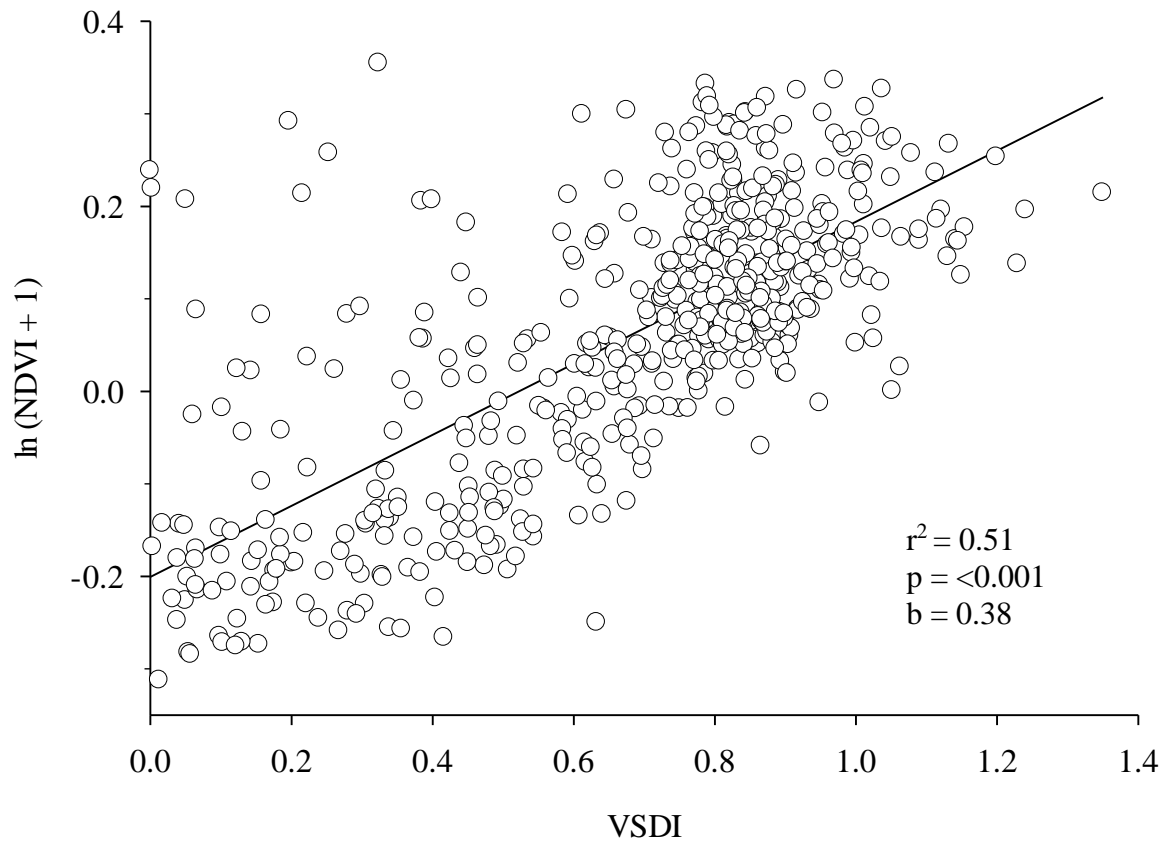


Figure 7. Correlation among productivity (NDVI) and structural diversity (VSDI), as represented by the linear relationship between ln-transformed NDVI and VSDI.

an unknown amount of irrigation during the summer months. The remaining two plots were adjacent main channel, suggesting possible ground water influence.

When considered simultaneously, the five metrics used to represent complexity and the diversity metric (GESD, PI, FA, FL, GI, and VSDI) increased along both axes (PC1 and PC2) of the PCA plot (Fig. 8). Together, PC1 and PC2 explained 70% of the total variance of the complexity metrics (axis 1 = 52.8%, axis 2 = 18.7%; Fig. 8). Complexity metrics were most highly and positively correlated with PC1 scores; VSDI, however, was displayed having a positive correlation between PC1 and PC2 (Fig. 8). There was also a positive relationship between NDVI scores along PC1 ($r^2 = 0.26$, $p < 0.001$), and PC2 NDVI ($r^2 = 0.16$, $p < 0.001$). When considered together using a multiple regression, PC1 + PC2 had high explanatory power in predicting NDVI ($r^2 = 0.42$, $p < 0.001$; Table 4). These results are indicative of a positive correlation among plot complexity metrics and NDVI values.

When VSDI was included with heterogeneity and connectivity metrics to test the collective relationship between these complexity metrics and NDVI values the AICc model of best fit included VSDI, GESD, FL, GI, and PI (Table 5), and the collective predictors were robustly related to NDVI ($P < 0.001$) with greatest explanatory power among all models (i.e., $r^2=0.58$, Table 6). NDVI values increased with increasing VSDI, FL, GI, and PI, but decreased with increasing GESD (Table 6). Of all complexity metrics, VSDI had the greatest explanatory power in predicting NDVI (partial $r^2 = 0.37$; Table 6). Connectivity variables collectively accounted for a moderate amount of explained variance (partial $r^2 = .18$), and GERD accounted for the least explanatory power (partial $r^2 = .03$; Table 6).

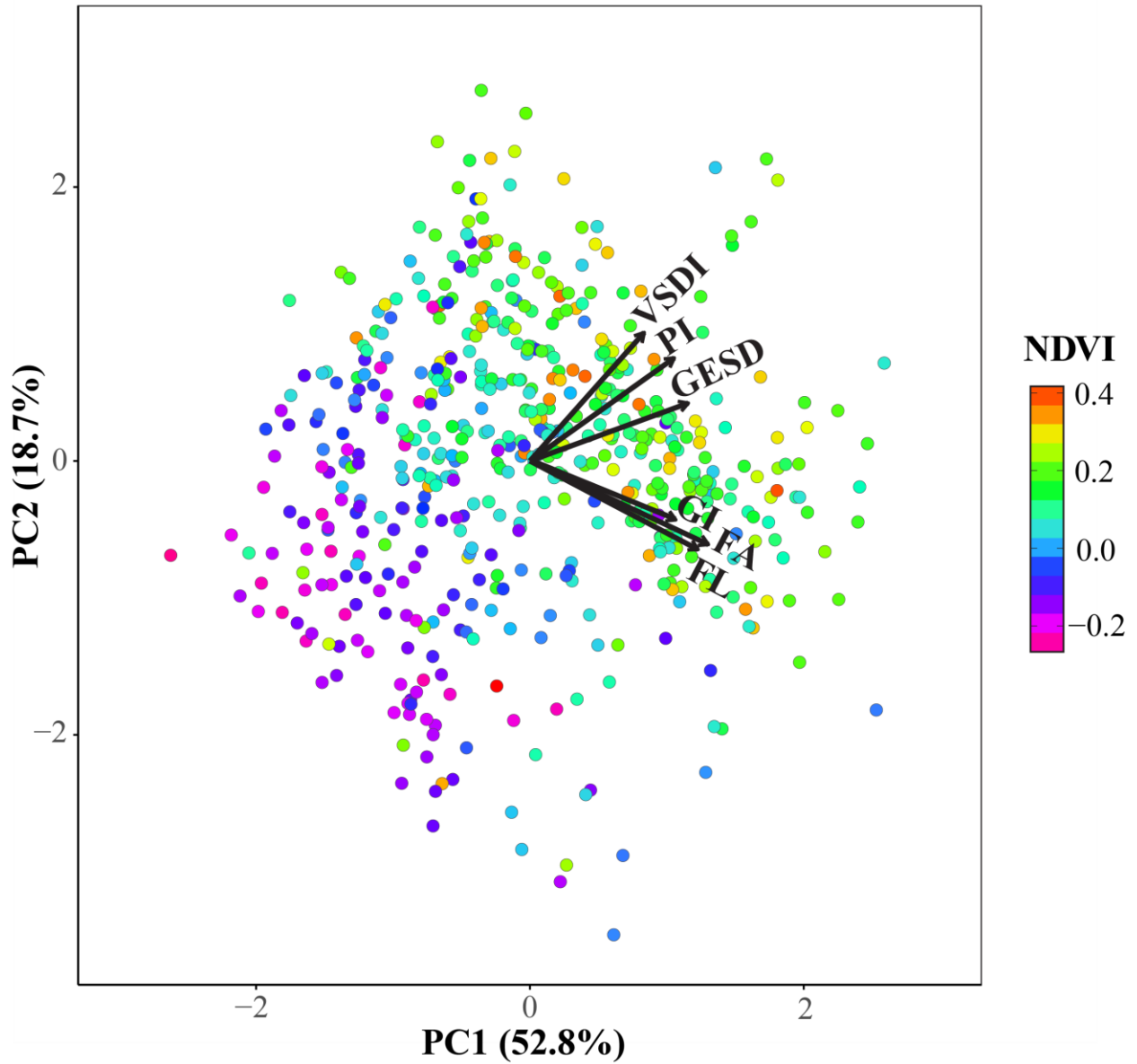


Figure 8. The relationship between complexity and NDVI was assessed using and PCA. A positive correlation was detected among all complexity metrics and NDVI values. Together, PC1 and PC2 explained a great amount of the total variance of the complexity metrics.

Table 4. Results of multiple regression analysis used to determine the relationship among NDVI and PC1 and PC2 of the PCA. Analysis results reflects the relationship among complexity metrics (represented by PC1 and PC2) and NDVI values

| Parameter | Estimate | SE | P | Partial r ² |
|-----------|----------|-------|--------|------------------------|
| PC1 | 0.044 | 0.003 | <0.001 | 0.26 |
| PC2 | 0.058 | 0.005 | <0.001 | 0.16 |

Multiple R-squared: 0.42, Adjusted R-squared: 0.42
F-statistic: 198.5 on 2 and 548 DF, p-value: < 0.001

Table 5. Results of AICc model of best-fit selection used to determine the relationship among NDVI and topographic heterogeneity, structural diversity, and connectivity metrics. The best-supported model is highlighted in bold.

| Fixed | AICc | Δ AICc |
|-----------------------------------|-----------------|---------------|
| VSDI + GESD + FL + GI + PI | -1012.48 | 0 |
| VSDI + GESD + FA + FL + GI + PI | -1011.59 | 0.88 |
| VSDI + GESD + FL + PI | -1008.51 | 3.97 |
| VSDI + GESD + FA + GI + PI | -1007.33 | 5.15 |
| VSDI + GESD + GI + PI | -1007.32 | 5.16 |
| VSDI + GESD + FA + FL + PI | -1006.46 | 6.02 |

Table 6. Results of multiple regression analysis predicting NDVI from AICc selected model of best fit represented by GESD, VSDI, PI, FL, and GI complexity metrics

| Parameter | Estimate | SE | P | Partial r ² |
|-----------|----------|-------|--------|------------------------|
| VSDI | 0.330 | 0.017 | <0.001 | 0.370 |
| PI | 0.030 | 0.004 | <0.001 | 0.132 |
| GESD | -0.043 | 0.009 | <0.001 | 0.030 |
| GI | 0.078 | 0.032 | 0.014 | 0.027 |
| FL | 0.023 | 0.009 | 0.007 | 0.022 |

Multiple R-squared: 0.58, Adjusted R-squared: 0.58
F-statistic: 151.3 on 5 and 545 DF, p-value: < 0.001

Discussion

Floodplain biophysical complexity was represented in this study using metrics of topographic heterogeneity, structural diversity, and connectivity and each was found to be a significant predictor of floodplain forest productivity. Topographic heterogeneity and structural diversity collectively represent the spatial heterogeneity dimension of complexity, and together with connectivity reflect two of the central dimensions of landscape biocomplexity (Cadenasso et al. 2006). Through this research, I was able to quantify the relationship floodplain biophysical complexity and terrestrial primary production, while also addressing a potential mechanistic relationship among complexity, structural diversity, and productivity.

Past studies of riverine complexity include investigations into the relationships between complexity and geomorphic and hydrologic divers (Scown et al. 2016), complexity and biodiversity (Hauer et al. 2016), and complexity and fish productivity (Luck et al. 2010). Here, I extend this long history of inquiry by quantitatively linking characteristics of a landscape renowned for its complexity as a terrestrial-aquatic interface to a functional metric fundamental to all ecosystems, primary productivity. To do this, I explored the relationships and potential causal association among complexity, structural diversity, and productivity (Figure 1A) by first quantifying the association between complexity (i.e., heterogeneity and connectivity metrics) and a biomass-based measure of vegetation structural diversity (i.e., the complexity – diversity hypothesis), and then extended the causal chain to address the relationship between diversity and a measure of productivity (i.e., the diversity – productivity hypothesis) across a representative portion of the riverscape, and over more than 500 floodplain patches. With an alternative perspective, vegetation structural diversity was then

grouped with connectivity and heterogeneity to address its potential expression as a component of biophysical complexity and its influence on terrestrial primary production (i.e., complexity – productivity hypothesis).

Connectivity is an ecosystem function concept that has been researched extensively in both aquatic and terrestrial systems. Early research quantifying hydrologic connectivity in floodplains included Ward et al. (1999), in which distance from the main channel was employed as a connectivity indicator. Ward's research displayed a positive relationship in which an increase in distance from the main channel resulted in enhanced species richness. Malard et al. (2000) later developed a surface hydrologic connectivity index, representing connectedness to the main channel, which showed that riverscape heterogeneity rose with surface connectivity during the spring and summer. Most recently, Scown et al. (2016) used spatial correlogram modeling to quantify the connectivity dimension of a complexity index, which increased with increasing patchiness across the landscape. The capability to quantitatively address hydrologic connectivity has evolved over the years with a growing awareness of the relationship among connectivity, diversity, and production, as well advancements in technological capacity.

By incorporating FL, FA, GI, and PI in this study, overland flow, within plot connectivity, and lateral inundation from the main channel were represented, with equal opportunity to influence NDVI. FL and FA reflect within and among plot connectivity caused by overland flow, rather than lateral inundation from the main channel. FL is a useful metric for quantifying connectivity; larger values indicate greater potential distance and time traveled by water across the landscape, and thus more extensive flow paths linking to the point of interest. Similarly, greater FA values reflects greater connectedness to upslope environments, representing a greater influence from the surrounding inundated terrestrial landscapes. Overland

hydrologic connectivity has been shown to play an important role in regulating hillslope and riparian runoff, altering residence time, and linking streams to their upland environment (McGuire et al. 2005, Jencso et al. 2009, 2010, Emanuel et al. 2014). These links can have significant implications for ecosystem function by maintaining ecological integrity, enhancing productivity, maintaining habitat, and regulating nutrient and organic matter exchange (Mertes 1997, Tockner et al. 1999, Snyder et al. 2003, Sommer et al. 2004, Freeman et al. 2007).

Within plot connectivity was addressed using GI, and represents the potential flow of water, energy, and nutrients within a sample plot. GI is a direct measure of the number of corridors across the landscape. Forman and Godron (1986) define corridors as, “narrow strips of land which differ from the matrix on either side.” Research into the role corridors in floodplains is extensive and highlights the importance of these conduits in enhancing ecosystem function. Greater hydrologic corridor connectivity in floodplains enable the dispersal capacity of biota (Johansson et al. 1996, Schalk and Luhring 2010), enhance biodiversity (Tockner et al. 1999, Karaus et al. 2013), increase habitat (Gurnell and Petts 2002, Amoros and Bornette 2002), and retain as well as disperse nutrients and water (Larsen et al. 2015).

Unlike the other connectivity measures derived from topographic character alone, PI was computed using HEC-RAS inundation modeling, and combines topography with flow paths leading from the main channel. In contrast to FA, FL, and GI, PI is indicative of lateral inundation during the flood-pulse, and it reflects a plots connectedness to the main channel, rather than the up-gradient environment. The vast majority of connectivity research pertaining to riverine systems has focused on this form of connectivity. Greater connectivity with the main channel has been shown to enhance spatio-temporal variability in habitat type (Arscott et al. 2002, Van Der Nat et al. 2003, Whited et al. 2007), impact plant community composition and

age (Salo et al. 1986, Hupp 2000, Bendix and Hupp 2000, Gurnell and Petts 2006), and affect the abundance and distribution of aquatic and terrestrial communities (Ward et al. 1999, Jenkins and Boulton 2003, Ballinger and Nally 2006, Leyer and Chiarucci 2006, Hauer et al. 2016). In the rocky mountain region of North America, it is imperative to include a main-channel component in connectivity analysis, as many ecosystems are dependent on the spring flood-pulse (Junk et al. 1989, Bayley 1995, Poff et al. 1997).

Vegetative structural diversity indices have been used to determine the relationship between foliage height diversity and species diversity (MacArthur and MacArthur 1961, Kohn 1967, Karr and Roth 1971, Greenstone 1984, Rosenzweig and Abramsky 1993, Tews et al. 2004), as well as determining the efficacy of a structural diversity as a proxy for ecosystem health (Debussche et al. 2001, Kalacska et al. 2007, Listopad et al. 2015). Through this study, I was able to broaden our understanding of the importance of environmental complexity in dictating ecosystem function by quantifying its impact on primary production in a floodplain landscape. Incorporating a vegetative component also bolstered the spatial heterogeneity dimension of biophysical complexity. In the context of this study, VSDI reflects variability in vegetation structure, and it is an effective metric in that it may represent species diversity, successional stage diversity, or a combination of both.

Topographic heterogeneity and connectivity vs. structural diversity

The assessment completed here for the Bitterroot River demonstrates that complexity, represented by topographic heterogeneity and connectivity, can be a significant driver of vegetative structural diversity in floodplain systems (Table 3). In the context of connectivity, PI accounted for the vast majority of the explanatory power, indicating that the degree of plot

connectedness to the main channel had the strongest control over determining VSDI. These findings are consistent with previous research which highlights the importance of connectivity, driven by flood-pulse regimes, in enhancing riparian plant diversity (Salo et al. 1986, Pollock et al. 1998, Johnson et al. 2016, Bornette, Amoros, and Lamouroux 1998). Similar to our research, Salo et al. (1986) identified a strong relationship between connectivity and diversity in an Amazon floodplain, and he attributed the relationship to intermediate disturbance patterns, and topographic spatio-temporal heterogeneity driven by the flood-pulse. Similarly, Pollack et al. (1998) found a positive correlation between connectivity and diversity, again attributing this phenomenon to flood regimes. It is clear from the abundant amount of research that floodplain vegetative structure and diversity is highly dependent on flood-pulse inundation regimes.

The low predictive power of GI, in conjunction with the AICc rejection of other connectivity metrics (Table 3), suggests that among and within patch connectivity (vs. connectivity to the main channel) has relatively little influence over VSDI in the floodplain. Therefore, overland flow of water potentially derived from precipitation or groundwater inundation of lateral habitat had much less control over VSDI than did water sourced laterally from the main channel. Mertes et al. (1997) explained how floodplains vary in their means of inundation. While some were highly dependent on main-channel, others became saturated by different means including groundwater, hyporheic water, precipitation, and upland flow, and in some cases even prevented main-channel water from entering the floodplain. In the coastal rivers of the Pacific Northwest region of the United States, means of riverine inundation patterns are relative to elevation (Naiman et al. 2010). Flooding in the highest elevation rivers were shown to be primarily snow-melt dominated, while those in the lowest are rainfall dominated. Our results are indicative of a floodplain whose vegetative structural diversity is highly dependent on main-

channel derived water, occurring as a result of spring snowmelt. These results corroborate previous research that has shown vegetation succession patterns to be dependent on main-channel derived flood patterns (Kalliola and Puhakka 1988).

Structural diversity vs. NDVI

VSDI was closely linked to NDVI and was found to be the strongest single predictor of NDVI in the study. This result suggests that spatial heterogeneity in vegetation structure is highly influential in determining rates of productivity in the floodplain. While VSDI was derived from the vertical distribution of biomass within sample plots, it likely reflects positive relationships between either species diversity (i.e., richness) and/or successional stage diversity, and plant productivity. These findings are consistent with the diversity-production hypothesis, and extend this train of thought to include a successional component that manifests in ecosystem properties like biomass distribution.

Topographic heterogeneity, structural diversity, and connectivity vs. NDVI

Maximum explanatory power was achieved when topographic heterogeneity, structural diversity, and connectivity metrics were combined to address variation in NDVI across the floodplain. The inclusion of VSDI as a complexity metric in combination with others caused an increase of 7% in predictive power over NDVI ($r^2=0.58$; Table 6), as compared to direct linkage of VSDI to NDVI ($r^2=0.51$; Fig. 7). By including a structural component in quantifying the heterogeneity dimension of complexity, I was better able to predict ecosystem productivity.

VSDI accounted for the vast majority of the explanatory power in this analysis, again underlining the influence of spatial variability of vegetation structure in determining rates of

productivity in the floodplain. GESD was the other spatial heterogeneity metric included in the model, and the only metric to have a negative slope. Scown et al. (2016) used several topographic heterogeneity metrics in part to develop a floodplain surface complexity index, but no correlations were drawn to productivity. The negative slope linking GESD and NDVI indicates that reduction in topographic variation is linked to increased productivity. Factors such as water retention time and material deposition potential may enhance productivity in flatter areas. More research is warranted to understand the relationship between the topographic heterogeneity component of complexity and terrestrial primary production.

Of all the connectivity metrics, PI was again the most influential while FL and GI together accounted for a very small amount of the model's ability to predict productivity. These results were consistent with the topographic heterogeneity and connectivity vs. structural diversity analysis, supporting the conclusion that a plot's connectedness to the main channel has greater control over productivity than within and among patch connectivity.

Conclusion

Through these analyses, I was able to quantify the association between complexity, vegetation structural diversity, and terrestrial primary production. First, the association among complexity (heterogeneity and connectivity) and vegetation structural diversity was explored to address the complexity-diversity hypothesis. I then extended this line of causality by investigating the relationship between vegetation structural diversity and terrestrial primary production (diversity-production hypothesis). Finally, vegetation structural diversity was included along with topographic heterogeneity and connectivity metrics to understand their collectively influence floodplain productivity.

Results from this study support a potential causal relationship among complexity, vegetative structural diversity, and terrestrial primary production. Increasing topographic heterogeneity and connectivity together enhanced vegetative structural diversity, while structural diversity was shown to have a positive and robust correlation with productivity. These findings supports the complexity-diversity hypothesis, the diversity-production hypothesis, and together suggest a relationship in which complexity enhanced vegetative diversity, and diversity drives productivity.

Collectively, topographic heterogeneity, structural diversity, and connectivity metrics had great explanatory power in predicting NDVI (Table 6), indicating a direct relationship in which complexity drives productivity, and supporting the complexity-production hypothesis. However, the great explanatory power of VSDI in this analysis as compared to the other explanatory metrics (Table. 6), in conjunction with the previous analyses, further supports a potential causal relationship among complexity, diversity, and production.

Modern advancements in GIS and remote sensing technologies have enabled scientists to further their understanding of the relationship between structure and function by monitoring such phenomena at the landscape scale, while maintaining fine resolutions. This study exemplifies the efficacy of geospatial technology in exploring the relationship between biocomplexity and productivity in a floodplain environment. LiDAR data, multispectral imaging, and GIS allowed us to quantify complexity and productivity metrics quickly, and across a large spatial scale at a very high resolution, a task that would have proven otherwise to be extremely difficult.

An abundant amount of time and effort has been invested in research supporting the notion that maintaining or restoring connectivity and the flood-pulse regime in aquatic systems is essential for sustaining ecological integrity (Mitsch and Gosselink 1986, Naiman and Decamps

1997, Heiler et al. 1995, Poff et al. 2007, Tockner and Stanford 2002, Peipoch et al. 2015).

Overland flow patterns showed very little control over ecosystem function in our analysis, and in both cases, PI was a much better predictor of VSDI and NDVI. These results underline the importance of maintaining a flood-pulse to ensure ecosystem function. Homogenization of the landscape through riverine alteration and management has been shown to sever patch connectivity to the main channel and across the landscape (Poff et al. 2007, Ward et al. 1999). Maintaining complexity, by ensuring the natural flood regime is sustained in floodplain ecosystems is therefore necessary to maintain biodiversity, production, and habitat in riverine environments.

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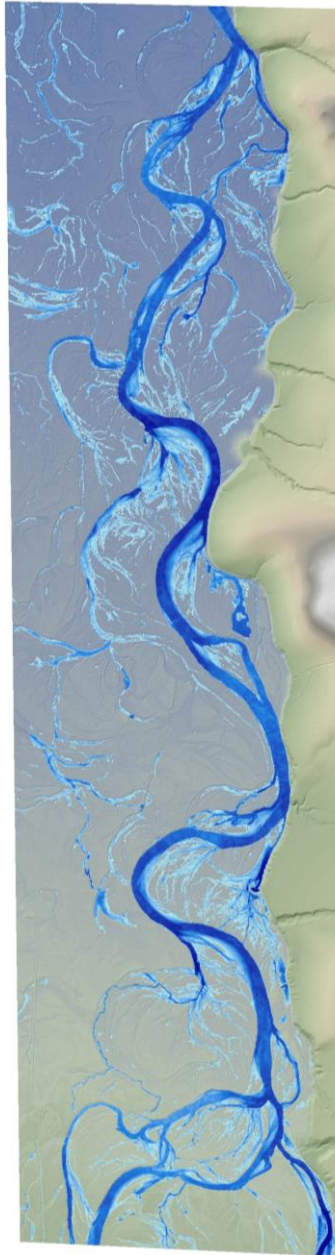
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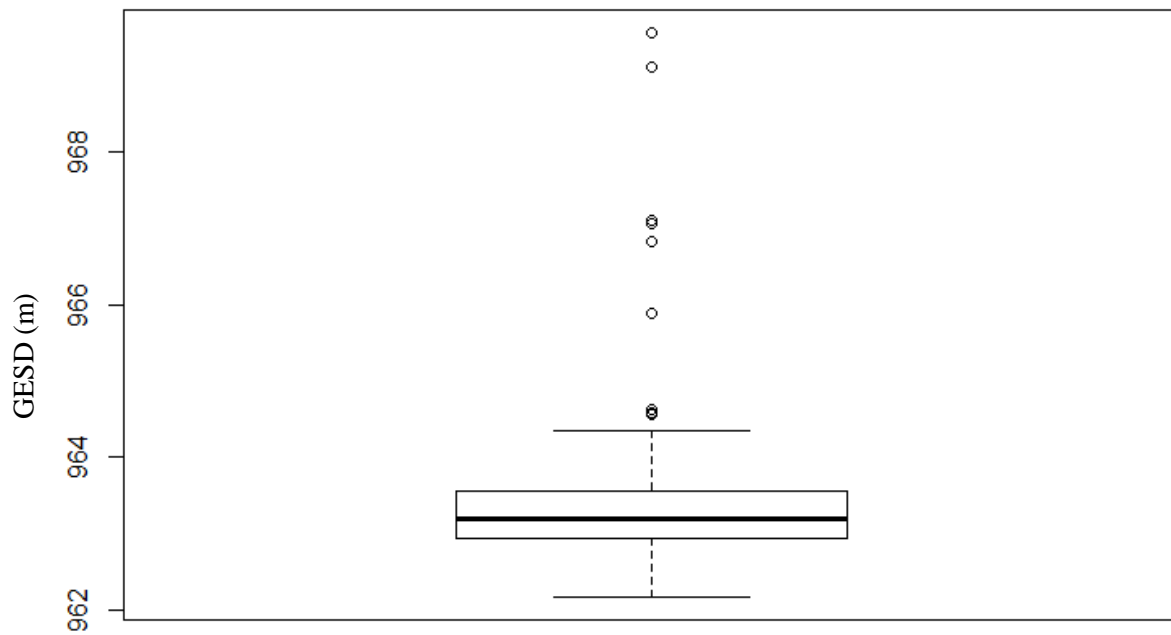
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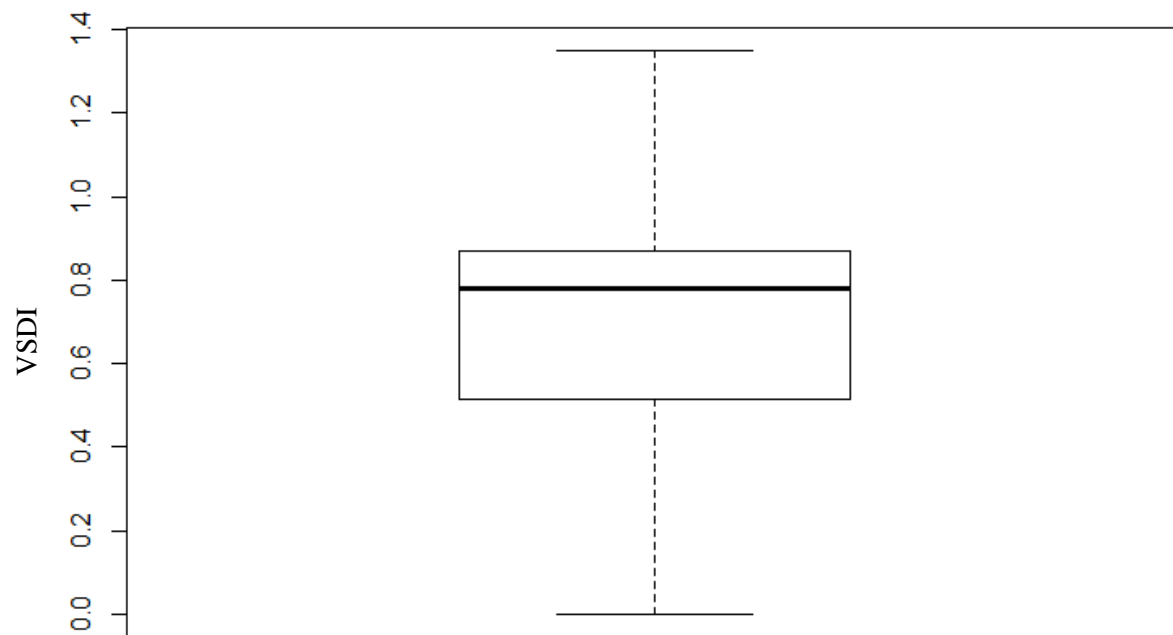
Appendix



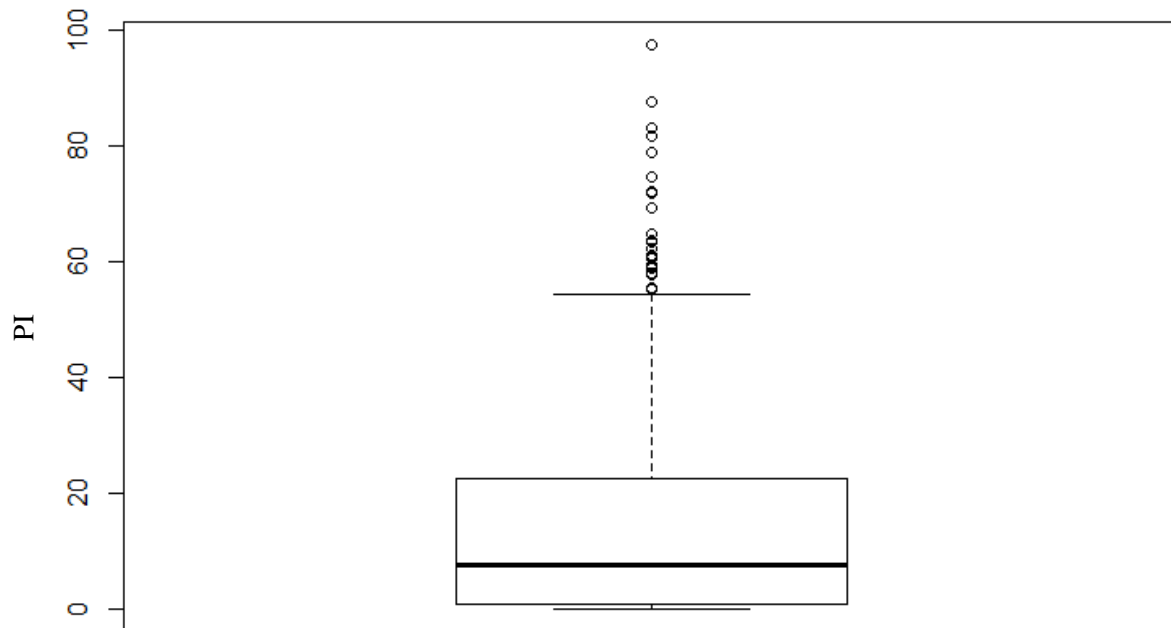
Appendix A. An inundation model was generated in HEC-RAS using the LiDAR derived DEM. Results in the form of a raster were exported and visualized in ArcGIS using the HEC-GeoRAS toolkit. The raster was overlain on the LiDAR DEM to determine how water is routed across the floodplain.



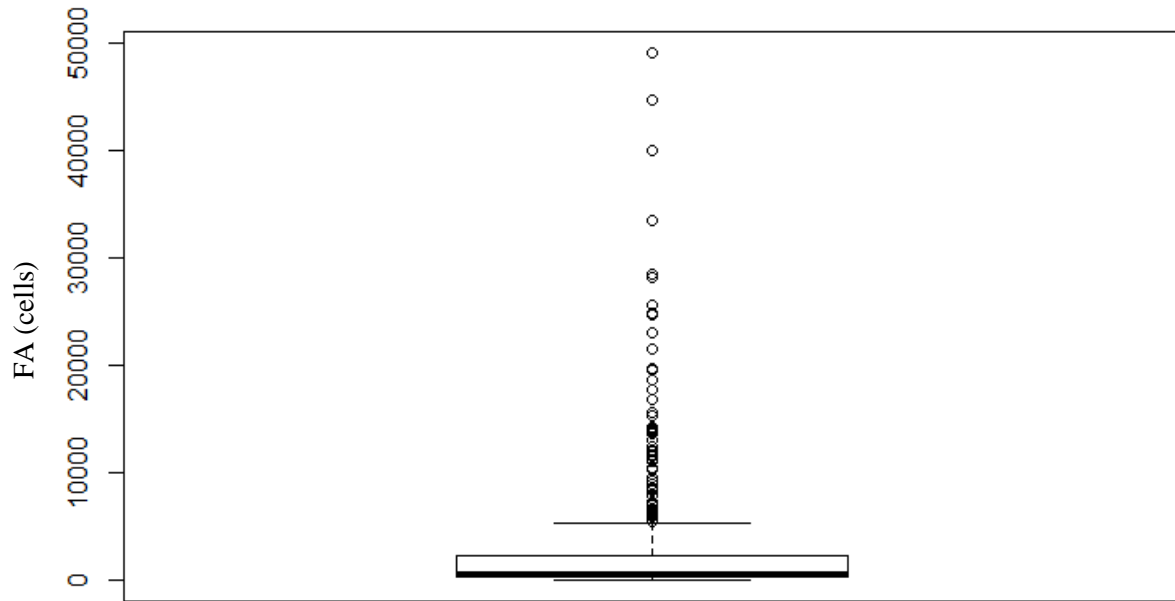
Appendix B. A box-and-whisker plot showing the distribution of GESD values across the floodplain.



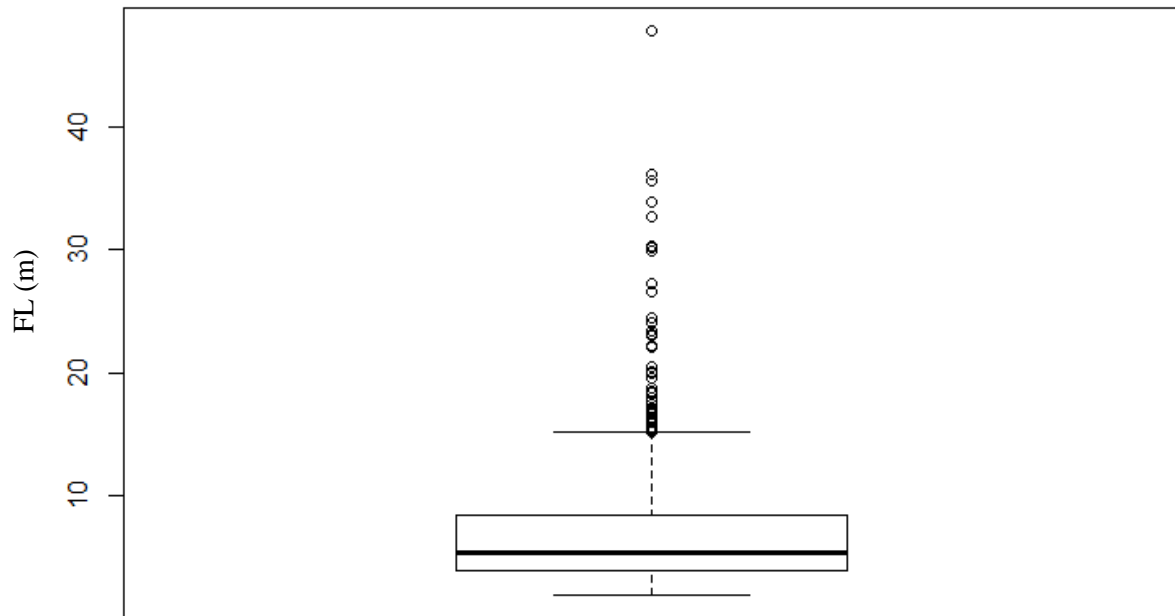
Appendix C. A box-and-whisker plot showing the distribution of VSDI values across the floodplain.



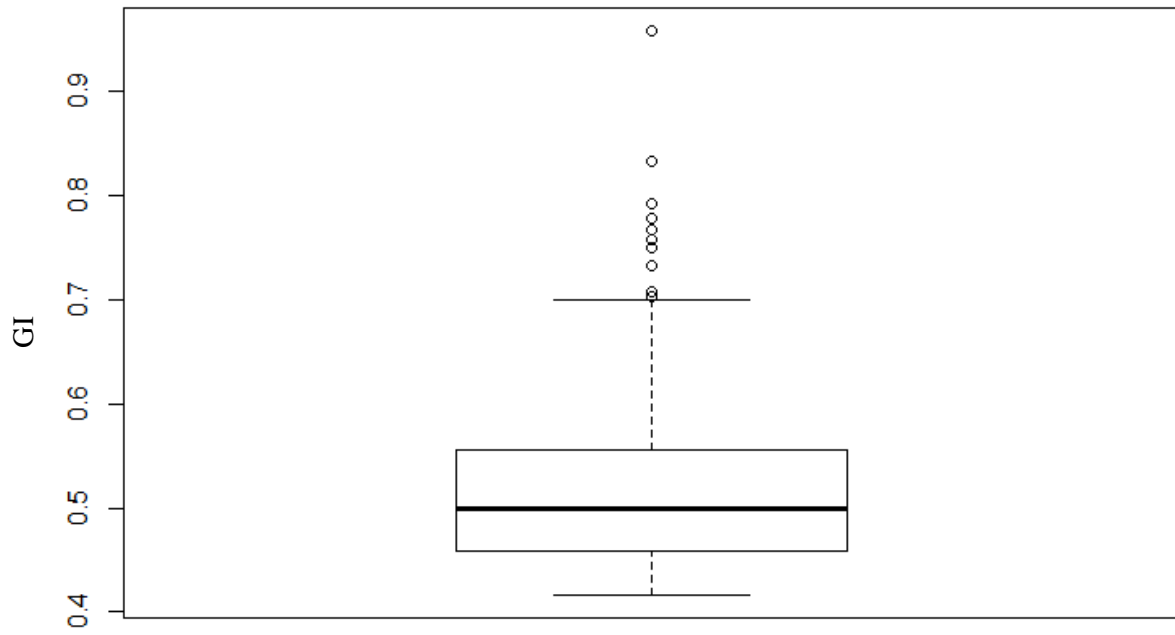
Appendix D. A box-and-whisker plot showing the distribution of PI values across the floodplain.



Appendix E. A box-and-whisker plot showing the distribution of FA values across the floodplain. FA units are in raster cells.



Appendix F. A box-and-whisker plot showing the distribution of FL values across the floodplain.



Appendix G. A box-and-whisker plot showing the distribution of GI values across the floodplain.