THE EFFECTS OF ENHANCED FLOWS ON COMMUNITY STRUCTURE AND
ECOSYSTEM FUNCTIONING IN A MONTANE UTAH RIVER SYSTEM

by

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A thesis submitted in partial fulfillment
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ABSTRACT

The Effects of Enhanced Flows on Community Structure and Ecosystem Functioning in a Montane Utah River System

by

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Utah State University, 2018

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Department: Watershed Sciences and the Ecology Center

Due to rapidly increasing human demand for freshwater within the last century, anthropogenically modified flow regimes are now a common feature of river systems worldwide. Modifications to the magnitudes and predictability of rivers’ flow regimes are known to negatively impact aquatic biodiversity, biological productivity, and ecosystem functions such as nutrient cycling. While previous research has focused on flow modifications associated with dams, there is a paucity of knowledge on how enhanced flows affect community structure and ecosystem functioning in rivers.

I collected macroinvertebrate community and ecosystem function data under natural and enhanced flow conditions throughout Sixth Water Creek and Diamond Fork River in central Utah. These data were supplemented with historical benthic macroinvertebrate data collected by BIO-West, Incorporated. I used linear mixed effects modeling and random forest regressions to determine whether a suite of flow metrics had relationships with benthic density, benthic community health, leaf breakdown,
chlorophyll-α growth, and stream metabolism. Additionally, I used linear mixed effects modeling to determine relationships between benthic and drift communities, and used nonparametric ordination methods to assess benthic community similarity across the river under multiple sampling years.

Here, I demonstrate that enhanced flows non-uniformly impact benthic macroinvertebrate communities across spatial scales, in addition to suppressing stream metabolism. While benthic communities were mostly unaffected by enhanced flows in the Sixth Water Creek tributary, benthic density and community health exhibited negative relationships with flow metrics in Diamond Fork River. Particularly in the Lower Diamond Fork mainstem, proportions of tolerant taxa increased logarithmically as maximum flow within 15 days increased, while benthic density exponentially decreased as mean monthly flows increased. Moreover, random forest regressions revealed that enhanced flows more negatively impacted gross primary production than ecosystem respiration in Sixth Water Creek and Lower Diamond Fork River. This disproportionate suppression of gross primary production shifted the river system towards a state of greater net heterotrophy. These results demonstrate the need to explicitly consider spatial gradients when investigating the effects of flow modifications on riverine communities, and also reveal how river ecosystems may be threatened with substantial losses to in-stream energy supplies under enhanced flows.

(163 pages)
PUBLIC ABSTRACT

The Effects of Enhanced Flows on Community Structure and Ecosystem Functioning in a Montane Utah River System

Joshua A. Epperly

Due to growing human demands for freshwater within the last century, manmade flow alterations are now a common characteristic of rivers worldwide. Alterations to the volume and timing of flows in rivers are known to negatively impact aquatic biodiversity, biological productivity and ecosystem functions such as nutrient cycling. While previous research has focused on the effects of flow reductions and spates, there is a lack of knowledge on how high flows across longer timespans (i.e. ‘enhanced flows’) impact the structure of river communities and the integrity of ecosystem functions.

The Utah Reclamation, Mitigation and Conservation Commission has expressed interest in reducing enhanced flows in a central Utah river so as to benefit aquatic habitat and native game fish. With their funding support, I collected aquatic invertebrate and ecosystem function data under natural and enhanced flow conditions throughout Sixth Water Creek and Diamond Fork River. These data were supplemented with historical invertebrate data collected by BIO-West, Incorporated. For each river segment, I tested whether flow volume and variation had relationships with the density and health of streambed invertebrate communities. I also sought to determine how these flow metrics affected leaf litter breakdown, primary production and stream metabolism (i.e. the production and respiration of organic matter).

Here, I demonstrate that enhanced flows impact streambed invertebrate communities differently in each river segment, in addition to suppressing stream
metabolism system-wide. While streambed communities were mostly unaffected by enhanced flows in Sixth Water Creek, density and community health exhibited negative relationships with flow metrics in Diamond Fork River. In the Lower Diamond Fork mainstem, proportions of pollution-tolerant taxa increased as peak flows increased, while streambed invertebrate density decreased as mean monthly flows increased. Moreover, enhanced flows appeared to severely impact the production of organic matter in Sixth Water Creek and Lower Diamond Fork River. This disproportionate suppression of production over respiration shifted the river towards greater reliance on out-of-stream energy sources. These results demonstrate the importance of considering spatial gradients when investigating community responses to flow alterations, and also reveal how river ecosystems are threatened with losses of in-stream energy supplies under enhanced flows.
ACKNOWLEDGMENTS

This work was funded through the Utah Reclamation, Mitigation and Conservation Commission (URMCC), who initially reached out to Utah State University scientists for research assistance on the Sixth Water Creek and Diamond Fork River system. This research project would not have existed without their backing. Additionally, I would like to thank BIO-West, Inc. for providing their historical invertebrate data, which greatly expanded the scope of my analyses.

I would like to thank everyone on the Diamond Fork project for creating a fun, challenging and intellectually stimulating atmosphere in which to conduct research. Particularly, I want to acknowledge my committee member Dr. Patrick Belmont and Team Sediment, who succeeded in the challenging task of getting me to appreciate the dynamics of dirt and rocks. Thank you to my research technicians Dylan Hackett, Sam Sedgwick, Dylan Anderson, Bryce Bollinger and Sarit Chanprame for their dedication in the lab, as well as Shaley Valentine, Hannah Moore and everyone else who assisted me with fieldwork in Diamond Fork Canyon. I would especially like to thank my advisors, Drs. Trisha Atwood and Edd Hammill. Not only have they shared their deep intellectual insight and trained me as an ecologist, but they have also been incredibly patient and supportive throughout the course of this project.

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CHAPTER I
INTRODUCTION

Flow is the master variable in river systems; it controls the distribution of nutrients, arranges the substrate and exerts a constant physical pressure on all trophic levels. Within the last few decades, the paradigm of the natural flow regime has become increasingly influential in river restoration (Poff et al., 1997). There has been a growing recognition among managers that restoring or imitating the magnitudes, frequencies and timing of flow events is essential for maintaining riverine community structures and the ecosystem functions they depend on (Bunn & Arthington, 2002). Yet, in the face of climate change and growing human demands for freshwater, anthropogenically modified flow regimes are becoming ubiquitous in river systems worldwide. If we are to successfully restore ecosystem health in regulated rivers, we must expand our knowledge of how riverine structure and function respond to modified flows across space and time.

Due to the pervasiveness of river regulation as well as societal impetus to reevaluate dams, there has been a recent upwelling of scientific focus on how modified flows affect riverine communities. Benthic macroinvertebrates have been a particularly well-studied subset of the riverine community because of their high fecundity and diversity, their conspicuous responses to environmental stressors, and their utility as bio-indicators (Huryn & Wallace, 2000; Kenney et al., 2009). The responses of macroinvertebrates to flow modification vary depending on the magnitude and direction of departure from the natural flow regime. Under baseflow reductions, benthic richness and proportions of sensitive taxa typically decline as habitat heterogeneity and connectivity are degraded (Dewson et al., 2007). Comparatively, high flow events and
augmented baseflows may directly reduce benthic density by flushing organisms into drift, in addition to impacting benthic richness (Kennedy et al., 2014). As river systems are gradients of environmental conditions, modified flows may non-uniformly alter habitat and resource availability across space (Lake, 2000). Thus, the responses of benthic communities to a given flow regime are often highly variable from headwater to mouth, which has implications for beta (β) diversity, connectivity, and river ecosystem functioning (Vannote et al., 1980; Gutiérrez-Cánovas et al., 2013; Heino et al., 2013).

Investigating river ecosystem functioning alongside structure may allow for a more robust, multi-trophic understanding of the effects of modified flows. Riverine communities are provided energy (i.e. carbon and nitrogen) through the internal contributions of primary producers and external contributions of coarse particulate organic matter (CPOM) (Cummins, 1974). Flow velocity is a highly influential variable for primary production, CPOM retention and CPOM processing in river systems. Scouring can remove periphyton biomass during moderate yet sustained flow increases, while aquatic vascular plants may experience widespread reductions during more intense high flow events (Biggs & Close, 1989; Biggs et al., 2005). Moreover, modified flows can directly alter thermal and nutrient regimes – the regulators of primary production in rivers (Hessen et al., 2002). In regards to external energy sources, high flow events and augmented baseflows may flush CPOM before it can enter a river’s food chain, interact with channel morphologies and substrate to reduce CPOM retention, and speed or slow the rates of CPOM processing through altering thermal regimes and microbial activity (Abelho, 2001; Quinn et al., 2009; Tank et al., 2010). Such changes in the standing stocks of these energy sources have direct, bottom-up effects on the biomass and
functional composition of macroinvertebrates (Fuller et al., 1986). All these functional processes may be reflected in stream metabolism, or the rates of organic matter production and respiration within a river (Tank et al., 2010). Modified flows have great potential to shift in-stream balances of production and respiration, which has implications for nutrient cycling and magnitudes of carbon fluxes (Hall & Tank, 2003; Uehlinger et al., 2003).

The Sixth Water (SXW) Creek and Diamond Fork (DF) River system in central Utah is an ideal system to research the ecological consequences of modified flows. This river system is located within the Spanish Fork River watershed and has historically been used to convey trans-basin flow imports to communities along the Wasatch Front. From 1913 to 2004, SXW Creek and DF River have been subjected to vastly augmented flow regimes throughout the 140-day irrigation season, resulting in long-term degradation of aquatic communities, reductions in habitat complexity, and alterations to channel morphologies and sediment transport (BIO-West, 2007). In 2004, the completion of the Diamond Fork Pipeline allowed for these flow imports to bypass the river system; however, the managers are still legally obligated to maintain mandated flow requirements. While not as severe as irrigation flows, these mandated flow requirements still feature baseflows that are higher than what is present in the river under natural conditions. I will subsequently be using the term ‘enhanced flows’ to collectively refer to these mandated flow requirements and natural high flow events such as spring runoff.

In this thesis, I investigated the effects of enhanced flows on macroinvertebrate community structure and ecosystem functioning in SXW Creek and DF River. Although previous research has established relationships between flow modifications and river...
ecosystem health, this project is novel in several regards. First, while river science has
typically focused on the effects of flow reductions and high flow events on structure and
functioning, my study system has experienced sustained increases to baseflow across
longer timespans. Second, I utilized a wide suite of metrics to assess how this river’s
ecosystem is affected by enhanced flows, which allowed for a more holistic, multi-
trophic understanding than what is common in the literature.

In Chapter II, I investigated (i) whether there was a relationship between flow
and benthic macroinvertebrate density / community composition; (ii) whether there was a
relationship between benthic density / composition and drift density / composition; and
(iii) how the similarity of communities across space and time were influenced by flow.
To analyze benthic and drift density / community composition, I used linear mixed
effects and random forests models featuring a suite of flow metrics. To analyze
community similarity, I used non-metric multidimensional scaling (NMDS) ordinations
and similarity percentage (SIMPER) analyses. My hypotheses were that (i) metrics of
benthic community health (e.g. EPT, Hilsenhoff Biotic Index) would respond negatively
to increases in flow in each river segment while benthic density would be less affected;
(ii) that the density and composition of benthic communities would be correlated with the
density and composition of drift communities; and (iii) that enhanced flows would
increase community similarity across the river system.

In Chapter III, I investigated (i) whether there were relationships between flow,
macroinvertebrate feeding group compositions, and measures of ecosystem functioning;
(ii) how enhanced flows altered stream metabolism across the river system; and (iii) how
macroinvertebrate feeding group compositions changed in response to enhanced flows.
As in Chapter II, I used linear mixed effects and random forest models to determine how ecosystem functioning responded to a suite of flow metrics. For ecosystem metabolism, I used the single-station open diel oxygen method to calculate differences in dissolved oxygen (mg/l) concentrations between day and night. Lastly, I used bar plots and linear mixed effects to investigate changes in feeding group compositions. I hypothesized that (i) enhanced flows would suppress both chlorophyll-a growth and leaf breakdown; (ii) enhanced flows would impact gross primary production more severely than ecosystem respiration; and (iii) enhanced flows would weaken preexisting spatial gradients of macroinvertebrate feeding groups by uniformly selecting for more tolerant taxa.
CHAPTER II

THE EFFECTS OF ENHANCED FLOWS ON MACROINVERTEBRATE COMMUNITY STRUCTURE IN SIXTH WATER CREEK AND DIAMOND FORK RIVER

Introduction

Aquatic macroinvertebrates have long been recognized as integral to riverine ecosystem health. In addition to comprising a major source of food for higher trophic levels, macroinvertebrates are bio-indicators of water quality and perform vital roles in energy cycling (Wallace & Webster, 1996). While many physical variables of rivers can determine the structure of macroinvertebrate communities in the benthos, arguably the most influential are substrate, temperature and flow (Allan, 1995). In general, stabilized substrate with ample organic detritus supports the highest abundance and diversity of macroinvertebrates (Allan, 1995; Wallace, 1997). Heterogeneous substrate templates with a variety of particle sizes may also provide refugia for macroinvertebrates from predation and hydraulic stress (Borchardt, 1993; Lancaster & Hildrew, 1993).

Comparatively, temperature influences benthic communities across broader spatial scales, as it sets distributional boundaries that are unique to each taxon. Species turnover is largely associated with thermal gradients in river systems, although local geomorphic contexts may cause abrupt and irregular transitions between benthic communities (Allan, 1995; Montgomery, 1999). Temperature also provides cues for hatching and emergence times and regulates the fecundity and body sizes of many taxa (Huryn & Wallace, 2000). For example, *Ephemerella* mayflies emerging from a cold-water tributary were nearly twice the mass of their counterparts in a nearby warm-water tributary of the same river.
system (Vannote & Sweeney, 1980). Lastly, dissolved oxygen concentrations - which are a limiting factor for pollution-sensitive taxa belonging to the mayfly (Ephemeroptera), stonefly (Plecoptera) and caddisfly (Trichoptera) orders - are inversely related to temperature (Allan, 1995). However, both substrate and temperature are in many ways dependent on flow, the ‘master variable’ that exerts a constant physical pressure on riverine communities (Poff et al., 1997).

Each macroinvertebrate taxon is specialized to live within a particular range of flows (i.e. functional niche). Filter feeders such as black flies (Simuliidae) and net-spinning caddisflies (Hydropsychidae) thrive in fast-flowing waters with high organic matter transport rates (Dewson et al., 2007), while other taxa such as Chironomid midges and snails are better suited to low velocity conditions (James et al., 2007). This spectrum of flow tolerances in aquatic macroinvertebrates has implications for community structure. For example, flow regimes with high disturbance frequencies can favor taxa with adaptations that allow for persistence, such as small body size, accelerated development, and clinging strategies (Poff & Ward, 1989; Huryn & Wallace, 2000). Moreover, flow arranges the matrix of suitable habitat and is indirectly related to variables such as temperature and dissolved oxygen. This is exemplified in the marked changes that flow reduction can bring to substrate, water quality, primary production and macroinvertebrates (Dewson et al., 2007). Reduced velocities are associated with increased benthic sedimentation, which can blanket heterogeneous habitats, clog interstitial spaces, and diminish taxonomic richness (Jones et al., 2012; Rolls et al., 2012). As water depths decrease with reduced velocities, in-stream temperatures can rise, which may promote the growth of filamentous algal mats that are less palatable to
macroinvertebrates than diatoms and periphyton (Suren et al., 2003; Dewson et al., 2007). Given the complex linkages between environmental variables, it is challenging for aquatic ecologists to develop general rules for flow’s influence on benthic communities. Nevertheless, there have been many recent efforts to establish correlations between macroinvertebrate metrics and flow alterations that can be applied across river systems.

There is evidence that the biological integrity of macroinvertebrate communities is correlated to the degree of flow alteration (Poff & Zimmerman et al., 2010; Carlisle et al. 2012). Common measures of macroinvertebrate community health include the relative abundances of Ephemeroptera, Plecoptera and Trichoptera orders (EPT), diversity indices, and tolerance indices such as the Hilsenhoff Biotic Index (HBI) (Kenny et al., 2009). In a recent study spanning 111 sites across the western United States, the upper limits of EPT abundance and richness were lowered as maximum flow and flow variation increased. Contrastingly, increases to these same flow metrics raised the lower limits of non-insect and tolerant taxa proportions within benthic communities (Konrad et al., 2008). Expanding on these results, Carlisle et al. (2012) found that augmented summer baseflows, depleted winter baseflows and daily to monthly flow variation were strongly correlated with declines in EPT richness and taxonomic richness. Both studies demonstrated that subsets of macroinvertebrate assemblages have differing responses to the same flow events, while broader macroinvertebrate metrics such as benthic density are less affected by streamflow alterations (Konrad et al., 2008; Carlisle et al., 2012). The weak responses of benthic density may be due to species replacement, where losses of sensitive taxa are compensated by gains of taxa with favored traits (i.e. faster growth rates, multivoltinism) (Brittain & Saltveit, 1989; Dewson et al., 2007). I hypothesized
that macroinvertebrate community health metrics would display negative correlations with flow metrics in SXW Creek and DF River, while benthic density would be less affected by enhanced flows due to species replacement.

The responses of benthic communities to flow alteration can be better understood by investigations of macroinvertebrate drift. In river systems, macroinvertebrate drift is integral to the recolonization of benthic communities and the transfer of energy to higher trophic levels (Brittain & Eikeland, 1988). Macroinvertebrate drift exhibits natural patterns such as seasonality and diel periodicity, and may further be influenced by flow alterations (Brittain & Eikeland, 1988). Sudden flow increases can dislodge organisms through bed mobilization and lead to severe, short-term reductions in benthic biomass (Bunn & Arthington, 2002). While such flow events certainly impact the benthic community as a whole, taxon-specific behavioral and morphological characteristics can lead to differential rates of dislodgement and population recovery. Clingers and filter feeders (e.g. Simuliidae) may be particularly resilient to dislodgement under flow pulses and high flow variation (Kennedy et al., 2016); contrastingly, the abundance of swimmer and collector-gatherer taxa (e.g. Ephemeroptera) in drift often increases with discharge (Kennedy et al., 2014; Rader, 1997). Moreover, while taxa that are well adapted for high frequencies of disturbance can exhibit rapid biomass recoveries, sensitive taxa with high drift propensities commonly experience sustained population reductions after high flow events (Vinson, 2001; Cross et al., 2011). Finally, invertebrates also deliberately enter the water column (i.e. ‘active drift’) in response to changes in predation intensity and resource availability; these rates of active drift may be altered by flow reductions and flow increases alike (James et al., 2007).
Drift communities are inherently subsets of benthic communities and are thus directly determined by the density of organisms in the benthos (O’Hop & Wallace, 1983; Turner & Williams, 2000; Kennedy et al., 2014). For example, following hydropeaking at Glen Canyon Dam, drift densities of amphipods, New Zealand mud snails, Simuliidae and Chironomidae in the Colorado River were proportional to their benthic densities (Kennedy et al., 2014). Yet other studies have found that the compositions and densities of drift communities in altered flow regimes were not predicted by the composition and density of the benthos (Hildebrand, 1974; Tonkin & Death, 2013). This suggests that density-independent factors such as sedimentation and resource depletion may also be strong drivers of drift rates (Rowe & Richardson, 2001; Larsen & Ormerod, 2010).

However, there is evidence that benthic density is a primary determinant of drift densities at seasonal timescales, while density-independent factors may cause drift variation at shorter timescales (Kennedy et al., 2014). Since I collected my data across seasonal timescales, I hypothesized that the densities of drift and benthic communities would be correlated in SXW Creek and DF River under both natural and enhanced flows. Although sudden flow increases can result in immediate relocation of benthic biomass into the water column, I expected flow to be only weakly associated with drift densities due to lag times between the start of high flow events and the start of my sampling events. Lastly, I expected that the composition of drift and benthic communities would also be correlated, and thus, that tolerant taxa in drift would increase under enhanced flows.

Macroinvertebrate drift is also the primary means of dispersal in river systems, linking local communities within the larger metacommunity (Leibold, 2004). Investigations into the ecological distances (or dis/similarities) between these local
communities can provide insight into $\beta$-diversity in river systems. Although there are several working definitions of $\beta$-diversity in the field of ecology, $\beta$-diversity can generally be understood as the variation in species compositions between sites (Legendre et al., 2008; Anderson et al., 2011). In river systems, benthic communities exhibit marked species turnover along physical gradients such as temperature, channel width, and substrate (Vannote et al., 1980; Gutiérrez-Cánovas et al., 2013). The rates at which these communities change across space and time are influenced by multi-scale factors. Across broader spatial scales, dispersal limitation and harsh environmental conditions may constrain both local ($\alpha$) diversity and $\beta$-diversity (Brown & Swan, 2010; Tonkin et al., 2014). Within local communities, disturbance frequencies (i.e. bed-mobilizing flows) and resource availability (i.e. primary production) can interact to generate distinct competitive outcomes that determine taxonomic richness (Huston, 1979; McCabe & Gotelli, 2000; Tonkin & Death, 2013).

System-wide declines in $\alpha$-diversity can result in biological simplification and declines in $\beta$-diversity in river systems. Given that diversity is often associated with functional redundancy, changes in $\alpha$- and $\beta$-diversity have strong implications for ecosystem health. Less diverse communities may be less able to perform important ecosystem functions, as losses of species with certain functional roles might not be compensated by equivalent species (Walker, 1992). I hypothesized that enhanced flows (i.e. high spring runoff, mandated flow requirements) would increase community similarity across the river by reducing the abundances of less common, sensitive taxa and increasing the abundances of more common, tolerant taxa. Particularly, I expected
communities in SXW Creek and DF River to become more homogenized under enhanced flows than they were under natural flow conditions.

In summary, my objectives for Chapter II are to: 1) determine how benthic community health and density are affected by enhanced flows in SXW Creek and DF River, 2) determine whether the density and composition of benthic and drift communities are correlated, and 3) determine how the similarity of communities across space and time is affected by enhanced flows.

**Methods**

**Background**

Diamond Fork River and its major tributary Sixth Water Creek are a river system in Utah County, UT, that drains approximately 404 square kilometers of mountainous terrain in the Wasatch Range (Fig. 1). Sixth Water (SXW) Creek is a relatively narrow headwater stream that passes through confined and partially confined valley settings until its confluence with Diamond Fork (DF) River. Its channel is predominantly composed of bedrock steps and boulders, and its reaches are punctuated with pools and beaver dams (Wilcock et al., 2018). Below the SXW and DF River confluence, DF River passes through a relatively flatter alluvial valley for about 17.7 kilometers before emptying into Spanish Fork River. This segment (Lower Diamond Fork) is less confined than SXW Creek, allowing for more active channel morphologies and floodplain development. The segment of DF River above the confluence (Upper Diamond Fork) is a sinuous headwater reach with significant canopy cover of willows (Salix spp.) and maples (Acer spp.). The river system has recently been a restoration focus of the Utah Reclamation Mitigation and Conservation Commission (URMCC), as it supports populations of game fish species
such as brown trout (*Salmo trutta*) and the endemic Bonneville cutthroat trout (*Oncorhynchus clarki utah*).

The SXW Creek and DF River system has experienced a long history of anthropogenically altered flow regimes. As early as 1913, trans-basin water imports have been conveyed through the Strawberry Tunnel pipeline and sent through SXW Creek and DF River for agricultural uses along the Wasatch Front. Until 2004, management agencies annually sustained augmented baseflows throughout the 140-day irrigation season. These augmented baseflows reached as high as 450 cubic feet per second (cfs) in Lower Diamond Fork (LDF) River – over 350 cfs greater than peak flows in the summer of 2016, a dry year with minimal spring runoff (Mitigation Commission, 2000). These augmented baseflows caused significant channel widening and incision, altered the

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**Fig. 1** Map of the Diamond Fork River watershed and the nine sampling sites used in this research.
river’s sediment transport regimes, and reduced habitat complexity and aquatic diversity (Mitigation Commission, 2000). In 1992, the US Congress enacted the Central Utah Project Completion Act (CUPCA), which permitted the construction of the Diamond Fork Pipeline. The current Diamond Fork Pipeline bypasses SXW Creek and DF River, delivering the majority of irrigation flow imports directly into Spanish Fork River (BIO-West, 2007). In 2004, CUPCA also established mandated flow requirements with the intention of maintaining optimal thermal conditions for trout populations. Presently, SXW Creek has mandated winter flows of 25cfs and summer flows of 32cfs, while LDF River has mandated winter flows of 60cfs and summer flows of 80cfs (BIO-West, 2012).

The URMCC is currently considering a removal or reduction of these mandated flow requirements. Previous sampling efforts of the ecological consulting company BIO-West, Inc. have indicated that the mandated flow regime may be inhibiting ecosystem recovery (BIO-West, 2012). BIO-West concluded that mandated flows were increasing sediment transport rates, promoting sedimentation and embeddedness in LDF River, and decreasing taxa richness in macroinvertebrate communities across time. Building on this baseline of data, the URMMC is now collaborating with Utah State University scientists to further assess how the mandated flow regime is impacting geomorphological processes, ecosystem functioning and biological communities.

Data Collection

To examine the effects of flow on community structure in the SXW Creek and DF River system, I collected data on benthic and drift macroinvertebrate communities in spring to fall of 2016 and 2017. The spatial level of my data structure was comprised of nine riffle sites across the continuum of the river system. Four of these sites were located
on SXW Creek and ranged from 13.07 to 0.12 kilometers above the tributary’s confluence with DF River. On DF River, two sites were located above the confluence and were unaffected by experimental flow regimes. The remaining three sites below the confluence represented the geomorphically dynamic segment of the river system that experienced the highest increases in flow. During the 2016 sampling season, baseflows were reduced to levels substantially below the requirements of CUPCA, allowing river conditions to become closer to their presumed historical conditions. Additionally, 2016 spring peak flows were minimal in both SXW Creek and DF River. The 2017 flow regime followed the requirements of 32cfs in SXW Creek and 80cfs in DF River. The river system also experienced high spring runoffs in 2017 that were sustained through April and June sampling events. USGS stream gages recorded peaks of 78.5cfs at Syar Tunnel (SXW Creek) on April 19, 2017 and 255cfs at Red Hollow (LDF River) on May 8, 2017 (Figs. 2, 3).

I collected one drift sample and three benthic samples at each riffle site. The drift samples were obtained by pounding two 300mm * 300mm, 150-micron mesh drift nets into the streambed at approximately 1/3 of the wetted channel width away from each bank and removing the nets after two hours. I ensured that my drift samples were only collected during daylight hours so as to limit any noise associated with diel variation in drift rates. The three benthic replicates were obtained by placing 300mm * 300mm Surber nets onto the streambed in river center and disturbing the substrate within the Surber’s frames. All samples were preserved in 70% ethyl alcohol. In the lab, I identified all insects to at least the family level and non-insects to at least the order level. Beginning with October 2016 samples, I identified all Ephemeroptera, Plecoptera, and Trichoptera
**Fig. 2** Daily flows (cfs) in SXW Creek as recorded by the USGS stream gage at Syar Tunnel, with orange representing 2016 and red representing 2017.

**Fig. 3** Daily flows (cfs) in LDF River as recorded by the USGS stream gage at Red Hollow, with orange representing 2016 and red representing 2017.
(EPT) to genus using the taxonomic keys provided in Merritt & Cummins (1996). I utilized a sub-sampling technique developed by the National Aquatic Monitoring Center, in which subsets of the sample are picked through until one reaches a fixed count of 600 – 800 organisms (Vinson & Hawkins, 1996).

My 2016 – 2017 benthic macroinvertebrate data were supplemented by data collected by BIO-West in 2005 – 2007 and 2012. They sampled from seven of my nine sites over this time period; only the two confluence sites (3FDF and 3F6W) were not included in their efforts. While BIO-West’s methods were generally compatible with mine, they used a 250-micron Hess type (0.086m²) bottom sampler to obtain their benthic replicates (BIO-West, 2013). They also did not employ the same sub-sampling techniques; thus, many of their final counts numbered in the 1000s. I controlled for these differences through several procedures. First, I standardized the areas of both Hess nets and Surber nets to m² to obtain density estimates. Additionally, for my community composition metrics, I generated random subsets of 700 organisms from BIO-West samples containing >800 organisms in R version 3.4.2 (R Core Team, 2017).

**Benthic Density and Community Composition Analyses**

I used linear mixed effects models and took an information theoretics approach to determine whether relationships existed between various flow metrics and five benthic response variables. Linear mixed effects (LME) modeling is an expansion of regression analysis that contains both fixed and random effects. LME modeling is best suited for hierarchical data structures typical of repeated measure or longitudinal studies, as it is able to account for variability from higher levels of the data (e.g. sample site, year) (Zuur et al., 2007). It accomplishes this by establishing these higher levels as random effects
and assuming that the variation within these groups conform to a normal distribution. After controlling for this variability, LME models are then able to determine general relationships between the response variable and the fixed effects (i.e. variables of interest) (Zuur et al., 2007).

The response variables in my LME models included: (1) density of organisms in the benthos per square meter; (2) the proportion of sampled taxa belonging to mayfly, stonefly and caddisfly (EPT) families; (3) richness, defined as the number of families within a sample; (4) Hilsenhoff Biotic Index (HBI) scores, which measure the pollution tolerances of taxa within a community; and (5) Simpson’s Diversity Index scores. While EPT taxa proportions and richness only consider the number of taxa present within the sampled area, the Hilsenhoff and Simpson indices account for both richness and evenness when assessing community health.

There exists a multitude of streamflow metrics that one may use to quantify components of a river’s flow regime (Poff et al., 1997; Konrad et al., 2008; Wenger et al., 2010). In river biomonitoring, selection of the most ecologically relevant streamflow metrics depends on the characteristics of the study system, the experimental design, and one’s specific research questions. For my LME models, I decided to use (1) mean monthly flow (MMF); (2) the coefficient of variation for MMF (CVmmf); and (3) the maximum daily flow rate $Q$ within 15 and 30 days of sample events ($Q_{\text{max15}}$, $Q_{\text{max30}}$) for my fixed effects. I selected MMF because it is a common metric that represents seasonal changes in flow (e.g. spring runoff and summer recession) (Carlisle et al., 2012); additionally, I found it appropriate to use monthly as opposed to longer timespans due to the two-month intervals between many sampling events. I calculated MMF by
averaging daily flow rates from the 30 days prior to the date that a sample was collected. I selected CVmmf to represent flow variation in this river system, as high temporal variation in flow has been found to disrupt life-history events (e.g. hatching, egg-laying) and deleteriously impact benthic community health (Poff & Ward, 1989; Konrad et al. 2008; Kennedy et al., 2016). I calculated CVmmf by dividing the standard deviation of daily flows by the mean of daily flows 30 days prior to each sampling event, and multiplying the quotient by 100. Finally, I selected maximum flow rate $Q$ to capture high-intensity, bed-mobilizing peak flow events that would otherwise be dampened in mean flow estimates. Correlation tests revealed that $Q_{\text{max}15}$ and 30 (as opposed to $Q_{\text{max}7}$ and 90) were repeatedly the most strongly correlated with my benthic response variables.

I performed log or square root transformations of my response variables and fixed effects and removed outlying or missing data points whenever necessary. Due to the wide variance of flows across the river system, I built separate models for SXW Creek, Upper Diamond Fork (UDF) River and Lower Diamond Fork (LDF) River. Benthic density models for each river segment only featured data from 2012, 2016 and 2017. Contrastingly, for my four remaining benthic response variables, I built models for 2005 – 2017 data and for 2016 – 2017 data (Table 1). I did this to assess whether 2016 – 2017 temperature (C) and dissolved oxygen (mg/l) data improved model fit if I included them as fixed effects.

For my richness, EPT taxa, and Simpson’s Diversity Index models, I selected site as a non-nested random effect and season within year as a nested random effect. Bartlett’s tests revealed the variances in these response variables to violate the law of
Table 1  The suite of linear mixed effects models constructed to test for relationships between flow and five benthic response variables. Here, EPT refers to the proportion of EPT taxa in a sample; Rich refer to the richness (# of families) in a sample, HBI refers to the Hilsenhoff Biotic Index, and SDI refers to Simpson’s Diversity Index. I did not build any 2016 – 2017 models for UDF River due to a paucity of data points.

<table>
<thead>
<tr>
<th>River</th>
<th>Density</th>
<th>EPT 05 - 17</th>
<th>EPT 16 - 17</th>
<th>Rich 05 - 17</th>
<th>Rich 16 - 17</th>
<th>HBI 05 - 17</th>
<th>HBI 16 - 17</th>
<th>SDI 05 - 17</th>
<th>SDI 16 - 17</th>
</tr>
</thead>
<tbody>
<tr>
<td>SXW Creek</td>
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<td>UDF River</td>
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<tr>
<td>LDF River</td>
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</table>

Homogeneity across space and time, validating the need for my random effect selections.

The structures of the null random intercept models for these response variables were:

\[ \hat{y}_i = \beta_{0j[i]}k[i] + \varepsilon_{j[i]}k[i] \]

\[ \beta_{0j} \sim N(\mu_{\beta_0}, \sigma_{\beta_0}^2), \text{ for } j = 1, \ldots, J \text{ site} \]

\[ \beta_{ok/l} \sim N(\mu_{\beta_0}, \sigma_{\beta_0}^2), \text{ for } k = 1, \ldots, K \text{ season within } l \text{ year} \]

\[ \varepsilon_{j[i]}k[i] \sim N(0, \sigma^2) \]

where \( \hat{y}_i \) is the response variable at observation \( i \), \( \beta_{0j[i]} \) is the intercept for site \( j \), \( \beta_{ok[i]} \) is the intercept for season \( k \) within \( l \) year, and \( N(\mu, \sigma^2) \) denotes a normal distribution with mean \( \mu \) and variance \( \sigma^2 \) around intercept \( \beta_0 \). Additionally, density and HBI scores of my sampled communities displayed strong unimodal trends across the sampling seasons.

Thus, for my density and HBI models, I included a quadratic term for day of year (DOY)
in my fixed effects and omitted the nested random effect of season. The structures of my null random intercept models for density and HBI were:

\[\hat{y}_i = \beta_{0j[i]k[i]} + \beta_1 x_i + \beta_2 x_i + \epsilon_{j[i]k[i]}\]

\[\beta_{0j} \sim N(\mu_{\beta_0}, \sigma^2_{\beta_0}), \text{ for } j = 1, \ldots, J \text{ site}\]

\[\beta_{0k} \sim N(\mu_{\beta_0}, \sigma^2_{\beta_0}), \text{ for } k\beta_{0j[i]k[i]} = 1, \ldots, K \text{ year}\]

\[\epsilon_{j[i]k[i]} \sim N(0, \sigma^2_{\epsilon})\]

This structure is similar to that of the previous models, except that \(\beta_{0k[i]}\) is now the intercept for year \(k\), \(\beta_1 x_i\) is observation \(i\) across day of year (DOY), and \(\beta_2 x_i\) is observation \(i\) across DOY².

To arrive at the optimal random effects structures, I used Bayesian information criterion (BIC), a method of weighing the likelihoods of a suite of candidate models that accounts for the number of parameters in a model and the sample size. In mathematical terms, \(\text{BIC} = -2\ell - K \log(n)\), where \(\ell\) is the likelihood function, \(K\) is the number of parameters and \(n\) is the sample size (Posada & Buckley, 2004). Additionally, I used Restricted Maximum Estimated Likelihood (REML) and considered \(\Delta \geq 4\) BIC score improvement as the threshold for a significant increase in model fit (Gelman & Hill, 2006). After selecting the random effects structures of the models with the lowest BIC scores, I determined the fixed effects of my models with a forward stepwise selection procedure. Here I used BIC, Maximum Likelihood (ML) and a \(\Delta \geq 4\) to compare full models with the selected random effect structures to null models with identical random effects. All of these linear mixed effects modeling analyses were performed using packages “lme4” and “arm” in R version 3.4.3 (R Core Team, 2017).
Regression analyses are predicated on the assumption of linear relationships (Zuur et al., 2007). However, I could not be certain that my observations conformed to this assumption. I employed random forest (RF) models to address this uncertainty and also to validate the accuracy of my benthic mixed effects models. Random forest models have several advantages over classical regression analyses that make them suitable for interpreting complex interactions between variables. First, RF models not make assumptions about the form of the relationship between a response and a predictor variable (Breiman, 2001). Additionally, they are non-parametric and thus do not rely on normal distributions (Cutler et al., 2007).

RF models are a form of ensemble learning, where a large number of classification or regression trees are grown from a training set of observations. At each step in the growth of a tree, the algorithm selects a value of a predictor variable that splits the training set into two new subsets, or nodes. These two nodes are composed of data points whose associated predictor variable values are either greater or lesser than the value at the split. With each successive split, the data points in a node become increasingly homogenous until maximum homogeneity is reached (Breiman, 1999). What differentiates RF models from earlier regression tree methods is that each tree begins with a bootstrapped sample (typically 63%) of the original observations, leaving behind a subset of “out of bag” observations. At each split, only a random subset of the predictor variables is considered, thus avoiding high correlation between trees. Eventually, each fully-grown tree predicts the values of the out-of-bag observations, and the final calculated values of the observations are selected by the majority vote of predictions (Breiman, 2001; Cutler et al., 2007). RF models provide several useful outputs: 1)
variable importance plots, in which the ranked importance of each variable is based on percent increases in mean square error of models with permuted out-of-bag data; and 2) partial dependence plots, which visually represent the relationships between predictor variables and the predicted values of a response variable (Cutler et al., 2007).

I constructed RF regression models for each of the five response variables previously used in linear mixed effects modeling. Again, SXW Creek, UDF River and LDF River each had their own separate suite of models, and every response variable except benthic density was tested across two time periods (2005 – 2017 and 2016 – 2017). I used the default 500 trees as well as the default percentage of predictor variables to consider at each split in a regression tree (p/3, where p is the number of variables). The predictor variables I included were: (1) mean monthly flow (MMF); (2) coefficient of variation for MMF (CVmmf); 3) the maximum daily volume of flow \( Q \) at 7, 15, 30, and 90-day time periods (\( Q_{max7, 15, 30, 90} \)); (4) year; (5) day of year (DOY); (6) elevation (m); and whenever possible, (7) temperature (°C) and (8) dissolved oxygen (mg/l).

To account for highly correlated predictor variables as well as nonessential predictor variables that generate noise, I used a variable reduction procedure developed by Christian Perry, a postdoctoral fellow at Utah State University. This procedure uses the results of variable importance plots to select and eliminate the least important predictor variable from each iteration. The output from this procedure is a more parsimonious RF regression model with a potentially higher \( R^2 \) value. My final variable importance plots and partial dependence plots consisted of the three variables remaining in our RF regression model after this reduction procedure. I measured final model performances with out-of-bag mean-square error and the percentage of variation
explained by each model. I performed these analyses using the “randomForest” package in R version 3.4.3 (R Core Team, 2017).

Drift Analyses

I used linear mixed effects models and took a hypothesis-driven approach to test whether a relationship existed between drift density (organisms per m$^2$) and benthic density (organisms per m$^2$). These models were relatively simple in comparison to my benthic density models, as I only included one response variable (drift density) and one predictor variable (benthic density). I constructed one system-wide model (i.e. all of SXW Creek and DF River) and separate models for SXW Creek and LDF River. For the system-wide model, I defined log-transformed drift density as a function of log-transformed benthic density while also accounting for the nested random effect of sample site within river and the non-nested random effect of sample year. Benthic density values were obtained by averaging the densities of the three Surber samples collected at the same sample site as the drift samples. The structure for my system-wide model was:

$$\hat{y}_i = \beta_{0j[i]} + \beta_1 x_i + \epsilon_{j[i]}$$

$$\beta_{0j} \sim N(\mu_{\beta_0}, \sigma_{\beta_0}^2), \text{ for } j = 1, \ldots, J \text{ site within } l \text{ river}$$

$$\beta_{0k} \sim N(\mu_{\beta_0}, \sigma_{\beta_0}^2), \text{ for } k = 1, \ldots, K \text{ year}$$

$$\epsilon_{j[i]} \sim N(0, \sigma_{\epsilon}^2)$$

where $\hat{y}_i$ is log drift abundance at observation $i$, $\beta_{0j[i]}$ is the intercept for site $j$ within $l$ river, $\beta_{0k[i]}$ is the intercept for year $k$, $\beta_1 x_i$ is observation $i$ across log-transformed benthic density, and $N(\mu, \sigma_{\epsilon}^2)$ denotes a normal distribution with mean $\mu$ and variance $\sigma^2$
around intercept $\beta_0$. I compared this system-wide model to the intercept-only null model that defined log drift abundance as a function of the intercept.

My full models for SXW Creek and LDF River defined log-transformed drift density as the function of log-transformed benthic density while also accounting for the non-nested random effects of sample site and sample year. I then compared these full models to intercept-only null models that defined log-transformed drift density as a function of the intercept. The structures of these full models and intercept-only null models were identical to their counterparts in the system-wide analysis, with the exception that this time $j$ was a non-nested site, not a site nested within a year. Additionally, a square-root transformation of benthic density was necessary for the LDF River model, rather than a log transformation. For the system-wide, SXW Creek and LDF River models, I considered $\Delta \geq 4$ BIC score improvements over the intercept-only null models to indicate statistically significant increases in model performance (Gelman & Hill, 2006). These linear mixed effects modeling analyses were performed using packages “lme4” and “arm” in R version 3.4.3 (R Core Team, 2017).

My omission of flow metrics and seasonality from these drift models warrant further explanation. As discussed earlier, there is evidence that drift density in rivers is strongly correlated to the density of the benthos, although density-independent explanations such as resource availability have also been observed (Hildebran, 1974; Turner & Williams, 2000; Kennedy et al., 2014). Factors such as flow and seasonality primarily act as controls on benthic density, which in turn influences the number of organisms entering the water column. Preliminary analyses in SXW Creek and DF River revealed a hump-shaped relationship between benthic density and seasonality, in addition
to correlations between benthic density and flow metrics. Thus, I suspected that including seasonality and flow in my drift models would cause correlation issues and increase redundancy. Additionally, while my drift samples were inherently composed of organisms that had travelled from upstream of my sample sites, I could not assume how far these organisms had travelled. Although drift distances can vary greatly between taxa and across environmental contexts, some research has shown most drift distances to be between a few centimeters to tens of meters (Brittain & Eikeland, 1988). Thus, I made the conservative assumption that drift density would be more correlated to the density of the same sample site rather than the density of the nearest upstream site.

*Community Similarity*

I used non-metric multidimensional scaling (NMDS), permutational multivariate analysis of variance (PERMANOVA) and Similarity Percentage (SIMPER) analyses to assess how system-wide community similarity changed between 2016 and 2017. NMDS is an ordination method that visualizes the ranked distances between communities by reducing a multi-dimensional dataset to fewer dimensions. NMDS searches for an optimal arrangement of communities on a $k$-dimensional plane and selects the solution that most minimizes stress (i.e. departure from a monotonic relationship between the distances in the original multi-dimensional dataset and the distances in the new $k$-dimensional dataset) (Lattin et al., 2003). NMDS has several advantages over other common ordination techniques. First, it does not assume strong linear relationships among variables, as does Principal Coordinates Analyses. Second, its use of ranked distances reduces transformation problems associated with Euclidean distances (Holland, strata.uga.edu). PERMANOVA is a non-parametric statistical test that is frequently
employed in conjunction with NMDS due to its competence with nested, random data structures and its ability to measure multiple response variables. While PERMANOVA is also capable of testing null hypotheses for two or more groups of communities, I mainly used it to understand how much variation in community similarity was being explained by each of my predictor variables (Anderson, 2017).

I produced NMDS plots for communities across the river system in all sampling months from 2016 to 2017, hypothesizing that the 2017 plots would reveal communities between SXW Creek and LDF Rivers to be more homogenized than they were in 2016. I also generated NMDS plots for SXW Creek and LDF River with benthic data from 2005 to 2017 to assess community changes within each river across larger timescales. Lastly, I plotted the predictor variables mean monthly flow (mmf), variation in mean monthly flow (CVmmf), elevation (elev), and when available, temperature in degrees Celcius (temp) and dissolved oxygen in mg/l (DO) to determine how each of these variables were influencing the distances between communities.

Lastly, I used SIMPER analyses to interpret the results of NMDS and PERMANOVA. SIMPER analyses break down the Bray-Curtis matrices underlying NMDS ordinations and determine the average percent contributions of taxa to dissimilarities between two groups (Clarke, 1993). I performed SIMPER analyses between three LDF River sites (BMH, DFC and MO) and three SXW Creek sites (USW, RC, BST) in 2016 and 2017 to compare the number of significant taxa contributions to between-river dissimilarity in both years. Additionally, I performed separate analyses for SXW Creek and LDF River, comparing communities between the 2016 and 2017
sampling months (April, June, August) to assess how the relative abundances of taxa in these rivers changed from one sampling year to the next.

**Results**

*Benthic Density and Community Composition Analyses*

Overall, I found that models with flow metrics performed significantly better than intercept-only null models for (1) benthic density in UDF and LDF Rivers, (2) richness in UDF and LDF Rivers, and (3) Hilsenhoff Biotic Index (HBI) scores in LDF River. Contrastingly, there were no models with improved performances over intercept-only null models for any of the five benthic response variables in SXW Creek. Although I observed significant increases in benthic density and HBI scores and significant declines in Simpson’s Diversity Index scores between 2016 and 2017 (Fig. 4), these changes were not explained by any of my predictor variables, including temperature (°C) or dissolved oxygen (mg/l). Unpaired Student’s t-tests showed that between 2016 and 2017,

![Box plots of benthic density (left) and Simpson’s Diversity Index (right) in SXW Creek in 2016 and 2017. Each box represents data from all four SXW Creek sites in April, June and August of that year.](image)
mean density increased from 16,707 to 34,894 (P = 0.0013) the mean HBI score increased from 4.83 to 5.08 (P = 0.042), and the mean Simpson's Diversity Index score decreased from 0.696 to 0.566 (P = 0.002) in SXW Creek.

The final 2012 – 2017 benthic density models for UDF and LDF River each had BIC values that were improvements over those of their respective null models by δ ≥ 4. The addition of log-transformed mean monthly flow (logMMF) to the UDF River intercept-only null model decreased the BIC value by 7.18. For LDF River, adding logMMF and the interaction of logMMF with day of year decreased the BIC value by 19.39. The notations for each of these final density models are:

1) Density in UDF River:

\[
\hat{y}_i = 158.82_{\text{site}[i]}(\text{season/year}[i]) + -24.88 \times \log \text{MMF} + \epsilon_{\text{site}[i]k[i]} \\
\beta_0_{\text{site}[i]} \sim N(158.82, 22.99^2) \\
\beta_0_{\text{season/year}[i]} \sim N(158.82, 11.9^2) \\
\epsilon_{\text{site}[i]k[i]} \sim N(0, 27.02^2)
\]

2) Density in LDF River:

\[
\hat{y}_i = -630.56_{\text{site}[i]}(\text{year}[i]) + 16.62 \times \log \text{MMF} + 5.87 \times \text{DOY} + -212.83 \times z\text{DOY}^2 + -0.499 \times \log \text{MMF}:\text{DOY} + \epsilon_{\text{site}[i]k[i]} \\
\beta_0_{\text{site}[i]} \sim N(-630.56, 0.000037^2) \\
\beta_0_{\text{season/year}[i]} \sim N(158.82, 13.69^2) \\
\epsilon_{\text{site}[i]k[i]} \sim N(0, 33.26^2)
\]

Where \(\hat{y}_i\) is benthic density in 1) UDF River or 2) LDF River; the fixed effects are 1) logMMF in UDF River or 2) logMMF, DOY, zDOY^2 and the interaction term
logMMF:DOY in LDF River; the random effects of 1) site and season within year are the $j^{th}$ and $k^{th}$ within $l^{th}$ groupings in UDF River or 2) site and season are the $j^{th}$ and $k^{th}$ groupings in LDF River, and residual variance $\epsilon_{(j)(l)(k)(i)}$ is 1) 27.02$^2$ in UDF River or 2) 33.26$^2$ in LDF River.

I found that benthic density had negative correlations with mean monthly flow in both UDF and LDF River, even after accounting for spatial and temporal trends. Although there were low density values across the entire range of MMF in both models, high density values became more infrequent as MMF increased (Fig. 5). In UDF River, there appeared to be density values of 30,000 individuals per meter squared until 20cfs. Above 20cfs, there was a gap in the data; then beginning around 35cfs, density values were dramatically reduced. The final UDF River model did not have large explanatory power, as residual variance slightly increased from that of the null. Comparatively, the final LDF River model showed a more continuous decline in density as MMF increased, and residual variance was reduced by 23.03% from the null model to the final model (Fig. A1). These observed density responses likely accounted for the negative correlations between benthic richness and flow variables in Diamond Fork River. While my UDF and LDF richness models respectively had BIC improvements of 7.89 and 11.13 over their null models when Q-max flow variables were added, they only marginally decreased residual variance (1.69% and 3.96%, respectively). I attributed this to the fact that richness had moderate correlations with density in both rivers, with Pearson’s coefficients of 0.405 for UDF River and 0.329 for LDF River.
In LDF River, Hilsenhoff Biotic Index (HBI) scores were positively correlated with increases in 15-day maximum flow (Qmax15) between 2005 and 2017 (Fig. 9). The final random slope model featuring log-transformed Qmax15 (logQ15), DOY and a DOY quadratic term (zDOY²) as fixed effects had a BIC score improvement of 11.01 above a null model with only DOY and zDOY². However, residual variance did not decrease from the null model to the final model, suggesting that logQ15 improved model fit while not accounting for any leftover model uncertainty that could not be explained by DOY and zDOY². Additionally, the random effect of site explained little variance, as the three sites were tightly clustered around the grand mean (Fig. 6). The notation for the final random slope model of 2005 to 2017 HBI scores in LDF River is:

\[ \hat{y}_i = -4.934 + 1.128_{(site)[i]} \times \log Q15 + 0.024 \times DOY + -1.349 \times zDOY^2 + \epsilon_{(site)[i](year)[i]} \]
\[ \beta_{1(site)}[i] \sim N(1.128, 0.0237^2) \]
\[ \epsilon_{(site)[i](year)[i]} \sim N(0, 0.698^2) \]

Where \(\hat{y}_i\) is the Hilsenhoff Biotic Index score of the average benthic sample in LDF River, \(\log Q_{15}\), \(\text{DOY}\) and \(z\text{DOY}^2\) are the fixed effects, and the random effects of site and year are the \(j^{th}\) and \(k^{th}\) groupings, respectively, with a residual variance \(\epsilon_{j[i]k[i]}\) of 0.698².

Both benthic density and HBI scores in LDF River displayed unimodal curves across sampling season. To simultaneously assess the influence of flow while visualizing

**Fig. 6** Final random slope model for Hilsenhoff Biotic Index scores in LDF River from 2005 to 2017 (n = 106). The dashed lines represent sites (BMH = Below Monk’s Hollow, DFC = Diamond Fork Campground, MO = Motherload) and the solid line represents the grand mean.
these seasonal trends, I plotted benthic density and HBI scores across DOY. I then produced simulations depicting the response curves of benthic density and HBI scores across DOY if the flow metrics were held constant at their maximum and minimum observed observations (Figs. 7, 8). The minimum and maximum values of MMF were 37cfs and 167.7cfs, respectively, while the minimum and maximum values of Qmax15 were 41.8cfs and 209cfs. These simulations reveal that increases to mean monthly flow lower the unimodal curve of benthic density across the seasons, while increases to 15-day maximum flow raise the unimodal curve of HBI scores across the seasons.

**Fig. 7** Benthic density (organisms per m²) across day of year (DOY) in LDF River from 2012 to 2017 (n = 78). The black line represents the grand mean of my final model, while the red and blue lines represent simulations of benthic density across DOY at minimum (37cfs) and maximum (167.7cfs) mean monthly flow (MMF) observations in LDF River, respectively.
**Fig. 8** Hilsenhoff Biotic Index (HBI) scores (y-axis) across day of year (DOY) (x-axis) in LDF River from 2005 to 2012. The red and blue lines represent simulations of HBI scores across DOY at minimum (41.8cfs) and maximum (209cfs) Qmax15 values, respectively.

**Table 2** Water quality and degrees of organic pollution associated with Hilsenhoff Biotic Index (HBI) scores of benthic macroinvertebrate communities.

<table>
<thead>
<tr>
<th>HBI score</th>
<th>Water Quality</th>
<th>Degree of Organic Pollution</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 – 3.75</td>
<td>Excellent</td>
<td>Organic pollution unlikely</td>
</tr>
<tr>
<td>3.75 – 4.25</td>
<td>Very Good</td>
<td>Possible slight organic pollution</td>
</tr>
<tr>
<td>4.26 – 5.01</td>
<td>Good</td>
<td>Some organic pollution probable</td>
</tr>
<tr>
<td>5.01 – 5.75</td>
<td>Fair</td>
<td>Fairly substantial organic pollution likely</td>
</tr>
<tr>
<td>5.76 – 6.50</td>
<td>Fairly Poor</td>
<td>Substantial pollution likely</td>
</tr>
<tr>
<td>6.51 – 7.25</td>
<td>Poor</td>
<td>Very substantial pollution likely</td>
</tr>
<tr>
<td>7.26 - 10</td>
<td>Very Poor</td>
<td>Severe organic pollution likely</td>
</tr>
</tbody>
</table>
Many of the same variables selected as fixed effects in my LME models were selected as most influential for benthic density and HBI scores by random forest regressions. For 2012 – 2017 benthic density in LDF River, the three predictor variables selected by variable reduction procedures were day of year (DOY), temperature (°C) on the day of sampling (temp_day) and mean monthly flow (MMF) (Fig. 9). Together, DOY, temp_day and MMF explained 63.84% of the variance in the data. Partial dependence plots depicted benthic density as having an increasing unimodal relationship with DOY, an exponentially increasing relationship with temp_day, and an exponentially decreasing relationship with MMF (Fig. 10). Comparatively, variable reduction procedures for benthic density in SXW Creek selected DOY, elevation and maximum flow within 90 days of sampling (Qmax90) as the most influential variables, explaining 48% of variation. Here, the strongest trend to emerge was that of density increasing exponentially across the range of elevation (Fig. 11). Random forest results for the Hilsenhoff Biotic Index in SXW Creek were less clear, as HBI scores appeared to sharply decline across the range of Qmax7 while increasing slightly across Qmax30.

Random forest variable reduction procedures selected DOY, MMF and 30-day maximum flow (Qmax30) as the most influential variables for 2005 – 2017 HBI scores in LDF River, together explaining 49.4% of the variance (Fig. 12). Partial dependence plots depicted HBI scores as increasing and plateauing across the ranges of DOY, MMF and Qmax30 (Fig. 13). Overall, these random forest results agreed with the results of my mixed effects models, and indicate that the density of organisms and the proportions of sensitive taxa in the LDF River benthos are strongly influenced by season, flow metrics, and the interaction of season and flow metrics.
Fig. 9 Variable importance plot for benthic density in LDF River from 2012 to 2017. X-axis shows the percentage increase in a model’s mean squared error (%IncMSE) when values for a given variable are permuted. The three variables selected by the variable reduction procedure are ranked from most important (top) to least important (bottom).

Fig. 10 Partial dependence plots for benthic density (organisms per m²) in LDF River from 2012 to 2017. Plot show the predicted relationships between benthic density (y-axis) and the three most important predictor variables selected by random forest (x-axis).
Fig. 11 Partial dependence plots for benthic density (organisms per m$^2$) in SXW Creek from 2012 to 2017. Plots show the predicted relationships between benthic density (y-axis) and the three most important predictor variables selected by random forest (x-axis).

Fig. 12 Variable importance plot for Hilsenhoff Biotic Index (HBI) scores in LDF River from 2005 – 2017. X-axis shows the percentage increase in model mean squared error when values of each variable are permuted. The three variables selected by the variable reduction procedure are ranked from most important (top) to least important (bottom).
Fig. 13 Partial dependence plots for Hilsenhoff Biotic Index scores in LDF River from 2005 to 2017. Plots show the predicted relationships between HBI scores (y-axis) and the three most important predictor variables selected by random forest (x-axis).

*Drift Analyses*

I found that drift density was highly correlated with benthic density in my system-wide model as well as my separate models for SXW Creek and LDF River (Figs. 14, 15, 16). The final random-intercept, system-wide model defining log-transformed drift density as a function of log-transformed benthic density with year and site within river as random effects had a BIC score improvement of 37.25 over the corresponding null model. Additionally, the final system-wide model decreased residual variance by 46.7%, and the residuals displayed no trends when plotted against log-transformed benthic density (Fig. A2). This decrease in variance was primarily due to the addition of benthic density and not the random effect structure, as the relationship between drift density and
benthic density did not vary much between years or sites within rivers. The notation for this random-intercept system-wide model is:

\[
\hat{y}_i = -0.25 (\text{year})_{[i]} (\text{site/river})_{[i]} + 0.867 \times \log \text{density} + \epsilon_{(\text{year})[i](\text{site/river})[l]}
\]

\[
\beta_0(\text{year})_{[i]} \sim N(-0.25, 0)
\]

\[
\beta_0(\text{site/river})_{[i]} \sim N(-0.25, 0.108^2)
\]

\[
\epsilon_{(\text{year})[i](\text{site/river})[l]} \sim N(0, 0.904^2)
\]

Where \(\hat{y}_i\) is the log-transformed drift density (organisms per m\(^2\)), the fixed effect is log-transformed benthic density (log density), and the random effects of year and site within river are \(j\)th and \(k\) within \(l\)th groupings, with a residual variance \(\epsilon_{j[i]k/l[i]}\) of 0.904\(^2\).

**Fig. 14** Log-transformed drift density (organisms per m\(^2\)) (y-axis) across benthic density (organisms per m\(^2\)) (x-axis) in SXW Creek and DF River (\(n = 62\)). The black line represents the grand mean of the random-intercept, system-wide drift density model.
The final random-intercept drift density models for SXW Creek and LDF River both featured log-transformed benthic density as a fixed effect and site and year as random effects. In SXW Creek, the addition of benthic density resulted in a BIC score improvement of 7.3 and a decrease in residual variance by 29.31%. The increase in model fit for LDF River was even stronger with a BIC score improvement of 10.93 and a 71.1% decrease in residual variance (Fig. A3).

The higher leftover residual variance in SXW Creek did not appear to be accounted for by the random effects of year or site (Fig. 15). This suggests that there are likely other factors explaining variance in drift density that are unrelated to temporal and spatial gradients. Comparatively, in my final LDF River model, I observed wider between-site variance in drift density. Drift density displayed a decreasing downstream trend, with the highest abundances in Below Monk’s Hollow (BMH) site and the lowest abundances in the Motherload (MO) site (Fig. 16). Subsequent visualizations revealed that the entire river system exhibited this trend in 2016 and 2017, with drift densities generally decreasing alongside elevation from headwaters to mainstem sites (Fig. 17).

The strong correlation between drift and benthic density led me to suspect that decreases in the relative abundances of taxa in the benthic community would be reflected in the drift community. I did not find any significant differences in taxa proportions in drift samples from SXW Creek between 2016 and 2017. In LDF River, unpaired t-tests revealed that the percentage of Chironomidae midges in drift samples significantly increased from a mean of 11.4% in 2016 to a mean of 31.4% in 2017 (P = 0.046) (Fig. 18). Additionally, drift abundances of the caddisfly family Helicopsychidae significantly
Fig. 15 Log-transformed drift density (organisms per m$^2$) (y-axis) across benthic density (organisms per m$^2$) (x-axis) in SXW Creek (n = 28). The black line represents the grand mean of the random-intercept drift density model.

Fig. 16 Log-transformed drift density (organisms per m$^2$) (y-axis) across benthic density (organisms per m$^2$) (x-axis) in LDF River (n = 21). The black line represents the grand mean of the random-intercept drift density model and the dashed colored lines represent the sites.
**Fig. 17** Box plot of drift density (organisms per m$^2$) across an elevational gradient in SXW Creek and DF River from 2016 to 2017. From left to right, the river segments are SXW Creek (blue sites), UDF River (yellow sites), and LDF River (green sites).

**Fig. 18** Box plot of the proportions of organisms in LDF River drift samples (April – August) that are Chironomidae. The 2016 sampling year had minimal spring runoff and no mandated flow requirements, while 2017 had high spring runoff and mandated flow requirements.
decreased from 24.33 in 2016 to 1.56 in 2017 (P = 0.041). This decrease in Helicopsycheidae was reflected in a strong but non-significant 71% decrease in Trichoptera percentages in drift samples from LDF River in 2017 (P = 0.13). Lastly, there was a non-significant 60.85% decrease in overall LDF River drift density from 2016 to 2017 (P = 0.33). These dramatic but non-significant results are likely due to the low sample sizes of 2016 and 2017 drift samples (n = 9) that I used for comparison in my t-tests for LDF River.

Community Similarity

NMDS plots revealed that the river system had comparable seasonal trends of community similarity in 2016 and 2017. In both sampling years, communities formed distinct river clusters (SXW, UDF and LDF) in April, became more homogenized in June, and separated back into river clusters in August (Figs. A4 – A9). Additionally, my predictor variables had consistent influences on the spread of the data between the two years. Communities in SXW Creek were more closely grouped around the elevation vector, indicating elevation to be the most influential driver of community variance within that river segment. Comparatively, LDF River communities were more closely grouped around temperature, mean monthly flow (mmf) and variation in flow (CVmmf). Dissolved oxygen was generally insignificant in explaining community variance, and alternated between associations with SXW Creek and LDF River from month to month. PERMANOVA analyses revealed that these five predictor variables collectively explained an average of 45% of the variance in 2016 and 40% in 2017. Elevation and mean monthly flow were overall the most influential variables, each having significant P-
values (P < 0.05) every month. In 2016, elevation consistently explained the most variance, with an $R^2$ of 0.20 in April, 0.11 in June, and 0.21 in August. In April and June 2017, the two flow metrics (mmf and CVmmf) became the most important drivers of community variance before being surpassed by elevation again in August.

I additionally found that in 2017, communities within DF River were spread farther apart (i.e. more dissimilar) than they were in 2016. Qualitative comparisons of NMDS plots from each sampling year (Figs. 19, 20) revealed that in 2016, communities were tightly clustered by river system while exhibiting some overlap (Fig. 19). By contrast, 2017 communities in UDF and LDF River were scattered farther from one another and from the centroid of the data (Fig. 20). Analyses of group dispersion with the “betadisper” function in the R “vegan” package partially confirmed these qualitative assessments. April was the only month where the distance to the centroid for the average community was greater in 2017 (0.503 out of 1) than in 2016 (0.416 out of 1). In June and August, distances to the centroid were equivalent between the two sampling years.

NMDS plots of benthic data from 2005 – 2017 revealed distinct long-term trends in community similarity in SXW Creek and LDF River. Generally, communities in SXW Creek displayed the highest similarity with other communities from the same sample site (USW, RC, BST) regardless of the year they were collected; thus, there did not appear to be any conspicuous temporal shifts in community structure in this river segment between 2005 and 2017 (Fig. 21). Comparatively, communities from the LDF River sites Diamond Fork Campground (DFC) and Motherload (MO) exhibited strong within-year, rather than within-site, similarity trends (Fig. 22). While 2005 – 2012 communities in DFC and MO were clustered closely together, 2016 communities appeared to have
Fig. 19 NMDS plot of SXW Creek & DF River benthic communities in 2016. SXW Creek sites are in blue, UDF River sites are in yellow, and LDF River sites are in red. The five predictor variables are elevation (elev), coefficient of variation for mean monthly flow (CVmmf), mean monthly flow (mmf), temperature (temp) and dissolved oxygen (DO). $R^2 = 0.253$. 
Fig. 20 NMDS plot of SXW Creek & DF River benthic communities in 2017. SXW Creek sites are in blue, UDF River sites are in yellow, and LDF River sites are in red. The five predictor variables are elevation (elev), coefficient of variation for mean monthly flow (CVmmf), mean monthly flow (mmf), temperature (temp) and dissolved oxygen (DO). $R^2 = 0.336$. 
undergone significant changes in structure. This was evidenced in the migration of 2016 communities away from the cloud of 2005 – 2012 communities on the two-dimensional NMDS plane. By 2017, DFC and MO communities displayed significant dissimilarities to one another and to communities from all years prior. This may partly be due to the paucity of organisms in several benthic samples from April 2017. By August 2017, however, benthic samples had abundances comparable to those from earlier years. Thus, I inferred that changes in structure were at least partially responsible for the considerable ecological distances of 2017 communities from earlier sampling years.

![NMDS plot of benthic communities in three SXW Creek sites: Upper Sixth Water (USW), Ray’s Crossing (RC) and Below Syar Tunnel (BST). Plotted communities are comprised of samples from April and from the end of the sampling season of each year (2005 – 2012 = September, 2016 = October, 2017 = August). Elev R^2 = 0.139 (P < 0.001), mmf R^2 = 0.031 (P = 0.029), CVmmf R^2 = 0.045 (P = 0.006), total R^2 = 0.215.](image-url)
**Fig. 22** NMDS plot of benthic communities in two Lower Diamond Fork sites: Diamond Fork Campground (DFC) and Motherload (MO). Plotted communities are comprised of samples from April and from the end of the sampling season of each year (2005 = September, 2016 = October, 2017 = August). Elev $R^2 = 0.013$ (P = 0.53), mmf $R^2 = 0.10$ (P < 0.001), CVmmf $R^2 = 0.069$ (P < 0.001), total $R^2 = 0.185$.

SIMPER analyses provided evidence that communities across the river system, and particularly communities between SXW Creek and DF River, did not become more homogenized under the enhanced flow regime in 2017. While there were fewer taxa whose populations were significantly different between SXW Creek and LDF River in 2017, the cumulative contribution of these taxa to between-river dissimilarity was higher in 2017 (0.435) than in 2016 (0.385) (Table 3). In 2016, the highest contributors to Bray-Curtis dissimilarity scores between SXW Creek and LDF River were Chironomidae
Table 3 SIMPER analyses between SXW Creek and LDF River in 2016 and 2017. The Number of Taxa column shows the number of taxa that were significantly contributing (P < 0.05) to overall Bray-Curtis dissimilarities between the two river segments. The Combined Contribution column shows the combined proportional contribution of those taxa (out of 1) to between-group dissimilarity. The Top Three Taxa column shows the three taxa with the highest proportional contributions within that given year.

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of Taxa</th>
<th>Combined Contribution</th>
<th>Top Three Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016</td>
<td>22</td>
<td>0.385</td>
<td>Chironomidae, Glossosomatidae, Helicopsychidae</td>
</tr>
<tr>
<td>2017</td>
<td>18</td>
<td>0.435</td>
<td>Chironomidae, Elmidae, Uenoidae</td>
</tr>
</tbody>
</table>

midges and the caddisfly families Helicopsychidae and Glossosomatidae, whose populations were well established in LDF River. In 2017, the highest contributors were Chironomidae, Elmidae riffle beetles and Uenoidae, a caddisfly family restricted to the headwater reaches of the river system.

The most noticeable changes occurred within the communities in LDF River, which exhibited far more temporal variability than the relatively stable SXW Creek communities. In SXW Creek, most changes between 2016 and 2017 occurred within the populations of three dominant taxa – Chironomidae, Elmidae and Baetid mayflies (Table 4). In June 2017, the average sample abundance of Chironomidae populations nearly doubled, while the populations of Baetidae and Elmidae significantly decreased to below half of their respective June 2016 abundances. The populations of these taxa balance out again by August, suggesting that the observed differences in June 2016 and 2017 could have been due to either stochastic processes or to these populations rebounding after natural runoff. I additionally compared populations from the Upper Sixth Water (USW)
site between 2005 and 2017 – two years with roughly analogous spring and summer hydrographs. This SIMPER analysis revealed that the populations of dominant taxa in this headwater site (i.e. Baetidae, Chironomidae, Uenoidae, Elmidae) did not significantly differ in 2005 and 2017.

**Table 4** SIMPER analyses between 2016 and 2017 in SXW Creek. For each month, influential taxa with significant P-values are listed. The **Average** column shows the average contribution (out of 1) of that taxon to overall between-group dissimilarity, **2016** and **2017** show the average taxon abundances in each sampling year, and **P** shows the probability of getting a larger or equal average contribution in random permutation of the group factor. **Green** denotes Plecoptera and **Blue** denotes Ephemeroptera.

<table>
<thead>
<tr>
<th>River</th>
<th>Month</th>
<th>Taxa</th>
<th>Average</th>
<th>2016</th>
<th>2017</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>SXW</td>
<td>April</td>
<td>Perlodidae</td>
<td>0.010</td>
<td>7.75</td>
<td>2.67</td>
<td>0.039*</td>
</tr>
<tr>
<td>SXW</td>
<td>June</td>
<td>Chironomidae</td>
<td>0.182</td>
<td>285.0</td>
<td>492.5</td>
<td>0.001***</td>
</tr>
<tr>
<td>SXW</td>
<td>June</td>
<td>Baetidae</td>
<td>0.065</td>
<td>110.92</td>
<td>45.67</td>
<td>0.014**</td>
</tr>
<tr>
<td>SXW</td>
<td>June</td>
<td>Elmidae</td>
<td>0.028</td>
<td>68.67</td>
<td>27.5</td>
<td>0.009**</td>
</tr>
<tr>
<td>SXW</td>
<td>August</td>
<td>Elmidae</td>
<td>0.019</td>
<td>61.58</td>
<td>35.5</td>
<td>0.022*</td>
</tr>
<tr>
<td>SXW</td>
<td>August</td>
<td>Empididae</td>
<td>1.33</td>
<td>0.25</td>
<td>5.08</td>
<td>0.038*</td>
</tr>
</tbody>
</table>

SIMPER analyses of Diamond Fork River communities revealed more significant between-year differences in this river segment. In UDF River, the populations of Elmidae and several Ephemeroptera families significantly declined in April and June 2017 (Table A1). By August, however, some of their populations had rebounded and surpassed 2016 abundances. In contrast, LDF River displayed dramatic reductions in the abundances of the caddisfly families Helicopsychidae and Glossosomatidae that persisted across the entire 2017 sampling campaign (Table 5). Additionally, Elmidae populations were significantly reduced across all months in 2017.
Table 5  SIMPER analyses between 2016 and 2017 in LDF River. For each month, the three most influential taxa with significant P-values are listed. Blue denotes Ephemeroptera and red denotes Trichoptera.

<table>
<thead>
<tr>
<th>River</th>
<th>Month</th>
<th>Taxa</th>
<th>Average</th>
<th>2016</th>
<th>2017</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>LDF</td>
<td>April</td>
<td>Glossosomatidae</td>
<td>0.231</td>
<td>104.89</td>
<td>2.11</td>
<td>0.001***</td>
</tr>
<tr>
<td>LDF</td>
<td>April</td>
<td>Helicopsychidae</td>
<td>0.069</td>
<td>31.00</td>
<td>1.89</td>
<td>0.001***</td>
</tr>
<tr>
<td>LDF</td>
<td>April</td>
<td>Baetidae</td>
<td>0.065</td>
<td>26.56</td>
<td>5.33</td>
<td>0.010**</td>
</tr>
<tr>
<td>LDF</td>
<td>June</td>
<td>Elmidae</td>
<td>0.028</td>
<td>33.11</td>
<td>4.00</td>
<td>0.001***</td>
</tr>
<tr>
<td>LDF</td>
<td>June</td>
<td>Glossosomatidae</td>
<td>0.023</td>
<td>26.56</td>
<td>0.78</td>
<td>0.001***</td>
</tr>
<tr>
<td>LDF</td>
<td>June</td>
<td>Hydropsychidae</td>
<td>0.008</td>
<td>8.89</td>
<td>2.11</td>
<td>0.043*</td>
</tr>
<tr>
<td>LDF</td>
<td>August</td>
<td>Helicopsychidae</td>
<td>0.047</td>
<td>65.44</td>
<td>10.33</td>
<td>0.002**</td>
</tr>
<tr>
<td>LDF</td>
<td>August</td>
<td>Glossosomatidae</td>
<td>0.046</td>
<td>64.77</td>
<td>10.33</td>
<td>0.002**</td>
</tr>
<tr>
<td>LDF</td>
<td>August</td>
<td>Elmidae</td>
<td>0.013</td>
<td>22.00</td>
<td>6.78</td>
<td>0.006**</td>
</tr>
</tbody>
</table>

I compared LDF communities between 2007 and 2017 to examine whether the declines in Helicopsychidae and Glossosomatidae could be attributed to peak runoff alone of runoff compounded by mandated summer flow requirements of 60 – 80cfs. 2007 was the most suitable year for comparison, as it featured the same mandated summer flow requirements and a less extreme spring runoff event. In 2007, the highest recorded daily flow at Motherload was 118.9cfs compared to a highest daily flow of 328.9cfs in 2017. I found that the populations of Helicopsychidae and Glossosomatidae were barely established in LDF River in 2007; even their diminished 2017 populations were a significant increase over that year. Subsequent visualizations showed that the populations of these caddisfly families became prominent in LDF River anywhere between 2013 and 2016 and experienced sharp declines in 2017 (Fig. 23).

Discussion

Anthropogenic flow regimes are becoming an increasingly common feature of river systems in the 21st century, particularly in regions where human development is faced with sustained threats of water insecurity (Poff et al., 1997). Flow regimes associated with pipelines and dams can deleteriously impact river ecosystems through increasing or decreasing the frequencies of disturbances (Poff et al., 1997; Cortes et al., 2002; Biggs et al., 2005), altering thermal, nutrient and sediment regimes (Cortes et al., 2002; Grams & Schmidt, 2005; Dewson et al., 2007; Hall et al., 2015), and promoting invasive species and generalist taxa (Bunn & Arthington, 2002; Konrad et al., 2008; Poff & Zimmerman, 2010; Kennedy et al., 2016). To recommend restorative flow regimes for
degraded river systems, it will be necessary to have a more complete understanding of how aquatic communities are related to flow metrics across spatial and temporal scales.

In Chapter II, I sought to understand how benthic and drift macroinvertebrate communities are structured by flow metrics in the Sixth Water Creek and Diamond Fork River system. For each river segment, I analyzed how benthic density and community health responded to a range of natural and anthropogenic flows, while also investigating the relationships between benthic and drift communities. Additionally, I utilized long-term benthic data to assess how flow influenced benthic community similarities across spatial and temporal scales. My results provide insight into how flow non-uniformly affects benthic and drift communities across river continua, which has implications for both freshwater management and for future research on ecological processes such as community assembly.

There were noticeable differences in the responses of benthic communities to natural and anthropogenic flow increases between the SXW Creek tributary and the DF River mainstem. In SXW Creek, there were no flow variables selected by Bayesian Information Criterion (BIC) procedures that significantly improved model fit for the full suite of benthic density and community health metrics. Random forest regressions for SXW Creek explained 47.3% and 70.3% of variance for density and Hilsenhoff Biotic Index (HBI) scores, respectively. However, the only linear result that emerged from these regressions was a positive, exponential relationship between density and elevation. Comparatively, in the DF River mainstem, benthic density, richness and HBI scores were all negatively associated with increases in mean monthly flow, 30-day maximum flow, and flow variation. Lastly, although drift density was highly correlated with benthic
density in both SXW Creek and DF River, only mainstem drift communities exhibited declines in density and EPT proportions in 2017. These results strongly suggest that macroinvertebrate communities in the DF River mainstem are more vulnerable to natural and anthropogenic flow increases than communities in the SXW Creek tributary, which may be attributable to underlying physical gradients.

Although all river systems are geomorphically dynamic and spatially variable, it has long been recognized that certain environmental conditions change predictably across their continua (Vannote et al., 1980; Montgomery, 1999; Rempel et al., 2000). In addition to self-evident gradients of elevation, temperature and channel width, substrate composition and the ability of the river to transport substrate are key characteristics that exhibit longitudinal patterns (Church, 2002). Due to the accumulation of runoff in drainage basins, velocity and hydraulic stress typically increase from headwaters to downstream (Rempel et al., 2000; Church, 2002). Consequently, substratum in headwater reaches are relatively more heterogeneous and have high percentages of large grain sizes (i.e. cobbles, boulders) that cannot be moved by the current; comparatively, gravel and finer grain sizes often predominate substratum in higher-order depositional zones. These physical gradients are profound sculptors of benthic density, diversity and community composition patterns in river systems. Hydraulic stress and substrate composition determine everything from the frequency of bed-moving disturbances (Death & Winterbourn, 1995; Townsend et al., 1997) to the availability of flow refugia and food resources (Lancaster & Hildrew, 1993; Allan, 1995) to the connectivity of habitat patches within the metacommunity (Lake, 2000).
The SXW Creek and DF River system exhibits pronounced physical gradients in addition to wide variability in flow conditions between the tributaries and mainstem. SXW Creek process domains are confined by the surrounding valley and feature boulders and cobbles as the prevailing bed materials, although localized anomalies also occur. DF River process domains (particularly beginning at the Monk’s Hollow reach) are characterized by active floodplains, high percentages of loose gravel, and gradual narrowing and incision of stream channels (Wilcock et al., 2018). Additionally, SXW Creek and DF River feature differing magnitudes of high flow events and - to a lesser extent - mandated summer flows. In 2017, peak flows were greater than average annual flows by 2.17x and 3.17x in SXW Creek and Lower Diamond Fork, respectively, while mandated summer flows were 1.4x and 2.0x greater than 2016 baseflows, respectively. Reflecting these physical gradients, benthic communities displayed varying levels of stability and taxonomic turnover across my nine sampling sites.

Benthic communities in SXW Creek did not exhibit any significant relationships with flow metrics between 2005 and 2017 after accounting for spatial and temporal variation. While I observed significant increases in mean benthic density and HBI scores as well as significant decreases in diversity in SXW Creek between 2016 and 2017, these changes were not correlated with changes in any environmental variables that I measured. Community similarity analyses revealed that benthic communities in SXW Creek experienced negligible shifts in community structure across time. The only significant difference between 2016 and 2017 communities that persisted across the entire sampling season was a 2017 decline in the populations of the rifflle beetle Elmidae. When I compared Bray-Curtis dissimilarities of Upper Sixth Water communities between 2007
and 2017, I only observed significant 2017 increases in several secondary taxa, while changes in dominant taxa such as Chironomidae, Baetidae mayflies and Uenoidae caddisflies were insignificant and relatively minor.

Contrastingly, benthic communities in DF River exhibited strong temporal and spatial variability as well as declines in density, richness and HBI scores in response to increases in multiple flow metrics. Within DF River, the strength of benthic responses to flow varied between Upper Diamond Fork (UDF) and Lower Diamond Fork (LDF). After establishing site, season and year as random effects, UDF and LDF density models with added flow metrics had BIC score improvements of 7.18 and 19.39 over their respective null models. Additionally, only LDF River communities experienced sustained seasonal increases in HBI scores under higher summer flows. Investigations into community similarity in LDF River revealed distinct temporal shifts across the sampling years, culminating with persistent, flow-induced reductions in the populations of dominant caddisfly taxa Glossosomatidae and Helicopsychidae in 2017. Although UDF River communities experienced significant declines in EPT families in 2017, their populations rebounded to and even surpassed 2016 levels by August. Overall, these results coupled with geomorphology findings suggest that benthic communities in this river system are strongly influenced by the interaction of discrete disturbance events and augmented summer baseflows.

Over the decades, ecologists have defined disturbance events in numerous ways and have presented several prevailing hypotheses on their roles in structuring communities (Connell, 1978; Huston, 1979; Resh et al., 1988; Lake, 2000). While some have described disturbances in terms of their specific biotic consequences (Sousa, 1984;
Townsend & Hildrew, 1994), I will use a primarily abiotic definition that may be more universally applied across river systems: a disturbance is a discrete physical event that damages a habitat occupied by populations or communities (Lake, 2000). Disturbance events such as flood pulses can replenish river communities by augmenting the transfer of organic matter between floodplains and channels (Junk et al., 1989). Additionally, intermediate frequencies of disturbance can interact with productivity to promote high primary and secondary diversity in the benthos by counteracting competitive exclusion (Townsend et al., 1997; McCabe & Gotelli, 2000; Cardinale et al., 2006). However, disturbance regimes that are characterized by high unpredictability and inadequate recovery times may disrupt ecological processes and degrade the health of benthic communities (Brittain & Saltviet, 1989; Carlisle et al., 2012; Kennedy et al., 2016). I suspect that hydraulic and substrate gradients in the SXW Creek and DF River system are responsible for varying frequencies and magnitudes of disturbances between the tributaries and the mainstem, and that benthic recovery from these disturbances in LDF River is being hindered by augmented summer baseflows.

In September 2017 we subjected the river system to two, five-day step flow events to determine thresholds of bed movement and ecosystem decline. The first event raised baseflows to 50cfs in SXW Creek and 100cfs in LDF River; the second occurred nine days after and raised baseflows to 100cfs and 150cfs, respectively. Geomorphology researchers Jabari Jones and Jacob Stout found that the transport rates and distances travelled of rocks during high flow events increased incrementally from headwater to downstream sites (Wilcock et al., 2018). There was minimal bed movement in the two uppermost SXW Creek sites during both step flow events, while the lowermost SXW
Creek sites had rates of transport that were comparable to LDF River under 100cfs. In LDF River, bed movement occurred at all sites under 100cfs; under 150cfs, rocks of all grain sizes travelled tens of meters away from their original locations.

These geomorphology results suggest that the relatively loose, gravel and cobble-dominated substratum in LDF River may be disturbed in flows around 150cfs or higher, which occurred in one or more LDF River sites for an estimated 66 days during spring and summer 2017. Contrastingly, we were not able to identify a flow disturbance threshold in SXW Creek, as both step flow spates failed to significantly mobilize the bed across all SXW Creek sites. The increases in community HBI scores in LDF River as a response to maximum flow within 30 days (Qmax30) indicate that discrete high flow pulses may be disproportionately impacting sensitive taxa, such as those belonging to the orders Ephemeroptera, Plecoptera and Trichoptera (EPT). The dramatic reduction of Helicopsychidae and Glossosomatidae caddisfly populations in 2017 is likely the primary driver of the relationship between community HBI scores and Qmax30 in LDF River.

The Helicopsychidae and Glossosomatidae caddisfly families are mainly composed of obligate scraper species that aggregate on substratum surfaces to feed on periphyton (Cummins & Klug, 1979). Under high velocity conditions, these taxa often shift their aggregations from exposed surfaces to protected crevices and downstream ends of rocks (Kovalak, 1976; Vaughn, 1987); however, this behavioral adaptation may do little to prevent mortality in disturbance events that mobilize the substrate itself. In unstable substrates, a macroinvertebrate taxon’s rate of dislodgement is strongly dependent on whether or not it seeks refugia in deeper sediment – a strategy that many caddisfly taxa do not exhibit (Holomuzki & Biggs, 2000). Disproportionate mortality of
these sensitive taxa and other scrapers (i.e. Elmidae riffle beetle) may increase in-situ primary producer biomass through releases from herbivory (Rosemond et al., 1993; Feminella & Hawkins, 1995), impede energy transfer to higher trophic levels via producer-consumer imbalances (Bowman et al., 2005), and decrease diversity by opening up space for more generalist taxa (Brittain & Saltveit, 1989; Troelstrup & Hergenrader, 1990). One limitation that may have affected the accuracy of the above results is that I only collected benthic samples from the center of the stream where hydraulic stress was greatest, while ignoring stream margins that may have sheltered more resilient populations (Rempel et al., 2000). However, it is striking that out of the six years of benthic data from LDF River, Helicopsychidae and Glossosomatidae constituted high proportions of sampled communities in 2016 alone – the year with the lowest spring runoffs and minimal increases to summer baseflows. This provides evidence that the observed vulnerability of these taxa to high flow events is not an artifact of my experimental design, but rather a response that persists across years.

The higher frequency of bed-mobilizing flow events in the mainstem does not entirely account for the overall response of benthic density to mean monthly flow across the river system. In historical terms, the SXW Creek and DF River system commonly experiences spring runoff magnitudes equal to or higher than those in March – June 2017; thus, while one should expect that such events may temporarily perturb the benthos, it is less probable that they would cause sustained degradation of communities. Moreover, while the density and composition of UDF communities recovered to 2016 levels by August 2017, the declines in LDF benthic communities persisted across all 2017 sampling events. I suspect that benthic communities in LDF River were prevented from
recovering after spring runoff due to the additive effects of augmented baseflows. While it has long been understood that flow events such as spates cause threshold responses in the benthos (Death & Winterbourn, 1995; Poff et al., 1997), there has been recent recognition that macroinvertebrate metrics may also exhibit linear relationships with anthropogenic flow alterations (Konrad et al., 2008; Poff & Zimmerman, 2010; Carlisle et al., 2012). Large-scale studies of river systems across the western United States have revealed that benthic community compositions – and, to a lesser extent, densities - are increasingly impacted across gradients of streamflow variability, baseflow depletion, and maximum flow (Konrad et al., 2008; Carlisle et al., 2012). Given that some bed movement was observed in LDF River at 100cfs, macroinvertebrate individuals may have experienced elevated hydraulic stress as they foraged and maintained positions under the mandated 80cfs, thus hindering population recoveries. These reductions in benthic density may result in decreases in functional and species diversity (Wallace & Webster, 1996) as well as in overall food availability for fish species such as brown trout (Salmo trutta) and Bonneville cutthroat trout (Oncorhynchus clarkii utah).

The spatial and temporal trends in benthic density were reflected in drift communities. Across the SXW Creek and DF River system, drift density at a site was highly correlated with that site’s benthic density. This tight correlation resulted in a unimodal peak in drift densities in August and a gradient of drift densities decreasing downstream, which conformed to the seasonal and elevational gradients of benthic density in both years. Notably, while SXW Creek drift densities and compositions were stable between the two sampling years, 2017 drift communities in LDF River exhibited
significant decreases in proportions of Helicopsycheidae significant increases in proportions of Chironomidae.

These drift results suggest that the number of organisms entering the water column in this river system is highly density-dependent. Bottom-up benthic controls on drift density and composition have been observed in large regulated rivers (Kennedy et al., 2014) and unregulated first-order streams (Turner & William, 2000). In the case of LDF River in 2017, the decreased presence of Trichoptera in drift was likely linked with declining Trichoptera populations in the benthos. The increased proportions of the generalist taxa Chironomidae could either have been attributable to their increased densities in the benthos or to the fact that they are passive drifters whose densities in the water column are often correlated with discharge (Brittain & Eikeland, 1988). Of course, density-independent factors such as resource depletion, habitat degradation and changes in flow may also temporarily increase rates of active drift (Hildebrand, 1974; Larsen & Ormerod, 2010); however, there is evidence that these factors regulate drift variation at shorter-term timescales (i.e. days), while benthic density may be the primary regulator of drift across longer timescales (i.e. weeks to months) (Rowe & Richardson, 2001; Dewson et al., 2007; Kennedy et al., 2014). I suspect that the rising limb of spring runoff in 2017 caused a short-term spike of passive drift as beds were mobilized and organisms were removed from the benthos – an event that was not captured by the first sampling effort in April 2017. As I only sampled drift across the river system three times in 2016 and four times in 2017, it is likely that I missed daily to weekly variation in drift rates under changing abiotic conditions. Despite this, the synchrony between the spatial and temporal patterns of drift density and benthic density highlights the importance of density-
dependent structuring of drift communities. In LDF River, the suppression of benthic density and EPT under the 2017 flow regime was partially mirrored in drift communities. Since drift is the primary mode of dispersal for aquatic macroinvertebrates, declines in drift abundance and diversity may feed back to affect colonization rates, the recovery of sensitive taxa, and connectivity between local communities.

Overall, these Chapter II results can improve our understanding of how foundational ecological processes operate in regulated river systems. Due to their conspicuous responses to stressors and their oftentimes-high levels of alpha (α) and beta (β) diversity, benthic macroinvertebrate communities have long been valuable subjects for research on community assembly (Poff, 1997; Vinson & Hawkins, 1998; Chase & Ryberg, 2004). As in any ecosystem, riverine macroinvertebrate communities are all comprised of species that possess the traits required to pass through a nested series of filters (Poff et al., 1997). However, assembly in river systems is unique in the sense that many of these filters change unidirectionally from headwaters to mouths (Vannote et al., 1980). There is evidence that benthic communities are structured by distinct processes in tributaries and mainstems due to varying intensities of key filters such as disturbance frequencies (Clarke et al., 2008; Brown & Swan, 2010; Brown et al., 2011). For example, Brown & Swan (2010) posited that in New England stream networks, headwater communities were structured primarily by species sorting (i.e. competition) due to their geographic isolation and harsher environmental conditions. Benthic communities in the mainstems, however, were the outcomes of both species sorting and dispersal processes, as higher dispersal rates may have allowed for species to colonize localities with less-than-ideal environmental conditions (Brown & Swan, 2010).
Interestingly, the SXW Creek and DF River system appears to exhibit spatial trends contrary to those observed by Brown & Swan (2010): stable benthic communities in the more benign tributaries, and fluctuating communities in the harsher, more disturbance-prone mainstem. In SXW Creek, community similarities and drift densities were generally unchanged across years and flow conditions. In LDF River, benthic and drift densities were suppressed by the 2017 flow regime, which in turn may have caused a divergence of local communities. This suggests that community resilience and the likelihood of species extirpations are dependent on underlying riverine gradients, and also reaffirms the importance of tributaries in sustaining $\alpha$- and $\beta$-diversity (Finn et al., 2011). However, several limitations of this study warrant some caution when interpreting these Chapter II results.

It is possible that my dataset did not have the temporal breadth to accurately capture long-term dynamics in this river system’s benthos. The pace at which a community adjusts to or recovers from disturbances depends on both current environmental conditions and the history of the landscape it inhabits (Cuddington, 2001). For example, past land use within watersheds (i.e. agriculture, mining) can oftentimes be stronger predictors of stream biodiversity than present-day disturbances (Harding et al., 1998). The SXW Creek and DF River system has experienced over a century of vastly augmented flows; it was only in 2004 that managers decided to draw the flow regime down to the current mandated flow requirements. It may be the case that the long-term recoveries of these benthic communities from pre-2004 flows are either adding noise or influencing the trends I observed. In a more immediate timescale, it also may be problematic to conclude that benthic communities in LDF River are highly vulnerable to
flow increases based on data from a limited window (e.g. samples from three mainstem sites between April and August 2017). Lastly, the original intent of this study was to measure the effects of anthropogenic flow increases on structure and functioning – not the combined effects of high spring runoff and anthropogenic flow increases. While UDF River has served as a valuable control, there were inherent levels of uncertainty that came with ascribing benthic responses to specific flow events. Some of these shortcomings were simply outside the scope of this study to address; moreover, the inclusion of previous BIO-West data into my models produces confidence that these benthic responses to flow are cross-year, cross-observer phenomenon.

There are several managerial implications in the distinctions between SXW Creek and DF River community responses to changing flow conditions. Both the long-term temporal stability of communities in SXW Creek and the recovery of UDF River communities in 2017 are testaments to the vital roles of headwaters and tributaries in the structuring of river ecosystems. Tributaries have been found to increase diversity and productivity immediately downstream of their confluences with mainstems (Fernandes *et al*., 2004; Kiffney *et al*., 2006) and have also been demonstrated to serve as refugia for mainstem species from stressors such as flow regulation (Robinson *et al*., 1998). Additionally, there has also been increasing recognition that headwater streams, due to characteristics such as greater habitat heterogeneity and geographic isolation, can support high levels of endemism and β-diversity (Clarke *et al*., 2008; Finn *et al*., 2011; Biggs *et al*., 2017). This is a call for managers to adapt conservation strategies that acknowledge the network structure of rivers, rather than maintaining linear perspectives that tend to overemphasize mainstem sampling efforts and restoration projects (Altermatt, 2013).
These Chapter II results also add to the growing body of knowledge on altered flow regimes by demonstrating that sustained increases in flow can non-uniformly degrade benthic communities across rivers. Specifically in the SXW Creek and DF River system, mandated summer flow requirements of 60 and 80cfs may potentially be deleterious not just to macroinvertebrate species but also to the target game fish species that these requirements were intended to protect (e.g. brown trout and Bonneville cutthroat trout). Decreases in benthic and drift density can have direct impacts on the bioenergetics of fish populations by causing individuals to gain fewer calories per unit of effort (Hayes et al., 2000; Rosenfeld et al., 2005). To avoid such gaps between intended and actual ecological consequences, managers must explicitly consider the hydrographic and physical contexts of their river systems when deciding whether to implement environmental flows as restoration strategies. In an era of ever-increasing anthropogenic modifications to rivers, a comprehensive understanding of the spatial and temporal dynamics of the benthos under altered flows will be crucial to protecting worldwide riverine ecosystem integrity.
Literature Cited


CHAPTER III
THE EFFECTS OF ENHANCED FLOWS ON ECOSYSTEM FUNCTIONING AND FUNCTIONAL FEEDING GROUPS IN SIXTH WATER CREEK AND DIAMOND FORK RIVER

Introduction

In assessing river health, it is essential to complement investigations of community structure with investigations of ecosystem functioning. Primary producers and terrestrial organic matter are vital to riverine ecosystem functioning, and comprise the autochthonous (in-stream) and allochthonous (out-of-stream) sources to a river’s energy budget (Wallace & Webster, 1996). Primary producers substantially contribute to carbon standing crops and dissolved oxygen concentrations through photosynthetic activity and are often the dominant energy pathway in river segments with scant canopy cover (Odum, 1956; Lamberti & Steinman, 1997). Contrastingly, the decomposition of primary producers and terrestrial organic matter alike is the major process by which nutrients are cycled in net heterotrophic river segments (Cummins, 1974; Abelho et al., 2001). While landscape features (e.g. land use, geology, riparian cover) strongly determine the balance of autochthonous and allochthonous energy supplies across river systems (Bunn et al., 1999; Allan, 2002), in-stream conditions can regulate the rates at which these supplies are incorporated into the food web.

Establishment of primary producers (i.e. periphyton, algae, vascular plants) is controlled jointly by velocity and substrate, while growth is regulated by light attenuation, nutrients and benthic communities (Odum, 1956). In a comparative study of nine rivers, in-stream nutrient loads explained 56% of variance in chlorophyll-α (Biggs &
Close, 1989). However, when flooding events caused these rivers’ hydrographs to rise, periphyton biomass was greatly reduced through scouring and substrate instability, and the influences of light and nutrients were muted (Biggs & Close, 1989). The effects of flow variability on primary producers have been described as existing on a continuum, with high flow events reducing biomass through ‘drag-disturbance’ and lower-magnitude flow events affecting colonization rates and energy uptake (Biggs et al., 2005). While periphyton biomass is more vulnerable to low to moderate-magnitude flow events, macrophyte biomass reduction occurs primarily during less frequent, high-intensity flow events (Biggs et al., 2005). Conversely, reduced flows may either suppress primary producers through the deposition of suspended sediment or convert low-biomass diatom assemblages to high-biomass algal mats (Dewson et al., 2007). One more consideration is the directional, accumulative effects of flow and nutrients that can result in spatially heterogeneous templates of primary production (Skidmore et al., 1998; Bunn et al., 1999). These autochthonous dynamics are important to investigate in river ecosystems, as primary productivity exerts a bottom-up control on scraper macroinvertebrate taxa and may also interact with disturbance frequencies to influence benthic species richness (Fuller et al., 1986; Tonkin et al., 2013).

Course particular organic matter (CPOM) retention and processing are critical processes through which allochthonous inputs may enter a river’s energy budget. Previous research has identified flow as the most important variable for CPOM retention, followed by submerged wood and periphyton biomass (Quinn et al., 2009). High flow events can strongly regulate CPOM retention by flushing CPOM out of the river system or fragmenting CPOM through physical abrasion (Tank et al., 2010). Additionally, as a
river’s discharge increases, water levels may submerge woody debris, macrophytes and other features that snag leaves out of suspension in lower velocities (Abelho, 2001). Upon being retained in the benthos, CPOM is then acted on by temperature, nutrients and biotic forces. Warmer temperatures and nutrient additions may speed up the breakdown of retained CPOM through their effects on metabolism and microbial activity (Tank et al., 2010). CPOM energy transfer is also strongly aided by aquatic hyphomycetes, bacteria and shredder macroinvertebrate taxa that release nitrogen and carbon while breaking down leaf mass (Cummins, 1974; Heiber & Gessner, 2002). Much research has focused on the relative contributions of microorganisms and shredder taxa to CPOM breakdown across spatial gradients. Irons et al. (1994) provided evidence that microbial activity becomes less important and shredder activity more important for breakdown at higher latitudes and elevations. In headwater streams with strong terrestrial-aquatic interfaces, CPOM comprises a large portion of food resources for macroinvertebrate communities, particularly shredder taxa (Vannote et al., 1980).

I hypothesized that enhanced flows in 2017 would suppress primary production in SXW Creek and DF River through colder temperatures, scouring and bed instability, while also suppressing CPOM processing through colder temperatures and reductions in shredder taxa. I expected that the impacts of enhanced flows on primary production and CPOM would depend in part on the relative availabilities of autochthonous and allochthonous energy sources across the river system. For example, in the LDF River mainstem, where higher light attenuation may promote the relative dominance of primary producers, enhanced flows would have more pronounced effects on primary production.
than CPOM. These changes in ecosystem functioning across the river system would likely be reflected in stream metabolism.

Stream metabolism, or the rate of organic matter production and consumption within a riverine food web, is a direct measure of ecosystem health (Tank et al., 2010). The two components of stream metabolism are gross primary production (GPP), defined as the amount of carbon fixated through photosynthesis, and ecosystem respiration (ER), defined as the sum of plant and animal respiration (Young et al., 2008). GPP and ER have typically been quantified through the open diel oxygen method, which requires monitoring diel changes in dissolved oxygen and estimating reaeration coefficients (Odum, 1956; Demars et al., 2015). Overall, stream metabolism can provide insight into the spatial and temporal dynamics of organic matter processing and reveal whether river ecosystems are net autotrophic (i.e. creating more energy than is being consumed in-stream) or net heterotrophic (i.e. consuming more energy than is being created in-stream).

Production (or GPP) to respiration (or ER) ratios are commonly used to determine the placement of rivers on the autotrophic-heterotrophic spectrum (Tank et al., 2010). If production surpasses respiration (P:R > 1), it is likely that in situ primary producers are the dominant carbon source supporting the river ecosystem. Conversely, if respiration surpasses production (P:R < 1), it is likely that the river ecosystem is more reliant on allochthonous energy sources such as leaves (Young et al., 2008). In addition to changing across spatial gradients, P:R ratios also exhibit strong seasonal variation in rivers, reflecting peak primary production in the summer and peak leaf fall in autumn (Lamberti & Steinman, 1997; Uehlinger, 2006). Flow events may disrupt the spatial and temporal patterns of P:R ratios by significantly impacting primary producers, organic matter and
heterotrophs alike (Uehlinger & Naegeli, 1998; Uehlinger et al., 2003; Acuña et al., 2004). Particularly, previous research has provided evidence that GPP is less resilient to flow disturbances than ER, which is manifested in widespread decreases in P:R ratios during high flow events (Young & Huryn, 1996; Uehlinger & Naegeli, 1998; Uehlinger et al., 2003). This may be due to high flows mobilizing the substrates colonized by primary producers while leaving intact the hyporheic zone, where a high proportion of ER occurs (Uehlinger & Naegeli, 1998; Young et al., 2008). Although high flows can certainly reduce the biomass of organic matter and macroinvertebrates (Bunn & Arthington, 2002; Acuña et al., 2004), there is limited evidence of P:R ratios shifting towards autotrophy as a result of such disturbances.

The responses of gross primary production (GPP) and ecosystem respiration (ER) to flow events are difficult to generalize, as they are largely dependent on the environmental conditions and climatic contexts of each river system (Young & Huryn, 1996; Uehlinger & Naegeli, 1998; Uehlinger, 2003). I hypothesize that in SXW Creek and DF River, enhanced flows will suppress both components of stream metabolism while disproportionally impacting GPP over ER. First, since algae and macrophytes are limited to exposed surfaces of the substrate, I expect high flow events to strongly decrease primary producer biomass through scouring and bed mobilization. Mandated summer flows may also limit GPP by lowering in-stream temperatures and decreasing light attenuation. Regardless of the direction of change, shifts in stream metabolism have implications for both nutrient cycling and the functional composition of macroinvertebrate communities.
A central tenet of ecology is that food resources and their consumers interact with one another through both bottom-up and top-down pathways. While food resource availability can act as a bottom-up control on the biomass and composition of higher trophic levels (Fuller et al., 1986; Hall et al., 2000), fluctuating populations of higher trophic levels can likewise alter food resource biomass through trophic cascades (Kratina et al., 2012) or changes in herbivory pressure (Huryn, 1998). The functional feeding group (FFG) classification approach has been developed to investigate such interactions between benthic macroinvertebrates and their food resources (Cummins & Klug, 1979). The FFG approach differentiates macroinvertebrate taxa into five general groups based on their morphological and behavioral traits for resource acquisition: 1) predators, 2) scrapers, 3) shredders, 4) gatherers, and 5) filterers (Wallace & Webster, 1996). This allows researchers to track changes in the functional integrity of benthic communities and determine the strength of trophic linkages, which may profoundly affect energy flow in river ecosystems (Troelstrup & Hergenrader, 1990; Wallace & Webster, 1996). For example, studies that have experimentally reduced shredder biomass and richness have demonstrated this feeding group to be functionally important for leaf breakdown and nutrient cycling within rivers (Andersen & Sedell, 1979; Lughart & Wallace, 1992; Jonsson et al., 2001). Although the FFG approach is limited in its ability to account for facultative feeders (Hawkins et al., 1982; Mihuc, 1997), it has nonetheless revealed patterns in benthic community composition that can be applied across river systems.

The River Continuum Concept (RCC) describes river systems as exhibiting longitudinal gradients of characteristics such as elevation, riparian cover and channel width (Vannote et al., 1980). The RCC also posits that functional feeding groups are
organized across these gradients in ways that maximize the utilization of available energy. Under this paradigm, 1st to 3rd order headwater streams with significant terrestrial inputs (P:R < 1) should contain higher proportions of taxa that shred leaves (i.e. shredders), while midsized reaches with primary producers dominating the food base (P:R > 1) should contain higher proportions of taxa that scrape algae (i.e. scrapers) (Vanote et al., 1980). While the RCC may be strongly predictive of benthic macroinvertebrate assemblages in temperate forest regions (Culp & Davies, 1982; Grubbaugh et al., 1996) and, to a lesser extent, tropical regions (Greathouse & Pringle, 2006), it has limited utility for rivers in arid regions with strong temporal variation of in-stream conditions and less discernable riparian gradients (Winterbourn et al., 1981). Moreover, river systems are dynamic and oftentimes do not conform to the RCC’s generic longitudinal gradients. Tributaries can produce discontinuities in community structure and food resources via inputs of sediment, organic material and nutrients (Bruns et al., 1984; Kiffney et al., 2006). Montgomery (1999) also argued that landscape-scale patterns create distinct process domains in rivers, where geomorphologic processes such as erosion and deposition are determinants of community structure. A proper understanding of the structural and functional gradients in river systems may better allow for managers to account for spatial variability in biomonitoring and river restoration.

The SXW Creek and DF River system diverges from classical RCC explanations in several notable ways. First, previous geomorphological measurements reveal that channel widths do not gradually increase but instead display an hourglass pattern from headwaters to mouth (Wilcock et al., 2018). Second, terrestrial inputs might be more equitably distributed across the river system – both Upper Sixth Water Creek and Lower
Diamond Fork River sites feature significant riparian vegetation along their banks. I thus hypothesized that FFG gradients in this river system would not conform to the predictions of the RCC. However, I expected that primary production would still be higher in the lower reaches than in the headwaters due to other factors such as light attenuation, temperature and nutrient accumulation. I also hypothesized that enhanced flows - and particularly increases in flow variability and maximum flow rates - would weaken any FFG gradients present under natural flow conditions by selecting for generalist, disturbance-tolerant taxa across the river system.

In summary, my objectives for Chapter III are to: 1) determine how primary production (as measured by chlorophyll-a growth) and CPOM processing (as measured by leaf breakdown) are affected by enhanced flows and the functional composition of the benthos, 2) determine how stream metabolism is affected by enhanced flows, and 3) understand how FFG and stream metabolism gradients in SXW Creek and DF River change in response to enhanced flows.

**Methods**

*Data Collection*

I installed tiles and leaf packs (coarse and fine) at the nine riffle sites from Chapter II so as to determine how flow influenced allochthonous and autochthonous energy supplies across the river system (Table 6). My schedule for installing these tiles and leaf packs followed the schedule established for macroinvertebrate data collection. During each sampling event from 2016 to 2017, I secured tiles and leaf packs to rebar along the edge of the channel at the upstream, midstream and downstream locations at my riffle sites. Once installed, tiles and leaf packs remained in the river for an average of
two months until being retrieved during the next sampling event. Upon removal in the field, all tiles and leaf packs were immediately stored in dry ice until they were transferred to laboratory freezers.

Table 6 Retrieval schedule for tiles, coarse leaf packs and fine leaf packs in SXW Creek and DF River. Blue numbers denote that all three tiles or leaf packs were retrieved from the site on that given date, while red numbers denote incomplete retrievals (2 or less).

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The 200-cm² surface areas of the tiles were composed of uneven shale designed to mimic natural substrate for periphyton to colonize. During the 2016 sampling year, I attached tiles to rebar with cable ties. This method resulted in many of the tiles being turned over by the current; thus, in 2017, I began to nail tiles directly into the substrate. In the laboratory, I extracted periphyton from the tiles by scrubbing known surface areas (25cm² in 2016, 50cm² in 2017) for 2.5 minutes and immersing the periphyton in 15ml of 95% ethyl alcohol. After 2 – 24 hours, I diluted the samples and performed in vitro chlorophyll-α analyses. This was accomplished with a fluorometer, which estimates chlorophyll-α content by detecting the amount of red light fluoresced from algal and cyanobacterial cells. Finally, I averaged chlorophyll-α growth values across all samples from the same tile, and then standardized these values to micrograms of chlorophyll-α per centimeter squared (μg/cm²). This standardization corrected for the variance in chlorophyll-α readings that may have resulted from scrubbing different-sized surface areas in 2016 and 2017.

I sewed together leaf packs of willow (Salix spp.), one of the most common riparian trees within the SXW Creek and DF River system. I secured these leaf packs within two types of mesh. Coarse-meshed leaf packs were comprised of two grams of willow contained within zip-tied squares of PVC deer block fencing with 5/8” x 5/8” openings. These openings were intended to allow shredder macroinvertebrate taxa to access the leaf packs (Hieber & Gessner, 2002). Fine-meshed leaf packs were comprised of one gram of willow leaves contained within 0.50mm² mesh bags. Since shredder taxa were unable to access the contents of these bags, I inferred that any breakdown of these fine-meshed leaf packs would be due to the activities of colonizing bacteria and aquatic
fungi (Petersen & Cummins, 1974). During sampling events, I secured both coarse and fine-meshed leaf packs to rebar locations at each site, making sure to place the packs perpendicular to the current.

In the laboratory, I thoroughly cleaned the leaf packs of insects and detritus before placing the remaining leaf masses in a drying oven at 50°C until they reached a constant dry weight. From these values, I calculated both the percentage of leaf mass remaining as well as the breakdown coefficient $k$, or the constant exponential loss of leaf mass per day (Petersen and Cummins, 1974). The $k$ coefficient for each leaf pack sample was calculated by dividing the natural logarithm of the percentage of mass remaining by the number of days the sample was in the stream.

Lastly, I installed MiniDOT® loggers at each site to record in-stream levels of dissolved oxygen (mg/l) and temperature (°C). These loggers were secured to rebar near the center of each riffle site in April 2016 and 2017 and retrieved at the end of the sampling season. These loggers recorded DO and temperature values at 10-minute intervals for the entirety of each field season. Once the loggers were returned to the laboratory, their data were compiled and averaged to obtain daily estimates of DO and temperature. In 2016, the range of mean monthly DO levels were 6.051 – 9.02 mg/l for SXW Creek and 7.36 – 9.024 for DF River. 2016 mean monthly temperature ranges were 7.45 – 15.88 °C for SXW Creek and 9.45 – 17.53 °C for DF River. 2017 was a comparatively colder year of stream temperatures with relatively higher concentrations of DO across the river system. There were a few instances per sampling year where loggers were buried under sediment – at the Ray’s Crossing (RC) and Below Syar Tunnel (BST) sites in 2016, and then at Diamond Fork Campground (DFC) and Motherload (MO) in
2017. These burying events resulted in lower recorded DO and temperature values than what would have been naturally occurring in the stream at those times. Thus, for my analyses, mean monthly values at those sites were averaged across the days of the month when these loggers were not impacted. I did not obtain any data from Guard Station in 2017, since the logger at that site became compromised.

*Leaf Breakdown and Chlorophyll-a Growth Analyses*

I used both linear mixed effects (LME) and random forest (RF) models to test whether flow metrics, macroinvertebrate composition metrics, and several other environmental variables were related to chlorophyll-a growth and leaf breakdown in SXW Creek and LDF River. As in Chapter II, there were spatial and temporal levels within my data structures that I needed to account for prior to determining the relationships between my response and predictor variables. Thus, I decided to establish sampling site and sampling season as random effects in my LME models. Sampling year was excluded as a random effect due to high correlations with flow and temperature.

Before continuing with LME and RF modeling, I obtained estimates of functional feeding group compositions for my sampled benthic invertebrate communities. I employed fuzzy coding methods of assigning feeding group designations to address several methodological issues (Chevenet *et al*., 1994; Tomanova *et al*., 2007). First, assigning a taxon to any one feeding group is problematic, as most are facultative in their feeding strategies (Mihuc, 1997). Further, feeding group assignments are typically most accurate at the species-level, and my lowest taxonomic resolution was genus (Lenat & Resh, 2001). Thus, I gave each taxon found in the benthic samples an “affinity score” that
represented the strength of its affiliation with a particular feeding group. The criterion for these scores were as follows:

- A taxon that did not exhibit a given feeding strategy was scored as 0 for that particular feeding strategy.
- A taxon that exhibited facultative behavior for a given feeding strategy was scored as 1 for that particular feeding strategy.
- A taxon that employed several feeding strategies equally was scored as 2 for each of those feeding strategies.
- A taxon that exhibited obligate behavior for one feeding strategy was scored as a 3 for that particular feeding strategy.

All the above affinity scores were based on feeding group charts in Merritt & Cummins (1996). I then weighed the scores of these taxa by their relative abundances to generate feeding group percentages for all benthic invertebrate samples. Lastly, I multiplied these percentages by the total density of organisms in the sample to arrive at feeding group densities.

For both SXW Creek and LDF River, I constructed LME models for: (1) percentage of coarse leaf pack remaining (%CR); (2) $k$ coefficient of coarse leaf pack breakdown ($k_C$); (3) percentage of fine leaf pack remaining (%FR); (4) $k$ coefficient for fine leaf pack breakdown ($k_F$) and (5) chlorophyll-$a$ growth ($\mu g/cm^2$). The fixed effects in my coarse leaf pack models were mean monthly flow in cfs (MMF), coefficient of variation for MMF (CVmmf), maximum flow within 30 days of sampling in cfs (Qmax30), temperature in degrees Celcius (temp), and the density of shredder invertebrate taxa from the previous sampling month (shred.dens). As I did not expect
flow to directly influence the breakdown of leaf packs within fine meshes, the only fixed
effects I included in my fine leaf pack models were dissolved oxygen (mg/l) and
temperature. Lastly, the fixed effects in my chlorophyll-\(a\) growth models were MMF,
CVmmf, Qmax30, scraper taxa density during tile installation (scrap.dens), temperature
in SXW Creek, and the density of Helicopsychidae and Glossosomatidae caddisflies
(HeGl.dens) during tile installation in LDF River. When necessary, I log-transformed or
square root-transformed my response variables and fixed effects to meet the assumption
of normal distributions. I did not build LME models for UDF River, as that river segment
did not feature enough data points of chlorophyll-\(a\) (\(n = 32\)), coarse (\(n = 34\)) or fine (\(n =
29\)) leaf packs to be statistically robust.

As in Chapter II, I compared models with added fixed effects to corresponding
intercept-only null models using Bayesian Information Criterion (BIC). Again, I
identified a BIC score improvement of \(\geq 4\) as my threshold for determining significance
(Gelman & Hill, 2006). In September 2017, the river system experienced an experimental
step flow regime, which was characterized by stretches of unaugmented baseflows
punctuated with two five-day high flow events (50cfs and 90cfs in SXW Creek, 100cfs
and 150cfs in LDF River). This step flow regime was implemented to determine flow
thresholds for bed mobilization and the flushing of organic matter and benthic
invertebrate biomass. Since the September 2017 flow regime did not feature the
mandated summer baseflows of prior sampling months, the step flow data points were not
directly comparable to earlier 2017 data points. Thus, I performed BIC selection
procedures for chlorophyll-\(a\) growth and leaf breakdown models with and without
September 2017 observations.
The structure of the intercept-only null models for the above five response variables was the following:

\[ \hat{y}_i = \beta_{0j[i]}k[i] + \varepsilon_{j[i]k[i]} \]

\[ \beta_{0j} \sim N(\mu_{\beta_0}, \sigma_{\beta_0}^2), \text{ for } j = 1, \ldots, J \text{ site} \]

\[ \beta_{0k/l} \sim N(\mu_{\beta_0}, \sigma_{\beta_0}^2), \text{ for } k = 1, \ldots, K \text{ season} \]

\[ \varepsilon_{j[i]k[i]} \sim N(0, \sigma^2_\varepsilon) \]

where \( \hat{y}_i \) is the response variable at observation \( i \), \( \beta_{0j[i]} \) is the intercept for site \( j \), \( \beta_{0k[i]} \) is the intercept for season \( k \), and \( N(\mu, \sigma^2_\varepsilon) \) denotes a normal distribution with mean \( \mu \) and variance \( \sigma^2_\varepsilon \) around intercept \( \beta_0 \).

Finally, I constructed Random Forest (RF) regression models for chlorophyll-\( a \) growth and the four previously mentioned leaf breakdown metrics in SXW Creek, UDF and LDF Rivers. The predictor variables I included in my chlorophyll-\( a \) growth models were: (1) day of year (DOY); (2) year; (3) MMF; (4) CVmmf; (5) Qmax30; (6) scraper density at time of tile installation (scraper.dens); (7) Helicopsychidae and Glossosomatidae density (HeGl.dens) at time of tile installation for LDF River; and (8) temperature (°C) and (9) dissolved oxygen (mg/l) for SXW Creek and LDF River. I included all the above predictor variables in my coarse leaf pack breakdown models with the exceptions of scraper.dens and HeGl.dens at time of installation, which I replaced with shredder density (shred.dens) at the time of installation. Fine leaf pack breakdown models did not feature any macroinvertebrate community composition metrics. I used the same variable reduction procedure from Chapter II to select for the three most important variables, which were included in my final variable importance and partial dependence plots. As with my LME models, I ran these procedures for datasets with and without step
flow observations. I performed these analyses using the “randomForest” package in R version 3.4.3 (R Core Team, 2017).

**Stream Metabolism Analyses**

I used the single-station diel oxygen method to estimate stream metabolism in SXW Creek and DF River (Odum, 1956; Demars *et al*., 2015). The single-station method allows one to calculate gross primary production (GPP) and ecosystem respiration (ER) by monitoring diel curves in dissolved oxygen (DO) concentrations at a given location. Additionally, this method requires a quantification of the reaeration coefficient $K$, which represents the rate at which the stream absorbs oxygen from the atmosphere (Churchill *et al*., 1962). Reaeration rates can be quantified either by injecting tracer gasses into the water column (Genereux *et al*., 1992; Demars *et al*., 2015) or by utilizing depth-velocity equations (Wilcock, 1982), with the former typically yielding more accurate results (Tank *et al*., 2010). Due to time and resource constraints, I selected the O’Connor and Dobbins method of calculating the reaeration coefficient with depth (m) and velocity (m/s) data for each site (O’Connor & Dobbins, 1958). These data were obtained from concurring geomorphological and fish surveys conducted by Utah State University researchers.

I used DO (mg/l) and temperature (°C) data from the MiniDOT® loggers I installed in 2016 and 2017 to determine GPP, ER and P:R ratios at each site. After converting the raw time-series data to usable formats, I inspected the data for compromised recordings. Given that the daily ranges in DO concentrations were largely between 6 – 10 mg/l across the sampling seasons, sharp declines or sustained intervals of concentrations at or below 4 mg/l suggested events of logger burial. Days that featured
such burial events were omitted from my analyses. Additionally, all recordings from Guard Station logger during the 2017 sampling season were not included, as they were stored in an unusable file type.

For each site, I calculated $K$ reaeration coefficients from annual average stream depth (m) and daily velocity (m/s) measurements using the “ODobbins” function. Sunrise and sunset times (MST) were determined for all days in each site’s DO time-series data frame using the “sunrise.set” function. Lastly, using the “SM” function and R code developed by Dr. Edd Hammill, I looped temperature-corrected $K$ coefficients, sunrise/sunset times, DO and temperature values through each day in a site’s data frame to produce daily estimates of GPP and ER. The “SM” function defined daily ER as mean nighttime net ecosystem production, corrected for the difference between average daytime and nighttime temperatures. The function also calculated daily GPP by subtracting ER from net ecosystem respiration at each 10-minute interval between sunrise and sunset, and then summing those resulting values. Daily P:R ratios were the quotient of daily GPP divided by the absolute value of daily ER. The “ODobbins”, “sunrise.set” and “SM” functions are all part of the “StreamMetabolism” package in R version 3.4.3 (R Core Team, 2017).

I used RF regressions to determine how flow and other environmental variables influenced GPP, ER and P:R ratios across the river system in 2016 and 2017. I obtained averages for GPP, ER and P:R ratios across 15-day intervals at each site from mid April to late September 2016 and from mid April to mid September 2017. I did not obtain any averages from 15-day time intervals that had fewer than seven data points. Additionally, I obtained average flows (cfs), coefficients of flow variation, and maximum daily flows for
each 15-day interval. I made separate, river system-wide models for GPP, ER and P:R ratios in each year to assess how these stream metabolism components change across spatial and temporal gradients. My predictor variables for these models were: (1) day of year (DOY); (2) elevation; (3) downstream distance from headwaters or confluence (river_km); (4) channel width; (5) average 15-day flow (CFS); (6) coefficient of variation for CFS (CVcfs); and (7) maximum flow within 15 days of sampling (Qmax15). I also made separate models of GPP, ER, and P:R ratios in SXW Creek and LDF River (2016–2017) to better understand the influence of flow metrics in each river segment. My predictor variables for these models were: (1) DOY; (2) temperature (temp); (3) CFS; (4) CVcfs; and (5) Qmax15. Lastly, I generated variable importance and partial dependence plots of the variables selected by reduction procedures. I performed these analyses using the “randomForest” package in R version 3.4.3 (R Core Team, 2017).

Functional Feeding Group Analyses

Before analyzing the influence of flow and stream metabolism metrics on particular feeding groups, it was first necessary to visualize the functional compositions of communities across space and time. For this purpose, I made bar plots of the densities and percentages of the five invertebrate feeding groups in SXW Creek and DF River: (1) predators, (2) scrapers, (3) shredders, (4) gatherers and (5) filterers. Benthic densities and percentages of feeding groups represent two different aspects of functional composition. While benthic density may convey information on a site’s carrying capacity for each feeding group, percentages may reveal the relative dominance of functional roles within the sampled community and more directly address how functional compositions change across space and time. I obtained site averages of these two metrics for 2016 and 2017 to
visualize the general spatial gradients of feeding groups in SXW Creek and DF River. These bar plots revealed benthic communities to be dominated by the scraper and gatherer groups; moreover, these groups also exhibited the most noticeable changes in densities and percentages across the continuum. I then obtained the monthly averages of the densities and percentages of these two groups and made separate bar plots for SXW Creek and LDF River. These initial visualizations informed subsequent analyses of gatherers and scrapers in this river system. All plots were made using the “gplots” package in R version 3.4.3 (R Core Team, 2017).

I constructed LME models for gatherer and scraper densities and percentages in SXW Creek and LDF River, utilizing a hypothesis-driven approach to test whether flow and stream metabolism metrics were significant predictors of these feeding groups after controlling for spatial and temporal variation. My fixed effects for my scraper models were MMF, Qmax30, and 15-day GPP, while my gatherer models featured the same two flow metrics but with 15-day ER instead of GPP. Where gatherers and scraper metrics exhibited strong unimodal trends across sampling season, I also included day of year (DOY) as a fixed effect in both my test models and their corresponding intercept-only null models. My random effects were site and year for models with DOY as a fixed effect, and site and month within year for models without DOY. Models with BIC improvements of $\geq 4$ over their corresponding nulls were considered significant (Gelman and Hill 2006). In the case of models with DOY, a BIC improvement of $\geq 4$ would indicate that the response variable was being significantly influenced by predictors other than sampling season. All of these analyses were performed using packages “lme4” and “arm” in R version 3.4.3 (R Core Team, 2017).
Results

Leaf Breakdown and Chlorophyll-a Growth Analyses

I found that while leaf breakdown increased system-wide under enhanced flows in 2017, SXW Creek and DF River exhibited varying degrees of change in this measure of ecosystem functioning. Since the experimental step-flow regime in September 2017 was not representative of this river system’s mandated summer flow requirements, I assessed whether my results still held when I removed fall observations from my analyses. Two-sample t-tests revealed that in SXW Creek, $K$ coefficients (i.e. the daily proportion of leaf mass loss) of 2017 coarse leaf packs were significantly higher than 2016 $K$ coefficients, regardless of whether I included ($P < 0.001$) or excluded ($P < 0.001$) fall observations (Table 2). Additionally, LME and RF models for SXW Creek revealed $K$ coefficients and percentages of coarse leaf pack mass remaining ($\%$CR) to respond positively and negatively to increases in flow metrics, respectively (Figs. 24, 25). Fine leaf pack breakdown also significantly increased in SXW Creek in 2017, but not as dramatically ($P = 0.009$ with fall observations) (Table 7). In DF River, there were significant increases in 2017 $K$ coefficients for coarse leaf breakdown ($P = 0.006$) and fine leaf breakdown ($P = 0.004$) in UDF as well as coarse breakdown ($P = 0.002$) in LDF; however, all these results became insignificant when I omitted fall observations (Table 7). Thus, it appeared that enhanced flows most strongly accelerated the conversion of leaves from coarse to fine particulate organic matter in SXW Creek.

The final LME models for $\%$CR and coarse leaf pack $K$ coefficients ($k_C$) in SXW Creek both had BIC scores that were significant improvements ($\delta \geq 4$) over those
Table 7 Mean $K$ coefficients of coarse and fine leaf packs across the river system between 2016 and 2017. All two-sample t-tests were conducted between sample groups of equivalent time periods. Significant p-values denote that the true difference in means is not equal to zero.

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<td>&lt; 0.001***</td>
<td>0.011</td>
<td>0.023</td>
<td>&lt; 0.001***</td>
</tr>
<tr>
<td>SXW:</td>
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</tr>
<tr>
<td>Fine leaf packs</td>
<td>0.013</td>
<td>0.022</td>
<td>0.009**</td>
<td>0.017</td>
<td>0.016</td>
<td>0.56</td>
</tr>
<tr>
<td>UDF:</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Coarse leaf packs</td>
<td>0.015</td>
<td>0.025</td>
<td>0.006**</td>
<td>0.017</td>
<td>0.028</td>
<td>0.06</td>
</tr>
<tr>
<td>UDF:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fine leaf packs</td>
<td>0.011</td>
<td>0.018</td>
<td>0.004**</td>
<td>0.015</td>
<td>0.018</td>
<td>0.30</td>
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<td></td>
</tr>
<tr>
<td>Coarse leaf packs</td>
<td>0.018</td>
<td>0.027</td>
<td>0.07</td>
<td>0.019</td>
<td>0.022</td>
<td>0.58</td>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fine leaf packs</td>
<td>0.012</td>
<td>0.017</td>
<td>0.002**</td>
<td>0.015</td>
<td>0.014</td>
<td>0.549</td>
</tr>
</tbody>
</table>

of their respective null models. In my analyses without 2017 step flow observations, the addition of log-transformed mean monthly flow (logMMF) as a fixed effect increased the model fit for %CR by 5.26 points over the intercept-only null model (Fig. 24).

Additionally, adding logMMF decreased residual variance by 22.1%. The annotated notation of my final SXW Creek random-intercept model for %CR is:
\[ \hat{y}_i = 1.37_{(\text{site}[i]) (\text{season}[i])} - 0.226 \times \log\text{MMF} + \varepsilon_{(\text{site}[i]) (\text{season}[i])} \]

\[ \beta_{0(\text{site}[i])} \sim N(1.37, 0.0348^2), \text{ for } j = 1, \ldots, J \text{ site} \]

\[ \beta_{0(\text{season}[i])} \sim N(1.37, 0.0558^2), \text{ for } k = 1, \ldots, K \text{ season} \]

\[ \varepsilon_{(\text{site}[i]) (\text{season}[i])} \sim N(0, 0.1394^2) \]

Where \( \hat{y}_i \) is the percentage of remaining coarse leaf pack mass, \( \log\text{MMF} \) is the fixed effect, the random effects of site and season are the \( j \)th and \( k \)th groupings, and residual variance \( \varepsilon_{(\text{site}[i]) (\text{season}[i])} \) is \( 0.1394^2 \).

**Fig. 24** The percentage of coarse leaf pack mass remaining (\%CR) as a function of mean monthly flow (MMF) in SXW Creek. The data in this model do not include step flow observations (\( n = 46 \)).
Fig. 25  $k$ coefficient for coarse leaf pack breakdown (y-axis) as a function of maximum flow within 30 days of sampling (Qmax30) (x-axis) in SXW Creek, 2016 – 2017. The data in this model included step flow observations ($n = 65$).

When I included step flow observations, the effects of flow metrics on coarse leaf pack breakdown were much more apparent. Here, log-transformed maximum flow within 30 days of sampling (logQ30) was a significant predictor of $k$ C, which linearly increased across the observed range of this flow metric (Fig. 25). Adding logQ30 increased the fit of my final random-intercept model by 24.00 points over its intercept-only null model and decreased residual variance by 43.2% (Fig. A10).

Plotting the random effect of site revealed distinct between-site variation in the slope of $k$ C against logQ30. Coarse leaf packs at Upper Sixth Water (USW) displayed the strongest responses to increasing Qmax30 and the weakest responses at Below Syar Tunnel (BST). The $k$ C slopes at Ray’s Crossing (RC) and Three Forks Sixth Water
(3F6W) were closer to the grand mean (Fig. 25). This may simply be due to noise in the coarse leaf pack dataset or may otherwise be attributed to between-site differences in other variables (i.e. shredder densities) that were not included in the final model. The annotated notation of my final random-intercept model for $k_C$ in SXW Creek is:

$$
\hat{y}_i = -0.033_{(site)[i]}(season)[i] + 0.047 \times \log Q30 + \varepsilon_{(site)[i]}(season)[i]
$$

$$
\beta_0_{(site)} \sim N(-0.033, 0.0109^2), \text{ for } j = 1, \ldots, J \text{ site}
$$

$$
\beta_0_{(season)} \sim N(-0.033, 0.0123^2), \text{ for } k = 1, \ldots, K \text{ season}
$$

$$
\varepsilon_{(site)[i]}(season)[i] \sim N(0, 0.0303^2)
$$

Where $\hat{y}_i$ is the percentage of remaining coarse leaf mass, $\log Q30$ is the fixed effect, the random effects of site and season are the $j$th and $k$th groupings, and residual variance $\varepsilon_{(site)[i]}(season)[i]$ is $0.0303^2$.

In addition to these LME results, there was some evidence that higher shredder densities may also have contributed to faster leaf breakdown in SXW Creek under enhanced flows in 2017. Average shredder densities in SXW Creek samples significantly increased from 1771 in 2016 to 4400 in 2017 ($P > 0.001$). A two-way ANOVA revealed that both shredder density and mean monthly flow were significant predictors of coarse leaf pack breakdown ($P = 0.002$ and $P > 0.001$, respectively), while the interaction of shredder density and mean monthly flow was not significant.

Random Forest (RF) models of leaf processing in SXW Creek & DF River validated the above LME models and also revealed the most important variables for fine and coarse leaf packs in LDF River. Qmax30, MMF, temp, DO and day of year were repeatedly identified as having the greatest influence on $k_C$ in SXW Creek with step
flow observations included. Variable reduction procedures selected multiple combinations of these five variables; however, the three that appeared to explain the most variance (~58%) were Qmax30, temp, and day of year. Partial dependence plots depicted $k^C$ as having a strong linear relationship with Qmax30 and unimodal relationships with temp and day of year (Fig. 26). The same five variables were also selected as most influential for %CR, which displayed exponential decreases across the observed ranges of MMF and Qmax30 and a unimodal curve across temperature.

**Fig. 26** Partial dependence plots of the $K$ coefficient for coarse leaf packs in SXW Creek (y-axis) against its three most important variables (x-axis): maximum flow within 30 days of sampling in cfs (Qmax30), temperature in degrees Celsius (temp), and day of year (DOY). Step flow observations are included (n = 64).
Fig. 27 Partial dependence plots of the percentage of coarse leaf pack mass remaining (%CR) in UDF River (top) and LDF River (bottom). In each river, %CR (y-axes) is plotted against its three most influential variables (x-axes). In UDF River, the variables from left to right are mean monthly flow in cfs (MMF), day of year (DOY), and maximum flow within 30 days of sampling in cfs (Qmax30). In LDF River, the variables are mean monthly flow in cfs (MMF), maximum flow within 30 days in cfs (Qmax30), and temperature in degrees Celcius (Temp). Step flow observations are included. N = 34 for UDF River and n = 40 for LDF River.

MMF and Qmax30 were also influential for coarse leaf breakdown in DF River.

In UDF River, %CR declined exponentially in response to increases in MMF and Qmax30; these two flow metrics combined with day of year explained ~64% of the variance in the data (Fig. 27). RF regressions for LDF River indicated that MMF, Qmax30, and temperature explained ~68% of variance in %CR when step flow
observations were included (Fig. 4). In LDF River, high %CR was maintained until a flow threshold of ~60cfs for Qmax30 or ~50cfs for MMF, after which any increases in flow precipitated rapid losses in leaf mass. Temperature appeared to have a strong, positive effect on %CR (Fig. 27), which may be attributable to its inverse correlation with flow; for example, late summer featured both the lowest flows and highest temperatures.

Overall, fine leaf pack breakdown results were less conclusive across the entire river system. In SXW Creek, day of year, temperature and dissolved oxygen explained about 40% of variance in the percentage of mass remaining in fine leaf packs (%FR), with %FR exhibiting declining U-shaped relationships across the ranges of these three variables. In LDF River, there were no clear relationships between %FR and day of year, temperature or dissolved oxygen, and the amount of variance that RF models explained was only slightly above 0%. Although fine leaf pack breakdown significantly increased in 2017, these changes did not appear to be highly correlated with the thermal and dissolved oxygen regimes.

Mirroring these yearly differences in leaf processing, chlorophyll-α growth on tiles increased in SXW Creek & DF River in 2017. Mean chlorophyll-α (μg/cm²) was marginally higher across LDF River sites than across SXW Creek sites in 2016, and this difference appeared to even stronger in 2017 (Table 8). In both years, UDF River featured the highest chlorophyll-α out of the three river segments. This was primarily attributable to tile samples from the Guard Station site, where mean monthly concentrations ranged from 0.314 to 1.857 μg/cm². Both SXW Creek and LDF River exhibited significant increases in chlorophyll-α in 2017, with mean annual concentrations increasing from 0.350 to 0.534 μg/cm² in SXW (P = 0.037) and from 0.328 to 0.648
μg/cm² in LDF (P = 0.011) (Figs. 28, 29; Table 8). These significant results were maintained regardless of whether I included or omitted fall observations (Table 3).

Neither LME modeling nor RF regression analyses provided much insight into the mechanisms driving this system-wide chlorophyll-a increase in 2017. In both SXW Creek and LDF River, intercept-only null models with site and season as random effects had the greatest model fit as identified by Bayesian Information Criterion. However, for LME modeling in LDF River, adding the coefficient of variation for MMF (CVmmf) as a fixed effect resulted in a nearly significant BIC score improvement of δ = 3.81. RF regression models for SXW Creek and UDF River did not reveal chlorophyll-a as having any clear relationships with predictor variables. After variable reduction procedures, a model with day of year, MMF and Qmax30 explained slightly less than 0% of variance in UDF River, while in SXW Creek, a model with day of year, DO and temp explained

<table>
<thead>
<tr>
<th>Table 8</th>
<th>Mean chlorophyll-a growth (μg/cm²) on tiles in each river segment between 2016 and 2017. All t-tests were conducted between sample groups of equivalent time periods. Significant p-values denote that the true difference in means is not equal to zero.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2016 avg. μg/cm² (with fall data)</td>
</tr>
<tr>
<td>SXW Creek: Chlorophyll-a</td>
<td>0.350</td>
</tr>
<tr>
<td>UDF River: Chlorophyll-a</td>
<td>0.399</td>
</tr>
<tr>
<td>LDF River: Chlorophyll-a</td>
<td>0.328</td>
</tr>
</tbody>
</table>
**Fig. 28** Chlorophyll-α growth (μg/cm²) on SXW Creek tile samples in 2016 and 2017.

**Fig. 29** Chlorophyll-α growth (μg/cm²) on LDF River tile samples in 2016 and 2017.
about -10% of variance in SXW Creek. These negative values indicate that the value of any given chlorophyll-a sample in these river segments is best predicted as being equal to the overall mean of chlorophyll-a samples, which indicates poor model performance.

In LDF River, chlorophyll-a appeared to be moderately influenced by sampling season as well as several flow metrics (Fig. 30). Together, CVmmf, day of year and MMF explained ~42% of variance in chlorophyll-a without step flow observations. Chlorophyll-a exhibited a hump-shaped seasonal trend across day of year and also attained highest concentrations when CVmmf was below 5cfs. When September 2017 data points were added, the three most important variables had less explanatory power (~26% of variance). Overall, these inconclusive results suggest that 2017 increases in chlorophyll-a growth are not strongly correlated with changes in in-stream conditions.

![Variable importance plot for chlorophyll-a in LDF River, 2016 – 2017. X-axis shows the percentage increase in mean squared error (%IncMSE) when values for a given variable are permuted. Variables are arranged in descending order of their importance. Step flow observations are not included (n = 44).](image-url)
Stream Metabolism Analyses

My stream metabolism analyses revealed SXW Creek & DF River to be a net heterotrophic system (P:R < 1). At every site, ecosystem respiration (ER) (O₂ mg/l d⁻¹) exceeded gross primary productivity (GPP) (O₂ mg/l d⁻¹) for the entirety of miniDOT logger recordings in both years. Moreover, there were apparent temporal and spatial trends of ER and GPP in 2016. GPP and ER peaked from mid August to mid September 2016 at SXW Creek sites such as USW, RC and BST. At lower elevation sites (3F6W, BMH, DFC, MO), these peaks occurred earlier in the season from June to August 2016. GPP also exhibited a distinct U-shaped trend across the river continuum in 2016, which is reflected in the highest (USW) and lowest (MO) elevation sites having the highest mean annual production to respiration (P:R) ratios of 0.225 and 0.285, respectively (Fig. 31). I suspect that this trend was driven by the combined influence of factors such as channel width, light attenuation and nutrient inputs.

Fig. 31 Box plot of mean 15-day production to respiration (P:R) ratios in SXW Creek & DF River, 2016. Sites are ordered from highest to lowest elevation, left to right.
In most sites across the river, 2017 ER and GPP were noticeably reduced relative to metabolic rates in 2016 (Fig. 32). However, GPP appeared to be more strongly suppressed than ER, resulting in significant declines in P:R ratios in 2017. Two-sample t-tests between 2016 and 2017 revealed mean annual P:R ratios to decline from 0.195 to 0.134 in SXW Creek (P < 0.001) and from 0.259 to 0.167 in LDF River (P = 0.002) (Fig. 33). Unfortunately, since the Guard Station logger was compromised in 2017, I was unable to use UDF River as a reference for P:R ratios across the two sampling years.

System-wide RF regression models explained noticeably less variance in stream metabolism metrics in 2017 than in 2016. In both years, variable reduction procedures repeatedly selected spatial and temporal variables such as width (m), elevation (m), river kilometer, and day of year as most predictive of GPP, ER and P:R in SXW Creek and DF River. Several flow metrics were also selected; however, they generally displayed ambiguous, nonlinear relationships with stream metabolism. Between 2016 and 2017, the percentage of variance explained by the three most important variables declined from ~65% to ~49% for GPP, ~71% to ~49% for ER, and ~78% to ~53% for P:R ratios.

Noticeably, the system-wide spatial and temporal trends displayed by GPP and P:R ratios in 2016 were muted in 2017. In 2016, GPP had an increasing relationship with channel width, a unimodal relationship with day of year, and a U-shaped trend across elevation; in 2017, all these relationships flattened out (Fig. 34). As previously observed, 2016 P:R ratios had a U-shaped relationship with elevation and a positive linear relationship with width, in addition to exhibiting distinct peaks in mid to late summer. Contrastingly, 2017 P:R ratios were relatively uniform across sampling sites and seasons (Fig. A11).
Fig. 32 Ecosystem respiration ($O_2$ mg/l d$^{-1}$) and gross primary productivity ($O_2$ mg/l d$^{-1}$) at the Below Syar Tunnel site, SXW Creek (top) and Below Monk’s Hollow site, LDF River (bottom), 2016 and 2017. Ecosystem respiration (ER) is represented by the red lines and gross primary productivity (GPP) by the blue lines. Solid and dashed lines represent 2016 and 2017, respectively.
**Fig. 33** Box plots of P:R ratios in SXW Creek (left) and LDF River (right) in 2016 (natural flow year) and 2017 (enhanced flow year). Each box is comprised of average 15-day P:R ratio data from April to October in a given river segment and year. N = 31 for SXW Creek boxes and n = 19 for LDF River boxes.

**Fig. 34** Partial dependence plots of system-wide gross primary productivity (O₂ mg/l d⁻¹) in 2016 (top) and 2017 (bottom). For each year, gross primary productivity (GPP) (y-axes) is plotted against its three most influential variables (x-axes). In 2016, the variables from left to right are width (m), day of year (DOY), and elevation in meters (Elev). In 2017, the variables are width (m), Elev, and DOY. N = 89 for 2016 and n = 59 for 2017.
RF models of system-wide stream metabolism metrics did not by themselves indicate that enhanced flows were suppressing GPP and ER in 2017. This is likely due to the wide variability in flow metrics across SXW Creek & DF River, which may have been obscuring the effects of flow at smaller spatial scales. My separate RF models for SXW Creek and LDF River provided more insight into the relationships between flow and stream metabolism within each river segment. Out of the three stream metabolism metrics, models of GPP had the most explanatory power, explaining ~50% and ~46% of variance in SXW Creek and LDF River, respectively. 15-day mean flows (CFS), coefficient of variation for CFS (CVcfs), and maximum flow within 15 days of sampling (Qmax15) all negatively affected GPP, particularly in LDF River (Fig. 12). In LDF River, GPP exponentially decreased across CFS and had a linear, negative relationship with CVcfs. Additionally, the positive correlation between GPP and temperature was much stronger in LDF River than in SXW Creek (Fig. 35). P:R ratios generally mirrored the relationships that GPP had with flow, temperature and season (Fig. A12). Compared to GPP and P:R ratios, visualizations of my ER models revealed more ambiguous relationships (Fig. A13). While there was some evidence of a negative, threshold relationship between ER and CFS in LDF River, the low model R$^2$ (~12%) should warrant skepticism. Overall, these RF models suggest that primary production was more vulnerable to enhanced flows than autotrophic and heterotrophic respiration, which may have caused a system-wide shift towards higher net heterotrophy.

*Functional Feeding Group Analyses*

Gatherers and scrapers were the dominant feeding groups within benthic communities in not just the two sampling years of this project, but also in the historical
Fig. 35 Partial dependence plots of gross primary productivity (O₂ mg/l d⁻¹) in SXW Creek (top) and LDF River (bottom). For each river segment, gross primary productivity (GPP) (y-axes) is plotted against its three most influential variables (x-axes). In SXW Creek, the variables from left to right are 15-day mean flow in cfs (CFS), day of year (DOY), and maximum flow within 15 days in cfs (Qmax15). In LDF River, the variables are 15-day mean flow in cfs (CFS), day of year (DOY), and maximum flow within 15 days in cfs (Qmax15). N = 73 for SXW Creek and n = 51 for LDF River.

data collected by BIO-West. From 2005 to 2017, these two feeding groups represented an annual average of 64.9% of organisms in SXW Creek, 65.1% in UDF River and 57.4% in LDF River. While shredders, filterers and predators have important functional roles and comprised the remainder of sampled communities, they did not exhibit any observable trends in initial visualizations of 2016 and 2017 (Figs. A14, A15). Contrastingly, 2016 scraper percentages had increasing downstream trends, surpassing gatherer percentages in
LDF River (Fig. A14). In 2017, gatherers were significantly more dominant across SXW Creek & DF River, while scrapers experienced uniform declines.

Both gatherer and scraper benthic densities exhibited distinct changes across the river system in 2017. April to August gatherer densities doubled in SXW Creek (P = 0.0013) from 2016 to 2017 while declining negligibly in DF River (Fig. 36). April to August scraper densities displayed marginally significant increases in SXW Creek (P = 0.0502), negligible declines in UDF River, and a significant plunge in LDF River (P = 0.002) between the two years (Fig. 37). These density changes were reflected in the relative contributions of these feeding groups to benthic communities. In 2016, scrapers were the dominant feeding group in LDF River; in 2017, gatherers overtook scrapers in LDF River and became the dominant feeding group system-wide (Fig. A14, A15).

![Bar plot of mean April – August gatherer benthic densities (organisms per m²) in SXW Creek & DF River, 2016 & 2017.](image)

**Fig. 36** Bar plot of mean April – August gatherer benthic densities (organisms per m²) in SXW Creek & DF River, 2016 & 2017.
LME modeling revealed these two feeding groups to be differentially affected by flow and stream metabolism metrics across the river system. In SXW Creek, adding 15-day P:R ratios resulted in the scraper density model having a BIC score improvement of 10.57 over the null model with day of year (DOY) and the quadratic term DOY² as fixed effects. Interestingly, this final model did not decrease residual variance, nor did it enhance prediction accuracy of scraper densities across P:R ratios. P:R ratios were also had significant Pearson correlations with gatherer and scraper densities in SXW Creek (Table 9). However, when these two feeding groups were plotted against P:R ratios, the relationships were non-linear and there were several outliers that I suspected were disproportionately contributing to the significant correlations. Thus, it appeared that the
Table 9  Pearson correlation coefficients between gatherer and scraper metrics and mean monthly flow (MMF), gross primary productivity (GPP), and production to respiration (P:R) ratios.

<table>
<thead>
<tr>
<th></th>
<th>Density ~ MMF</th>
<th>Density ~ GPP</th>
<th>Density ~ P:R</th>
<th>Percentage ~ MMF</th>
<th>Percentage ~ GPP</th>
<th>Percentage ~ P:R</th>
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<td></td>
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<td></td>
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</tr>
<tr>
<td>Gatherers</td>
<td>-0.279*</td>
<td>0.399***</td>
<td>0.547***</td>
<td>-0.104</td>
<td>0.021</td>
<td>0.230</td>
</tr>
<tr>
<td>Scrapers</td>
<td>-0.177</td>
<td>0.352**</td>
<td>0.465***</td>
<td>0.035</td>
<td>0.018</td>
<td>-0.25*</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gatherers</td>
<td>-0.39***</td>
<td>NA</td>
<td>NA</td>
<td>0.57***</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>Scrapers</td>
<td>-0.61***</td>
<td>NA</td>
<td>NA</td>
<td>-0.497***</td>
<td>NA</td>
<td>NA</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gatherers</td>
<td>-0.348**</td>
<td>0.588***</td>
<td>0.636***</td>
<td>0.66***</td>
<td>-0.239*</td>
<td>-0.111</td>
</tr>
<tr>
<td>Scrapers</td>
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<td>0.664***</td>
<td>0.639***</td>
<td>-0.543***</td>
<td>0.267</td>
<td>0.140</td>
</tr>
</tbody>
</table>

Higher densities of both feeding groups and the increased proportions of gatherers in 2017 SXW Creek communities were weakly associated with flow and stream metabolism.

In LDF River, gatherers and scrapers varied in the strength of their responses to flow and stream metabolism. Adding log-transformed mean monthly flow (log\text{MMF}) significantly increased fit over null models with DOY and DOY^2 as fixed effects, improving the BIC scores of the gather and scraper density models by 5.42 and 7.26, respectively. While the final gatherer density model had only slightly less residual variance over its corresponding null (2.4%), the scraper model had a notable decrease of 15.9%. The annotated notations of my final random-intercept models for gatherer and scraper densities in LDF River are:
1) Gatherer densities:

\[ \hat{y}_i = -148.04_{(site)[i][year][i]} - 16.07 \times \log\text{MMF} + 1.54 \times \text{DOY} - 71.44 \times \text{zDOY}^2 + \epsilon_{(j)[i][k][i]} \]

\[ \beta_0_{(site)} \sim N(-148.04, 8.491 \times 10^{-7}) \), for \( j = 1, \ldots, J \) site

\[ \beta_0_{(year)} \sim N(-148.04, 0) \), for \( k = 1, \ldots, K \) year

\[ \epsilon_{(j)[i][k][i]} \sim N(0, 18.31^2) \]

2) Scraper densities:

\[ \hat{y}_i = -703.64_{(site)[i][year][i]} + 39.68 \times \log\text{MMF} + 6.42 \times \text{DOY} - 189.39 \times \text{zDOY}^2 - 0.73 \times \log\text{MMF}:\text{DOY} + \epsilon_{(j)[i][k][i]} \]

\[ \beta_0_{(site)} \sim N(-703.64, 4.971^2) \), for \( j = 1, \ldots, J \) site

\[ \beta_0_{(year)} \sim N(-703.64, 19.903^2) \), for \( k = 1, \ldots, K \) year

\[ \epsilon_{(j)[i][k][i]} \sim N(0, 18.584^2) \]

Where \( \hat{y}_i \) is the benthic density of 1) gatherers or 2) scrapers; 1) \( \log\text{MMF}, \text{DOY} \) and \( \text{zDOY}^2 \) or 2) \( \log\text{MMF}, \text{DOY}, \text{zDOY}^2 \) and the interaction term \( \log\text{MMF}:\text{DOY} \) are the fixed effects, the random effects of site and season are the \( j \)th and \( k \)th groupings, and residual variance \( \epsilon_{(j)[i][k][i]} \) is 1) \( 18.31^2 \) or 2) \( 18.584^2 \).

When I visualized these final models across DOY, I observed that gatherer densities did not respond as strongly as scraper densities to changes in mean monthly flow (Figs. 38, 39). For both feeding groups, I simulated the seasonal trends of benthic density if MMF were held constant at its minimum (37cfs), mean (81cfs) and maximum (167.7cfs) observed values. Although increases to MMF lowered the unimodal curve of
gatherer densities across DOY, gatherer densities under minimum and maximum MMF did not strongly deviate from the grand mean of the final model (Figure 38). Contrastingly, minimum and maximum MMF values were shown to dramatically raise and lower the unimodal curves of scraper densities across DOY, respectively (Fig. 39).

**Fig. 38** Gatherer density (organisms per m$^2$) across day of year (DOY) in LDF River from 2016 to 2017. The red, black and blue lines represent simulations of gatherer density across DOY at minimum (37cfs), mean (81cfs) and maximum (167.7cfs) mean monthly flow (MMF) values, respectively.
**Fig. 39** Scraper density (organisms per m²) across day of year (DOY) in LDF River from 2016 to 2017. The red, black and blue lines represent simulations of scraper density across DOY at minimum (37cfs), mean (81cfs) and maximum (167.7cfs) mean monthly flow (MMF) values, respectively.

The differing responses of gatherer and scraper densities to mean monthly flow likely prompted shifts in the overall percentages of these two feeding groups within LDF River benthic communities. Scraper percentages in LDF River had a negative relationship with MMF (P < 0.001) (Fig. 40). Contrastingly, gatherer percentages had a positive relationship with MMF (P < 0.001) and a significant, negative Pearson correlation with GPP (Fig. 40, Table 9). The opposing trends of gatherer and scraper percentages in LDF River highlight the strong role of flow in organizing the functional composition of benthic communities. The potential influence of stream metabolism on gatherer and scraper dynamics in LDF River was not detected in LME modeling.
Fig. 40  Gatherer (top) and scraper (bottom) proportions across log-transformed mean monthly flow (cfs) in LDF River, 2016 to 2017 (n = 52).
Discussion

In Chapter III, I sought to understand how enhanced flows influence overall ecosystem functioning as well as the spatial gradients of stream metabolism and functional feeding groups (FFGs) in SXW Creek and DF River. For each river segment, I used LME and RF modeling of leaf litter breakdown and chlorophyll-a growth to test for relationships between flow metrics and the standing stocks of allochthonous and autochthonous energy sources. Secondly, with time-series data from MiniDOT loggers, I estimated gross primary productivity (GPP), ecosystem respiration (ER) and production to respiration (P:R) ratios and then used RF modeling to determine how these stream metabolism metrics were affected by enhanced flows. Lastly, I visualized the spatial gradients of stream metabolism and FFGs under two years of distinct flow regimes to assess the applicability of the River Continuum Concept for my study system. My results demonstrate that enhanced flows may significantly and non-uniformly alter ecosystem functioning, stream metabolism rates and the functional composition of the benthos across river systems. Moreover, I also found that the spatial gradients of stream metabolism and FFGs differed strongly between the two sampling years and oftentimes diverged from explanations offered by the River Continuum Concept.

When considering only leaf breakdown and chlorophyll-a results, it appeared that enhanced flows stimulated ecosystem functioning in 2017. Flow metrics in SXW Creek had significant, positive correlations with $K$ coefficients of leaf breakdown ($kC$) and significant, negative correlations with percentages of coarse leaf pack mass remaining (%CR). Maximum flow $Q$ appeared to be a particularly strong control on leaf breakdown in SXW Creek, as evidenced by the significant improvements in LME model fit with the
addition of Qmax30 as a fixed effect. Moreover, RF regressions also showed %CR as exhibiting threshold responses to flow metrics in DF River; these thresholds of leaf mass loss occurred around 10cfs in UDF River and 50-60cfs in LDF River. When compared with the equivocal influence of shredder densities, these strong linkages between flow and breakdown metrics suggest that leaf breakdown was being augmented primarily through physical abrasion. Physical abrasion is an often-overlooked mechanism of leaf breakdown in rivers and may particularly assume a dominant role during flood events (Abelho, 2001). While leaf breakdown has typically been conceptualized as having three distinct processes (i.e. leaching, conditioning, fragmentation) (Cummins, 1974), some have argued that this conceptualization downplays the influence of abiotic forces (Gessner et al., 1999). In the absence of other factors, higher physical abrasion associated with enhanced flows may bypass this three-part process and accelerate breakdown rates.

Notably, leaf breakdown responded more strongly to flow increases in SXW Creek than in DF River. While this may be due to high turbulence and flow heterogeneity in the headwaters, there was also evidence to suggest that shredder macroinvertebrates were more actively contributing to leaf breakdown in SXW Creek. Not only did SXW Creek shredder densities increase 2.5x from 2016 to 2017, a two-way ANOVA revealed shredder densities to be a significant predictor of %CR in this river segment. The influence of shredders on ecosystem functioning has been found to decrease downstream in relation with altitude (Graca et al., 2001), and it is quite possible that this biotic gradient was contributing to the different magnitudes of change in leaf breakdown between SXW Creek and DF River. However, the negligible, system-wide increases of fine leaf pack breakdown in 2017 are more difficult to account for with biotic
mechanisms. Bacteria and aquatic fungi are understood to be less metabolically active in
colder water temperatures and are oftentimes more involved in leaf breakdown in high-
order streams than in headwaters (Irons III et al., 1994; Graca et al., 2001). Since the
river system exhibited colder in-stream temperatures in 2017, one might expect the
contributions of these microbial populations to leaf breakdown to be reduced. Thus,
hydraulic stress may also have been a driver of increased fine leaf pack breakdown under
the 2017 flow regime. Since I did not measure bacterial and fungal biomass on my leaf
packs, these interpretations are far from conclusive and warrant further research.

The significant, system-wide increase in chlorophyll-\(a\) growth in 2017 was not
well explained by LME or RF modeling. Additionally, increases in primary productivity
during and immediately after high flow events are not commonly observed in the
literature. While algae and periphyton may be released from herbivory following
reductions in scraper populations (Rosemond et al., 1993; Huryn, 1998), there was
equivocal evidence of strong top-down controls on primary production in the SXW Creek
and DF River system. My chlorophyll-\(a\) results conflicted with the observed between-
year changes in stream metabolism, and I suspect that this discrepancy may be due to
methods and shortcomings associated with tile installations. First, autotrophy in river
systems can exist anywhere along a spectrum from algae-dominated to macrophyte-
dominated (Biggs et al., 2005; Dewson et al., 2007; Rolls et al., 2012). While the
biomasses of both algae and macrophytes can be greatly reduced under “drag-
disturbance” high flow events, long durations of low flows may promote the takeover of
macrophytes (Biggs et al., 2005). It is possible that system-wide decreases of GPP in
2017 were linked to changes in macrophyte biomass not detected by chlorophyll-\(a\)
measurements from my tiles. Moreover, placing tiles along the stream margins in both years and nailing them into the substrate in 2017 may have protected these tiles’ periphyton stocks from the hydraulic stress faced by periphyton in other sections of the channel. Thus, it is possible that increases in chlorophyll-a growth on installed tiles and decreases in overall GPP occurred simultaneously within the same year.

Stream metabolism analyses revealed the river to be a net heterotrophic system. Even under natural flow conditions, P:R ratios rarely surpassed 0.5 throughout the river. In 2016, SXW Creek & DF River exhibited a distinct U-shaped gradient in primary production, with highest P:R ratios occurring in the topmost and bottommost elevations. As mentioned earlier, this may be explained by the influence of factors such as light attenuation and nutrient inputs. Not only were the SXW Creek headwaters and DF River mainstem less shaded than mid-elevation sites (i.e. Guard Station, Three Forks sites), field observations of macrophyte biomass below the Syar Tunnel and Monk’s Hollow Outlets suggested that these flow release structures were contributing substantial nutrient loads to the river. In 2017, these spatial trends of GPP were muted, and both GPP and ER uniformly declined throughout the river system. However, RF models of stream metabolism metrics in SXW Creek and LDF River provided evidence that flow metrics (i.e. CFS, CVcfs, Qmax15) more strongly suppressed GPP than ER. This resulted in a system-wide shift in P:R ratios towards greater net heterotrophy.

Disproportionate declines in GPP during natural and anthropogenic spates have been observed in river systems worldwide, and this phenomenon has often been attributed to GPP being less resilient to high flows than ER (Young & Huryn, 1996; Uehlinger & Naegeli, 1998; Uehlinger et al., 2003). Autotrophic activity is mostly
restricted to streambed surfaces; thus, bed-mobilizing and scouring events may result in large reductions in primary producer biomass. Contrastingly, heterotrophs have access to the hyporheic zone, where they can process organic matter free from the influence of flow disturbances (Uehlinger & Naegeli, 1998; Boulton et al., 2010). This zone may provide substantial contributions to ecosystem functioning, as hyporheic respiration has been found to constitute as much as 87% of total ER in some rivers (Mulholland et al., 1997; Naegeli & Uehlinger, 1997). I suspect that the lopsided reductions in GPP and ER in SXW Creek & DF River were at least partly due to the hyporheic zone acting a source of resiliency for ER, where processes such as nutrient uptake and organic matter decomposition were able to continue undisturbed. Despite this potential heterotrophic advantage, enhanced flows still suppressed ER in 2017. This was likely caused by reductions in benthic macroinvertebrate density and, where density did not decline, reductions in autotrophic respiration and decreased energy uptake (Biggs et al., 2005).

One area of uncertainty is how stream metabolism in SXW Creek and DF River will rebound from enhanced flows. Temporal and spatial recovery patterns of GPP are especially variable; primary producers may even exhibit increases after initial declines from high flows (Uehlinger et al., 2003). Additionally, some have posited that high flow events contract reaches of high primary productivity, which expand during subsequent periods of low flow (Minshall et al., 1985; Young & Huryn, 1996). Regardless of this uncertainty, the uniform decreases in GPP and ER within the observed timespan have significant implications for river health. Declines in stream metabolism under enhanced flows may negatively impact carbon fixation, organic matter turnover lengths, and ultimately, the integrity of biological communities (Meyer & Edwards, 1990; Hall et al.,
2016). In SXW Creek & DF River, system-wide losses in autochthonous energy under enhanced flows may force the stream ecosystem to be more reliant on allochthonous energy sources. If leaves and terrestrial organic matter are not compensating for these losses and are instead being rapidly evacuated from river reaches, then it is possible that the carrying capacity of this ecosystem will be reduced.

In 2017, GPP and P:R ratios were uniformly low and exhibited little change across the river continuum. This system-wide suppression of primary productivity was mirrored in the system-wide suppression of scrapers and the promotion of collector-gatherers. Gatherer densities and percentages significantly increased across the river system under enhanced flows, and in LDF River, gatherer populations were more resilient to flow than scraper populations. Based on feeding group classifications from Merrit & Cummins (1996), many taxa that belong primarily to the gatherer guild also display facultative feeding strategies (e.g. Chironomidae, Oligochaeta, Baetid mayflies). Contrastingly, the Helicopsychidae and Glossosomatidae taxa that exhibited the strongest declines in LDF River are obligate scrapers. Gatherer taxa may also benefit from their strong associations with “flow-avoiding” strategies, as was observed in the Fraser River in British Columbia (Rempel et al., 2000). These flow-induced shifts in P:R ratios and the functional composition of the benthos demonstrate that paradigms which overemphasize predictable gradients and temporal stability (i.e. the River Continuum Concept) are too simplistic (Montgomery, 1999).

There were several study limitations that should be considered while interpreting these results. First, my methods of installing tiles for chlorophyll-α growth analyses were not consistent between the two sampling years. During the 2016 sampling season, I
secured tiles to rebar using zap straps; in 2017, I nailed these tiles directly into the substrate. These methodological differences, in addition to the placement of tiles along the stream margins, may have produced misleading results. Second, calculating the reaeration coefficient from width and depth is less accurate than tracer gas methods for estimating stream metabolism (Tank et al., 2010). Width and depth data do not capture the turbulence of a reach, which strongly influences the rate that oxygen is exchanged between the atmosphere and the stream. Some have suggested the use of Monte-Carlo simulations to incorporate uncertainty into stream metabolism estimations (McCutchan Jr. et al., 1998); such methods may have been beneficial to adapt. Despite this, the striking differences in stream metabolism between the years suggest that my methods still picked up on a system-wide trend. Finally, the low and inconsistent taxonomic resolution of my macroinvertebrate identification may have prevented me from detecting subtler changes in FFG compositions, particularly in feeding groups that were not overly abundant within the community. However, family or genus-level identification is more acceptable when assessing large between-site and across-time differences, or when the study system is not very speciose (Lenat & Resh, 2001). My FFG methods were likely best suited for comparing system-wide differences between the sampling years, rather than for tracking the temporal dynamics of feeding groups in individual sites.

Overall, the research conducted in Chapter III has both ecological and managerial implications. My results indicate that enhanced flows have the potential to suppress net ecosystem production in river systems, which may impact biological carrying capacities and the efficiency of organic carbon processing. Moreover, enhanced flows have the potential to weaken gradients of stream metabolism that are present in unregulated rivers.
In SXW Creek and DF River, there is equivocal evidence that the widespread suppression of GPP was contributing to the system-wide increases in gatherer taxa in 2017. Some have observed certain feeding groups to outperform others under stressful abiotic conditions such as hydrological variability in the tailwaters of dams (Troelstrup & Hergenrader, 1990; Ellis & Jones, 2013). While there was strong evidence that increases in mean monthly flow were promoting gatherers over scrapers in LDF River, I was unable to assess the degree to which these changes in FFG compositions were occurring independently of changes in GPP. Going forward, my results should prompt further research into the relative influences of flow and resource availability on feeding group dynamics.

Lastly, the conflicting results of my chlorophyll-\(a\) and stream metabolism analyses show that it may be ideal for managers to use suites of ecosystem function metrics rather than relying on one or two. If I were to have measured ecosystem functioning solely through leaf breakdown and chlorophyll-\(a\) growth, I would have more likely concluded that enhanced flows were bolstering resource availability in SXW Creek and DF River. However, my stream metabolism analyses provided evidence for an overall negative impact of enhanced flows on net ecosystem production in 2017. Thus, managers should adapt holistic approaches to quantifying ecosystem functioning in regulated rivers so that they may compare the utility of existing methods and increase the accuracy of their diagnoses.
Literature Cited:


CHAPTER IV
CONCLUSION

Despite a growing recognition of the importance of natural flow regimes for maintaining river ecosystem health, free-flowing rivers are becoming increasingly rare worldwide. As of 2006, only 64 out of 177 (~36%) rivers longer than 1000km globally are unobstructed by dams and unmodified by anthropogenic flow regimes (World Wide Fund for Nature, 2006). Currently, the majority of river systems in the western United States are being regulated under state and federal projects to provide humans with agriculture, industrial and municipal water amidst arid landscapes. Flow modifications are known to degrade river systems by increasing or decreasing the frequencies of disturbance events (Dewson et al., 2007; Kennedy et al., 2014), upsetting sediment budgets (Grams & Schmidt, 2005; Ligon et al., 1995), altering thermal regimes (Hall et al., 2015; White et al., 2016), and decreasing ecosystem productivity and aquatic biodiversity (Brittain & Saltviet, 1989; Kennedy et al., 2016). However, despite detailed understandings of how flow reductions and high flow spates impact river health (Cortes et al. 2002; Rolls et al., 2012.), few studies have investigated the effects of sustained increases to baseflow magnitudes on community structure and ecosystem functioning. Given the complex responses of river ecosystems to flow modification, it will be necessary for managers to adapt holistic, multi-trophic monitoring approaches under enhanced flow regimes.

The purpose of my research on the SXW Creek and DF River system was to understand the dynamics of macroinvertebrate communities and ecosystem functions across a range of flow conditions. To determine how community health and structure
responded to increases in flow, I collected benthic and drift data under natural flow conditions in 2016 and enhanced flow conditions in 2017, in addition to utilizing historical data collected by BIO-West from 2005 – 2012. I used a combination of linear modeling, nonparametric modeling, and community ordination techniques to address my Chapter II research questions. I found that increases to flow non-uniformly impacted benthic density, sensitive taxa, and drift composition from headwaters to mouth. I concluded that the dual stressors of natural and anthropogenic flow increases were suppressing LDF River communities in 2017, and particularly the populations of sensitive taxa such as several families of caddisfly.

In Chapter III, I investigated how enhanced flows affected leaf breakdown rates, chlorophyll-\(a\) growth, and stream metabolism in SXW Creek and DF River, in addition to assessing the spatial linkages between ecosystem functioning and macroinvertebrate functional feeding groups. I found that leaf breakdown accelerated as flows increased, while stream metabolism and gross primary productivity in particular were negatively impacted by enhanced flows in 2017. This disproportionate suppression of gross primary productivity caused the river system to shift towards greater net heterotrophy. Additionally, the functional composition of macroinvertebrate communities significantly changed between the two years. In 2017, enhanced flows appeared to cause a system-wide decline in scraper taxa and a system-wide increase in collector-gatherer taxa. Lastly, the spatial gradients of stream metabolism and functional feeding groups that were present in 2016 became homogenized in 2017 flow conditions.

Overall, the distinct ecological responses to enhanced flows within each river segment have implications for both the field of ecology and for managers of regulated
rivers. Despite relatively uniform changes to ecosystem functioning in 2017, mainstem macroinvertebrate communities were more vulnerable to flow increases than tributary communities, which was likely due to the influences of substrate instability and hydraulic stress compounding downstream. This affirms recent work demonstrating that the processes guiding community assembly (i.e. species sorting, dispersal) vary across river continua, and particularly between tributaries and mainstems (Brown & Swan, 2010; Finn et al., 2011; Heino et al., 2013). These results should motivate managers of regulated rivers to more explicitly consider tributaries and headwaters as refugia for sensitive species and sustainers of aquatic biodiversity. In addition to these differences between tributaries and mainstems, the reorganization of structural and functional gradients between 2016 and 2017 demonstrate the need for ecologists to view rivers as temporally and spatially dynamic, rather than as linear systems that change predictably from headwaters to mouth (Vannote et al., 1980; Montgomery, 1999; Toone et al., 2012). Lastly, the system-wide declines of gross primary productivity in 2017 demonstrates that river ecosystems may be vulnerable to losses of in-stream energy supplies under enhanced flows. My research on SXW Creek and DF River reveals the importance of using suites of structural and functional metrics to assess the impacts of modified flow regimes on river systems. Based on the output of this thesis, I recommend managers to strive for comprehensive understandings of the environmental and ecological variability of their river systems before considering mandated flows as restoration strategies.
Literature Cited:


APPENDIX: SUPPORTING FIGURES
Fig. A1  Distribution of residuals around zero for the final benthic density model (yellow) and the null benthic density model (blue) in LDF River. The y-axis is the frequency (# of data points) of a given residual value within the model. The x-axis is the residual value, or the difference between the observed and predicted value of benthic density (organisms m$^2$).
Fig. A2  Residuals plotted against the fixed effect of log-transformed benthic density (organisms per m²) for the random-intercept, system-wide model (left) and the null model (right) of drift density (organisms per m²) in SXW Creek & DF River, 2016 – 2017.

Fig. A3  Distribution of residuals around zero for the final drift density models (yellow) and the null drift density model (blue) in SXW Creek (left) and LDF River (right). The y-axis is the frequency of a specific residual value within the model, and the x-axis is the residual value, or the difference between the observed value and predicted model value of drift density (organisms m²).
**Fig. A4** NMDS plot of SXW Creek & DF River benthic communities in April 2016. SXW Creek sites are in blue, UDF River sites are in yellow, and LDF River sites are in red. The five predictor variables are elevation (elev), coefficient of variation for mean monthly flow (CVmmf), mean monthly flow (mmf), temperature (temp) and dissolved oxygen (DO). $R^2 = 0.458$. 
Fig. A5  NMDS plot of SXW Creek & DF River benthic communities in June 2016. SXW Creek sites are in blue, UDF River sites are in yellow, and LDF River sites are in red. The five predictor variables are elevation (elev), coefficient of variation for mean monthly flow (CVmmf), mean monthly flow (mmf), temperature (temp) and dissolved oxygen (DO). $R^2 = 0.377$. 
Fig. A6 NMDS plot of SXW Creek & DF River benthic communities in August 2016. SXW Creek sites are in blue, UDF River sites are in yellow, and LDF River sites are in red. The five predictor variables are elevation (elev), coefficient of variation for mean monthly flow (CVmmf), mean monthly flow (mmf), temperature (temp) and dissolved oxygen (DO). $R^2 = 0.459.$
Fig. A7  NMDS plot of SXW Creek & DF River communities in April 2017. SXW Creek sites are in blue, UDF River sites are in yellow, and LDF River sites are in red. The five predictor variables are elevation (elev), coefficient of variation for mean monthly flow (CVmmf), mean monthly flow (mmf), temperature (temp) and dissolved oxygen (DO). \( R^2 = 0.467 \).
Fig. A8  NMDS plot of SXW Creek & DF River communities in June 2017. SXW Creek sites are in blue, UDF River sites are in yellow, and LDF River sites are in red. The five predictor variables are elevation (elev), coefficient of variation for mean monthly flow (CVmmf), mean monthly flow (mmf), temperature (temp) and dissolved oxygen (DO). $R^2 = 0.664$. 

- SXW Creek
- UDF River
- LDF River
**Fig. A9** NMDS plot of SXW Creek & DF River communities in August 2017. SXW Creek sites are in blue, UDF River sites are in yellow, and LDF River sites are in red. The five predictor variables are elevation (elev), coefficient of variation for mean monthly flow (CVmmf), mean monthly flow (mmf), temperature (temp) and dissolved oxygen (DO). $R^2 = 0.663$. 
Table A1  SIMPER analyses between 2016 and 2017 in UDF River. For each month, the three most influential taxa with significant P-values are listed. The **Average** column shows the average contribution (out of 1) of a taxon to overall between-group dissimilarity, 2016 and 2017 show the average taxon abundances in each sampling year, and **P** shows the probability of getting a larger or equal average contribution in random permutation of the group factor. **Blue** denotes Ephemeroptera and **Red** denotes Trichoptera.

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<td>0.003**</td>
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**Fig. A10**  Residuals plotted against log-transformed Qmax30 for the final intercept-only model (left) and the intercept-only null model (right) of the \( K \) coefficient for coarse leaf packs in SXW Creek.
2016

Fig. A11  Partial dependence plots of system-wide production to respiration (P:R) ratios in 2016 (top) and 2017 (bottom). In each year, P:R ratios (y-axes) are plotted against their three most influential variables (x-axes). In 2016, the variables from left to right are elevation in meters (Elev), width in meters, and day of year (DOY). In 2017, the variables are elevation and 2017 (bottom). In 2016, the variables are Elev, 15-day mean flow in cfs (CFS), and width in meters. N = 89 for 2016 models and n = 59 for 2017 models.
Fig. A12  Partial dependence plots of production to respiration (P:R) ratios in SXW Creek (top) and LDF River (bottom). For each river segment, P:R ratios (y-axes) are plotted against their three most influential variables (x-axes). In SXW Creek, the variables from left to right are day of year (DOY), 15-day mean flow in cfs (CFS), and maximum flow within 15 days in cfs (Qmax15). In LDF River, the variables are temperature in degrees Celsius (Temp), DOY, and Qmax15. N = 73 for SXW Creek and n = 51 for LDF River.
Partial dependence plots of ecosystem respiration (O₂ mg/l d⁻¹) in SXW Creek (top) and LDF River (bottom). For each river segment, ecosystem respiration (ER) (y-axes) is plotted against its three most influential variables (x-axes). In SXW Creek, the variables from left to right are 15-day mean flow in cfs (CFS), temperature in degrees Celcius (temp), and coefficient of variation for 15-day mean flow in cfs (CVcfs). In LDF River, the variables are CFS, day of year (DOY), and CVcfs. N = 73 for SXW Creek and n = 51 for LDF River.
Fig. A14  Bar plot of mean functional feeding group percentages within all benthic communities in 2016.

Fig. A15  Bar plot of mean feeding group percentages within all benthic communities in 2017.