Title

The Influence of Flow Variation on Community Composition in Streams and Rivers

Author

Saffarinia, Parsa

Publication Date

2019

UNIVERSITY OF CALIFORNIA
RIVERSIDE

The Influence of Flow Variation on Community Composition in Streams and Rivers

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Evolution, Ecology, and Organismal Biology

by

Parsa Saffarinia

December 2019

Dissertation Committee:
    Dr. Kurt E. Anderson, Chairperson
    Dr. Jeffrey Diez
    Dr. Marko Spasojevic

The Dissertation of Parsa Saffarinia is approved:

Committee Chairperson

University of California, Riverside

Acknowledgements

I am deeply grateful for the guidance of my advisor, Kurt Anderson. I thank my dissertation committee members Jeff Diez and Marko Spasojevic. As a first generation academic, I will always have a special appreciation to those who encouraged me early in my career, especially Kurt Anderson, Mary Power, David Herbst, and Scott Cooper. Several others notably contributed to my dissertation work, including William Walton, Matt Daugherty, David Reznick, James Sickman, Mary Gauvain, Caitlin Eliason, Hossien Saffarinia, Soraya Saffarinia, Haley Saffarinia, Kai Palenscar, Heather Dyer, Larry Brown, Kerwin Russell, Brett Mills, Bruce Medhurst, Brandon McNellis, Kenjiro Quides, Michala Philips, Emily Naylor, Matthew Green, Ryan Conway, Lisa Dong, and Brian Wang. Funding for this dissertation was provided by the National Science Foundation (Integrative Graduate Education and Research Traineeship), the institute for the study of ecological and evolutionary climate impacts, the Center for Conservation Biology, the Valentine Eastern Sierra Nevada Research Grant, and the U.S. Fish and Wildlife Service.

ABSTRACT OF THE DISSERTATION

The Influence of Flow Variation on Community Composition in Streams and Rivers

by

Parsa Saffarinia

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal Biology
University of California, Riverside, December 2019
Dr. Kurt E. Anderson, Chairperson

Global change has severely impacted the flow regimes of river systems across the globe, and the species inhabiting those systems now find themselves adapted to hydrographs that no longer exist. This includes many of the flow regimes in California, as streams are experiencing an altered precipitation cycle and a system of dams, culverts, and wastewater treatment plants that have transformed rivers that were once naturally flowing into occasionally concrete-lined channels. In the following chapters, I report the results of several studies aimed at understanding the relationship between flow variability and the persistence of ecological communities in river systems, particularly diatoms and benthic macroinvertebrates. In chapter one, I utilize a set of high-elevation experimental stream channels to subject the stream benthic community to a gradient of drought treatments. In this study, I found that pool habitat serves as a better refuge to benthic macroinvertebrates than riffles, contingent on the presence of hyporheic flow. Additionally, perennial flow–adapted communities appear to resist flow reduction, up to the point when surface flow is lost. My second chapter examines the relationship between benthic macroinvertebrate community composition and flow regimes, spatial connectivity, and environmental variables at large spatial scales and long temporal scales. I found that spatial processes, such as drainage density and upstream area, and flow metrics, such as flow variability and zero-flow days, best explain temporal beta diversity in macroinvertebrate communities at the multi-catchment scale. Chapter three explores the impact of urban flow disturbance, in the form of effluent discharge from wastewater treatment plants and storm runoff, on benthic diatom and macroinvertebrate communities through space and time. I found that macroinvertebrates in such systems are resistant to flow perturbations, compositionally reflected in a relatively disturbance-tolerant community, while the diatoms reflected fast-paced resilience strategies. While erratic flow shutdowns from wastewater treatment plants result in losses of taxa and lower densities of individuals, large storm events further compound flow regime disturbance in the urban stream system. Overall in this dissertation, I demonstrate that flow disturbance is a strong predictor of benthic freshwater communities, and that determining the extent of hydrological disturbance at the correct timescale is critical to the conservation of freshwater biodiversity.

Table of Contents

List of Figures

List of Tables

Introduction

The relationship between disturbance and biodiversity is a long and storied one in ecology, notably starting with investigations of the resistance and resilience of communities of taxa (Holling 1973, Levin and Paine 1974). In freshwater systems, one of the most influential disturbances is flow variability (Resh et al. 1988), as altered streamflow patterns exert a strong effect on communities that inhabit freshwater systems and are considered to be a master variable dictating most other environmental conditions in rivers (Power et al. 1995). The effect of flow disturbance on aquatic communities has been quantified primarily through alpha and beta diversity in several contexts and spatiotemporal scales, including: (1) small-scale experimental setups (Walters and Post 2011), (2) catchment-wide analyses (Costa and Melo 2007), and (3) urban environments (Walsh et al. 2005). In turn, in this dissertation, the relationship between flow disturbance and aquatic communities will be examined in these three specific cases.

More recently, stream mesocosm setups have allowed manipulation of environmental conditions beyond typical extremes and greater control over experimental settings, allowing testing of the effects of environmental conditions that are projected to become more frequent due to climate change (Ledger et al. 2011). Experimental droughts can select for taxa with faster life cycles (Ledger 2012) and alter their functional stability (Leigh et al. 2019) by creating advantageous conditions for individuals that can reproduce quickly while surface flow conditions exist. Alternatively, experimental drought can result in generalist communities (Doretto et al. 2018) in which those individuals with specialized life cycles are unable to persist, especially in the remaining spatially constricted stream pool habitat (Verdonschot et al. 2014). However, even generalist taxa can be lost in drought conditions when hyporheic flow ceases (Vander Vorste et al. 2015), but more studies are needed to quantify the tolerances of aquatic insects to extreme drought at longer timescales (Aspin et al. 2019).

Studies investigating flow disturbance that examine beta diversity patterns compliment those focused on local alpha diversity (such as mesocosm experiments) by explicitly incorporating dispersal and connectivity between communities and processes that operate at larger spatial and temporal scales. For instance, location within a river network (central versus isolated), upstream area, and location relative to confluence have been shown to affect assemblage structures in freshwater communities (Hitt and Angermeier 2008, Thornbrugh and Gido 2010). Further, the inherent dendritic connectivity of river networks and the resulting drainage density can also increase in more central locations, leading to more movement of individuals between metacommunities, which are defined as communities linked by dispersal through space (Leibold et al. 2004b, Carrara et al. 2014).

The drivers of patterns in metacommunities have traditionally been investigated by examining both local environmental factors and the spatial factors that impact dispersal, and the most commonly explored structuring concepts within metacommunity theory are species sorting and mass effects (Altermatt et al. 2011). While species sorting implies that communities are structured by local habitat, mass effects are usually observed in habitats with high connectivity and a resulting high dispersal rate (Leibold et al. 2004a, Tolonen et al. 2017). In turn, flow disturbance can increase or decrease dispersal between metacommunities in a river network with river drying or flooding (Datry et al. 2013). Additionally, considering that flow variability dictates other local environmental conditions, the relative importance of local processes, when compared to dispersal distance and space, can be investigated by determining the amount of flow variability in a watershed, although further research is needed to link beta diversity to flow variability at large spatial scales (Heino et al. 2015).

Anthropogenic impacts on river networks can transform river catchments that were once flow-connected into a mosaic of dry and wet reaches, disrupting movement between metacommunities and degrading historically pristine environmental conditions (Meyer et al. 2005). Dams, water impoundments, agriculture, municipal water use, and wastewater treatment plants are a few of the many anthropogenic impacts on the communities inhabiting urban river systems (Tonkin et al. 2009). Wastewater treatment plants in particular can alter temperature cycles and introduce micropollutants and unique heterogeneity into flow regimes by emitting treated effluent at set times of the day, at set temperatures, and with varying water treatment processes (Kinouchi et al. 2007). Diatoms and aquatic insects have been used as the primary indicator species to determine the status of degradation brought about by anthropogenic activities, as these basal taxa serve as a vital food source for endangered species in the riverine food web at higher trophic levels (Silva et al. 2010, Tornés et al. 2018). Aquatic insect composition degrades rapidly with urbanization, and communities can transform into persistent, pollution-tolerant subsets of their original composition (Brown et al. 2005), indicating that few taxa in urban areas can adapt to anthropogenic pressures. More studies are needed to link anthropogenically altered hydrographs in urban catchments to benthic community responses, since doing so will not only benefit endangered species, but also inform environmental flow management in developed areas (Poff and Zimmerman 2010, Kaushal and Belt 2012).

In general, the main theme of this dissertation is the determination of the role that flow variation plays in structuring benthic freshwater communities at multiple spatial and temporal scales. I will also address the following three aims: (1) to examine how experimental drought conditions affect the persistence of aquatic insects, (2) to explore the relationship between flow variability, spatial connectivity and temporal beta diversity of the benthic community at large spatial scales, and (3) to determine the effect of novel, urbanized flow regimes and spatial heterogeneity on the persistence of the riverine benthic community.

In chapter one, I used a set of experimental stream channels at the Sierra Nevada Aquatic Research Laboratory to subject the aquatic insect community to a gradient of drought conditions over three years. Aquatic insect abundance decreased in a linear relationship with flow reduction, while there was a threshold effect for richness in which there were no major losses in taxa identity until the surface flow was lost. There were strong and significant trends in beta diversity partitions in response to flow reduction, especially with respect to abundance gradients. Large numbers of species were lost from channels with loss of surface flow, but species composition was not significantly changed. Communities in riffles appeared to respond to drought conditions faster than those in pools, indicating the role of pool habitat as refugia for at least a subset of the aquatic insect community.

In my second chapter, I utilized a large, publicly available dataset of benthic macroinvertebrates in California to determine the role that flow variability, local environment, and spatial metrics play in determining beta diversity at large spatial and long temporal scales in multiple catchments. By utilizing beta regression models, I found that zero-flow days, magnitude, and duration of high- and low-flow events significantly increased beta diversity through time, while slope and catchment area were the most significant spatial factors. Contrary to my predictions, the local environment explained relatively little variation in beta diversity through time.

For my third chapter, I determined how novel spatial and temporal heterogeneity in the environment and flow regime in an urbanized river affected the persistence of benthic diatoms and insects. In particular, I sampled the benthic community before and after a flow disturbance event imposed by a wastewater treatment plant and winter storm. I found that, while the benthic invertebrate community was tolerant and exhibited resistance strategies, the diatom community reflected resilient strategies in that its population crashed following flow perturbations but rebounded two weeks later. In general, this dissertation shows that droughts and zero-flow days, especially in historically perennial systems, strongly alter the diversity and abundance of benthic communities at both the local and regional scales, while these stressors are less significant when the species pool has been conditioned to disturbance. Overall, throughout this dissertation, I hope to demonstrate that the three dimensions of temporal variability, spatial connectivity, and environmental conditions dictated by flow regime are critical factors to consider when considering the persistence and conservation of communities in freshwater systems.

References

Altermatt, F., S. Schreiber, and M. Holyoak. 2011. Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. Ecology 92:859–870.

Aspin, T. W. H., K. Hart, K. Khamis, A. M. Milner, M. J. O'Callaghan, M. Trimmer, Z. Wang, G. M. D. Williams, G. Woodward, and M. E. Ledger. 2019. Drought intensification alters the composition, body size, and trophic structure of invertebrate assemblages in a stream mesocosm experiment. Freshwater Biology 74:33–11.

Brown, L. R., C. A. Burton, and K. Belitz. 2005. Aquatic assemblages of the highly urbanized Santa Ana River basin, California. American Fisheries Society.

Carrara, F., A. Rinaldo, A. Giometto, and F. Altermatt. 2014. Complex interaction of dendritic connectivity and hierarchical patch size on biodiversity in river-like landscapes. The American Naturalist 183:13–25.

Costa, S. S., and A. S. Melo. 2007. Beta diversity in stream macroinvertebrate assemblages: among-site and among-microhabitat components. Hydrobiologia 598:131–138.

Datry, T., S. T. Larned, K. M. Fritz, M. T. Bogan, P. J. Wood, E. I. Meyer, and A. N. Santos. 2013. Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. Ecography 37:94–104.

Doretto, A., E. Piano, E. Falasco, S. Fenoglio, M. C. Bruno, and F. Bona. 2018. Investigating the role of refuges and drift on the resilience of macroinvertebrate communities to drying conditions: An experiment in artificial streams. River Research and Applications 34:777–785.

Heino, J., A. S. Melo, L. M. Bini, F. Altermatt, S. A. Al-Shami, D. G. Angeler, N. Bonada, C. Brand, M. Callisto, K. Cottenie, O. Dangles, D. Dudgeon, A. Encalada, E. Göthe, M. Grönroos, N. Hamada, D. Jacobsen, V. L. Landeiro, R. Ligeiro, R. T. Martins, M. L. Miserendino, C. S. Md Rawi, M. E. Rodrigues, F. de O. Roque, L. Sandin, D. Schmera, L. F. Sgarbi, J. P. Simaika, T. Siqueira, R. M. Thompson, and C. R. Townsend. 2015. A comparative analysis reveals weak relationships between ecological factors and beta diversity of stream insect metacommunities at two spatial levels. Ecology and Evolution 5:1235–1248.

Hitt, N. P., and P. L. Angermeier. 2008. Evidence for fish dispersal from spatial analysis of stream network topology. Journal of the North American Benthological Society 27:304–320.

Holling, C. S. 1973. Resilience and Stability of Ecological Systems. Annual Review of Ecology and Systematics 4:1–23.

Kaushal, S. S., and K. T. Belt. 2012. The urban watershed continuum: evolving spatial and temporal dimensions. Urban Ecosystems 15:409–435.

Kinouchi, T., H. Yagi, and M. Miyamoto. 2007. Increase in stream temperature related to anthropogenic heat input from urban wastewater. Journal of Hydrology 335:78–88.

Ledger, M. E. 2012. Drought alters the structure and functioning of complex food webs. Nature Climate Change 3:223–227.

Ledger, M. E., F. K. Edwards, L. E. Brown, A. M. Milner, and G. Woodward. 2011. Impact of simulated drought on ecosystem biomass production: an experimental test in stream mesocosms. Global Change Biology 17:2288–2297.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004a. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004b. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leigh, C., T. W. H. Aspin, T. J. Matthews, R. J. Rolls, and M. E. Ledger. 2019. Drought alters the functional stability of stream invertebrate communities through time. Journal of Biogeography 31:831–13.

Levin, S. A., and R. T. Paine. 1974. Disturbance, Patch Formation, and Community Structure. Proceedings of the National Academy of Sciences of the United States of America 71:2744–2747.

Meyer, J. L., M. J. Paul, and W. K. Taulbee. 2005. Stream ecosystem function in urbanizing landscapes. Journal of the North American Benthological Society 24:602–612.

Poff, N. L., and J. K. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshwater Biology 55:194–205.

Power, M. E., A. Sun, G. Parker, W. E. Dietrich, and J. T. Wootton. 1995. Hydraulic Food-Chain Models. BioScience 45:159–167.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The Role of Disturbance in Stream Ecology. Journal of the North American Benthological Society 7:433–455.

Silva, D. de P., P. De Marco, and D. C. Resende. 2010. Adult odonate abundance and community assemblage measures as indicators of stream ecological integrity: A case study. Ecological Indicators 10:744–752.

Thornbrugh, D. J., and K. B. Gido. 2010. Influence of spatial positioning within stream networks on fish assemblage structure in the Kansas River basin, USA. Canadian Journal of Fisheries and Aquatic Sciences 67:143–156.

Tolonen, K. E., K. Leinonen, J. Erkinaro, and J. Heino. 2017. Ecological uniqueness of macroinvertebrate communities in high-latitude streams is a consequence of deterministic environmental filtering processes. Aquatic Ecology 52:17–33.

Tonkin, J. D., R. G. Death, and M. K. Joy. 2009. Invertebrate drift patterns in a regulated river: dams, periphyton biomass or longitudinal patterns? River Research and Applications 25:1219–1231.

Tornés, E., J.-R. Mor, L. Mandaric, and S. Sabater. 2018. Diatom responses to sewage inputs and hydrological alteration in Mediterranean streams. Environmental Pollution 238:369–378.

Vander Vorste, R., F. Malard, and T. Datry. 2015. Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. Freshwater Biology:n/a–n/a.

Verdonschot, R. C. M., A. M. van Oosten-Siedlecka, C. J. F. ter Braak, and P. F. M. Verdonschot. 2014. Macroinvertebrate survival during cessation of flow and streambed drying in a lowland stream. Freshwater Biology 60:282–296.

Walsh, C. J., A. H. Roy, J. F. J. O. T. Feminella, P. D. Cottingham, P. M. Groffman, and R. P. Morgan II. 2005. The urban stream syndrome: current knowledge and the search for a cure. Journal of the North American Benthological Society 24:706–723.

Walters, A. W., and D. M. Post. 2011. How low can you go? Impacts of a low-flow disturbance on aquatic insect communities. Ecological Applications 21:163–174.

Chapter 1:

Multi-season drought affects abundance, richness, and beta-diversity of insect communities in near-perennial streams

Abstract

Most climate change modeling scenarios predict increases in hydrologic extremes for freshwater systems. In particular, drought is expected to produce more frequent intermittent flows in near-perennial streams and rivers, potentially affecting many other aspects of their ecosystems. To determine the impacts of shifts in flow regimes on freshwater communities, I simulated flow losses over multiple seasons in the eastern Sierra Nevada region of California using a set of nine experimental stream channels. Aquatic insect communities were sampled several times before, during, and after drought treatments over a three-year period. Stream insect abundance declined in proportion with flow losses and species richness was subject to a flow threshold. Insect communities resisted drawdown until surface flow was lost, when only disconnected pools remained and significant losses in taxa were observed. Pools served as a refuge, with maintenance of stable communities for longer than in riffles. Community dissimilarities between treatments increased in riffles after the onset of drought, but decreased in pools and then stabilized. Beta diversity partitions suggested no strong shifts in community compositions, and indicated that the effects of drought were largely uniform across taxa until flow was fragmented. Upon restoration of flow, species abundance and richness returned to pre-treatment levels, whereas community dissimilarities decreased, indicating homogenization across treatment channels. Although insect communities in channels

were generally more tolerant than those in nearby streams, many of the taxa present in my system were resistant to drought conditions until surface flow connectivity was lost. My experiments demonstrate the importance of long-term experimental studies of flow alterations. Future studies should consider resilience over larger temporal and spatial scales.

Introduction

Climate change is a primary threat to biodiversity across the globe (Bellard et al. 2012). Current and future impacts on biodiversity can be assessed by measuring resilience of species to disturbances at all levels of biological organization (Oliver et al. 2015). Responses to flow disturbances are key measures of resilience in freshwater systems, because stream flow is a master variable that dictates the structure and dynamics of freshwater systems (Power et al. 1995, Zeiringer et al. 2018). Extreme flow events, such as those in drought, lead to changes in key abiotic variables such as dissolved oxygen (DO), temperature, and nutrient levels (Dahm et al. 2003, van Vliet and Zwolsman 2008). Additionally, flow connects parts of river systems both laterally and longitudinally, and dictates habitat complexity by influencing movement, spawning, and recruitment (Bunn and Arthington 2002). Freshwater taxa are among the most threatened globally, and studies of the effects of changing hydrological regimes on their resilience will be critical to their conservation under the conditions of climate change (Reid et al. 2018).

Rapidly shifting climate patterns have resulted in greater hydrologic extremes in freshwater systems (Siam and Eltahir 2017, Byun et al. 2019). In mid- to high-altitude streams and rivers, altered timing of extreme melt events has led to earlier peak flows (Maurer 2007, Musselman et al. 2017), which result in a lack of sustained baseflow late in the season and manifest as remarkably strong droughts and increased flashiness (Dettinger et al. 2004). Reduced and erratic flows are further compounded by anthropogenic influences on water use and distribution, such as those due to dams, diversions, and channels (Gronberg et al. 1998, Zimmerman et al. 2018).

Historically, studies of the effects of flow loss on aquatic organisms in natural systems have been hampered by the stochastic nature of droughts and the difficulties in establishing appropriate reference conditions (Boulton 2003, Wright et al. 2004). The severity of flow alterations varies spatiotemporally, as do rates and durations of changes in flow rates (Lake 2003, Lynch et al. 2018). Aquatic insects serve as bioindicators of stream conditions (Hodkinson and Jackson 2005) because they are highly sensitive to rapid shifts in the flow regimes, especially those associated with drought (Lytle and Poff 2004). Yet the full extent of this sensitivity and the mechanisms responsible are poorly understood.

In recent studies, experimental mesocosms have been used to study the effects of flow alterations under climate change scenarios. These systems can be manipulated to model environmental variability that has not yet been experienced (Walters and Post 2011, Aspin et al. 2019). The effects of experimental drought on aquatic insect communities have been observed in several regions of the world, albeit with varying results. Studies of streams in the lowlands of the Netherlands and in a temperate mixed-hardwood forest in northeastern USA showed no significant changes in community compositions following pronounced shifts in biomass due to drought treatments (Walters and Post 2011, Verdonschot et al. 2014). Other experiments suggest high species replacement following flow perturbations, with increased production of small, short-lived, high dispersing taxa following extreme drought events in English chalk streams and in streams in southwestern USA (Ledger et al. 2011, Bogan et al. 2015, Aspin et al. 2018a).

The lack of consistency between experimental drought studies may reflect evolutionary adaptation of stream-inhabiting taxa, but compositional shifts vary with environmental and geographical context. In a study of aridlands, Bogan *et al*. found that strong colonists persisted through supraseasonal droughts better than longer lived, weak dispersers, which were regionally extirpated (2015). However, in perennial systems few taxa have drought resistance and resilience strategies compared with those in intermittent streams, leading to catastrophic reductions in total insect biomass (Doretto et al. 2018). Hyporheic flows are important sources of drought resistance for insects, because many can burrow following losses of surface flow during dry periods (Vander Vorste et al. 2016). Although the roles of hyporheic flows have been demonstrated, most drought studies have been conducted for < 1 year and report limited comparisons of different systems. Thus, the ranges of flow variability that can be tolerated by taxa, the aspects of the perturbations that drive divergent community responses, and the factors that lead to recovery require further investigation.

Beta diversity is a measure of dissimilarity in taxonomic compositions between separate communities (Steinberg et al. 2011), and changes in this index are widely used to quantify divergence of aquatic communities following flow perturbations. Previous studies show significant divergence of communities following drought treatments (Doretto et al. 2018). Moreover, in intermittent streams that are subjected to higher drought stress, community dissimilarities can manifest as high nestedness, where the taxa present are a limited subset of those in natural flowing areas (Arscott et al. 2010). Conversely, Aspin *et al*. found unique assemblages of specialists following drought treatments of historically perennial streams, indicating high turnover and replacement by functional variants (2018b), albeit without the adaptations to extreme droughts that are found in communities of arid land streams (Boersma et al. 2013). Beta diversity methods have recently been adapted to partition abundance-based community measurements in consideration of balanced variations such as species replacement from site-site (turnover) and abundance gradients, and from individuals that are lost from one site to another (nestedness) ((Baselga 2013, 2017). Compared with previous approaches, recent methodological advances in partitioning of beta diversity will reveal mechanisms that contribute to community dissimilarity.

Although aquatic insect responses to experimental drought have been studied in streams world wide, the observations are context dependent and no studies have been performed in high altitude systems, such as those in North America. In the eastern Sierra Nevada in California, USA, stream insect communities are adapted to a perennial stream hydrology that is driven mostly by accumulated snow melt. Some regions of the Sierra Nevada are expected to become increasingly dry with the onset of climate warming, and shifts in hydrograph are expected to produce occasional peak flows from snow melt in the winter, instead of in the spring, and greater intermittency of flow (Maurer 2007, Swain et al. 2018). To determine the effects of these changes on aquatic insects, hydrological thresholds need to be identified for communities and the processes by which communities diversify in response to changes in flow regimes need to be examined.

Herein, I describe mesocosm experiments in which the effects of experimental drought and post-drought flow resumption on aquatic insects were quantified in the eastern Sierra Nevada. I established a flow-reduction gradient across a set of experimental channels and measured abundances and compositions of insect communities before, during, and after relaxation of drought conditions. My drought treatments were performed over two summers, with sampling after flow resumption in a subsequent season. My data represent substantial spatial and temporal heterogeneity of local stream habitats. These multi-season experiments provide insights into the long-term effects of drought gradients and flood events on changes in community composition in realistically structured stream habitats.

Methods

Study area

This study was performed at the Sierra Nevada Aquatic Research Laboratory (SNARL), a University of California Natural Reserve near Mammoth Lakes, CA (37º37’N, 118º50’ W). SNARL has an average elevation of 2154 m ASL with summer and winter temperatures ranging from 0ºC to 28ºC and −22ºC to 13ºC, respectively. SNARL straddles Convict Creek, which is a perennial oligotrophic stream that runs from the snowmelt-fed alpine lake Convict Lake. Typically, major hydrograph peaks occur in

June (700–5700 L/s), and discharge decreases rapidly afterwards, leveling to the base flow (100–300 L/s) from late October to April. On average, water temperatures are freezing in the winter, about 5ºC in March, and range between 12°C and 17°C in the summer (Jenkins et al. 1999).

Experiments were conducted in nine 50-m long channels, which were constructed of concrete and sealed with epoxy resin (Figure 1.1). The channels simulate alternating pool–riffle habitats and have six pools and riffles each. The channels are 1 m wide at the riffles. The pools average 1.5 m in diameter and contain fiberglass reinforced concrete sheets that simulate undercut banks. The substrate in the channels is approximately 30 cm deep and comprises silt, sand, gravel, and pebbles. Six parallel channels are connected to a top inlet basin, and three more are connected in parallel to a lower inlet basin. Both inlet basins are naturally fed from Convict Creek and the channels are arranged in a flow-through setup. To emulate natural drift colonization processes and water properties, no water was recycled. Because the flow is diverted directly from Convict Creek, insects can drift or oviposit naturally into the channels. Although no riparian vegetation is present immediately along the channels, previous studies demonstrated the presence of similar periphytic and aquatic insect communities as those in Convict Creek (Jenkins et al. 1999). Flow gates at the top of each channel were used to reduce or completely stop discharge into the channels.

For five years preceding the start of the project, the channels were naturally colonized by Convict Creek biota and experienced a similar hydrograph to that of Convict Creek. A large population of naturalized brown trout (*Salmo trutta*) is present in the creek. These were reportedly introduced to the region by German freshwater enthusiasts in the 1890s (Jenkins et al. 1999). Due to their invasive nature and ability to radically alter aquatic communities, fish were excluded from the channels by inserting double stacked, pre-cut 2 × 4 wood struts to the head of each channel.

Experimental design

Using a gradient of flow-reduction treatments, I simulated different levels of flow loss. As percentage flow losses, targeted flow reductions were 0% (control, free-flowing), 25%, 50%, 75%, and 100% (complete drought, dry riffles with hyporheic flow and isolated pools). Some deviation from target flow levels was noted over the study period (Figure 1.2). The top six channels were labeled A–F and the bottom three were labeled G–I (Figure 1.1). Specific flow-reduction increments were determined from average flow measurements in the Convict Creek hydrograph during the drought years of the past 50 years. The channels were assigned to flow-reduction (drought condition) treatments using a random number generator, although single random channels were selected as controls for the top six and bottom three channels. Flow into the channels was reduced by closing the inflow gates from the holding reservoir.

Flow was incrementally reduced over the course of 7 days after calculating the number of flow regulator turns needed to reduce discharge by a certain percentage. Drought conditions were implemented according to observed temporal flow reductions in the Convict Creek hydrograph. After establishing drought treatments, discharge from each channel was monitored daily and the flow gates were adjusted to compensate for variations in discharge from Convict Creek. Channel drying commenced on 7/19/14. On

July 12, 2015, a buildup of debris clogged the outlet of Convict Lake to Convict Creek. The US Forest Service cleared the dam and the discharge flooded some areas at SNARL. The flow gates were thus opened to prevent damage to the concrete structures. After the flood water passed through the channels, flow levels were restored to experimental drought conditions after four days and the field team arrived on-site. The flow-gates were opened on 8/23/15 to end the experimental drought period. Flow was unimpeded thereafter.

Sampling regime

Benthic insect communities were sampled once before drought treatments (7/18/14), several times during the drought treatments (7/26/14, 8/19/14, 8/25/14, 7/18/15, 7/25/15, 8/22/15), and once after flow restoration (7/26/16). Temperature, conductivity, and DO were measured using a YSI Professional Pro Plus, and discharge was calculated by measuring current velocity with a Marsh-McBirney Flo-Mate 2000 Electromagnetic Flow Meter. Environmental variables were measured in the same places and on the same days as biotic samples using standard methods (Hauer and Hill 2011).

Samples of benthic insects were taken upstream, in the middle, and downstream of riffle/pool pairs in each channel using a custom-made aluminum-frame surber sampler with a 250-μm mesh (900-cm^2 areas were sampled). Benthic habitats were brushed by hand, allowing attached biota to flow into the surber sampler and be collected into 200-ml containers attached to the end of the sampler's net for about 60 s. In channels with flow restrictions, water was hand-swept through the 250-μm aquarium net into the container and the surber net and container were then rinsed into a bucket. I removed large organic matter and rocks from samples and followed an elutriation protocol to clear benthic invertebrates from most organic matter. Care was taken to separate cased caddisflies and mollusks from the debris (as in Herbst et al. 2018). I then poured sample fractions through a 100-μm aquarium net into 250-ml containers containing 90% ethanol to be identified in the lab. I collected and combined two samples from representative habitats in each pool/riffle pair. To prevent re-sampling of habitats that were disturbed by surber sampling, I collected samples from every other pool/riffle. I also divided each section of the riffles and pools into 8 and randomly assigned single sections to each sampling date. In the laboratory, aquatic insects were identified at the genus level, with the exception of midges (chironomidae).

Benthic algae were sampled by brushing two cobbles that were randomly selected from the same upstream, middle, and downstream riffle/pool pairs as for the surber samples. After scrubbing with a nylon bristle brush, cobbles were rinsed and the resulting algal solutions were homogenized in the sample tray. Solutions were filtered through 1-µm glass fiber filters (GF/E filter) using a 60-ml syringe attachment. Samples were then labeled and stored on ice for transport to the lab. I extracted chlorophyll-a with cold ethanol for 24 h and then determined chlorophyll-a concentrations of using established fluorometric methods (Sartory and Grobbelaar 1984). Areas of sampled substrates were estimated from recorded measures of substrate length, width, height, and circumference and chlorophyll-a contents per unit area were calculated (Herbst and Cooper 2010).

Data analysis

Relationships between aquatic insect abundance, richness, discharge rates and dates, and pool *vs.* riffle habitats were identified using linear and polynomial regression functions. For each date/habitat combination, linear and polynomial regressions were restricted to second- and third-degrees and were fitted to the data. The best fit function was selected using Akaike information criterion (AIC) scores. I do not infer statistical significance in relationships between discharge and community metrics from these regressions, which are solely intended to describe visual patterns. To explain variations in total benthic invertebrate abundance and richness, I fitted a set of generalized linear models (GLM). Date, DO, temperature, chlorophyll-a, discharge, and a date*discharge interaction term were included as explanatory variables. I used GLM because assumptions of normality were rejected by Shapiro-Wilks tests of residuals. To avoid overdispersion, I employed poisson and negative binomial distributions for richness and abundance models, respectively. Changes in corrected AIC (ΔAICc) values were calculated to determine which combination of variables most parsimoniously correlated with variations in abundance and richness in aquatic insect communities. The top ten models for richness and abundance are presented. Analyses were conducted using the lme4, MASS, and bbmle packages in R (R Core Team, version 3.5.1).

Taxonomic total pairwise beta diversity and overall multiple-site dissimilarity were calculated using the betapart package in R. For total pairwise beta diversity, I calculated the Bray-Curtis dissimilarity index accounting for dissimilarity due to partitions of balanced variation with respect to abundance and unidirectional abundance gradients between pairs of sites in experimental channels. I utilized this framework to quantify the extent to which assemblages in some sites were subsets of others (shifts in composition), and to identify how beta diversity was influenced by gradients of abundances before, during, and after flow perturbations (Baselga 2017). To assess heterogeneity of species compositions among all sites over time, I calculated overall multiple-site dissimilarity using the same two components of the Bray-Curtis dissimilarity in abundance (Baselga 2017). I used summed dissimilarities because averaging pairwise dissimilarity measures over more than three pairs is reportedly problematic (Diserud and Odegaard 2007, Baselga 2013). To track overall site dissimilarity at each timepoint, I plotted multiple-site dissimilarity against sampling date regardless of channel treatments. Because 100% drought channels had zeros for all taxa, I inserted three dummy taxa with Bray-Curtis values of 1 into genus × site matrices. Dissimilarities between rows of zeros cannot be calculated. After investigating transformations and calculating beta diversity with or without sites, with zeros, and with or without dummy variables, the dummy variables capture all variations in the data while accounting for sites with only zeros.

Pairwise differences in discharge between channels on each sampling date were used as measures of drought intensity. I adopted Aspin *et al.*'s (2018b) term "drought intensity", but I did not ordinate my suite of environmental variables into one axis because my predictors did not collapse into similar axes as in their system. Most of the present variation was explained by discharge. I fit negative exponential models using the betapart package and the “decay.model” function, and examined decay in dissimilarity for balanced variations and abundance gradients relative to drought intensity (Rodríguez and Baselga 2018). This function adjusts a GLM with dissimilarity as the response variable and drought intensity as the predictor. I selected negative exponential decay models over the optional power-law functions by comparing AIC values for both. Goodness of fit from the models was assessed on pseudo R^2 values. Significant relationships between dissimilarity and drought were identified by randomizing drought intensity 9999 times and determining the proportion in which model deviance was smaller than that of the randomized model (Rodríguez and Baselga 2018).

Results

In this study, I established a gradient of flow perturbations (Figures 2 and 3) with water flow reductions ranging from ~98% (channels B and G) to slightly increased flow in control channels (channels A and I, see Figure 1.2). Riffles in channels B and G had zero surface flow and were reduced to hyporheic flows, allowing disconnected pools to remain wet, albeit with rapidly fluctuating dayly DO and temperatures. Pools in treated channels had relatively stable environments through June and July, but conditions became more extreme in late August, with temperatures fluctuating between 8.7°C and 28°C in dry channels, compared with 14°C–19°C in control channels. Insects were not present in dry riffles after 7/18/14, and I checked to a depth of ~25 cm into the hyporheic zone. The most dominant aquatic insect taxa across sampling dates were Ephemeroptera of the genus *Baetis,* Trichoptera of the genera *Micrasema, Wormaldia,* and *Hydroptila,* Coleoptera of the genus *Optioservus* and chironomid Dipterans. Of these, *Hydroptila,* *Optioservus,* and chironomids were the most abundant in pools during drying periods. *Drunella* and *Epeorus* Ephemeropterans and *Glossosoma* Trichopterans were most rare in drying pools.

Changes in stream insect abundance with flow perturbations

Regression models of discharge, chlorophyll-a, DO, date, and the date*discharge interaction had the lowest ΔAICc values for abundance (table 1). Date, discharge, and date*discharge were present in every model, and were within ΔAICc values of 3.0 for the most highly ranked model. The model with only discharge, date, and date*discharge had a ΔAICc value of 3.0. Because differences in support for the top-ranked models were generally small, I accepted the discharge, date, and date*discharge model as the most parsimonious for further analyses, given the ecology of my system (Burnham et al. 2010). A weak positive relationship was identified between aquatic insect abundance and discharge in riffles and a weak negative relationship was identified in pools before drought treatments. Post-drought, I observed more aquatic insects in higher flowing channels than in low flow and dry channels, in which insect numbers had generally intensified in riffles during 2014 (Figure 1.4). Yet no relationship was discernable between aquatic insect abundance and discharge rates in pools until 8/25/14, and this was stronger in riffles. Under the contrasting environmental disturbance of the 2015 flood, no relationship was found between aquatic insects and discharge in pools or riffles during sampling shortly after the flood event. At the end of the sampling season—well after the flood—a slightly positive relationship between discharge and aquatic insect abundance was identified in riffles. In 2016, average channel discharges increased dramatically with the resumption of flow, and a unimodal relationship between discharge and aquatic insect abundance was established. No relationship between discharge and aquatic insect abundance was found in pools (Figure 1.4).

Responses of stream insect richness to flow perturbations

The model with discharge and date had the lowest ΔAICc value for taxonomic richness of aquatic insects (table 1). In contrast with abundance, date was not significant factor in explaining richness, although when taken without the date interaction, discharge was a significant factor. In general, models that included discharge were the most consistent in explaining variations in aquatic insect richness across the experimental channels, but no relationship was identified between discharge and richness before flow perturbations, neither in pools nor riffles. Immediately after flow changes, aquatic insect richness exhibited a positive, saturating relationship with discharge, with an asymptote at around 13 in riffles (Figure 1.5). This relationship became more pronounced by 8/25/14. Aquatic insect richness in pools only responded to variations in discharge prior to drought conditions (8/25/14), with a slight positive linear relationship. The aquatic insect threshold effect carried through 2015 in riffles, but not in pools. In 2016, I found no relationship between aquatic insect richness and discharge in pools or riffles.

Community dissimilarity

Total dissimilarity between all sites increased immediately in riffles after drought perturbations ($\beta = 0.73–0.83$), whereas dissimilarity in pools stabilized after an immediate decrease (between $\beta = 0.70–0.75$, Figure 1.6). Upon establishment of drought conditions, community dissimilarities were consistently higher, except when the channels were flooded on 7/18/15, at which point community dissimilarities were close to pre-drought levels. Dissimilarity in the riffle communities increased again after the flood, and after a year of free flow, dissimilarities between all the sites markedly decreased to lower levels than before flow-reductions in the channels ($\beta = 0.65$, Figure 1.6). In pools, site-wide dissimilarity was relatively constant across drought periods, flood periods, and the flow resumption period ($\beta = 0.70$–0.72), but declined immediately after drought treatments ($\beta = 0.63$, Figure 1.6).

After partitioning dissimilarity into balanced variations and abundance gradients in riffles, a significant linear relationship ($R^2 = 0.139$, $p = 0.001$) weakly explained the decay in abundance gradient similarity due to flow before any perturbation (Figure 1.7, Supplemental Table 1.1). After drought treatments, the abundance gradient exhibited a saturating response across the drought intensity gradient that was best fit by the negative exponential function. This relationship remained significantly positive and non-linear ($R^2 = 0.175$–0.330, $p = 0.001$) until natural flow was restored. In 2016, when all channels had natural flow, the abundance gradient had a decreasing linear relationship with drought intensity ($R^2 = 0.141$, $p = 0.001$). In contrast, the relationship between balanced variation and flow was insignificant in riffles during all years.

In pools, balanced variations and abundance gradients showed linear responses across the flow gradient before drought treatments (Figure 1.7). These linear responses were weak but became significant immediately following flow perturbations ($R^2 = 0.075$, $p = 0.012$ for abundance gradient, $R^2 = 0.114$, $p = 0.004$ for balanced variation; Supplemental Table 1.1). On 8/19/14, responses between the two partitions started to diverge. The strength of the positive relationship with the abundance gradient increased significantly ($R^2 = 0.362$, $p = 0.001$), whereas that with the balanced variation became negative and was not significant until 8/25/14 (Supplemental Table 1.1). These relationships were reset immediately after the 2015 flood, and pre-flood patterns were re-established after 1 month. In 2016, both partitions exhibited positive relationships with drought intensity, but only the balanced variation was significantly explanatory in the distance-decay model ($R^2 = 0.130$, $p = 0.002$). These partitions suggest that there were no strong compositional shifts in the stream insect community over time, and that the main effect of the drought was to reduce abundances uniformly across taxa.

Discussion

Novel flow regimes, whether from direct anthropogenic manipulation or from climate change, are substantially altering communities in freshwater ecosystems. These alterations include simplification of community structures and shifts in dominant traits (Tonkin et al. 2018, Ruhí et al. 2018, Aspin et al. 2018a). As flow regimes are increasingly altered, a continuing challenge is to generalize about how biodiversity responds across different freshwater ecosystems and flow scenarios. In this study, I experimentally imposed a gradient of drought severity across nine experimental stream channels over multiple seasons and tested responses of aquatic insect communities to the imposition and relaxation of drought conditions. The present discharge manipulation had a strong, direct effect on community structure. In particular, insect abundance was reduced in direct proportion to the reduction in flow, whereas significant losses in richness were only observed in the most severe cases of flow reduction, in which surface flow was lost in riffles. Consequently, aquatic insect community composition remained relatively stable throughout the experiment, as indicated by the lack of a significant effect of the discharge*date interaction in richness models and the contrasting significant effect in abundance models (table 1). Beta diversity among channels was largely driven by changes in abundance, as indicated by positive abundance gradients, especially in pools, but was not related to compositional turnover, as indicated by minimal shifts in balanced variation (Figure 1.7). Thus, increases in beta diversity among channels were related to the loss of individual taxa in the driest channels, resulting in nested subsets of the original communities, with no replacement of lost taxa by other taxa.

Other studies of experimental flow reductions show that drought-affected communities shift towards smaller taxa with faster life cycles (Ledger et al. 2011, Aspin et al. 2018a), with strong dispersers replacing weak dispersers (Bogan et al. 2015) and the emergence of generalists (Doretto et al. 2018). Yet, I did not find pronounced changes in taxonomic or trait compositions. Rather, declines were evident across taxa and the most affected communities became nested-subsets of less affected communities. These consistent declines among taxa could be attributed to the source of water in my experimental channels. Convict Creek is a perennially flowing watercourse that does not regularly experience extreme low-flow events. Therefore, insect community adaptations to the perennial flow regime may have led to particular vulnerability (Lytle and Poff 2004). In arid systems where low-flow events are typical, taxa like the flightless Belostomatidae have been shown to crawl long distances to find water (Bogan et al. 2015). These disturbance-mitigating traits appear to be lacking in the insects at SNARL, for which constant densities were maintained in channels with sustained surface flows and rapidly declined in dry channels due to emigration or direct mortality. Skews in absolute abundance were less pronounced after the flood of 2015 than before it, yet the abundance gradient was reestablished rapidly, indicating a bias of drifting colonization toward higher-flowing channels (Figure 1.7).

The proximity of my experimental channels to the source community in Convict Creek (within 15m) could have provided an efficient colonization route into the channels via drift or oviposition. In agreement, close proximity of source communities reportedly promoted resilience at perturbed sites (Boersma et al. 2013). However, I conducted daily measurements using 250-μm nets that covered the widths of the channels at the inlets and recorded only negligible amounts of immigrating invertebrates at the start of the experiment. I attribute the lack of drift to growth of Elodea near the flow-gates in the channel heads at the start of drought treatments. These plants became very thick and may have closed off drift routes into the channels. Upstream crawling of insects into the channels was also unlikely because water falls approximately 2 m from the channels into the inlet basin. After a year of higher flows in 2016, drifting insects successfully and rapidly recolonized the channels and exhibited a preference for riffles. Drift migration likely increased after the 2015 flood event also. In areas without drift migration, such as headwater systems, drought scenarios could result in high community turnover—high community turnover has been found in drought studies with no migration in recirculating mesocosms (Aspin et al. 2019, Leigh et al. 2019).

A prolonged drought was recorded from 2012 to 2015 in the Sierras, likely resulting in unique environmental conditions and a limited taxa portfolio in my experimental channels (Herbst et al. 2019). Similarly, low background flow conditions from Convict Creek could have reduced migration of insects into the experimental channels. These conditions promoted excess growth of the lentic macrophyte Elodea (Robach et al. 1997). Benthic samples were taken from Convict Creek in the summer of 2014 and had a genus richness of 35 taxa, compared with only 15 in the channels. Limited numbers of taxa could constrain the aquatic insect response to flow losses, because particularly disturbance-sensitive taxa may have been extirpated before the experiment. Long-term studies during the prolonged drought found significant shifts in functional traits and aquatic insect compositions in the Sierra, where sensitive intolerant species were depleted and more tolerant generalists became dominant (Herbst et al. 2019). In line with my results, hyporheic flows in pools conferred some community resilience, whereas extreme flow losses resulted in significant decreases in richness, especially among riffle-type taxa (Herbst et al. 2019). Because Convict Creek was subject to a regional drought during my study, I posit that the pool of species was already limited to a set of taxa that are tolerant of low flow conditions.

In my experiments, pools emerged as a temporary refuge, as indicated by the maintenance of richness, abundance, and community dissimilarity, relative to those in riffles (approximately one month, Figures 4 and 7). The disturbance-mitigating effects of pools also emerged as beta diversity partitions. Specifically, pools exhibited a time-lag and maintained balanced variation and abundance gradients for longer than riffles during drought conditions. Pools also sustained community dissimilarity for longer than riffles, both in terms of composition and abundance gradients from site to site. Because environmental conditions were not degraded in pools until later in the summer, I only saw strong abundance gradients in pools in samples from later in the season (Figure 1.7). The impact of drought on aquatic insect beta diversity was minimal for several weeks (up to a month) because pools provided hospitable habitats during the start of drought periods. Under these conditions, channel pools had sustained hyporheic flows, with small amounts of water passing into dry flow-disconnected channels, and all channels had sufficient substrate (30 cm) to allow cooler water to flow underneath without evaporation, heating, or loss of oxygen. As the temperature regime of the pools became extreme a month later, fluctuating between 8.7°C and 28°C in dry channel pools, strong abundance gradients emerged.

My results show that pools maintain community dissimilarity and abundance gradients longer than riffles during drought periods, albeit with some caveats. First, the environmental heterogeneity between pools and riffles was not as pronounced in my system as in Convict Creek and other Sierra Nevada streams. Previous comparisons between pools and riffles in other small Sierra Nevada streams showed significant differences in environmental conditions and aquatic insect assemblages, suggesting that many taxa distributions respond to heterogeneity of pool / riffle environments (Herbst et al. 2018). Environmental conditions of pools influence their use as refuges during drought events (Doretto et al. 2018).

Second, considering the relatively low taxonomic diversity in the channels during my experiment, relatively few sensitive riffle specialists were present in the channels. Thus, the pre-drought community may have had a higher proportion of taxa with mixed habitat affinity (riffles and pools), enabling persistence in remnant pools for several weeks. This pool-tolerant taxonomic profile may explain why no strong shifts in composition were recorded. In another study, however, interactions between extreme temperature ranges, low flow, lack of pool refugia, and loss of substrate moisture with the contraction of hyporheic zones were most detrimental to aquatic insect diversity in streams during drought events (Rader and Belish 1999, Stubbington and Datry 2013, Vander Vorste et al. 2016). Remnant disconnected pools following complete flow loss can become overcrowded and then collapse following drying events, and riffle preferring taxa are unable to persist in interspersed pools (Verdonschot et al. 2014, Herbst et al. 2019). Thus, even pool-tolerant communities in the experimental channels were unable to persist through long-term drought conditions of over one month.

Low flows and drought can result in lasting shifts in environmental conditions, such as decreased organic matter availability and quality, alterations to riparian vegetation, and changes to the channel geometry (Stromberg et al. 2005, Ylla et al. 2010). At SNARL, cattail, bulrush, and some perennial grasses colonized the exposed banks of stagnant pools in low-flow and dry channels. This riparian vegetation was not present in pools of high-flowing channels, but it persisted into 2016, a year after natural flows were restored. Changes in riparian habitats may have influenced components of instream diversity that did not conform with my general findings of static community composition under most experimental flow conditions. For example, megaloptera of the genus *Sialis* established larval populations in low-flow pools, likely reflecting preference for stagnant flowing habitats in which eggs can be laid on objects over the water (Woodrum and Tarter 1973). Drought-stricken streams may therefore harbor some legacy effects when flow is lost for long enough. Future studies are required to consider experimental flow reductions in the context of structural habitat changes that may only manifest over longer timescales.

Aquatic insect populations recovered from drought treatments after flow resumption in 2016, suggesting that the channel-dwelling taxa can reestablish themselves in one year. With unperturbed flow from 7/25/2015 to 7/26/2016, species abundance and richness were restored to similar levels as those before the drought treatments were started in 2014. Further, in this year of natural flows, beta diversity became homogenous among channels, with greater similarity than before the drought treatment. My year-long time-scale of recolonization is longer than the durations of weeks or months reported in previous studies, and other work has shown that 21 days of recolonization is insufficient to establish pre-drying communities (Doretto et al. 2018). In the present study, dispersal (drift, crawling, and oviposition) between channel communities likely contributed to recolonization of drought-affected channels. Accordingly, dispersal mechanisms are vital determinants of community structure when sites are flow connected (Datry et al. 2015). Dispersal was most influenced by the presence of surface flow and high flow events. For example, trajectories of beta diversity were reset by the 2015 flood and by flow resumption in 2016. These observations suggest that individuals drifted into the channels to recolonize immediately following channel re-wetting, and adult insects later repopulated the channels via oviposition. Thus, an interaction between stream connectivity and the specific time-scales of my flow perturbation may have facilitated recolonization.

Taking a metacommunity perspective can help to generalize responses of aquatic insects to flow perturbations, because it explicitly considers extinction and recolonization dynamics for different taxa (Leibold et al. 2004, Heino et al. 2015, Downes et al. 2017). During drought, local community structured may most reflect species sorting, favoring disturbance and stress adapted taxa. In my experimental channels, inhospitable local environmental conditions, especially in the dry channels, abolished normal dispersal pathways and resulted in strong depleted abundance gradients (see also (Campbell et al. 2015, Aspin et al. 2018b, Leigh et al. 2019). Site-wide community dissimilarity was lower after flow was restored in my channels (Figure 1.7), suggesting that in future drought scenarios, mass effects may be crucial to recovery when rivers regain flow connectivity. In agreement, flow connectivity facilitated high dispersal rates between channels in a previous study, and the communities became more homogeneous when drought conditions were eased (Tonkin et al. 2017). The lower site-wide dissimilarity at SNARL may also follow higher flow in 2016 than in the previous two years, allowing for higher rates of drift. Moreover, high rates of source (Convict Creek) – sink (SNARL channels) dynamics may have overwhelmed local environmental processes and facilitated migration back into the channels.

This study demonstrates the importance of sustained surface flow connectivity in streams for the persistence of diverse and abundant insect communities. When surface flow is lost due to drought conditions, pools are sustained by hyporheic flows but demand resilience of insect communities that are adapted to perennial flows, and may not support sensitive species, such as riffle adapted taxa (Herbst et al. 2019). In regions that lack the hydrogeology to sustain groundwater inflows, such as those from springs, aquatic insects may be most imperiled by drought. In future studies, I recommend that routes of colonization before and after flow disturbances be controlled to determine the mechanisms through which taxa respond to disturbances and how they recolonize (Vander Vorste et al. 2016, Downes et al. 2017). Flow disturbance studies performed at larger spatial scales and during heterogeneous flow years may also indicate divergent persistence mechanisms of aquatic insects. Alternatively, spatial variations could be simulated in smaller experimental facilities by mimicking the unique dispersal and environmental conditions at different stream orders within the study system.

References

Arscott, D. B., S. Larned, M. R. Scarsbrook, and P. Lambert. 2010. Aquatic invertebrate community structure along an intermittence gradient: Selwyn River, New Zealand. Journal of the North American Benthological Society 29:530–545.

Aspin, T. W. H., K. Hart, K. Khamis, A. M. Milner, M. J. O'Callaghan, M. Trimmer, Z. Wang, G. M. D. Williams, G. Woodward, and M. E. Ledger. 2019. Drought intensification alters the composition, body size, and trophic structure of invertebrate assemblages in a stream mesocosm experiment. Freshwater Biology 74:33–11.

Aspin, T. W. H., K. Khamis, T. J. Matthews, A. M. Milner, M. J. O'Callaghan, M. Trimmer, G. Woodward, and M. E. Ledger. 2018a. Extreme drought pushes stream invertebrate communities over functional thresholds. Global Change Biology 25:230–244.

Aspin, T. W. H., T. J. Matthews, K. Khamis, A. M. Milner, Z. Wang, M. J. O'Callaghan, and M. E. Ledger. 2018b. Drought intensification drives turnover of structure and function in stream invertebrate communities. Ecography 117:1227–13.

Baselga, A. 2013. Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. Ecography 36:124–128.

Baselga, A. 2017. Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. Methods in Ecology and Evolution 8:799–808.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

Boersma, K. S., M. T. Bogan, B. A. Henrichs, and D. A. Lytle. 2013. Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. Freshwater Biology 59:491–501.

Bogan, M. T., K. S. Boersma, and D. A. Lytle. 2015. Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams. Freshwater Biology 60:2547–2558.

Boulton, A. J. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. Freshwater Biology 48:1173–1185.

Bunn, S. E., and A. H. Arthington. 2002. Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity. Environmental Management 30:492–507.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2010. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Byun, K., C.-M. Chiu, and A. F. Hamlet. 2019. Effects of 21st century climate change on seasonal flow regimes and hydrologic extremes over the Midwest and Great Lakes region of the US. Science of the Total Environment 650:1261–1277.

Campbell, R. E., M. J. Winterbourn, T. A. Cochrane, and A. R. McIntosh. 2015. Flow-related disturbance creates a gradient of metacommunity types within stream networks. Landscape Ecology 30:667–680.

Dahm, C. N., M. A. Baker, D. I. Moore, and J. R. Thibault. 2003. Coupled biogeochemical and hydrological responses of streams and rivers to drought. Freshwater Biology 48:1219–1231.

Datry, T., N. Bonada, and J. Heino. 2015. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. Oikos 125:149–159.

Dettinger, M. D., D. R. Cayan, M. K. Meyer, and A. E. Jeton. 2004. Simulated Hydrologic Responses to Climate Variations and Change in the Merced, Carson, and American River Basins, Sierra Nevada, California, 1900–2099. Climatic Change 62:283–317.

Diserud, O. H., and F. Odegaard. 2007. A multiple-site similarity measure. Biology Letters 3:20–22.

Doretto, A., E. Piano, E. Falasco, S. Fenoglio, M. C. Bruno, and F. Bona. 2018. Investigating the role of refuges and drift on the resilience of macroinvertebrate communities to drying conditions: An experiment in artificial streams. River Research and Applications 34:777–785.

Downes, B. J., J. Lancaster, A. Glaister, and W. D. Bovill. 2017. A fresh approach reveals how dispersal shapes metacommunity structure in a human-altered landscape. Journal of Applied Ecology 54:588–598.

Gronberg, J., N. M. Dubrovsky, and C. R. Kratzer. 1998. Environmental Setting of the San Joaquin-Tulare Basins, California. USGS Water-Resources Investigations Report 97-4205.

Hauer, F. R., and G. Hill. 2011. Methods in stream ecology. Pages 103–118 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in stream ecology. Second edition. Elsevier.

Heino, J., A. S. Melo, L. M. Bini, F. Altermatt, S. A. Al-Shami, D. G. Angeler, N. Bonada, C. Brand, M. Callisto, K. Cottenie, O. Dangles, D. Dudgeon, A. Encalada, E. Göthe, M. Grönroos, N. Hamada, D. Jacobsen, V. L. Landeiro, R. Ligeiro, R. T. Martins, M. L. Miserendino, C. S. Md Rawi, M. E. Rodrigues, F. de O. Roque, L. Sandin, D. Schmera, L. F. Sgarbi, J. P. Simaika, T. Siqueira, R. M. Thompson, and C. R. Townsend. 2015. A comparative analysis reveals weak relationships between ecological factors and beta diversity of stream insect metacommunities at two spatial levels. Ecology and Evolution 5:1235–1248.

Herbst, D. B., and S. D. Cooper. 2010. Before and after the deluge: rain-on-snow flooding effects on aquatic invertebrate communities of small streams in the Sierra Nevada, California. Journal of the North American Benthological Society 29:1354–1366.

Herbst, D. B., S. D. Cooper, R. B. Medhurst, S. W. Wiseman, and C. T. Hunsaker. 2018. A comparison of the taxonomic and trait structure of macroinvertebrate communities between the riffles and pools of montane headwater streams. Hydrobiologia 820:115–133.

Herbst, D. B., S. D. Cooper, R. B. Medhurst, S. W. Wiseman, and C. T. Hunsaker. 2019. Drought ecohydrology alters the structure and function of benthic invertebrate communities in mountain streams. Freshwater Biology 39:L10401–17.

Hodkinson, I. D., and J. K. Jackson. 2005. Terrestrial and Aquatic Invertebrates as Bioindicators for Environmental Monitoring, with Particular Reference to Mountain Ecosystems. Environmental Management 35:649–666.

Jenkins, T. M., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 80:941–956.

Lake, P. S. 2003. Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 48:1161–1172.

Ledger, M. E., F. K. Edwards, L. E. Brown, A. M. Milner, and G. Woodward. 2011. Impact of simulated drought on ecosystem biomass production: an experimental test in stream mesocosms. Global Change Biology 17:2288–2297.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leigh, C., T. W. H. Aspin, T. J. Matthews, R. J. Rolls, and M. E. Ledger. 2019. Drought alters the functional stability of stream invertebrate communities through time. Journal of Biogeography 31:831–13.

Lynch, D. T., D. R. Leasure, and D. D. Magoulick. 2018. The influence of drought on flow-ecology relationships in Ozark Highland streams. Freshwater Biology 63:946–968.

Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. Trends in Ecology & Evolution 19:94–100.

Maurer, E. P. 2007. Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. Climatic Change 82:309–325.

Musselman, K. N., N. P. Molotch, and S. A. Margulis. 2017. Snowmelt response to simulated warming across a large elevation gradient, southern Sierra Nevada, California. The Cryosphere 11:2847–2866.

Oliver, T. H., M. S. Heard, N. J. B. Isaac, D. B. Roy, D. Procter, F. Eigenbrod, R. Freckleton, A. Hector, C. D. L. Orme, O. L. Petchey, V. Proença, D. Raffaelli, K. B. Suttle, G. M. Mace, B. Martín-López, Ben A Woodcock, and J. M. Bullock. 2015. Biodiversity and Resilience of Ecosystem Functions. Trends in Ecology & Evolution 30:673–684.

Power, M. E., A. Sun, G. Parker, W. E. Dietrich, and J. T. Wootton. 1995. Hydraulic Food-Chain Models. BioScience 45:159–167.

Rader, R. B., and T. A. Belish. 1999. Influence of mild to severe flow alterations on invertebrates in three mountain streams. Regulated Rivers: Research & Management 15:353–363.

Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd, T. J. MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C. Vermaire, D. Dudgeon, and S. J. Cooke. 2018. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 7:401–25.

Robach, F., I. Eglin, and M. Tremolieres. 1997. Species richness of aquatic macrophytes in former channels connected to a river: a comparison between two fluvial hydrosystems differing in their regime and regulation. Journal of Animal Ecology 6:267.

Rodríguez, C. G., and A. Baselga. 2018. Variation among European beetle taxa in patterns of distance decay of similarity suggests a major role of dispersal processes. Ecography 41:1825–1834.

Ruhí, A., X. Dong, C. H. McDaniel, D. P. Batzer, and J. L. Sabo. 2018. Detrimental effects of a novel flow regime on the functional trajectory of an aquatic invertebrate metacommunity. Global Change Biology 12:466–17.

Sartory, D. P., and J. Grobbelaar. 1984. Extraction of chlorophyll a from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia

Siam, M. S., and E. A. B. Eltahir. 2017. Climate change enhances interannual variability of the Nile river flow. Nature Climate Change 7:350–354.

Steinberg, M. K., M. R. First, E. J. Lemieux, L. A. Drake, B. N. Nelson, D. M. Kulis, D. M. Anderson, N. A. Welschmeyer, and P. R. Herring. 2011. Comparison of techniques used to count single-celled viable phytoplankton. Journal of Applied Phycology 24:751–758.

Stromberg, J. C., K. J. Bagstad, J. M. Leenhouts, S. J. Lite, and E. Makings. 2005. Effects of stream flow intermittency on riparian vegetation of a semiarid region river (San Pedro River, Arizona). River Research and Applications 21:925–938.

Stubbington, R., and T. Datry. 2013. The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones. Freshwater Biology 58:1202–1220.

Swain, D. L., B. Langenbrunner, J. D. Neelin, and A. Hall. 2018. Increasing precipitation volatility in twenty-first- century California. Nature Climate Change 8:1–10.

Tonkin, J. D., D. M. Merritt, J. D. Olden, L. V. Reynolds, and D. A. Lytle. 2018. Flow regime alteration degrades ecological networks in riparian ecosystems. Nature Ecology & Evolution:1–10.

Tonkin, J. D., F. Altermatt, D. S. Finn, J. Heino, J. D. Olden, S. U. Pauls, and D. A. Lytle. 2017. The role of dispersal in river network metacommunities: Patterns, processes, and pathways. Freshwater Biology 63:141–163.

van Vliet, M. T. H., and J. J. G. Zwolsman. 2008. Impact of summer droughts on the water quality of the Meuse river. Journal of Hydrology 353:1–17.

Vander Vorste, R. V., R. Corti, A. Sagouis, and T. Datry. 2016. Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence. Freshwater Science 35:164–177.

Verdonschot, R. C. M., A. M. van Oosten-Siedlecka, C. J. F. ter Braak, and P. F. M. Verdonschot. 2014. Macroinvertebrate survival during cessation of flow and streambed drying in a lowland stream. Freshwater Biology 60:282–296.

Walters, A. W., and D. M. Post. 2011. How low can you go? Impacts of a low-flow disturbance on aquatic insect communities. Ecological Applications 21:163–174.

Woodrum, J. E., and D. C. Tarter. 1973. The Life History of the Alderfly, Sialis aequalis Banks, in an Acid Mine Stream. American Midland Naturalist 89:360.

Wright, J. F., R. T. Clarke, R. J. M. Gunn, N. T. Kneebone, and J. Davy-Bowker. 2004. Impact of major changes in flow regime on the macroinvertebrate assemblages of four chalk stream sites, 1997-2001. River Research and Applications 20:775–794.

Ylla, I., I. Sanpera-Calbet, E. Vázquez, A. M. Romaní, I. Muñoz, A. Butturini, and S. Sabater. 2010. Organic matter availability during pre- and post-drought periods in a Mediterranean stream. Hydrobiologia 657:217–232.

Zeiringer, B., C. Seliger, F. Greimel, and S. Schmutz. 2018. River Hydrology, Flow Alteration, and Environmental Flow. Pages 67–89 *in* Riverine Ecosystem Management. Springer International Publishing, Cham.

Zimmerman, J. K. H., D. M. Carlisle, J. T. May, K. R. Klausmeyer, T. E. Grantham, L. R. Brown, and J. K. Howard. 2018. Patterns and magnitude of flow alteration in California, USA. Freshwater Biology 63:859–873.

Figures

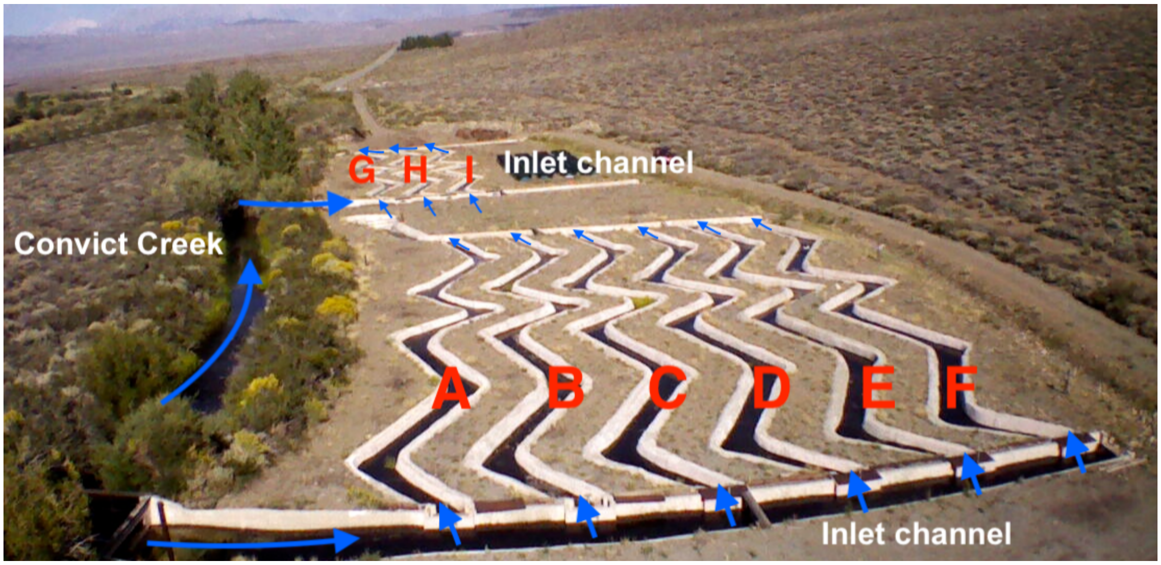


Figure 1.1. Layout of SNARL channels used in the experimental drought manipulation; letters refer to treatments as described in the text. Arrows denote the direction of flow.

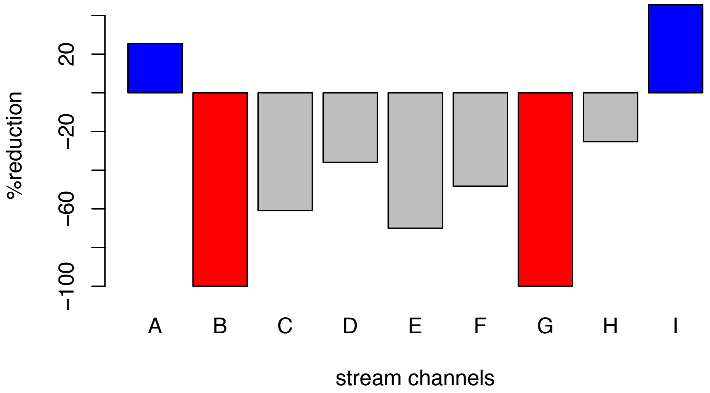


Figure 1.2 (left). Percentage changes in discharge from experimental channels at the Sierra Nevada Aquatic Research Laboratory (SNARL). Discharge rates are presented relative to pre-experimental levels and were maintained throughout the two-year period, except for the July 2015 flood. Blue bars, control channels; red bars functionally intermittent channels (complete drying); grey bars, moderately perturbed channels. Figure 1.3 (right). Comparison of the 98% flow-reduction channel (left, channel B) with a control channel (right, channel A) after drought treatments

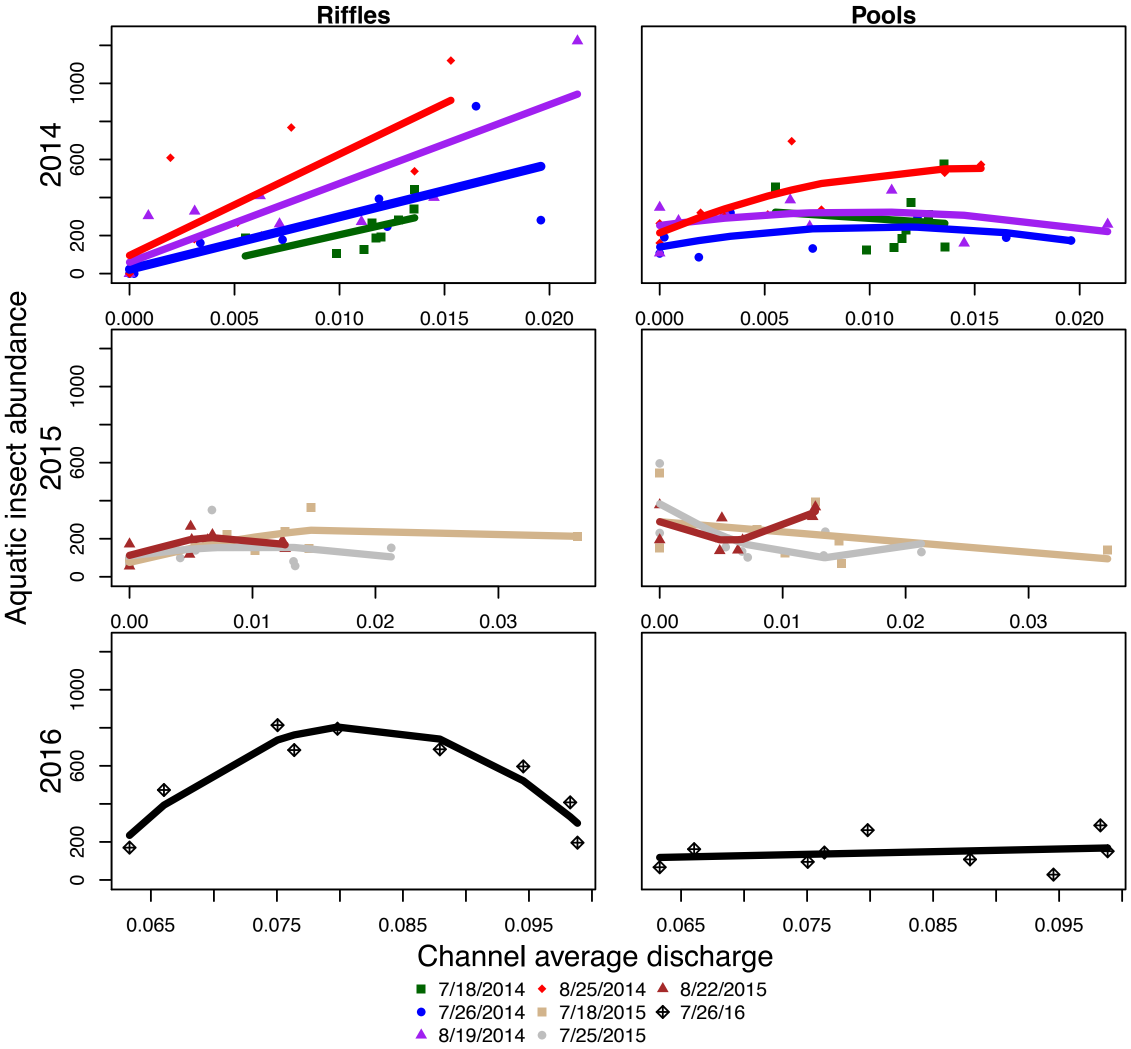


Figure 1.4. Relationships between aquatic insect abundance and average discharge over time in differing habitats (pool or riffle); trends were identified using best-fit polynomial models. Colors / shapes correspond with sampling dates.

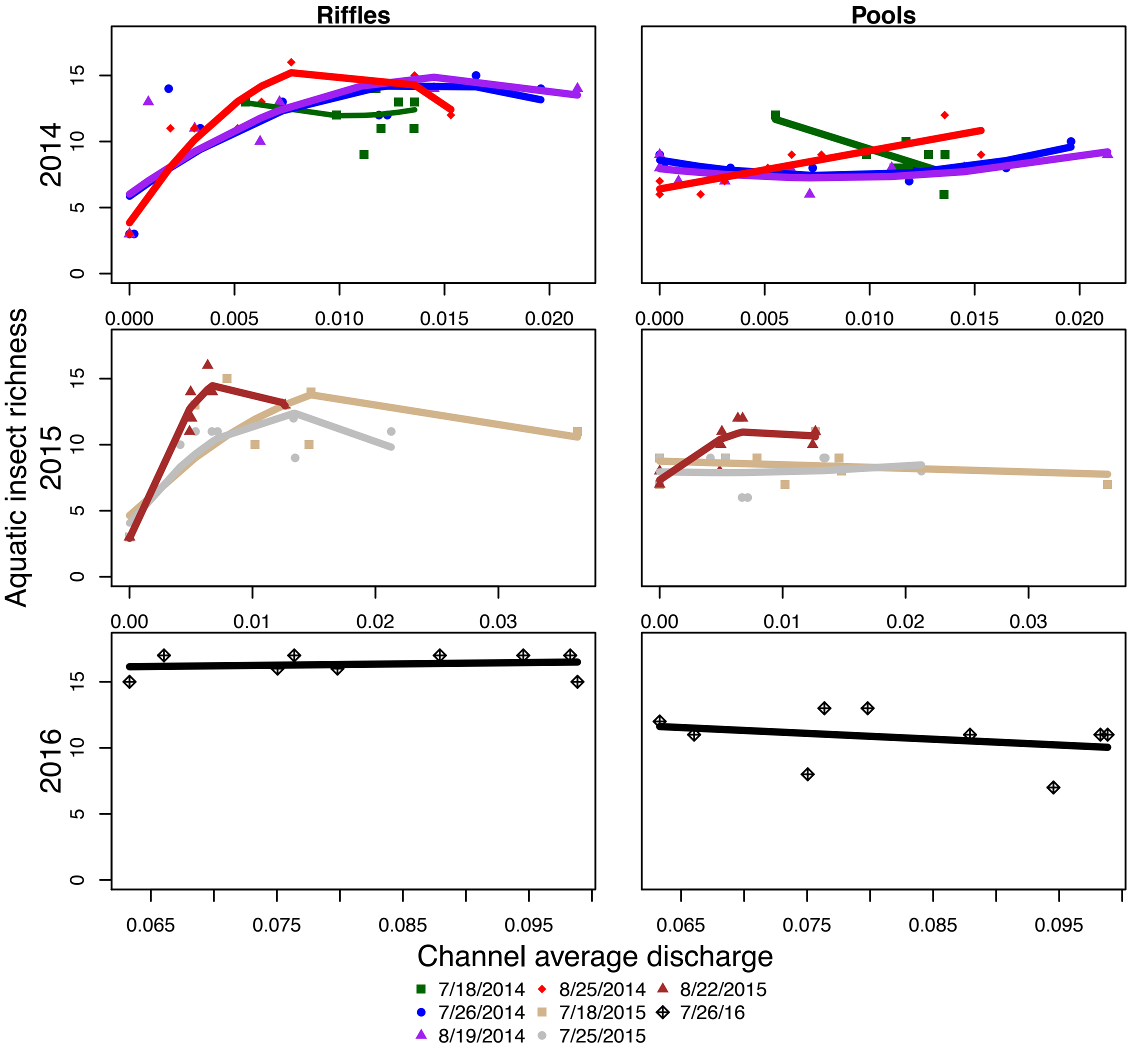


Figure 1.5. Relationships between aquatic insect richness and average discharge over time in differing habitats (pool or riffle); trends were identified using best-fit polynomial models. Colors / shapes correspond with sampling dates.

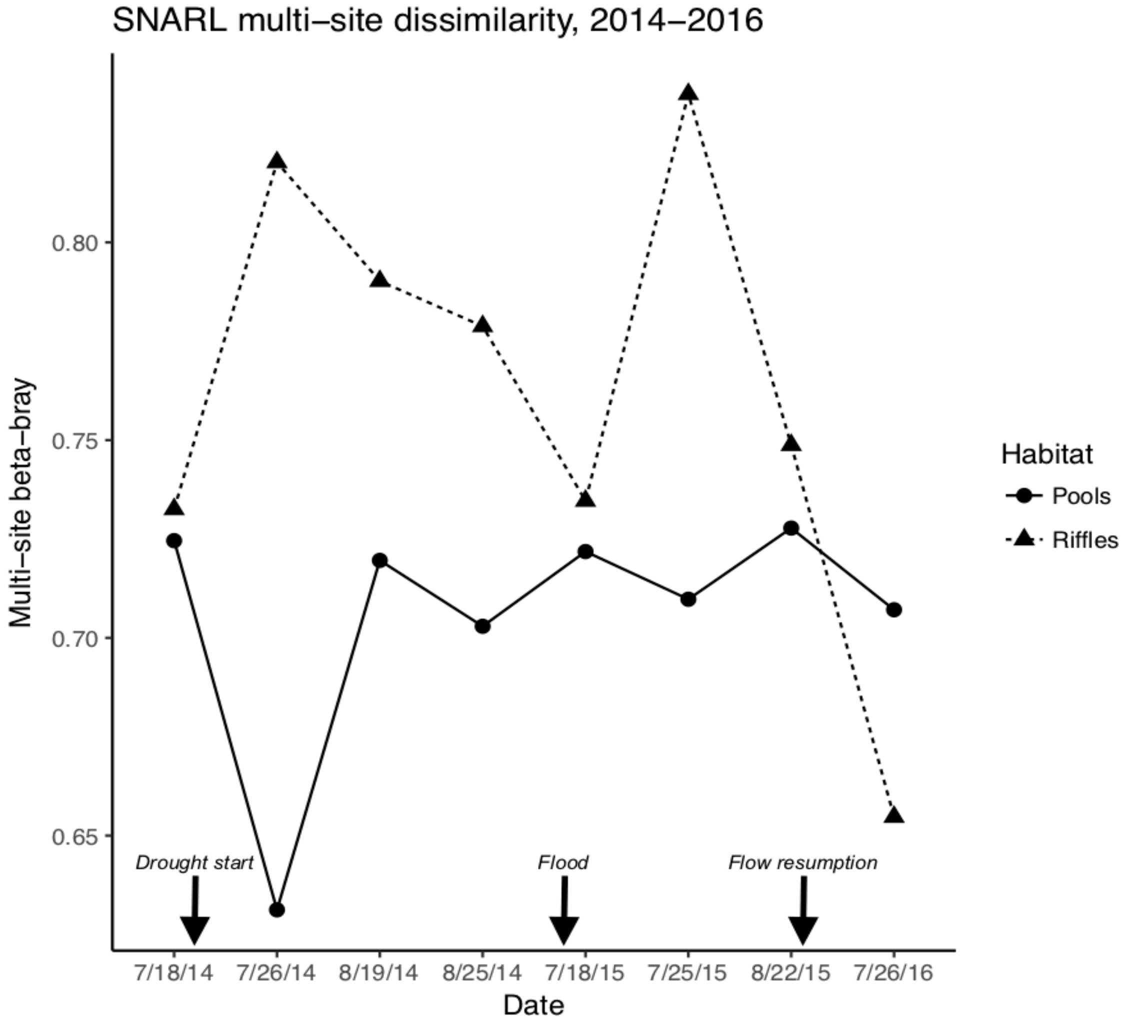


Figure 1.6. Multi-site beta dissimilarity on each sampling date; major flow changes are indicated with arrows. Dotted and solid lines represent beta dissimilarities in riffles and pools, respectively.

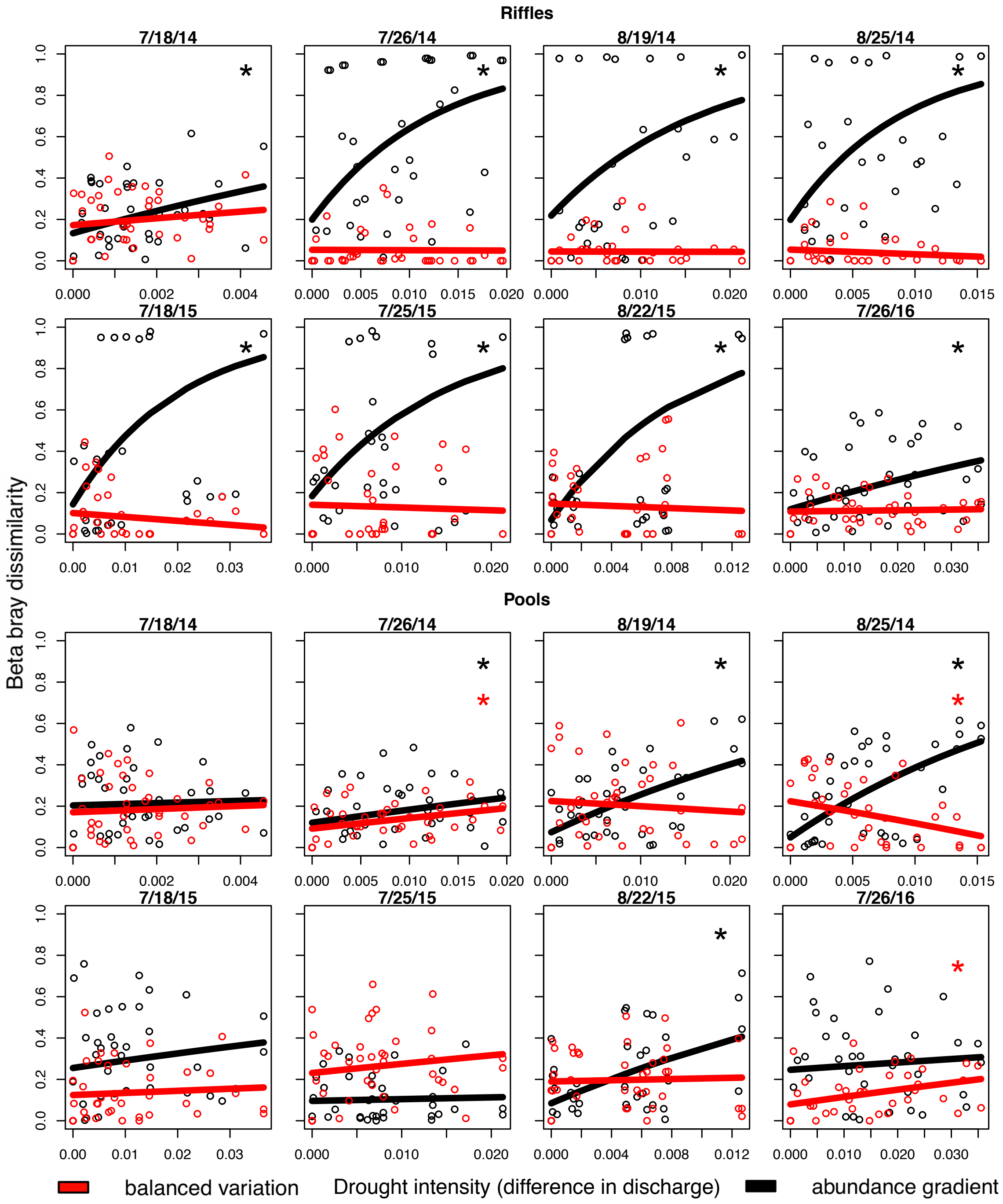


Figure 1.7. Partitioned pairwise beta-bray dissimilarity values in riffles (upper panels) and pools (lower panels); data are plotted against drought intensity on sampling days. The lines were fitted using negative exponential distance decay models. Black asterisks indicate significant relationships ($p < 0.05$) with abundance gradient, and red asterisks indicate significant relationships with balanced variation.

Tables

Table 1.1. GLM models used to explain variations in stream insect abundances (upper) and species richness (lower) across flow perturbation treatments. Models are ranked according to corrected Akaikes information criterion (AICc) values. Factors with significant effects in the model are listed in bold font ($p < 0.05$).

Model	**Model predictors**	**df**	**ΔAICc**	**AICc**
Abundance	**Discharge,** ChlA, DO, **Date, Date*Discharge**	7	0	976.5
	Discharge, DO, Date, Date*Discharge	6	0.2	976.7
	Date, ChlA, Discharge, Date*Discharge	6	0.3	976.8
	Discharge, ChlA, DO, Temp, **Date, Date*Discharge**	8	2.1	978.6
	Discharge, ChlA, Conductance, DO, **Date, Date*Discharge**	8	2.3	978.8
	Discharge, Date, Date*Discharge	5	3.0	979.5
	Discharge, ChlA, Conductance, DO, Temp, **Date**, **Date*Discharge**	9	4.2	980.7
	Discharge, Conductance, **DO**, Temp, **Date, Date*Discharge**	8	4.5	981.0
	ChlA, Conductance, Temp, **Date, Date*Discharge**	8	4.9	981.4
	Discharge, ChlA, Conductance, DO, Temp, Date	8	16.3	992.8
Richness	**Discharge**, Date	3	0	325.1
	Discharge, Date, Date*Discharge	4	0.3	325.4
	Discharge, ChlA, Date	4	2.2	327.3
	Discharge, ChlA, Date, Date*Discharge	5	2.6	327.7
	Discharge, Conductance, DO, Temp, Date	6	2.9	328.0
	Discharge, ChlA, DO, Temp, Date	6	4.0	329.1
	Discharge, Conductance, DO, Temp, Date, Date*Discharge	7	4.4	329.5
	Discharge, ChlA, Conductance, DO, Date	6	4.4	329.5
	Chla, DO, Date*Discharge	6	4.8	329.9
	Discharge, ChlA, Conductance, DO, Date, Date*Discharge	8	6.5	331.9

Supplemental tables

Supplemental Table 1.1. Distance-decay model outputs for both balanced variation and abundance gradient outputs in pools (above) and riffle (below). Significant models highlighted in yellow with p<.05.

Riffles

Date	**Dissimilarity partition**	**Slope**	**P-value**	**Pseudo-R^2**
7/18/14	*Abund grad*	*66.3*	*.001*	*.139*
	Balance var	20.5	.192	.021
7/26/14	*Abund grad*	*79.9*	*.001*	*.275*
	Balance var	-.19	.902	0
8/19/14	*Abund grad*	*58.8*	*.001*	*.175*
	Balance var	-.078	.953	0
8/25/14	*Abund grad*	*111.53*	*.001*	*.250*
	Balance var	-2.3	.21	.020
7/18/15	*Abund grad*	*48.80*	*.001*	*.175*
	Balance var	-2.05	.14	.027
7/25/15	*Abund grad*	*66.40*	*.001*	*.188*
	Balance var	-1.53	.714	0
8/22/15	*Abund grad*	*113.31*	*.001*	*.330*
	Balance var	-3.15	.596	.003
7/26/16	*Abund grad*	*8.80*	*.001*	*.141*
	Balance var	.357	.707	.001

Pools

Date	**Dissimilarity partition**	**Slope**	**P-value**	**Pseudo-R^2**
7/18/14	*Abund grad*	*7.12*	*.744*	*.001*
	Balance var	9.38	.585	.003
7/26/14	*Abund grad*	*7.46*	*.012*	*.075*
	Balance var	5.77	.004	.114
8/19/14	*Abund grad*	*21.88*	*.001*	*.362*
	Balance var	-3.16	.442	.006
8/25/14	*Abund grad*	*43.77*	*.001*	*.425*
	Balance var	-12.85	.003	.108
7/18/15	*Abund grad*	*4.96*	*.186*	*.022*
	Balance var	1.17	.513	.005
7/25/15	*Abund grad*	*.95*	*.708*	*.002*
	Balance var	5.89	.251	.018
8/22/15	*Abund grad*	*34.18*	*.001*	*.279*
	Balance var	1.85	.736	.001
7/26/16	*Abund grad*	*2.38*	*.447*	*.007*
	Balance var	4.01	.002	.130

Supplemental Table 1.2. Table of insects identified from SNARL channels. Midges (from suborder Nematocera) not identified to family or genus.

Order	**Family**	**Genus / species**
Ephemeroptera	Heptageniidae	Epeorus
Ephemeroptera	Baetidae	Baetis
Ephemeroptera	Ephemerllidae	Drunella
Ephemeroptera	Leptophlebiidae	Paraleptophlebia
Plecoptera	Nemouridae	Zapada columbiana
Trichoptera	Hydroptilidae	Hydroptila
Trichoptera	Philopotamidae	Wormaldia
Trichoptera	Brachycentridae	Micrasema
Trichoptera	Brachycentridae	Brachycentrus americanus
Trichoptera	Glossosomatidae	Glossosoma
Trichoptera	Hydropsychidae	Hydropsyche
Coleoptera	Elmidae	Optioservus
Diptera	Simuliidae	Simulium
Megaloptera	Sialidae	Sialis
Diptera	Nematocera(suborder)	Midges

Chapter 2:

Evaluating the influence of flow, space, environment and time on the beta diversity of riverine metacommunities at large spatial scales and long timescales

Abstract

River systems are ideal for the study of the spatial and temporal drivers of beta diversity because they contain multiple layers of spatial complexity at local and regional scales. The effects of flow variability, local environment and spatial location on beta-diversity patterns at long timescales were investigated using a large amount of publicly available benthic macroinvertebrate data from river networks in California. The results from beta regression models indicated that spatial factors, change in time, and two specific flow metrics were significant in explaining turnover in benthic macroinvertebrate metacommunities. Slope, drainage density, and upstream catchment area were most significant spatial factors, while significant long-term flow metrics corresponded to flow variability and zero-flow days. Finally, local environmental variables performed poorly in describing variation in beta diversity at long timescales. This study provides support for the hypothesis that the combination of spatial factors, especially drainage density, and long term flow variation can determine beta-diversity patterns of benthic macroinvertebrate metacommunities at large spatial scales.

Introduction

Spatial patterns of biological communities are influenced by conditions in the local environment, species interactions, and landscape biogeography (Cottenie 2005). Trends in community diversity and distribution are often studied by calculating beta diversity, which can be defined as the dissimilarity in community composition between sites in a given area (Anderson et al. 2006). River systems are ideal for the study of the spatial and temporal drivers of beta diversity because they contain multiple layers of spatial complexity at local and regional scales, which dictates the vertical movement of biota and physical water properties (Tonkin et al. 2018, Harvey and Altermatt 2019). River systems are composed of a dendritic structure, which is largely responsible for flow directionality and in turn, the dispersal of organisms (Tonkin et al. 2017). As our ecological understanding of rivers has advanced past classical linear concepts of biodiversity, such as the linear progression of communities advocated by the river continuum concept (Vannote and Minshall 1980), the dendritic structure of river networks, and more specifically their unidirectional flow patterns, can impose a unique hierarchical pattern of biodiversity (Altermatt 2013). The relative influence of spatial and temporal processes as drivers of beta diversity is an unresolved issue in ecology, especially in freshwater systems because of their dynamic environmental conditions and unique dendritic structure (Tonkin et al. 2017).

Given that flow has been defined as a master variable that can affect many other environmental conditions such as temperature, dissolved oxygen, and substrate transport in rivers (Power et al. 1995), spatial and temporal variation in catchment flow regimes can strongly influence beta-diversity patterns (Rolls et al. 2017). Spatial variation in hydrological connectivity, stream discharge magnitude and discharge duration have been shown to be particularly important in the determination of beta-diversity patterns, as these factors not only determine the dispersal ability of benthic macroinvertebrates through the river network, but also interact with the tolerance of taxa to local environmental conditions (Clarke et al. 2010b, Liu et al. 2013, Warfe et al. 2014, Leigh and Datry 2016). Additionally, slope can have a significant effect on flow regimes by facilitating higher and shorter or lower and longer peak discharge events, which can increase or decrease the strength of local environmental filtering (Nippgen et al. 2011). Empirical studies have also shown that the beta diversity of several freshwater communities is lowest when floods and high flow events are more frequent (by causing higher connectivity between metacommunities), while community dissimilarity increases when discharge is lost and fragmentation occurs (higher barriers to dispersal and homogenization of metacommunities) (Fazi et al. 2013, Starr et al. 2014). Zero-flow days are also a commonly reported factor in the determination of patterns of turnover, and results in nestedness (spatial subsets of metacommunities) (Datry et al. 2014) and replacement (compositional turnover) (Bogan et al. 2013), since surface flow loss is one of the strongest dispersal barriers. However, studies on beta-diversity patterns across regions with distinct hydrological characteristics are not found in the literature (Rolls et al. 2017), and they are necessary to generalize the response of beta diversity to flow regimes and better understand the interaction between spatially structured flow regimes and other environmental processes.

Dendritic network organization, the resulting connectivity between network branches and especially network position and structure can dictate beta-diversity patterns by restricting species dispersal (Altermatt 2013, Brown et al. 2017). The metacommunity paradigm, which highlights processes that structure communities beyond the local scale, has facilitated the progress and understanding of theory and analysis of the spatial patterns of beta diversity (Leibold et al. 2004, Winegardner et al. 2012). Benthic macroinvertebrate metacommunities are ideal for studying beta-diversity patterns because they inhabit dendritic river networks, and their spatial structure has been shown to affect community dynamics at local and regional scales (Tonkin et al. 2018). Further, the drivers of benthic macroinvertebrate turnover have been shown to be scale-dependent. Evidence suggests that headwater communities are structured more by local environmental conditions (sorting), while higher-order streams and mainstems are influenced more by distance and corresponding connectivity metrics, such as network position and upstream area (mass effects) (Schmera et al. 2017). However, studies that separate local and regional processes to explain shifts in beta diversity have been unpersuasive (Heino et al. 2015). Studies have suggested that local and regional factors are more connected than originally thought when the mechanisms behind process effects are considered. For example, flow regime can dictate both the local temperature profile and dispersal patterns at the regional scale (Mayfield and Stouffer 2017).

Though river networks are highly dynamic systems with considerable variation in environmental conditions and connectivity, most beta diversity studies have assumed that community assembly mechanisms are stable over time. However, stream metacommunities exhibit significant temporal variability in community assembly and resulting beta diversity (Datry et al. 2016, Ruhí et al. 2017). For example, beta diversity has been shown vary temporally due to changes in hydrological conditions, which renders assembly mechanisms more stable in perennially flowing streams (Sarremejane et al. 2017b). Context dependence reported in prior studies could be due to the absence of observations at temporal scales that were long enough to capture overall variability in beta diversity (Tonkin et al. 2016a). More studies are needed to fill the knowledge gaps related to the response of beta diversity to temporally structured habitat heterogeneity, local environmental conditions, and hydrological regimes.

Though local- and regional-scale studies are most commonly used to investigate compositional turnover in benthic macroinvertebrate metacommunities (Thompson and Townsend 2006, Brown and Swan 2010, Siqueira et al. 2012), they have also recently expanded to larger scales with varying biogeography (Swan and Brown 2014, Tonkin et al. 2015b, Seymour et al. 2016, Tonkin et al. 2016b, Dala-Corte et al. 2017), and even to the global scale (Heino et al. 2015). However, a smaller body of research has examined the relationship between beta diversity and temporal heterogeneity as it relates to environment, species composition, and hydrology (Ruhí et al. 2017, Sarremejane et al. 2017b). Additionally, though beta diversity has generally been shown to vary in response to flow variability, no study has determined which aspects of the hydrograph are driving beta-diversity patterns, especially in multiple regions with fluctuating hydrology characteristics and at long timescales.

I examined patterns of beta diversity in a large geographic area spanning the Sierra Nevada mountain range in California, United States. There is a considerable amount of spatial and temporal variation in environment and hydrology throughout this range in California, and as prior studies have shown that distinct flow regimes throughout this range strongly affect benthic macroinvertebrate assemblages (Lusardi et al. 2016), it was thus expected that beta diversity would respond strongly to gradients in environment and flow regime. A large number of streams spanning multiple orders (headwaters to mainstem) was examined, and the linkages between drivers of beta diversity were investigated. These drivers could be related to species sorting along gradients (Cottenie 2005), spatial processes such as location within a dendritic river network (Brown and Swan 2010), and/or temporal variability (Sarremejane et al. 2017b). The importance of these processes in structuring communities has been debated, and this may be contingent on the spatial and temporal scale of the study (Heino et al. 2014). Thus, by using a large, publicly available macroinvertebrate dataset, the effects of flow variability, environment, and spatial location on beta-diversity patterns at long timescales were investigated through multiple catchments in the Sierra Nevada mountain range in California, United States.

Given the stated objectives, the following hypotheses were developed: (1) throughout all sites, local environmental conditions, such as temperature and dissolved oxygen, are a significant explanatory variable in the prediction of beta diversity, followed by strictly spatial factors such as drainage density, (2) higher beta diversity between headwater sites is due to colonization limitation and low connectivity (species sorting), while lower beta diversity between mainstem sites in lower-order sections is due to higher homogenization of communities (mass effects), (3) after controlling for variability in space and environment, variation with respect to time alone would be a poor predictor of beta-diversity patterns, and (4) long-term flow regime variability, especially hydrograph metrics, such as zero flow days and flood intervals in each sampling area, can be used to predict beta diversity by providing more ecological context than environmental variables.

Methods

Benthic macroinvertebrates and site-level environmental variables

Publicly available data from the California Surface Water Ambient Monitoring Program (SWAMP) were used to conduct this study, which is accessible through the California Environmental Data Exchange Network (CEDEN, http://www.ceden.org). SWAMP organizes much of its aquatic sampling data by county, and I restricted my data collection effort to counties that generally fall within the Sierra Nevada mountain range and the southern portion of the Cascade mountain range. The sampling protocol for benthic macroinvertebrates is standardized across the SWAMP sampling network, which includes taking care to sample at multiple habitat types and regulating sampling effort. The lowest level of taxonomic resolution was genus, though some taxa such as chironomids were not identified down at this level. Genus is a finer level of taxonomic resolution than used in several prior studies (Heino 2011, Datry et al. 2014, Leigh and Datry 2016). At most SWAMP sampling sites, the environmental variables were also measured concurrently with benthic macroinvertebrate sampling. Thus, dissolved oxygen, pH, conductivity, temperature, and velocity data were also retrieved from the database. Substantial post-processing of the data was performed after it was downloaded from CEDEN. SWAMP sampling occurs throughout the year, and the sampling season is not standardized throughout the database. Further, sites are sometimes renamed from one sampling year to the next. Using ArcGIS (version 9.x) and National Hydrography Dataset

(NHDv2) stream layers, all sites sampled by CEDEN throughout the Sierra Nevada mountain range in California were mapped for all timepoints. I then focused data collection efforts in those California counties with the highest number of collection sites and timepoints for each site, taking care to combine site names that were sampled at the same site. To control for seasonal variation in benthic macroinvertebrate metacommunities while maximizing the large temporal timescale, the data were restricted to samples taken between June and September from 1998-2017. Additionally, sites that had at least two sampling timepoints were chosen, though this does not mean the sites were sampled annually. Frequently, sites were sampled once, and the following sampling events occurred after a random number of years had passed (anywhere between 1-15 years).

After scouring all counties in the vicinity of the Sierra Nevada mountain range for benthic macroinvertebrate community data, five counties were found to have sampling efforts with sufficient spatial and temporal scale to warrant inclusion in my dataset. While El Dorado, Alpine and Mono counties were all clustered south of Lake Tahoe, CA, Tehama and Plumas counties covered the northern end of the Sierra Nevada mountain range and a small part of the southern Cascade mountain range (Figure 2.1). The biotic samples had a temporal spread of 1998-2017, with a maximum spatial range of 450km and average total area between all samples of 36,000 km^2. The dataset included a total of 110 sites across 5 counties (Alpine, El Dorado, Mono, Plumas, and Tehama) with a total of 382 genera, spanning stream orders of 1-6, though the area upstream from sampling locations was used as a quantitative measure of site position within the network.

Flow

The SWAMP sampling locations were paired with long-term flow data by finding United States Geological Survey (USGS) stream flow gage sites. Gage locations within a 10 km buffer (Leigh and Datry 2016) and similar stream order to SWAMP sampling sites were found by using the Consortium of Universities for the Advancement of Hydrologic Science (CUAHSI) HydroClient web interface (data.cuahsi.org), and snapping gaged sites to an ArcGIS layer to determine distance to SWAMP sampling location. Entire hydrograph time series from paired flow gages were used, with an average span of 20 years per gage because long-term flow conditions are an important environmental filter for benthic macroinvertebrate metacommunities (Lytle and Poff 2004). The River Analysis Package (RAP 3.0.8) was used to calculate hydrograph metrics and contextualize the flow regime at each location at long timescales (Kennard et al. 2009). Twenty-six calculated flow metrics (Table 2.1) were chosen to evaluate critical parts of flow variability affecting biological patterns, such as flow magnitude, duration, frequency, timing and rate of change (Poff et al. 1997, Leigh and Datry 2016). Specific calculated metrics have been previously described in detail (Olden and Poff 2003, Kennard et al. 2009, Leigh and Datry 2016). After flow data were compiled for all sites, I ordinated the metrics using principal components analysis (PCA) to collapse flow variability information into various flow regime types, because several different flow metrics were related. Each principal component axis was then related to flow metrics loading most strongly along that axis. The most ecologically relevant PC axes were separated by county and plotted to visually determine the types of flow regimes by geography.

Stream network metrics

Upstream area (from the sampling location), channel slope, drainage density and land cover were calculated for each benthic macroinvertebrate sampling location. This was accomplished by constructing a landscape network (LSN) with the functional linkage of water basins and streams (FLoWS) ArcGIS geoprocessing toolset (Theobald et al. 2005), and subsequently, the spatial tools for the analysis of river systems (STARS) toolset was used to generate and format spatial data (Peterson and Ver Hoef 2014, Isaak et al. 2014). Catchment characteristics were derived from NDHPlusv2, while land cover was derived from the National Land Cover Database (NLCD). Each upstream area was square-root transformed, which is analogous to discharge volume and overall stream size (Leopold and Maddock 1953). To calculate a metric of environmental distance (environmental dissimilarity), site-specific environmental data were ordinated with PCA over all timepoints. Principal components with eigenvalues greater than 1 were kept, and environmental distance was defined as the Euclidian distance calculated between pairs of sites in multivariate space (Brown and Swan 2010).

Calculating beta diversity and statistical modelling framework

Temporal beta diversity was obtained by calculating Bray-Curtis community dissimilarity of genus abundance between all sites and timesteps using the betapart package for R (Baselga 2013). Similarly, the time difference between sampling periods was calculated (hereafter referred to as Δtime), and the relationships among temporal beta diversity, Δtime, environmental distance, stream network distance, and flow metrics were statistically tested in a beta regression framework. Beta regression was determined to be the ideal modelling framework because community dissimilarity values were between the unit interval (0,1) and the data violated assumptions of normality and equal variances (data appeared to be heteroskedastic). Assumptions of normality and equal variance were checked with Shapiro-Wilk's, Lavene's test, and bptest in the car package for R, as well as with Q-Q and cook's distance plots. Beta regressions are flexible with heteroskedasticity and incorporate extra precision parameters, which can depend on a set of similar or different regressors to account for extra variance in data (Zeileis and Cribari-Neto 2010). Collinearity between predictors was checked by examining the variance inflation factors (VIFs) in the car package after running beta regressions, and any predictors with a VIF greater than 2 were removed (Fox and Monette 1992). For NLCD land cover data, only %forest cover was used as a predictor because it resulted in the largest model performance improvement, while the inclusion of other land cover data increased the VIF above the acceptable range (Fox and Monette 1992). The addition of a precision parameter in the beta regression model was determined by checking the addition of all predictors as a precision parameter and comparing model performance with AIC tests between models with and without precision parameters. It was determined that using drainage density as a precision parameter accounted for the most unexplained variance and was used in the final modelling approach.

Since the importance of various environmental and spatial predictors has been context-dependent in previous studies (Tonkin et al. 2016a), I used AIC to select the best model for predicting temporal variation in beta diversity. Using the MuMIn package for R, I determined which top-ranked models had a ΔAICc less than 4. The relative importance of each predictor was obtained by summing Akaike weights (SW) in the top-ranked models. SW assists in detecting important predictors even if they are not included in the top model because they can be found if they appear often in other model formulations (Burnham et al. 2010, Giam and Olden 2015). Then, I model-averaged all models with a ΔAICc of less than 4 to account for model selection uncertainty and obtain robust predictions (Grueber et al. 2011), and coefficient estimates from model averaging output were used to understand the importance of predictors. From the beta regression, predicted univariate relationships between each independent variable and beta diversity (mean of the predicted beta distribution) were plotted to visually examine significant effects from the averaged model. The predicted 5% and 95% quantiles were also plotted on these graphs, which revealed increasing precision in the beta regression (i.e., 90% confidence interval around the mean) (Zeileis and Cribari-Neto 2010).

Results

In the ordinations of sampled environmental variables, the first four principal components explained 88% of the variation, and those were used to calculate Euclidian distance, which was used as the measure of environmental distance. For the ordination of the flow metrics, the first four principal component axes captured 83% of the variability, so these scores were used in further analyses. In the beta regression modelling approach, PC1 and PC4 were repeatedly identified as the most important predictors of flow variability (Tables 2.2 and 2.3). The flow metrics with the strongest loading on PC1 were related to rates and magnitudes of rises and falls in flow over time, while PC4 was related to the number of zero-flow days and the duration of flow rises and falls in the hydrograph. Plumas and Tehama counties were structured more by PC1, while Alpine, El Dorado, and Mono counties were structured more by PC4. However, most counties were generally structured more by PC1, and this axis explained most variations in flow metrics (Figure 2.2).

Twenty-three beta regression models (ΔAICc < 4) were chosen from a list of models with different combinations of predictors to explain temporal beta diversity of benthic macroinvertebrates. Out of the suite of the ten selected predictors, six were most important based on summed Akaike weights. Predictors of flow and catchment characteristics were most important in the explanation of beta diversity of benthic macroinvertebrates with an Akaike weight greater than 0.5 (slope, drainage density, Δtime, upstream area, PC1, and PC4 with SW of 1, 1, 1, 1, 0.91 and 0.86, respectively; Table 2.2). Forest cover, environmental distance, PC2 and PC3 were the least important predictors (SW of 0.40, 0.37, 0.27 and 0.21).

The results varied when the best beta regression model was used to evaluate the role of space (upstream area, channel slope, drainage density), environment (environmental distance, forest cover, flow metrics PC1 and PC4) and time in dictating turnover. Model averaging of all models with ΔAICc < 4 yielded corresponding estimated coefficient values for each predictor (Table 2.2), and univariate relationships between each predictor and temporal beta diversity over time were plotted with the best fitted statistical model. Upstream area and forest cover exhibited slightly positive relationships with beta diversity (estimated coefficients of 0.0007 and 0.0024; Figure 2.3E and 2.3H, Table 2.2). Drainage density, Δtime, and environmental distance exhibited stronger positive relationships with beta diversity (estimated coefficients of 0.7536, 0.3090 and 0.0415; Figures 2.3F, 2.3A and 2.3B; Table 2.2). Channel slope, PC1 and PC4 exhibited negative relationships with beta diversity (estimated coefficients of -2.4405, -0.0341 and -0.1635; Figures 2.3G, 2.3C and 2.3D; Table 2.2). However, since flow metrics were negatively related to PC1 and PC4, the more negative values on the x axis in Figures 2.3C and 2.3D signifies a stronger relationship with that metric. In other words, communities were more dissimilar when the rate and magnitude of rises and falls in flow was higher in the hydrograph (Figure 2.3C), while they were also more dissimilar when the number of zero-flow days was higher and the duration of flow rises and falls was higher (Figure 2.3D).

Discussion

Although local environmental conditions are known to structure metacommunities of benthic macroinvertebrates and fish in riverine systems (Brown and Swan 2010, Grönroos et al. 2013, Dala-Corte et al. 2017, Gansfort and Traunspurger 2019), point estimates of this historically important predictor were fairly weak in explaining beta diversity. Point estimates in this study included local environmental variables, such as dissolved oxygen and temperature, which were sampled when benthic macroinvertebrates were collected. Contrary to predictions made with hypothesis 1, there was little evidence to suggest that local habitat variability led to high community turnover in this study system. Spatial factors such as slope, drainage density, upstream catchment area and long-term flow metrics explained a substantially higher portion of turnover, even though temporal variation in these metrics were not included in our analyses. The explanation for this result may be twofold. First, network metrics, such as channel slope, drainage density and upstream area may provide more environmental context by explaining a more complex suite of variables than point-estimate environmental measurements. For instance, metacommunities inhabiting certain sections of catchments can have unique dispersal abilities that renders them more or less persistent in different environmental conditions. For varying local environmental conditions over time and space, point-estimate measurements may not have been able to accurately capture all the variability in metacommunity response (Cañedo-Argüelles et al. 2015).

Secondly, heterogeneity in network structure within and between catchments may be interacting with local environmental variables to impact metacommunities in different ways, and although I predicted that upstream locations would experience more turnover (hypothesis 2), the relationship appears to be inversely related. The results indicated that metacommunities occupying more dense central locations within river networks harbored higher beta diversity, regardless of patch size (Carrara et al. 2014), and in my system, sites with a lower upstream area did not have higher turnover over time, which rejects hypothesis 2. Instead, given low connectivity between patches at large spatial scales, metacommunities in more dense areas of catchments could be more influenced by mass effects and subsequently increase beta diversity between patches. Further, asynchrony between communities in nearby patches could be leading to high turnover. With temporally variable local environmental conditions, communities at large spatial scales are expected to be fluctuating in diversity through time, with different patches contributing more or less to beta diversity. Headwaters in dense areas could function similarly to lower mainstem sections that receive input from more patches, where higher dispersal in these sections is leading to more turnover through time (Schmera et al. 2017). In other words, patches in dense headwaters and mainstems both have higher amounts of patches close to each other, leading to higher dispersal and temporal beta diversity, given low connectivity between all patches. Additionally, slope had a strongly negative relationship and upstream area had a slightly positive relationship with beta diversity, which reinforces this theory because areas with lower slope are generally associated with mainstems and higher order, lower elevation sites, while sites with a lower upstream area tend to correspond to headwater locations. Though headwater metacommunities typically experience more disturbance and potentially more resulting dissimilarity (Göthe et al. 2013), after disturbances, they have a fixed set of colonists, and these same taxa could be reoccurring over time (Little and Altermatt 2018). Based on this reasoning, headwaters could still be impacted by species sorting effects (Brown and Swan 2010), but only at isolated and less central locations where environmental effects trump those of connectivity.

Hypothesis 3 stated that time would play less of a role than local environmental conditions, and environmental heterogeneity would precede temporal variability in driving beta diversity. Though temporal heterogeneity of environmental conditions is known to impact metacommunities (Sarremejane et al. 2017b), time in and of itself, when controlling for temporally structured environment and space, was found to be a significant predictor of turnover in benthic macroinvertebrate metacommunities in this study. This result could be attributed to an imperfect measure of environmental change and/or lagged effects of different populations. The sampled environmental variables (dissolved oxygen, pH, conductivity, temperature and flow velocity) may not have been the most important environmental drivers of beta diversity in the catchments analyzed in this study (Tolonen et al. 2017). Additionally, changes in environmental conditions may affect metapopulations at different timescales, as seasonal variation in environmental conditions can allow for time-sharing by different communities to persist in light of environmental change (Bogan and Lytle 2007). Further, it is improbable that beta diversity is driven by a set suite of environmental variables, given that local environmental changes can take years to move through populations, and the sensitivity and trait profile of individual taxa is variable through space and over time (Hawkins et al. 2014, Tonkin et al. 2015a). Alternatively, the significant time factor could be related to ecological drift and neutral processes (Gilbert and Levine 2017), which have been found to be important in structuring metacommunities, especially in relation to mass effects, high connectivity and high flow, by mediating dispersal (Sarremejane et al. 2017a, Dong et al. 2017). In this framework, long-term variations in environment and risk of mortality in connected sites are decoupled from species traits and sensitivity, which amounts to the dominance of neutral processes driving beta diversity.

Evidence was found to support my fourth prediction that long term-flow characteristics are important determinants of benthic macroinvertebrate beta diversity patterns over time. The two most influential aspects of the hydrograph that drove higher beta diversity were related to characterizing extreme flow variability at sites: the magnitude and duration of flow rises and falls and the number of zero-flow days (Figures 2.3C and 2.3D). It appears that variability in discharge rather than average discharge at a site drives turnover in this system. Prior research supports this conclusion, as others have found that metrics involving stream flow loss, such as duration without connected surface flow, act as a strong environmental filter, and drive patterns in benthic macroinvertebrate community composition (Clarke et al. 2010a). In other words, when metacommunities are distributed within a catchment that receives high variability in flow patterns, beta diversity increases because communities are repeatedly disturbed. However, it is important to note that the sites within this study primarily exhibited a perennial flow regime, and when metacommunities are more adapted to flow variability (such as in intermittent systems), patterns in beta diversity can be more variable as taxa can exhibit traits to mitigate effects of strong flow variability, such as dispersal strength (Leigh and Datry 2016).

Overall, my results indicate that temporal beta diversity of freshwater benthic macroinvertebrates strongly responded to long-term hydrological context and spatial factors. These findings highlight the importance of biomonitoring sampling regimes implemented at long timescales because discrete point-estimate sampling of local environmental conditions does not always reflect patterns in riverine metacommunity turnover. Furthermore, the results of this study reinforce that we cannot assume headwaters are always subject to high species sorting effects and defined by their local habitat. Other spatial factors can be stronger predictors of community dissimilarity. In general, more studies should incorporate the temporal variability in dendritic river networks to properly understand community assembly mechanisms, as these highly dynamic systems are in constant flux. Additionally, by incorporating functional traits into the examination of temporal heterogeneity in beta diversity, the strength and direction of the effects on biodiversity can be ascertained because traits can be directly linked to dispersal ability and persistence in patches of a river network.

References

Altermatt, F. 2013. Diversity in riverine metacommunities: a network perspective. Aquatic Ecology 47:365–377.

Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9:683–693.

Baselga, A. 2013. Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. Ecography 36:124–128.

Bogan, M. T., and D. A. Lytle. 2007. Seasonal flow variation allows “time-sharing” by disparate aquatic insect communities in montane desert streams. Freshwater Biology 52:290–304.

Bogan, M. T., K. S. Boersma, and D. A. Lytle. 2013. Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. Freshwater Biology 58:1016–1028.

Brown, B. L., and C. M. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. Journal of Animal Ecology 79:571–580.

Brown, B. L., C. Wahl, and C. M. Swan. 2017. Experimentally disentangling the influence of dispersal and habitat filtering on benthic invertebrate community structure. Freshwater Biology 63:48–61.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2010. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Cañedo-Argüelles, M., K. S. Boersma, M. T. Bogan, J. D. Olden, I. Phillipsen, T. A. Schriever, and D. A. Lytle. 2015. Dispersal strength determines meta-community structure in a dendritic riverine network. Journal of Biogeography 42:778–790.

Carrara, F., A. Rinaldo, A. Giometto, and F. Altermatt. 2014. Complex interaction of dendritic connectivity and hierarchical patch size on biodiversity in river-like landscapes. The American Naturalist 183:13–25.

Clarke, A., J. Rosenfeld, R. Mac Nally, N. Bond, and P. S. Lake. 2010a. Flow permanence affects aquatic macroinvertebrate diversity and community structure in three headwater streams in a forested catchment. Canadian Journal of Fisheries and Aquatic Sciences 67:1649–1657.

Clarke, A., R. Mac Nally, N. Bond, and P. S. Lake. 2010b. Flow permanence affects aquatic macroinvertebrate diversity and community structure in three headwater streams in a forested catchment. Canadian Journal of Fisheries and Aquatic Sciences 67:1649–1657.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

Dala-Corte, R. B., F. G. Becker, and A. S. Melo. 2017. The importance of metacommunity processes for long-term turnover of riffle-dwelling fish assemblages depends on spatial position within a dendritic network. Canadian Journal of Fisheries and Aquatic Sciences 74:101–115.

Datry, T., N. Bonada, and J. Heino. 2016. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. Oikos 125:149–159.

Datry, T., S. T. Larned, K. M. Fritz, M. T. Bogan, P. J. Wood, E. I. Meyer, and A. N. Santos. 2014. Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. Ecography 37:94–104.

Dong, X., D. A. Lytle, J. D. Olden, T. A. Schriever, and R. Muneepeerakul. 2017. Importance of neutral processes varies in time and space: Evidence from dryland stream ecosystems. PLoS ONE 12:e0176949–14.

Fazi, S., E. Vázquez, E. O. Casamayor, S. Amalfitano, and A. Butturini. 2013. Stream Hydrological Fragmentation Drives Bacterioplankton Community Composition. PLoS ONE 8:e64109–10.

Fox, J., and G. Monette. 1992. Generalized Collinearity Diagnostics. Journal of the American Statistical Association 87:178–183.

Gansfort, B., and W. Traunspurger. 2019. Environmental factors and river network position allow prediction of benthic community assemblies: A model of nematode metacommunities. Nature Publishing Group 9:14716–10.

Giam, X., and J. D. Olden. 2015. Quantifying variable importance in a multimodel inference framework. Methods in Ecology and Evolution 7:388–397.

Gilbert, B., and J. M. Levine. 2017. Ecological drift and the distribution of species diversity. Proceedings of the Royal Society B: Biological Sciences 284:20170507–10.

Göthe, E., N. Friberg, M. Kahlert, J. Temnerud, and L. Sandin. 2013. Headwater biodiversity among different levels of stream habitat hierarchy. Biodiversity and Conservation 23:63–80.

Grönroos, M., J. Heino, T. Siqueira, V. L. Landeiro, J. Kotanen, and L. M. Bini. 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. Ecology and Evolution 3:4473–4487.

Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699–711.

Harvey, E., and F. Altermatt. 2019. Regulation of the functional structure of aquatic communities across spatial scales in a major river network. Ecology 100:e02633–9.

Hawkins, C. P., H. Mykrä, J. Oksanen, and J. J. Vander Laan. 2014. Environmental disturbance can increase beta diversity of stream macroinvertebrate assemblages. Global Ecology and Biogeography 24:483–494.

Heino, J. 2011. A macroecological perspective of diversity patterns in the freshwater realm. Freshwater Biology 56:1703–1722.

Heino, J., A. S. Melo, and L. M. Bini. 2014. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. Freshwater Biology 60:223–235.

Heino, J., A. S. Melo, L. M. Bini, F. Altermatt, S. A. Al-Shami, D. G. Angeler, N. Bonada, C. Brand, M. Callisto, K. Cottenie, O. Dangles, D. Dudgeon, A. Encalada, E. Göthe, M. Grönroos, N. Hamada, D. Jacobsen, V. L. Landeiro, R. Ligeiro, R. T. Martins, M. L. Miserendino, C. S. Md Rawi, M. E. Rodrigues, F. de O. Roque, L. Sandin, D. Schmera, L. F. Sgarbi, J. P. Simaika, T. Siqueira, R. M. Thompson, and C. R. Townsend. 2015. A comparative analysis reveals weak relationships between ecological factors and beta diversity of stream insect metacommunities at two spatial levels. Ecology and Evolution 5:1235–1248.

Isaak, D. J., E. E. Peterson, J. M. Ver Hoef, S. J. Wenger, J. A. Falke, C. E. Torgersen, C. Sowder, E. A. Steel, M.-J. Fortin, C. E. Jordan, A. S. Ruesch, N. Som, and P. Monestiez. 2014. Applications of spatial statistical network models to stream data. Wiley Interdisciplinary Reviews: Water 1:277–294.

Kennard, M. J., S. J. Mackay, B. J. Pusey, J. D. Olden, and N. Marsh. 2009. Quantifying uncertainty in estimation of hydrologic metrics for ecohydrological studies. River Research and Applications 16:n/a–n/a.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leigh, C., and T. Datry. 2016. Drying as a primary hydrological determinant of biodiversity in river systems: a broad-scale analysis. Ecography 40:487–499.

Leopold, L. B., and T. Maddock. 1953. The hydraulic geometry of stream channels and some physiographic implications.

Little, C. J., and F. Altermatt. 2018. Do priority effects outweigh environmental filtering in a guild of dominant freshwater macroinvertebrates? Proceedings. Biological sciences 285:20180205–9.

Liu, J., J. Soininen, B.-P. Han, and S. A. J. Declerck. 2013. Effects of connectivity, dispersal directionality and functional traits on the metacommunity structure of river benthic diatoms. Journal of Biogeography 40:2238–2248.

Lusardi, R. A., M. T. Bogan, P. B. Moyle, and R. A. Dahlgren. 2016. Environment shapes invertebrate assemblage structure differences between volcanic spring-fed and runoff rivers in northern California. Freshwater Science 35:1010–1022.

Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. Trends in Ecology & Evolution 19:94–100.

Mayfield, M. M., and D. B. Stouffer. 2017. Higher-order interactions capture unexplained complexity in diverse communities. Nature Ecology & Evolution 1:1–7.

Nippgen, F., B. L. McGlynn, L. A. Marshall, and R. E. Emanuel. 2011. Landscape structure and climate influences on hydrologic response. Water Resources Research 47:164–17.

Olden, J. D., and N. L. Poff. 2003. Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. River Research and Applications 19:101–121.

Peterson, E., and J. M. Ver Hoef. 2014. STARS: An ArcGIS toolset used to calculate the spatial information needed to fit spatial statistical models to stream network data. Journal of Statistical Software 56.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. BioScience 47:769–784.

Power, M. E., A. Sun, G. Parker, W. E. Dietrich, and J. T. Wootton. 1995. Hydraulic Food-Chain Models. BioScience 45:159–167.

Rolls, R. J., J. Heino, D. S. Ryder, B. C. Chess am, I. O. Growns, R. M. Thompson, and K. B. Gido. 2017. Scaling biodiversity responses to hydrological regimes. Biological Reviews 93:971–995.

Ruhí, A., T. Datry, and J. L. Sabo. 2017. Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. Conservation Biology 343:1080–10.

Sarremejane, R., H. Mykrä, N. Bonada, J. Aroviita, and T. Muotka. 2017a. Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. Freshwater Biology 62:1073–1082.

Sarremejane, R., M. Cañedo-Argüelles, N. Prat, H. Mykrä, T. Muotka, and N. Bonada. 2017b. Do metacommunities vary through time? Intermittent rivers as model systems. Journal of Biogeography 44:2752–2763.

Schmera, D., D. Árva, P. Boda, E. Bódis, Á. Bolgovics, G. Borics, A. Csercsa, C. Deák, E. Á. Krasznai, B. A. Lukács, P. Mauchart, A. Móra, P. Sály, A. Specziár, K. Süveges, I. Sziválk, P. Takács, M. Tóth, G. Várbíró, A. E. Vojtkó, and T. Erős. 2017. Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. Freshwater Biology 63:74–85.

Seymour, M., K. Deiner, and F. Altermatt. 2016. Scale and scope matter when explaining varying patterns of community diversity in riverine metacommunities. Basic and Applied Ecology 17:134–144.

Siqueira, T., L. M. Bini, F. O. Roque, S. R. Marques Couceiro, S. Trivinho-Strixino, and K. Cottenie. 2012. Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. Ecography 35:183–192.

Starr, S. M., J. P. Benstead, and R. A. Sponseller. 2014. Spatial and temporal organization of macroinvertebrate assemblages in a lowland floodplain ecosystem. Landscape Ecology 29:1017–1031.

Swan, C. M., and B. L. Brown. 2014. Using rarity to infer how dendritic network structure shapes biodiversity in riverine communities. Ecography 37:993–1001.

Theobald, D., J. Norman, E. Peterson, and S. Ferraz. 2005. Functional linkage of watersheds and streams (FLoWS): network-based ArcGIS tools to analyze freshwater ecosystems. Proceedings of the 2005 ESRI International User Conference.

Thompson, R., and C. Townsend. 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. Journal of Animal Ecology 75:476–484.

Tolonen, K. E., K. Leinonen, J. Erkinaro, and J. Heino. 2017. Ecological uniqueness of macroinvertebrate communities in high-latitude streams is a consequence of deterministic environmental filtering processes. Aquatic Ecology 52:17–33.

Tonkin, J. D., A. Sundermann, S. C. Jähnig, and P. Haase. 2015a. Environmental Controls on River Assemblages at the Regional Scale: An Application of the Elements of Metacommunity Structure Framework. PLoS ONE 10:e0135450–19.

Tonkin, J. D., D. M. Merritt, J. D. Olden, L. V. Reynolds, and D. A. Lytle. 2018. Flow regime alteration degrades ecological networks in riparian ecosystems. Nature Ecology & Evolution:1–10.

Tonkin, J. D., J. Heino, A. Sundermann, P. Haase, and S. C. Jähnig. 2016a. Context dependency in biodiversity patterns of central German stream metacommunities. Freshwater Biology 61:607–620.

Tonkin, J. D., J. Heino, and F. Altermatt. 2017. Metacommunities in river networks: The importance of network structure and connectivity on patterns and processes. Freshwater Biology 63:1–5.

Tonkin, J. D., R. D. Tachamo Shah, D. N. Shah, F. Hoppeler, S. C. Jähnig, and S. U. Pauls. 2016b. Metacommunity structuring in Himalayan streams over large elevational gradients: the role of dispersal routes and niche characteristics. Journal of Biogeography 44:62–74.

Tonkin, J. D., S. Stoll, S. C. Jähnig, and P. Haase. 2015b. Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. Oikos 125:686–697.

Vannote, R. L., and G. W. Minshall. 1980. The river continuum concept. Canadian journal of fisheries and aquatic sciences. 37:130–137.

Warfe, D. M., S. A. Hardie, A. R. Uytendaal, C. J. Bobbi, and L. A. Barmuta. 2014. The ecology of rivers with contrasting flow regimes: identifying indicators for setting environmental flows. Freshwater Biology 59:2064–2080.

Winegardner, A. K., B. K. Jones, I. S. Y. Ng, T. Siqueira, and K. Cottenie. 2012. The terminology of metacommunity ecology. Trends in Ecology & Evolution 27:253–254.

Zeileis, A., and F. Cribari-Neto. 2010. Beta regression in R. Journal of Statistical Software.

Figures

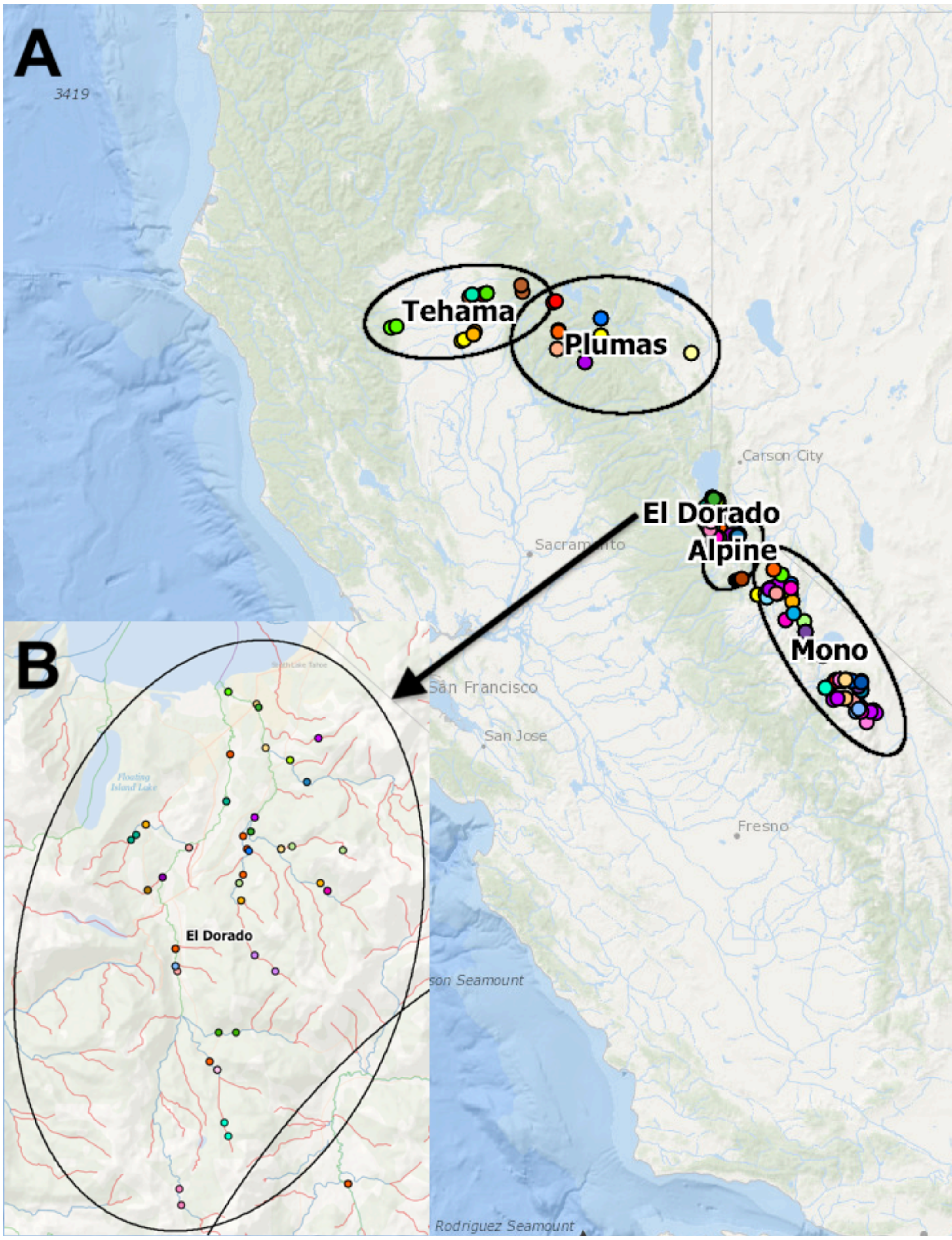


Figure 2.1. Map of sampling sites of aquatic insects by SWAMP (A), with a zoomed map of the El Dorado catchment (B), as an example, demonstrating dendritic structure and spatial variation in sampling sites, both across the state and within catchments.

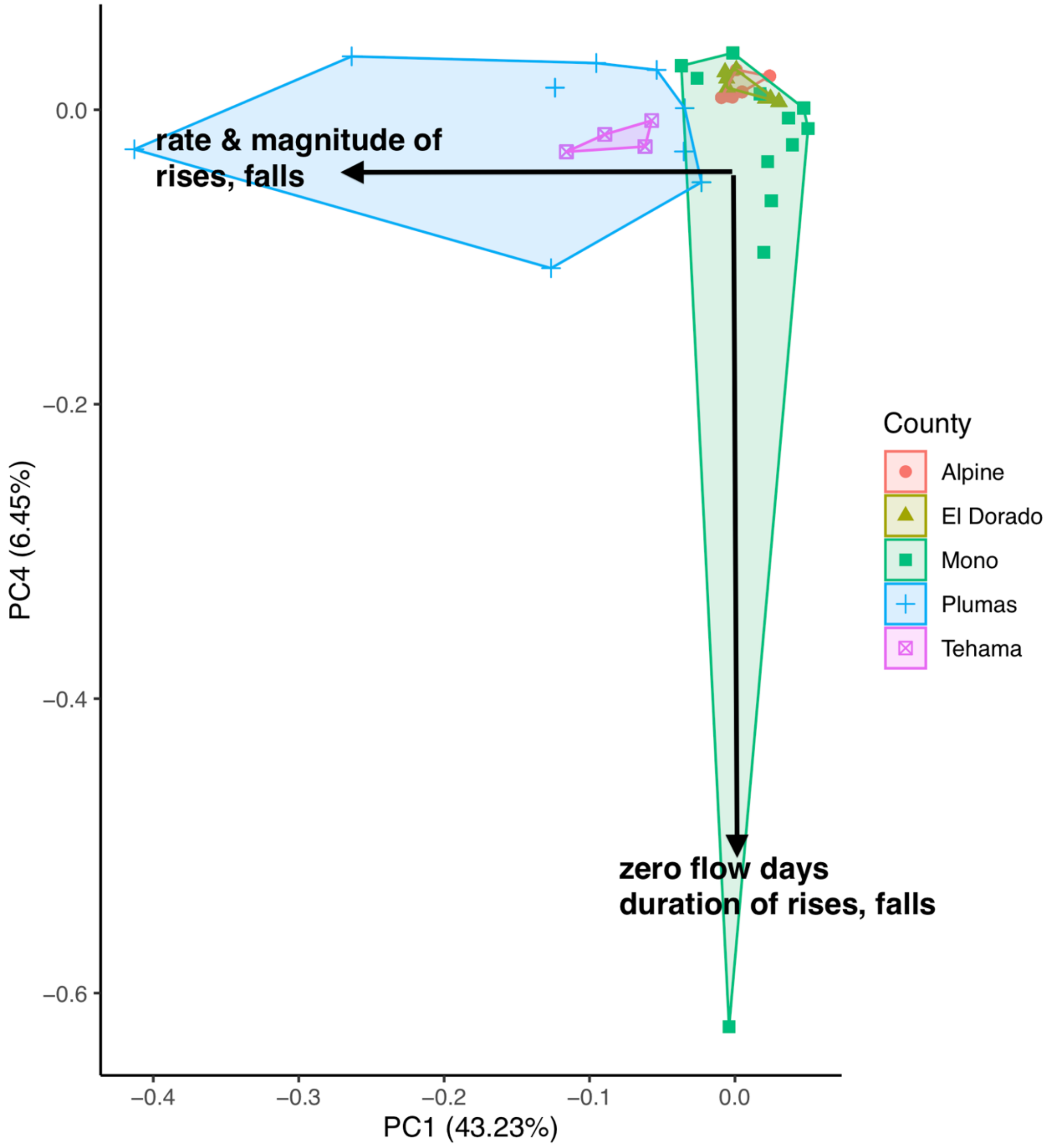


Figure 1.2. PCA of flow metrics calculated in RAP, from USGS flow gage data. PC1 and PC4 are plotted since they were the most significant in explaining beta diversity in statistical modeling approach. Points grouped by county.

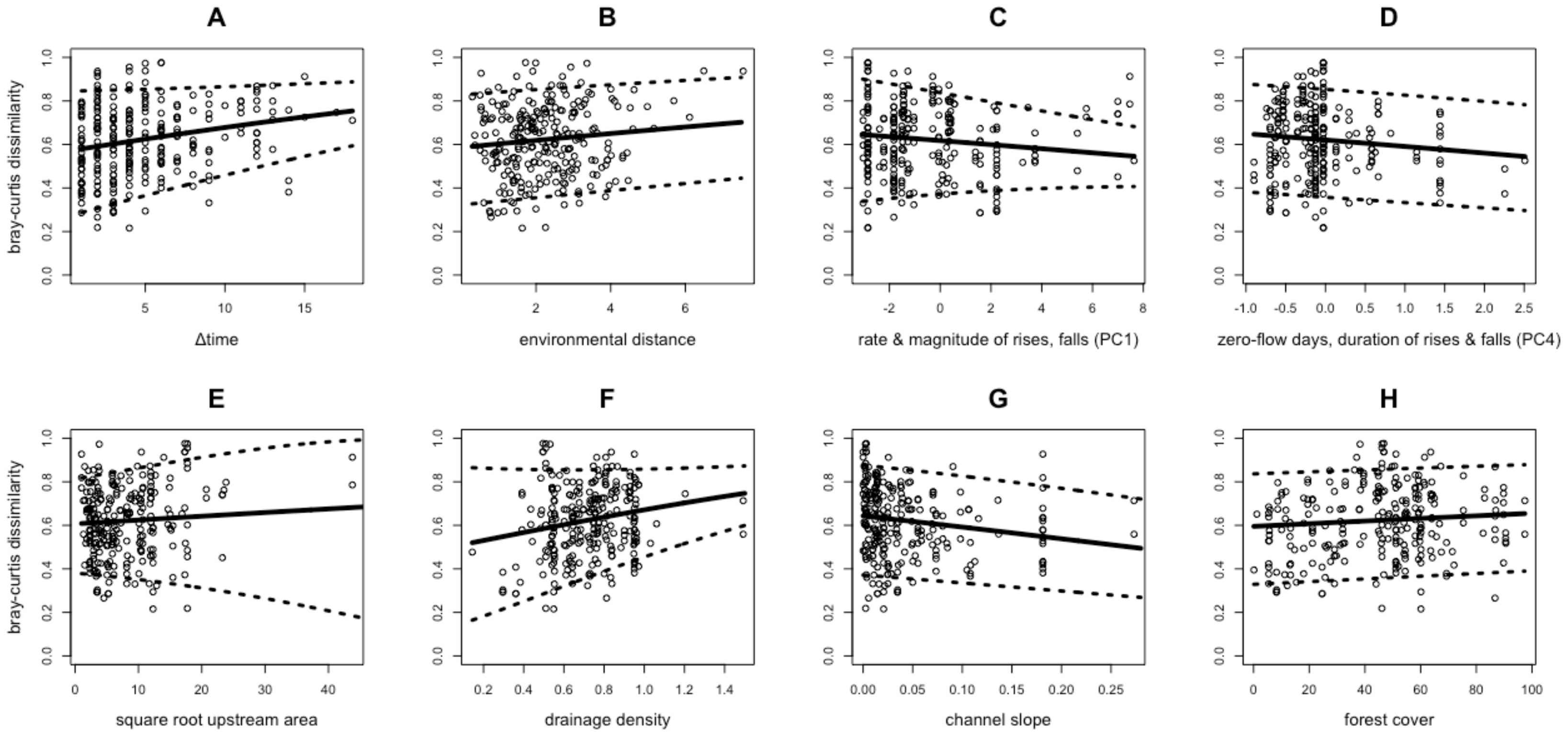


Figure 2.3. Plotted regression line for the mean of the predicted beta distribution used in modeling approach, examining relationship between community dissimilarity and A) change in time, B) environmental distance, C) rate and magnitude of rises and falls, D) zero flow days and duration of rises and falls, E) upstream area (square root transformed), F) drainage density, G) channel slope, and H) forest cover. Environmental distance measured as Euclidian distance between environmental measures in multivariate space. Dotted lines are 5% and 95% quantiles, showing the 90% confidence interval of the model.

Tables

Table 2.1. List of all hydrograph metrics calculated from the RAP program (3.0.8). ARI represents annual flood return interval.

Flow metrics calculated with RAP
Minimum
Maximum
Zeros
Longest High Spell
Mean of High Spell Peaks
Mean Duration of High Spell
Mean period Between High Spells
Longest Low Spell
Mean of Low Spell troughs
Mean Duration of Low Spell
Mean period Between Low Spells
Mean magnitude of Rises
Mean duration of Rises
Mean rate of Rise
Mean magnitude of Falls
Mean duration of Falls
Mean rate of Fall
Baseflow Index
Flood Flow Index
Mean Daily Baseflow
Predictability based on monthly mean daily flow
Constancy based on monthly mean daily flow
Contingency based on monthly mean daily flow
Partial series 1 Yr ARI
Partial series 2 Yr ARI
Partial series 10 Yr ARI

Table 2.2. Coefficient estimates from model averaging of beta regressions with a delta AICc of less than 4. Relative importance of each predictor calculated as how many times that variable was selected in top models.

Response variable	**Predictor**	**Coefficient estimate**	**Relative importance (SW)**
Temporal beta diversity	Slope	-2.4404601	1.00
	Drainage density	0.7535826	1.00
	Δtime	0.3090173	1.00
	Upstream area	0.0007923	1.00
	PC1	-0.0341396	0.91
	PC4	-0.1635418	0.86
	Forest cover	0.0024172	0.40
	Environmental distance	0.0415317	0.37
	PC2	-0.0177084	0.27
	PC3	0.0165038	0.21

Table 2.3. Output of dredge function from MuMIn package for R from the full beta regression. All combinations of predictors were included and removed, while only models with a delta AICc of less than 4 are presented. Cells with a value of 0 represent a predictor that was dropped from that model

intercept	**Δtime**	**drainage density**	**environmental distance**	**forest cover**	**PC1**	**PC2**	**PC3**	**PC4**	**slope**	**upstream area**	**df**	**Loglik**	**AICc**	**delta AICc**	**weight**
-0.241	0.04	0.754	0	0	-0.035	0	0	-0.164	-2.411	0.001	9	133.273	-247.82	0	0.082
-0.289	0.04	0.674	0	0.002	-0.034	0	0	-0.16	-2.5	0.001	10	134.209	-247.528	0.293	0.071
-0.35	0.039	0.777	0.042	0	-0.035	0	0	-0.158	-2.426	0.001	10	133.966	-247.041	0.78	0.056
-0.277	0.039	0.815	0	0	-0.032	-0.019	0	-0.179	-2.43	0.001	10	133.843	-246.795	1.026	0.049
-0.399	0.04	0.7	0.042	0.002	-0.034	0	0	-0.154	-2.507	0.001	11	134.906	-246.738	1.082	0.048
-0.236	0.04	0.743	0	0	-0.035	0	0.021	-0.152	-2.322	0.001	10	133.49	-246.09	1.731	0.035
-0.311	0.04	0.731	0	0.002	-0.033	-0.015	0	-0.172	-2.499	0.001	11	134.528	-245.983	1.838	0.033
-0.376	0.038	0.833	0.039	0	-0.032	-0.018	0	-0.172	-2.436	0.001	11	134.436	-245.798	2.022	0.03
-0.285	0.04	0.675	0	0.002	-0.034	0	0.007	-0.157	-2.466	0.001	11	134.229	-245.385	2.435	0.024
-0.342	0.039	0.767	0.04	0	-0.035	0	0.018	-0.148	-2.346	0.001	11	134.126	-245.178	2.642	0.022
-0.287	0.037	0.869	0	0	-0.036	0	0	0	-2.624	0.001	8	130.866	-245.153	2.667	0.022
-0.342	0.038	0.788	0	0.003	-0.036	0	0	0	-2.72	0.001	9	131.899	-245.072	2.749	0.021
-0.413	0.039	0.749	0.039	0.002	-0.033	-0.013	0	-0.164	-2.502	0.001	12	135.146	-245.018	2.802	0.02
-0.272	0.039	0.803	0	0	-0.032	-0.018	0.018	-0.168	-2.352	0.001	11	133.999	-244.925	2.896	0.019
-0.18	0.042	0.677	0	0	0	0	0	-0.172	-2.122	0.001	8	130.692	-244.806	3.015	0.018
-0.406	0.036	0.891	0.047	0	-0.036	0	0	0	-2.624	0.001	9	131.716	-244.706	3.114	0.017
-0.463	0.037	0.81	0.047	0.003	-0.036	0	0	0	-2.708	0.001	10	132.769	-244.647	3.173	0.017
-0.396	0.04	0.7	0.041	0.002	-0.034	0	0.003	-0.152	-2.49	0.001	12	134.91	-244.547	3.273	0.016

-0.227	0.043	0.596	0	0.002	0	0	0	-0.168	-2.215	0.001	9	131.613	-244.5	3.32	0.016
-0.23	0.041	0.761	0	0	0	-0.025	0	-0.189	-2.177	0.001	9	131.605	-244.484	3.336	0.016
-0.276	0.037	0.839	0	0	-0.036	0	0.036	0	-2.447	0.001	9	131.533	-244.339	3.481	0.014
-0.29	0.041	0.701	0.042	0	0	0	0	-0.165	-2.15	0.001	9	131.38	-244.034	3.787	0.012
-0.368	0.038	0.823	0.037	0	-0.033	-0.017	0.015	-0.163	-2.367	0.001	12	134.55	-243.827	3.993	0.011

Chapter 3:

Effects of novel spatial and temporal heterogeneity on benthic macroinvertebrate and diatom communities in an urbanized watershed

Abstract

Water quality, distribution, and flow are constantly being altered in rivers in urban watersheds, subjecting aquatic communities to novel spatial and temporal heterogeneity in the environment. Thus, the conservation of threatened species within urban watersheds and an understanding how novel spatial temporal heterogeneity is impacting indicator taxa is of paramount concern. In this study, I documented the relationship between benthic macroinvertebrate and diatom communities with flow perturbations in a transect of an urbanized river in Southern California, USA. In particular, I analyzed trends in the richness and abundance of diatom communities in relation to a flow shutdown event by a wastewater treatment plant and urban storm runoff events. I found that while the diatom community reflected resilience strategies, rebounding quickly after disturbance, the benthic macroinvertebrates resisted flow loss and storm events, reflecting a disturbance-tolerant community. These results have implications to the conservation of endangered fish species, such as the Santa Ana Sucker, which depend on a thriving basal food web for survival.

Introduction

Freshwater ecology has placed spatial and temporal heterogeneity in a central role in structuring communities, viewing it as fundamental to describing patterns and ultimately to managing freshwater diversity (Cooper, Barmuta, Sarnelle, Kratz, & Diehl, 1997; Hutchinson, 1953; Vannote & Minshall, 1980; Winemiller, Flecker, & Hoeinghaus, 2010). Additionally, urban growth is increasing and subjecting freshwater communities to novel gradients in spatial and temporal heterogeneity (Paul & Meyer, 2001), with many of the resulting effects, such as altered hydrographs, simplified channel morphology, and novel biological communities, being encapsulated in the serial discontinuity concept (Stanford & Ward, 2001), and the urban stream syndrome (Walsh et al., 2005). Urban rivers generally comprise a network of highly controlled waterways that maximize efficiency and the predictability of flow distribution, especially in the southwest US (Wohl, 2018). The resulting flow regimes typically exhibit reduced natural seasonality, flow connectivity, and increased artificial flow signals, such as dam releases and flash floods caused by large areas of impervious surface (Kennedy et al., 2016; Ruhí, Dong, McDaniel, Batzer, & Sabo, 2018). For example, losses in flow connectivity compounded with urban discharge can lead to the removal of dispersal pathways (Blakely, Harding, & McIntosh, 2006; Richmond, Backlin, Galst-Cavalcante, O'Brien, & Fisher, 2017), the alteration of substrate transport patterns (Blakely et al., 2006; Nedeau, Merritt, & Kaufman, 2003), and other myriad changes in water quality. Moreover, different urban water management activities within urban rivers, such as water retention, reuse, irrigation, hydropower, and flood control, can each introduce idiosyncratic alterations of physical structure, nutrient loadings, temperature changes, and the source, timing, and rate of discharge, thereby introducing novel spatial heterogeneity. For example, hydropeaking practices by dams result in unique patterns of discharge, while elevated stream temperatures have been directly related to the location of wastewater treatment plant effluent discharge and proximal downstream environments (Kinouchi, Yagi, & Miyamoto, 2007; Ruhí et al., 2018). Thus, patterns of spatial and temporal heterogeneity in habitat types and quality in urban rivers may depend on geographical context and human needs (D. B. Booth, Roy, Smith, & Capps, 2016; Konrad & Booth, 2005; Ripl, 2003).

Wastewater treatment plants (WWTPs) are characteristic features of urban river networks that strongly influence patterns of environmental heterogeneity (Luo et al., 2014; Ziajahromi, Neale, & Leusch, 2016). Despite improved treatment capability, many WWTPs discharge treated sewage water, including numerous contaminants such as nutrients (eutrophication), pharmaceuticals, personal care products, flame retardants, and pesticides (Bai et al., 2018; Carey & Migliaccio, 2009), directly into urban rivers. Since WWTPs emit effluent at large volumes, the natural dilution capacity of contaminants and nutrients in river systems can be inhibited (Lake, 2003; Sánchez-Morales, Sabater, & Muñoz, 2018). In addition to the altered constituent profile, effluent temperature regimes are highly variable and dependent on the specific treatment practices of the WWTP. In particular, elevated temperatures have been found in winter and spring due to the prevalence of WWTP effluent (Kinouchi et al., 2007).

In addition to altering the environment, WWTPs have been shown to have strong impacts on biodiversity patterns in urban rivers. Altered habitat patches due to effluent flow facilitate the invasion and establishment of resilient generalist communities throughout the riverine food web, replacing taxa requiring more pristine conditions (Bourassa, Fraser, & Beisner, 2017; Drury, Rosi-Marshall, & Kelly, 2013; Roy, Rosemond, Paul, Leigh, & Wallace, 2003; Tornés, Mor, Mandaric, & Sabater, 2018). Moreover, WWTP effluent has been shown to decrease the abundance and diversity of benthic bacterial communities (Drury et al., 2013), decrease algal diversity (Tornés et al., 2018), increase benthic macroinvertebrate density while decreasing diversity (Coimbra, Graca, & Cortes, 1996; Morrissey, Boldt, Mapstone, Newton, & Ormerod, 2012; Van Dam, Mertens, & Sinkeldam, 1994; Wright, Chessman, Fairweather, & Benson, 1995), and lower the richness and abundance of fish (Galib et al., 2018; Northington & Hershey, 2006). Cross-ecosystem effects may also occur, as significantly altered benthic macroinvertebrate communities above and below WWTPs have been shown to impact the presence of insectivorous bats (Kalcounis-Rueppell, Payne, Huff, & Boyko, 2007).

Despite their degraded conditions, many urban streams are home to threatened and endangered species (Morley & Karr, 2002; Silver et al., 2018), and effluent flows from WWTPs can supplement low base flow in rivers and expand available habitats for native species in certain circumstances (Nedeau et al., 2003). WWTP effluent output tends to elevate discharge year-round, with effluent flows comprising a fraction or even the entirety of the flow present depending on the time of year (Goodrich, Kepner, Levick, & Wigington, 2018). In some cases, effluent discharge represents the only source of running water for some species in flow-disconnected landscapes (Boyle & Fraleigh, 2003). Thus, effluent has been used to restore habitats for species of concern, and urban river food webs and many conservation plans have been created for urban rivers that rely on effluent for habitat creation (Linke, Turak, & Nel, 2010). Despite research on the effects of urbanization on the physical properties of rivers and the potential for WWTPs to positively and negatively impact biodiversity, no clear picture has emerged about how effluent, by creating novel spatial and temporal heterogeneity, can influence freshwater communities (Bourassa et al., 2017; Hassett et al., 2018).

Effluent-dominated freshwater systems, which are home to numerous species of conservation concern, are particularly common in the arid southwest USA. In the Santa Ana River watershed, the largest watershed entirely within southern California, USA, there are over 20 species relying on a food web persisting within a valley dominated in part by river processes (ICF International, 2014). The WWTPs emitting effluent into the Santa Ana River have unique discharge and water property characteristics, which in turn lead to notable temporal heterogeneity with respect to flow variability, and to spatial heterogeneity with respect to the novel stream habitats created by each WWTP and surrounding urban structures. Efforts are underway to document the habitat requirements of focal species of conservation concern, such as the Santa Ana sucker (*Catostomus santaanae*) and the Arroyo chub (*Gila orcuttii*), in order to preserve them under the multi-species Upper Santa Ana Habitat Conservation Plan (ICF International, 2014). Yet, the distributions of the lower trophic levels that support the persistence of these threatened species are poorly understood. This lack of understanding is compounded by the fact that much of the temporal and spatial heterogeneity in the system is imposed by WWTP effluent dynamics, and studies documenting the effects of novel WWTP-imposed flow and habitat heterogeneity on freshwater communities are scarce.

Here, I investigated how the benthic community (diatoms and benthic macroinvertebrates) responds to temporal and spatial heterogeneity driven by WWTPs and associated urban structures in the Santa Ana River. Specifically, I asked: (1) what is the magnitude of responses by urban stream communities to temporal flow perturbations from changes in WWTP discharge and urban runoff?; (2) do benthic communities return to pre-perturbation conditions—and if so, how quickly?; and (3) does community response depend on local environmental conditions, i.e., are spatial patterns of density and richness reestablished after disturbance?. Answering these questions will assist in the management of benefits for threatened freshwater species experiencing novel spatiotemporal heterogeneity in urban systems.

Methods

Study site

The Santa Ana River is embedded within the Santa Ana watershed in southern California, with a majority of its headwaters originating in the San Bernardino Mountains. This region is subject to a Mediterranean climate with wet, cold winters and hot, dry summers. Historically, the Santa Ana watershed was a large branching river network with meandering courses, shifting ocean outlets, and large flood events. However, after the 1950s, much of the network was dammed and otherwise managed with flood control infrastructure, leading to permanent hydrologic isolation throughout the watershed (Richmond et al., 2017). Due to modern-day water diversions, much of the streambed is dry downstream of Seven Oaks Dam, only wetting during infrequent winter storm events. Further, natural flow has become short-lived but with greater intensity (flashy or high peak flows). Seven Oaks Dam is located in the upper portion of the Santa Ana River, in the San Bernardino Mountains, northeast of Redlands, California. Between

Seven Oaks Dam and western Riverside County, the stream channel becomes re-wetted due to WWTP effluent discharge. The first major treatment plants that wet the dry Santa Ana River below Seven Oaks Dam are in Colton and Rialto, CA (Figure 3.1). The WWTP in Colton, the Rapid Infiltration and Extraction (RIX) facility, employs the use of ultraviolet (UV) radiation and soil percolation to treat water to tertiary standards, while a second WWTP in the neighboring City of Rialto (hereafter "Rialto") employs a traditional chlorination–dichlorination treatment method to treat water to tertiary standards. The Rialto WWTP releases water 1.2 km upstream of the RIX plant, and this effluent flows over an unlined concrete channel before dropping into a river bed dominated by a variable mix of cobble, pebbles, and sediment (Figure 3.1). Rialto effluent meets RIX effluent adjacent to a "plunge pool" where the RIX WWTP discharges, and their combined discharge provides the majority of the flow in Santa Ana River, especially during the drier parts of the year (Figure 3.2). During the study period, RIX outflow averaged 29.5 million gallons per day, while Rialto outflow averaged 5.96 million gallons per day in 2016 at its discharging locations.

Historically, the RIX treatment plant introduced unique flow regimes into the Santa Ana River. Although flow is emitted at a standard discharge rate for most of the year, the RIX plant needs to halt effluent discharge several times per year in order to access and maintain its UV lamps. These flow shutdowns result in significant losses of discharge in the Santa Ana River, up to a complete loss of surface water (Figure 3.3). Despite being quite severe, these flow shutdowns can be brief (2–6 hours). They do not appear in daily discharge reports from the RIX WWTP (Figure 3.2), as the plant increases flows immediately following shutdowns to compensate, resulting in typical daily average discharge values being reported. Since Rialto discharge is much lower than that of RIX, it is typically not enough to offset high percolation rates in the riverbed. In the winter, flashy flows that result from precipitation runoff over impervious surfaces also contribute to the overall discharge present in the upper Santa Ana River, and several of these events took place in November–December 2016, in the same month as a major RIX shutdown (Figures 2, 3).

Much of the work from this study in part supported the Upper Santa Ana Habitat Conservation Plan, as the freshwater benthic community (diatoms, benthic macroinvertebrates) can serve as an indicator of ecosystem function in watersheds, and 22 species of conservation concern are listed under a draft Upper Santa Ana Habitat Conservation Plan (ICF International, 2014). These species include fish such as the Santa Ana sucker (*Catostomus santaanae*) and the Arroyo chub (*Gila orcuttii*), plants such as the Santa Ana River woolly-star (*Eriastrum densifolium ssp. sanctorum),* amphibians such as the Arroyo toad *(Anaxyrus californicus*) and the mountain yellow-legged frog *(Rana muscosa*), birds such as the southwestern willow flycatcher (*Empidonax traillii extimus*) and the least Bell's vireo (*Vireo bellii pusillus*), and mammals such as the San Bernardino kangaroo rat (*Dipodomys merriami parvus*).

Field sampling

In order to document the effects of urban-influenced flow regimes and spatial locations relative to WWTPs on diatom and benthic macroinvertebrate communities, I sampled along a transect that captured the influence of outflow from two WWTPs on three occasions in a single season. I sampled at sites above and below the location of the RIX outflow immediately before a flow shutdown event on November 16, 2016, and two times afterwards on December 1, 2016 and December 12, 2016. There were also several storm runoff events during the sampling period. Since the Rialto plant still releases water during RIX flow shutdown events, part of the river between Rialto and RIX remains wet, and it thus served as a point of comparison with downstream sites. In total, I included eight sampling sites along the transect: three in the Rialto channel, one at the RIX outflow, and four downstream of the RIX outflow (Figure 3.1).

I measured habitat variables and diatom and benthic macroinvertebrate (BMI) densities according to the reachwide benthos multihabitat procedure defined by the standard operating procedures of the California Surface Water Ambient Monitoring Program (Ode, Fetscher, & Buusse, 2016). Dissolved oxygen (DO) and temperature were measured at sampling locations using a YSI Professional Plus. I collected BMIs using a 500-µm D-net and gently brushed all substrate in front of the D-net for ca. 30 seconds. Diatoms were collected in the field by choosing three fist-sized rocks from the same habitats from which the BMIs were collected. Rocks were then transported with a fine-mesh aquarium net to a tray in the field, where the rock was scraped with a plastic wire brush. All biofilm was brushed off the rock, and the rock was rinsed with clean water. Then, 1.5-ml of diatom solution was extracted from scrapings and immediately frozen on dry ice in the field.

During September 2016 and 2017, annual fish surveys were performed in the study area to determine the status of the Santa Ana sucker, the Arroyo chub, and numerous invasive species. These surveys were conducted by a collaborative team of United States Geological Survey researchers, United States Fish and Wildlife researchers and other agency staff, and citizen-scientists. Methods included snorkeling, electrofishing, and seining, depending on the microhabitat type being surveyed. Physical habitat surveys were also conducted during this time, documenting canopy cover, substrate profile, reach width, reach depth, and flow velocity. Santa Ana sucker and other fish populations were estimated using the abundance value from one survey method (seine, electro-fishing, snorkel) depending on the efficacy of the method given the field conditions at each site (Wulff, Brown, & May, n.d.). Daily measurements of temperature were also taken with remote sensors along the transect. These physical habitat survey data are included here to describe long-term spatiotemporal variability in stream habitats along the upper Santa Ana River. Physical habitat data from these surveys were used in this study, and data from fish surveys are available in the Supplementary Figures, as diatoms have been shown to be the primary food source of the Santa Ana sucker (Greenfield, Ross, & Deckert, 1970).

Diatoms were cleared of organelles and other organic matter with a diluted bleaching method (Carr, Hergenrader, & Troelstrup, 1986). Diatoms were diluted with the bleach solution and vortexed to break up any clumps of material. Afterward, the bleach was decanted using continuous inoculation with deionized water. Diatoms in cleaned samples were then identified to genus using the Flow-CAM particle imaging system (Fluid Imaging Technologies, Inc.) following the methods of (Camoying & Yñiguez, 2016). The cleaned diatom solution was filtered through a 100-µm plastic mesh before being run through the Flow-CAM system. Although a 100-μm filter could exclude some individuals, I determined that a 100-μm deep flow cell (FC100) would yield the most precise results. I assigned field density values for diatoms by converting from diatoms captured per ml by Flow-Cam to the amount of surface area scrubbed per rock in the field. BMIs were sorted and identified to genus using dissecting microscopes in the laboratory, with the exception of chironomids, which were only identified to family. BMI abundance was converted to density by dividing abundances by surface area sampled (.09m^2 area sampled each time).

Data analysis

To quantify patterns of spatial habitat heterogeneity along the Santa Ana River, I used data collected from annual USGS-led surveys of the river from September 2016 as well as DO and temperature measures taken during benthic sampling. I performed a principal component analysis (PCA) of scaled and centered environmental variables to visually determine which variables were most associated with different river locations. Factors ordinated and sorted by location included mean channel depth, mean channel width, mean width:depth ratio, mean velocity, mean canopy cover, and mean substrate type (Supplementary Figures). To better relate time of sampling to the hydrograph present in the selected section of the Santa Ana River, I plotted discharge from the treatment plants and from a nearby USGS gage (U.S. Geological Survey, 2019) through time using the EcoHydRology package for R (ver. 3.5.2). The gage helped determine the amount of storm flows contributing to overall discharge in the channel, and I paired these data with a local precipitation gage (Riverside County Flood Control, 2019).

In order to determine the effects of the unique environmental conditions in each location I sampled, I examined the richness and density of diatoms and BMIs by distance from the most upstream site sampled (which was Rialto channel). The recovery of diatom and BMI communities was assessed for each site by examining proportional changes through time. To understand overall system resilience, proportions were also calculated by averaging density and richness values. To examine shifts in community composition through time in response to flow perturbation, I plotted total average densities of diatoms for each genus across all sampling locations. Since trends in BMI composition involved more taxa, I conducted a non-metric multidimensional scaling (NMDS) ordination for each sampling date.

I used generalized linear models to determine how unique sampling locations and date explained variation in the density and richness of diatoms and BMIs. I determined site groupings for the location factor in statistical models by examining ordinations of physical data grouped by location, the results of which showed that sites in Rialto channel have similar environmental conditions, suggesting a natural a priori grouping of all Rialto sites in the statistical model (R1–3, Figure 3.4). However, sites SA-1, SA-2, SA-3, SA-4, and SA-5 exhibited more variable environmental conditions in the PCA. Therefore, I used a suite of statistical models with different groupings of SA sites to determine whether differences in environmental variables at different spatial scales translated into differences in density and richness. Diatom density was log-standardized using the decostand function in the vegan package for R (Anderson, Ellingsen, & McArdle, 2006; Legendre & Gallagher, 2001). Model type and distribution were selected between negative binomial and Gaussian depending on Shapiro-Wilks tests on residuals and examining model fit for homogeneity of variances and normality. Statistical modeling was performed using MASS, fBasics, lme4, vegan, ggfortify, and ggplot2 packages for R.

Results

I found that the uppermost sites in Rialto channel were consistently clustered around principal component axes structured by mean canopy cover and substrate profile, while sites downstream of the RIX outflow were structured by mean velocity, depth, and channel width (Figures 3 and 4). In general, sites R-1, R-2, and R-3 were characterized by higher canopy cover, narrower wetted width, and larger substrate (Supplemental Figures 3.2, 3.4, and 3.5). The RIX outflow plunge pool (SA-1) was notably faster-flowing and deeper than all other locations (Supplemental Figures 2.1 and 2.3). Channel width increased moving downstream of SA-1, and the river in this section becomes braided with a tendency to meander across the floodplain. Total discharge increases below RIX since base flow is composed of effluent from two WWTPs, while canopy decreases and substrate generally becomes smaller, especially in the absence of scouring floods. Yearly temperature measurements taken near the Rialto and RIX outflows show that Rialto channel experiences greater overall fluctuations in temperature following ambient fluctuations (between 20°C and 30°C), while RIX water is less variable (between 22°C and 27.5°C, Figure 3.5). This means that in the winter, RIX outflow is warmer than

Rialto outflow; and in the summer, Rialto outflow is considerably warmer than RIX outflow (usually about a 5°C difference in temperature, Figure 3.3).

The native Arroyo chub and Santa Ana sucker increased in average abundance moving downstream of the RIX and Rialto effluent outflows during September 2016 and 2017, while invasive yellow bullhead catfish were more abundant upstream in the Rialto outflows above RIX (Supplemental Figures). Diatom density increased moving downstream of the Rialto–RIX transect prior to the RIX shutdown on November 16, 2016, except for slight decreases at the RIX outflow (Figure 3.6). The statistical model in this study provided strong evidence for increases in diatom density moving downstream, with SA-4 and SA-5 having higher densities than SA1-3 (Table 3.1). Diatom richness was higher in sites downstream of the RIX outflow relative to upstream sites, although the statistical model provided only limited evidence for differences between upstream and downstream sites.

Both diatom density and richness appeared to be strongly affected by the combined RIX shutoff and high storm flows that occurred between the first and second sampling events (Figure 3.6, Table 3.1). Diatom density dropped to levels near zero at all sites two weeks after the RIX flow shutdown, while richness in turn dropped by one-half or more depending on the site. Non-effluent discharge increased between the second and third samples, and there were fewer high discharge events and no shutdowns. In this period, diatoms re-established communities with densities and richness similar to pre-shutdown levels (Figure 3.6, Table 3.1). Both aggregate diatom density and richness as well as the spatial variation in these were very similar to patterns observed in the first sample period.

Despite changes in density and richness over the sampling period, the overall composition of the diatom community did not change greatly. In the first sample, diatoms of the genera *Fragilaria, Synedra, and Gomphonema* had the highest average densities in the transect. Two weeks later, most diatoms had densities close to zero, suggesting similar susceptibilities among the diatom genera to the flow perturbations. Four weeks later, *Gomphonema* replaced *Fragilaria* as the most common diatom genus, exhibiting substantially higher densities compared to other diatoms (over 25 individuals per substrate sampled), while other diatoms had similar relative abundances (Figure 3.7).

In contrast with diatoms, BMI density and richness generally decreased moving downstream from Rialto on the first sampling date (Figure 3.8, Table 3.1). Sites above RIX tended to be dominated by Helicopsyche caddisflies, while Baetis mayflies and Libelulid dragonflies were mostly found far below RIX. BMI density and richness decreased in most locations after the shutdown and runoff perturbations. Sites upstream of RIX that were subjected to runoff events but not to the flow shutdown showed the greatest decrease in both density and richness; changes downstream of RIX were generally lower in magnitude, with SA-4 increased in density and richness. BMI density and richness appeared to trend toward levels similar to those observed in the first sample by December 12, 2016. Increases in both density and richness were largest in the Rialto channel, while changes at most sites downstream of RIX were not particularly substantial. NMDS ordinations on the BMI community largely visually mirror density and richness effects from the statistical modeling; shifts in composition in Rialto channel were more pronounced than those in RIX, although they both returned to the same composition levels following perturbation (Figure 3.9).

Discussion

Urban watersheds are subject to novel patterns of spatiotemporal heterogeneity that affect the biological communities inhabiting them (Wohl, 2018). Embedded within a Mediterranean climate, the Santa Ana River is subject to massive water extraction for human use. In turn, much of the upper watershed is entirely reliant on WWTP effluent flows to prevent riverbed drying, although parts of the original riverbed remain dry. This unique flow distribution results in sections of the river being transformed into an intermittent flow regime wherein only large flood events in the winter re-wet dry reaches, while other sections remain perennial due to WWTP effluent. In the summer, flow shutdown events represent an isolated perturbation through time; although in the winter, flow shutdowns were found to be compounded with flood events to impose a unique disturbance regime on the instream community In accordance to objectives (1) and (2), the magnitude of response of diatom and BMI communities to spatial and temporal variation was different. The sampled diatom community exhibited resilience strategies whereby their populations declined more strongly after flow perturbation but also exhibited faster recovery, though dominant taxa appeared to be shifted at the end of the study. On the other hand, the BMI community was most negatively impacted in the upstream Rialto channel compared to below the RIX WWTP following flow perturbations—despite recovering, the community did not achieve pre-perturbation levels. Further, even though some taxa were negatively affected by flow perturbations, pre-existing spatial heterogeneity in community distributions reasserted itself following disturbances in accordance to the location of WWTPs within the watershed, affirming objective (3) in that local environment strongly structured the benthic community.

Resistance and resilience to disturbance

The diatom community reacted strongly to flow perturbation, as a strong decline in abundance and richness was observed immediately after the flow shutdown and November flood events, although populations at least partially recovered within the timescale of the study (Figure 3.6). This result can be interpreted as the studied diatom taxa having low resistance but potentially high resilience to flow perturbations. The recolonizing taxa were similar except for the two most dominant genera. There could be multiple reasons for why *Gomphonema* replaced *Fragilaria* as the most dominant genus following flow perturbation. The interaction of flow disturbance timing with the stage of diatom community development has been found to be important. Factors such as season, flow rate before disturbance, and presence of other algae taxa have been determined to be significant in explaining the persistence of diatoms (Peterson & Stevenson, 1992). Although priority effects may have influenced the higher presence of *Gomphonema* at the end of the sampling period, a higher taxonomic resolution and a larger sampling timescale are needed to confirm this. Seasonal succession is likely to have been a more contributing factor, since the high frequency of flow disturbances, compounded by both the shutdown and floods, may have rendered the environmental conditions too difficult for both taxa to persist, since they can form chains, stalks, and colonies which render them more vulnerable to perturbations and grazing (B-Béres et al., 2017; Passy, 2007; Tornés, Acuña, Dahm, & Sabater, 2015). I posit that the dominant source of colonists from Rialto into the RIX channel shifted seasonally, which is why I observed a difference in dominant taxa after the observed flow perturbations (Korhonen, Köngäs, & Soininen, 2013). Nonetheless, *Fragilaria* and *Gomphonema* are considered cosmopolitan taxa which occupy a wide range of ecological conditions, and they have been found to coexist in other polluted waters (Wojtal, 2003).

In contrast to diatoms, the lack of a strong response from the BMI community to flow perturbations may have been due to the BMIs in the Santa Ana River being a resistant, disturbance-tolerant group. Other studies have shown that BMI assemblages in pristine locations are sensitive to urbanization gradients and tend to degrade in composition, resulting in urbanized, degradation-tolerant communities forming quite rapidly, and the taxa in the Santa Ana River reflect this (Brown, Burton, & Belitz, 2005; Brown et al., 2009). Dragonflies of the genera *Libelulla* and *Sympetrum* are relatively disturbance-tolerant, are well distributed in the region, and are capable of flying to other sources of water during flow perturbations (Ferreras-Romero, Márquez-Rodríguez, & Ruiz-García, 2009). Caddisfly filter-feeders of genus *Oecetis* are also tolerant to polluted waters, and these taxa reflect the general trend of disturbance tolerance across the insect community sampled (Hilsenhoff, 1987).

Considering the different life strategies of BMIs and diatoms within this study, the mechanisms that allow for the persistence of diatoms and BMIs may therefore also be different. While the BMI community, by persisting through the effects of flow perturbations, is reflective of a disturbance-resistant community, diatoms within the same genus can have vastly different levels of disturbance tolerance (Fore & Grafe, 2002; Hill et al., 2001; Morin et al., 2015; Stevenson et al., 2008). Thus, the faster reproductive cycle of the diatoms may have enabled them to quickly recolonize previously dry areas via free-flowing upper areas of the watershed in Rialto channel, exhibiting low resistance, but high resilience (Tornés, Acuña, Dahm, & Sabater, 2015). Sequential flow perturbations may have proven especially detrimental to the persistence of BMI and diatom communities in the Santa Ana River. The second (12/01/16) sampling event measured recovery after a flow shutdown and two runoff flood events. However, there was also a third runoff flood event before the December 12, 2016, sampling date (Figure 3.2). BMI and diatom communities did not respond as strongly to the third runoff event. These results suggest that although BMI and diatom communities tend to be stress-adapted and able to withstand flood events in isolation, a flow shutdown paired with a flood event may prove catastrophic.

Novel spatial and temporal heterogeneity

In watersheds subject to less flow impairment and a lower amount of total discharge composed of WWTP effluent, flow perturbations (in the form of droughts or floods) can structure communities differently compared to systems that have more flow impairment. Rivers with less flow impairment and higher connectance typically contain communities with higher taxonomic and functional diversity and higher food web stability (Cross et al., 2013), while flow perturbations in less degraded systems can lead to novel spatial heterogeneity with redistributions of preferred habitat, resulting in unique community assembly trajectories (S. G. Fisher, Gray, Grimm, & Busch, 1982; Lake, 2003; Marks, Power, & Parker, 2000; Power, Parker, & Dietrich, 2008; Stanley, Buschman, Boulton, Grimm, & Fisher, 1994). In contrast, the perturbations imposed by WWTPs and flow runoff in the system covered by this study are twofold: they impose a constant, time-independent effect on the river network by continually releasing effluent at a constant temperature and flow rate, but they also impose a temporally random effect of flow shutdowns and runoff which dries or floods parts of the riverbed. Thus, in the Santa Ana River, and potentially other WWTP effluent-dominated watersheds, flow perturbations do not reset the system for long. When flow returns after shutdowns, it is emitted at a constant rate which quickly re-asserts previous spatial patterns of available habitat and resulting communities. Floods caused by urban runoff result in the occasional movement of the river channel in the river basin and can re-structure the riverine habitat, which can compound the effects of flow shutdowns. Thus, communities within the Santa Ana River are subject to constant WWTP effluent and time-variable runoff floods. However, even in the face of pronounced drying events and urban floods, patterns of diatom and insect distributions are re-established within four weeks.

Total community abundance and richness are consistently lower when approaching the WWTP plants, and their flow regimes not only decrease the prevalence of BMI and diatom communities but also promote the prevalence of invasive species. The unique physical water properties of WWTP effluent impose novel spatial heterogeneity in the system and drive differences in communities between sites. Urban streams have been shown to exhibit extremely fluctuating and high thermal regimes as a result of impervious concrete-lined channels (Somers et al., 2013). Water flowing into Rialto channel from the Rialto WWTP is extremely warm and cannot support healthy native fish populations in the summer and autumn, and additionally tends to closely track ambient temperatures due to the water running over a shallow, concrete-lined channel for 100 m. Effluent from RIX has a constant temperature throughout the year, which has allowed for the successful colonization and year-round establishment of a cosmopolitan tropical filamentous red alga thought to have been introduced from the aquarium trade, *Compsopogon caeruleus* (Junior, Branco, & Gomes, 1999). In turn, invasive yellow bullhead catfish (*Ameiurus natalis*), largemouth bass (*Micropterus salmoides*), green sunfish (*Lepomis cyanellus*), and other non-native fish thrive in the warmer water and constant flow regime established from the WWTPs. In particular, yellow bullhead catfish have been observed living in Santa Ana sucker egg-laying habitats, and largemouth bass have been found with entire bodies of Santa Ana suckers inside their stomachs. Aside from the temporal disturbance of flow shutdowns and floods, I believe that due to the consistent prevalence of *Compsopogon*, an elevated temperature profile, and invasive fish populations, both BMIs and diatoms have a difficult time establishing populations near the RIX WWTP outflow. Following drying events and flood flows throughout the year, consistent flow regimes from effluent outflow promote the persistence of a novel food web, likely created with the establishment of the WWTPs.

In the present study, I identified both novel flow and temperature regimes in an urbanized watershed as well as different aspects of the benthic riverine community that responds to this unique gradient of heterogeneity. Also, I observed that the effects of urban spatiotemporal heterogeneity were not uniform across the sampled communities. Future research is needed to determine whether the taxa are responding to different environmental drivers, such as temperature, or are subject to species interactions, especially since it is unknown whether pre-disturbance communities in the Santa Ana River resemble assemblages present at other, less-disturbed sites in the region that respond to well-documented habitat heterogeneity. Therefore, the management of urban rivers in relation to the preservation of biodiversity should consider the different types of heterogeneity being introduced into the system. For instance, in working with the US Fish and Wildlife Service and local water districts, the operators of the RIX WWTP have been able to implement measures to reduce extreme desiccation events and resulting surface flow disconnection by using groundwater wells near the effluent outflow which activate and release water into the Santa Ana River when flow shutdowns occur. This action demonstrates the importance of research on urban rivers and its relevance to conservation outcomes, as studies such as this can provide a baseline for use in the assessment of the efficacy of restoration efforts and other conservation actions. Further research in the Santa Ana watershed will increase understanding of how novel spatiotemporal heterogeneity imposed on urban streams affects imperiled species as well as how to conserve urban streams in the face of continued human population expansion.

References

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, *9*(6), 683–693. http://doi.org/10.1111/j.1461-0248.2006.00926.x

B-Béres, V., Török, P., Kókai, Z., Lukács, Á., T-Krasznai, E., Tóthmérész, B., & Bácsi, I. (2017). Ecological background of diatom functional groups_ Comparability of classification systems. *Ecological Indicators*, *82*, 183–188. http://doi.org/10.1016/j.ecolind.2017.07.007

Bai, X., Lutz, A., Carroll, R., Keteles, K., Dahlin, K., Murphy, M., & Nguyen, D. (2018). Occurrence, distribution, and seasonality of emerging contaminants in urban watersheds. *Chemosphere*, *200*, 133–142. http://doi.org/10.1016/j.chemosphere.2018.02.106

Blakely, T. J., Harding, J. S., & McIntosh, A. (2006). Barriers to the recovery of aquatic insect communities in urban streams. *Journal of Animal Ecology*, *51*(9), 1634–1645. http://doi.org/10.1111/j.1365-2427.2006.01601.x

Booth, D. B., Roy, A. H., Smith, B., & Capps, K. A. (2016). Global perspectives on the urban stream syndrome. *Freshwater Science*, *35*(1), 412–420. http://doi.org/10.1086/684940

Bourassa, A. L., Fraser, L., & Beisner, B. E. (2017). Benthic macroinvertebrate and fish metacommunity structure in temperate urban streams. *Journal of Urban Ecology*, *3*(1), 267–14. http://doi.org/10.1093/jue/jux012

Boyle, T. P., & Fraleigh, H. D., Jr. (2003). Natural and anthropogenic factors affecting the structure of the benthic macroinvertebrate community in an effluent-dominated reach of the Santa Cruz River, AZ. *Ecological Indicators*, *3*(2), 93–117. http://doi.org/10.1016/S1470-160X(03)00014-1

Brown, L. R., Burton, C. A., & Belitz, K. (2005). Aquatic assemblages of the highly urbanized Santa Ana River basin, California. *American Fisheries Society*.

Brown, L. R., Cuffney, T. F., Coles, J. F., Fitzpatrick, F., McMahon, G., Steuer, J., et al. (2009). Urban streams across the USA: lessons learned from studies in 9 metropolitan areas. *Journal of the North American Benthological Society*, *28*(4), 1051–1069. http://doi.org/10.1899/08-153.1

Camoying, M. G., & Yñiguez, A. T. (2016). FlowCAM optimization: Attaining good quality images for higher taxonomic classification resolution of natural phytoplankton samples. *Limnology and Oceanography: Methods*, *14*(5), 305–314. http://doi.org/10.1002/lom3.10090

Carey, R. O., & Migliaccio, K. W. (2009). Contribution of Wastewater Treatment Plant Effluents to Nutrient Dynamics in Aquatic Systems: A Review. *Environmental Management*, *44*(2), 205–217. http://doi.org/10.1007/s00267-009-9309-5

Carr, J. M., Hergenrader, G. L., & Troelstrup, N. H. (1986). A Simple, Inexpensive Method for Cleaning Diatoms. *Transactions of the American Microscopical Society*, *105*(2), 152. http://doi.org/10.2307/3226387

Coimbra, C. N., Graca, M., & Cortes, R. M. (1996). The effects of a basic effluent on macroinvertebrate community structure in a temporary Mediterranean river. *Environmental Pollution*, *94*(3), 301–307.

Cooper, S. D., Barmuta, L., Sarnelle, O., Kratz, K., & Diehl, S. (1997). Quantifying spatial heterogeneity in streams. *Journal of the North American Benthological Society*, *16*(1), 174–188. http://doi.org/10.2307/1468250

Cross, W. F., Baxter, C. V., Rosi-Marshall, E. J., Hall, R. O., Kennedy, T. A., Donner, K. C., et al. (2013). Food-web dynamics in a large river discontinuum. *Ecological Monographs*, *83*(3), 311–337. http://doi.org/10.1890/12-1727.1

Drury, B., Rosi-Marshall, E., & Kelly, J. J. (2013). Wastewater Treatment Effluent Reduces the Abundance and Diversity of Benthic Bacterial Communities in Urban and Suburban Rivers. *Applied and Environmental Microbiology*, *79*(6), 1897–1905. http://doi.org/10.1128/AEM.03527-12

Ferreras-Romero, M., Márquez-Rodríguez, J., & Ruiz-García, A. (2009). Implications of anthropogenic disturbance factors on the Odonata assemblage in a Mediterranean fluvial system. *International Journal of Odonatology*, *12*(2), 413–428. http://doi.org/10.1080/13887890.2009.9748354

Fisher, S. G., Gray, L. J., Grimm, N. B., & Busch, D. E. (1982). Temporal Succession in a Desert Stream Ecosystem Following Flash Flooding. *Ecological Monographs*, *52*(1), 93–110. http://doi.org/10.2307/2937346?ref=no-x-route:be3e54b737f72757f4b24d00a631ec3a

Galib, S. M., Mohsin, A. B. M., Parvez, M. T., Lucas, M. C., Chaki, N., Arnob, S. S., et al. (2018). Municipal wastewater can result in a dramatic decline in freshwater fishes: a lesson from a developing country. *Knowledge & Management of Aquatic Ecosystems*, *22*(419), 37–12. http://doi.org/10.1051/kmae/2018025

Goodrich, D. C., Kepner, W. G., Levick, L. R., & Wigington, P. J., Jr. (2018). Southwestern Intermittent and Ephemeral Stream Connectivity. *JAWRA Journal of the American Water Resources Association*, *54*(2), 400–422. http://doi.org/10.1111/1752-1688.12636

Greenfield, D. W., Ross, S. T., & Deckert, G. D. (1970). Some aspects of the life history of the Santa Ana sucker, Catostomus (Pantosteus) santaunae (Snyder). *Calif Fish Game*.

Hassett, B. A., Sudduth, E. B., Somers, K. A., Urban, D. L., Violin, C. R., Wang, S.-Y., et al. (2018). Pulling apart the urbanization axis: patterns of physiochemical degradation and biological response across stream ecosystems. *Freshwater Science*, *37*(3), 653–672. http://doi.org/10.1086/699387

Hilsenhoff, W. L. (1987). An Improved Biotic Index of Organic Stream Pollution. *The Great Lakes Entomologist*, *20*(1), 1–10.

Hutchinson, G. E. (1953). The concept of pattern in ecology. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *105*, 1–12. http://doi.org/10.2307/4064466

ICF International. (2014). Phase 1 Report: Upper Santa Ana River Habitat Conservation Plan. March. (ICF 00455.13). Redlands, CA.

Junior, O. N., Branco, C. C., & Gomes, R. V. (1999). Microhabitat and plant structure of Compsopogon coeruleus (Compsopogonaceae, Rhodophyta) populations in streams from São Paulo State, southeastern Brazil. *Cryptogamie Algologie*, *20*(2), 75–87. http://doi.org/10.1016/S0181-1568(99)80008-7

Kalcounis-Rueppell, M. C., Payne, V. H., Huff, S. R., & Boyko, A. L. (2007). Effects of wastewater treatment plant effluent on bat foraging ecology in an urban stream system. *Biological Conservation*, *138*(1-2), 120–130. http://doi.org/10.1016/j.biocon.2007.04.009

Kennedy, T. A., Muehlbauer, J. D., Yackulic, C. B., Lytle, D. A., Miller, S. W., Dibble, K. L., et al. (2016). Flow Management for Hydropower Extirpates Aquatic Insects, Undermining River Food Webs. *BioScience*, *66*(7), 561–575. http://doi.org/10.1093/biosci/biw059

Kinouchi, T., Yagi, H., & Miyamoto, M. (2007). Increase in stream temperature related to anthropogenic heat input from urban wastewater. *Journal of Hydrology*, *335*(1-2), 78–88. http://doi.org/10.1016/j.jhydrol.2006.11.002

Konrad, C. P., & Booth, D. B. A. F. (2005). Hydrologic changes in urban streams and their ecological significance. *American Fisheries Society Symposium*.

Korhonen, J. J., Köngäs, P., & Soininen, J. (2013). Temporal variation of diatom assemblages in oligotrophic and eutrophic streams. *European Journal of Phycology*, *48*(2), 141–151. http://doi.org/10.1080/09670262.2013.779390

Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, *48*(7), 1161–1172. http://doi.org/10.1046/j.1365-2427.2003.01086.x

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*(2), 271–280. http://doi.org/10.1007/s004420100716

Linke, S., Turak, E., & Nel, J. (2010). Freshwater conservation planning: the case for systematic approaches. *Freshwater Biology*, *56*(1), 6–20. http://doi.org/10.1111/j.1365-2427.2010.02456.x

Luo, Y., Guo, W., Ngo, H. H., Nghiem, L. D., Hai, F. I., Zhang, J., et al. (2014). A review on the occurrence of micropollutants in the aquatic environment and their fate and removal during wastewater treatment. *Science of the Total Environment*, *473-474*(C), 619–641. http://doi.org/10.1016/j.scitotenv.2013.12.065

Marks, J. C., Power, M. E., & Parker, M. S. (2000). Flood disturbance, algal productivity, and interannual variation in food chain length. *Oikos*, *90*(1), 20–27.

Morley, S. A., & Karr, J. R. (2002). Assessing and restoring the health of urban streams in the Puget Sound basin. *Conservation Biology*, *16*(6), 1498–1509. http://doi.org/10.1046/j.1523-1739.2002.01067.x

Morrissey, C. A., Boldt, A., Mapstone, A., Newton, J., & Ormerod, S. J. (2012). Stable isotopes as indicators of wastewater effects on the macroinvertebrates of urban rivers. *Hydrobiologia*, *700*(1), 231–244. http://doi.org/10.1007/s10750-012-1233-7

Nedeau, E. J., Merritt, R. W., & Kaufman, M. G. (2003). The effect of an industrial effluent on an urban stream benthic community: water quality vs habitat quality. *Environmental Pollution*, *123*(1), 1–13.

Northington, R. M., & Hershey, A. E. (2006). Effects of stream restoration and wastewater treatment plant effluent on fish communities in urban streams. *Freshwater Biology*, *51*(10), 1959–1973. http://doi.org/10.1111/j.1365-2427.2006.01626.x

Ode, P. R., Fetscher, A. E., & Buusse, L. B. (2016). Standard Operating Procedures (SOP) for the Collection of Field Data for Bioassessments of California Wadable Streams: Benthic Macroinvertebrates, Algae, and Physical Habitat.

Standard Operating Procedures (SOP) for the Collection of Field Data for Bioassessments of California Wadeable Streams: Benthic Macroinvertebrates, Algae, and Physical Habitat. *SWAMP Bioassessment Procedures*.

Passy, S. I. (2007). Diatom ecological guilds display distinct and predictable behavior along nutrient and disturbance gradients in running waters. *Aquatic Botany*, *86*(2), 171–178. http://doi.org/10.1016/j.aquabot.2006.09.018

Paul, M. J., & Meyer, J. (2001). Streams in the urban landscape. *Annu. Rev. Ecol. Syst.*, *32*(1), 333–365. http://doi.org/10.1146/annurev.ecolsys.32.081501.114040

Peterson, C. G., & Stevenson, R. J. (1992). Resistance and Resilience of Lotic Algal Communities: Importance of Disturbance Timing and Current. *Ecology*, *73*(4), 1445–1461. http://doi.org/10.2307/1940689

Power, M. E., Parker, M. S., & Dietrich, W. E. (2008). Seasonal Reassembly of a River Food Web: Floods, Droughts, and Impacts of Fish. *Ecological Monographs*, *78*(2), 263–282. http://doi.org/10.2307/27646132?ref=no-x-route:51b1031fe0f2c424d9f6f8e47add058d

Richmond, J. Q., Backlin, A. R., Galst-Cavalcante, C., O'Brien, J. W., & Fisher, R. N. (2017). Loss of dendritic connectivity in southern California's urban riverscape facilitates decline of an endemic freshwater fish. *Molecular Ecology*, *27*(2), 369–386. http://doi.org/10.1111/mec.14445

Ripl, W. (2003). Water: the bloodstream of the biosphere. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *358*(1440), 1921–1934. http://doi.org/10.1098/rstb.2003.1378

Riverside County Flood Control. (2019). San Jacinto Daily Rainfall Gage. Retrieved from https://data.countyofriverside.us/Land-Use-and-Environment/San-Jacinto-Daily-Rainfall-Station-186/irhj-j2uf

Roy, A. H., Rosemond, A. D., Paul, M. J., Leigh, D. S., & Wallace, J. B. (2003). Stream macroinvertebrate response to catchment urbanisation (Georgia, U.S.A.). *Freshwater Biology*, *48*(2), 329–346. http://doi.org/10.1046/j.1365-2427.2003.00979.x

Ruhí, A., Dong, X., McDaniel, C. H., Batzer, D. P., & Sabo, J. L. (2018). Detrimental effects of a novel flow regime on the functional trajectory of an aquatic invertebrate metacommunity. *Global Change Biology*, *12*, 466–17. http://doi.org/10.1111/gcb.14133

Sánchez-Morales, M., Sabater, F., & Muñoz, I. (2018). Effects of urban wastewater on hyporheic habitat and invertebrates in Mediterranean streams. *Science of the Total Environment*, *642*(C), 937–945. http://doi.org/10.1016/j.scitotenv.2018.06.132

Silver, B. P., Hudson, J. M., Smith, C. T., Lujan, K., Brown, M., & Whitesel, T. A. (2018). An urban stream can support a healthy population of coastal cutthroat trout. *Urban Ecosystems*, *11*(3), 1–14. http://doi.org/10.1007/s11252-017-0711-0

Somers, K. A., Bernhardt, E. S., Grace, J. B., Hassett, B. A., Sudduth, E. B., Wang, S., & Urban, D. L. (2013). Streams in the urban heat island: spatial and temporal variability in temperature. *Freshwater Science*, *32*(1), 309–326. http://doi.org/10.1899/12-046.1

Stanford, J. A., & Ward, J. V. (2001). Revisiting the serial discontinuity concept. *Regulated Rivers: Research & Management*, *17*(4-5), 303–310. http://doi.org/10.1002/rrr.659

Stanley, E. H., Buschman, D. L., Boulton, A. J., Grimm, N. B., & Fisher, S. G. (1994). Invertebrate Resistance and Resilience to Intermittency in a Desert Stream. *American Midland Naturalist*, *131*(2), 288–300.

Tornés, E., Acuña, V., Dahm, C. N., & Sabater, S. (2015). Flood disturbance effects on benthic diatom assemblage structure in a semiarid river network. *Journal of Phycology*, *51*(1), 133–143. http://doi.org/10.1111/jpy.12260

Tornés, E., Mor, J.-R., Mandaric, L., & Sabater, S. (2018). Diatom responses to sewage inputs and hydrological alteration in Mediterranean streams. *Environmental Pollution*, *238*, 369–378. http://doi.org/10.1016/j.envpol.2018.03.037

U.S. Geological Survey. (2019). USGS Surface-Water Daily Data for California. Retrieved from https://waterdata.usgs.gov/ca/nwis/dv/?site_no=11062810&agency_cd=USGS

Van Dam, H., Mertens, A., & Sinkeldam, J. (1994). A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. *Netherland Journal of Aquatic Ecology*, *28*(1), 117–133. http://doi.org/10.1007/BF02334251

Vannote, R. L., & Minshall, G. W. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137. http://doi.org/10.1139/f80-017

Walsh, C. J., Roy, A. H., Feminella, J. F. J. O. T., Cottingham, P. D., Groffman, P. M., & Morgan, R. P., II. (2005). The urban stream syndrome: current knowledge and the search for a cure. *Journal of the North American Benthological Society*, *24*(3), 706–723. http://doi.org/10.1899/04-028.1

Winemiller, K. O., Flecker, A. S., & Hoeinghaus, D. J. (2010). Patch dynamics and environmental heterogeneity in lotic ecosystems. *Journal of the North American Benthological Society*, *29*(1), 84–99. http://doi.org/10.1899/08-048.1

Wohl, E. (2018). Rivers in the Anthropocene: The U.S. perspective. *Geomorphology*, 1–10. http://doi.org/10.1016/j.geomorph.2018.12.001

Wojtal, A. (2003). Diatoms of the genus Gomphonema Ehr. [Bacillariophyceae] from a karstic stream in the Krakowsko-Czestochowska Upland. *Acta Societatis Botanicorum Poloniae*, *72*(3).

Wright, I. A., Chessman, B. C., Fairweather, P. G., & Benson, L. J. (1995). Measuring the Impact of Sewage Effluent on the Macroinvertebrate Community of an Upland Stream - the Effect of Different Levels of Taxonomic Resolution and Quantification. *Australian Journal of Ecology*, *20*(1), 142–149. http://doi.org/10.1111/j.1442-9993.1995.tb00528.x

Wulff, M. L., Brown, L. R., & May, J. T. (n.d.). Native Fish Population and Habitat Study, Santa Ana River, California, 2015: U.S. Geological Survey data release. (USGS California Water Science Center, Ed.).

Ziajahromi, S., Neale, P. A., & Leusch, F. D. L. (2016). Wastewater treatment plant effluent as a source of microplastics: review of the fate, chemical interactions and potential risks to aquatic organisms. *Water Science and Technology*, *74*(10), 2253–2269. http://doi.org/10.2166/wst.2016.414

Figures

Figure 3.1. Benthic macroinvertebrate and diatom sampling locations relative to effluent outflows in the upper Santa Ana River near Colton, California, USA. Map data: Google Earth.

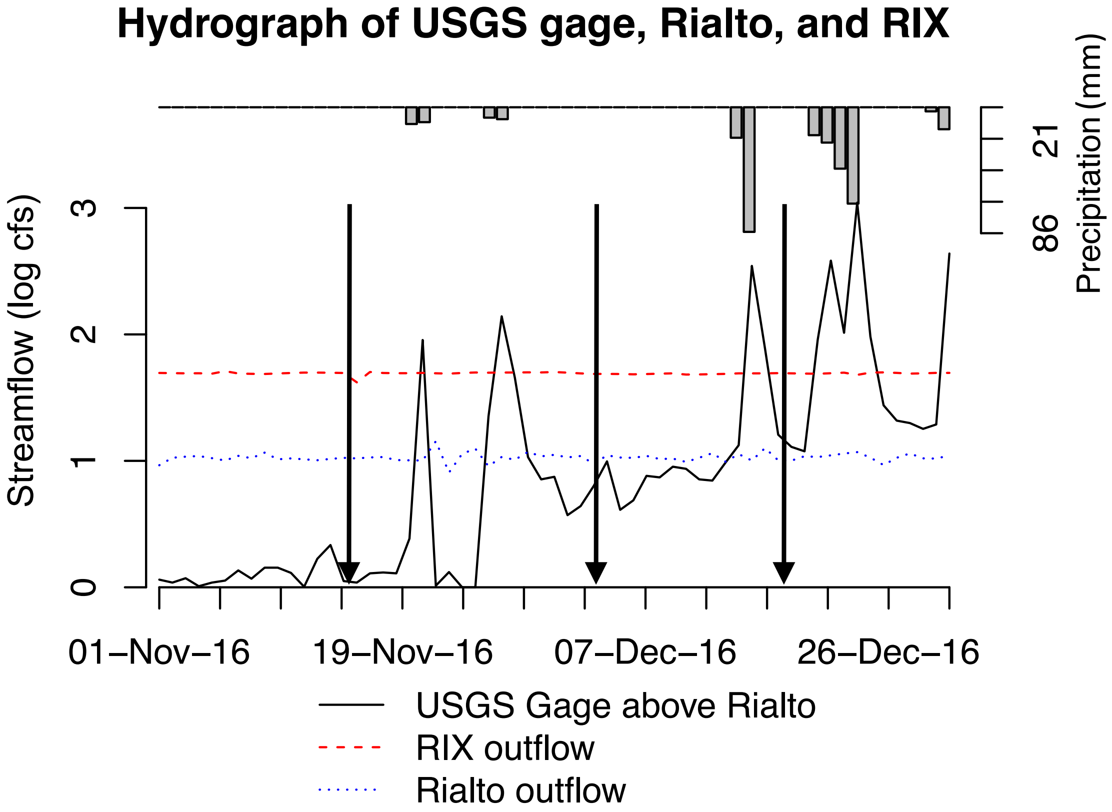


Figure 3.2. Flow dynamics in the upper Santa Ana River. (1) USGS flow gage data gathered upstream of the Rialto WWTP outflow, serving as a proxy for background flow conditions driven by precipitation (black line, gage 11062810). Precipitation data were gathered from a nearby rain gage (data.countyofriverside.us). (2) Discharge rates from the RIX WWTP (dashed red line) and the Rialto WWTP (dotted blue line) at their outflows to the Santa Ana River. Black arrows indicate sampling events, while the first black arrow also represents when a RIX flow shutdown occurred. Flow shutdowns from RIX are not seen in this figure because the plant compensated for shutdowns by increasing flows after shutdowns to arrive at similar daily discharge averages.

Figure 3.2. Photo collage of flow dynamics and habitat heterogeneity in the Santa Ana River. Flow being restored to a dry riverbed after a flow shutdown in 2016 (A); Santa Ana sucker found stranded on a dry riverbed (B); Santa Ana sucker and Arroyo chub facing severe habitat constriction to a draining pool during a summer flow shutdown (C); and a downstream photo of Rialto WWTP effluent transitioning from the concrete transport channel to the riverbed during a mild storm event (D).

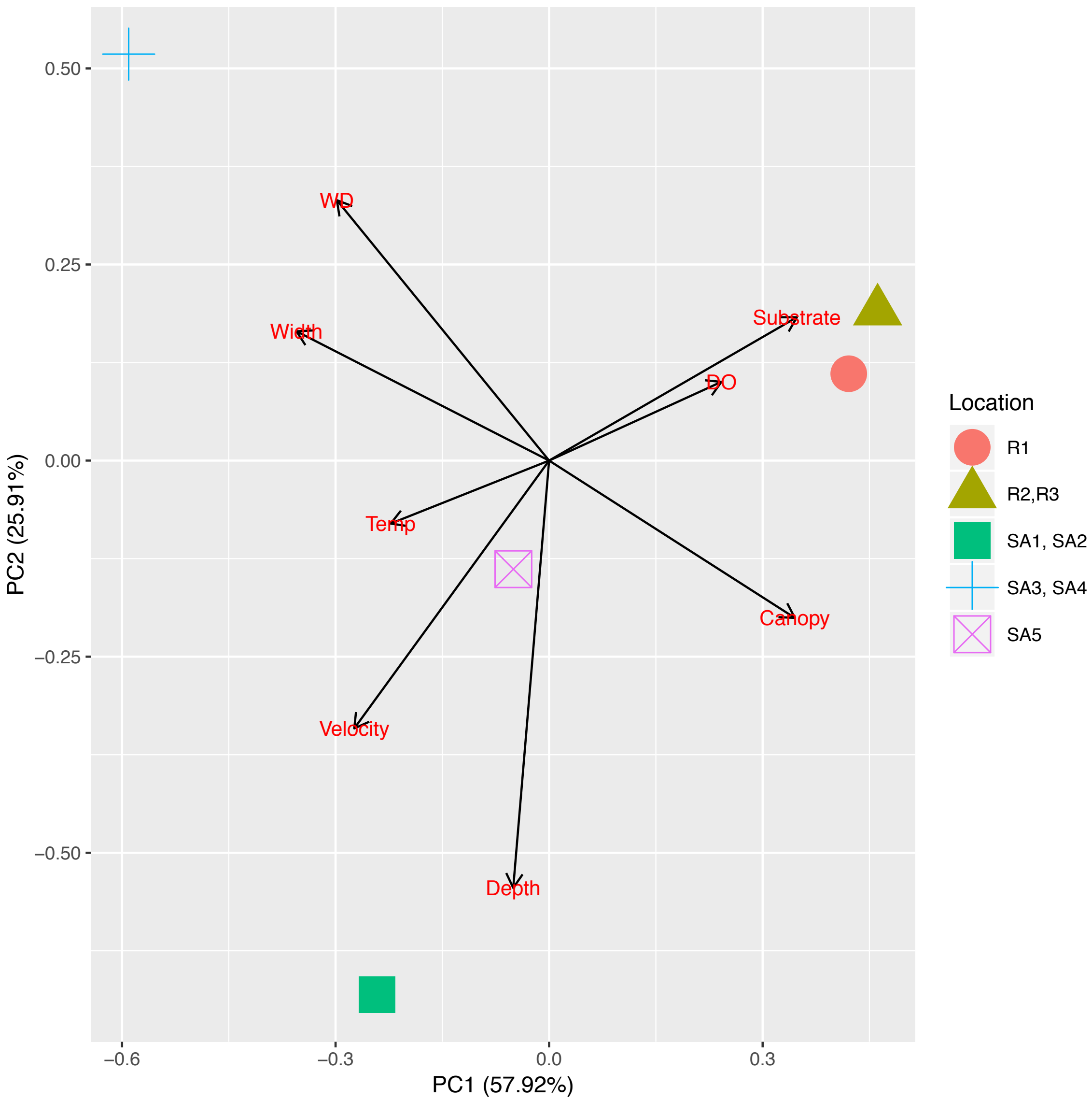


Figure 3.3. PCA of environmental variables at sampling locations of diatoms and BMIs measured during a USGS-led river survey in September 2016. Variables ordinated include mean flow velocity, mean depth, mean canopy cover, mean substrate profile, mean width:depth ratio, and mean width. Since sites measured for environmental variables overlapped with more than one of our sampling sites, our sites were grouped into the areas closest to where USGS survey data were taken.

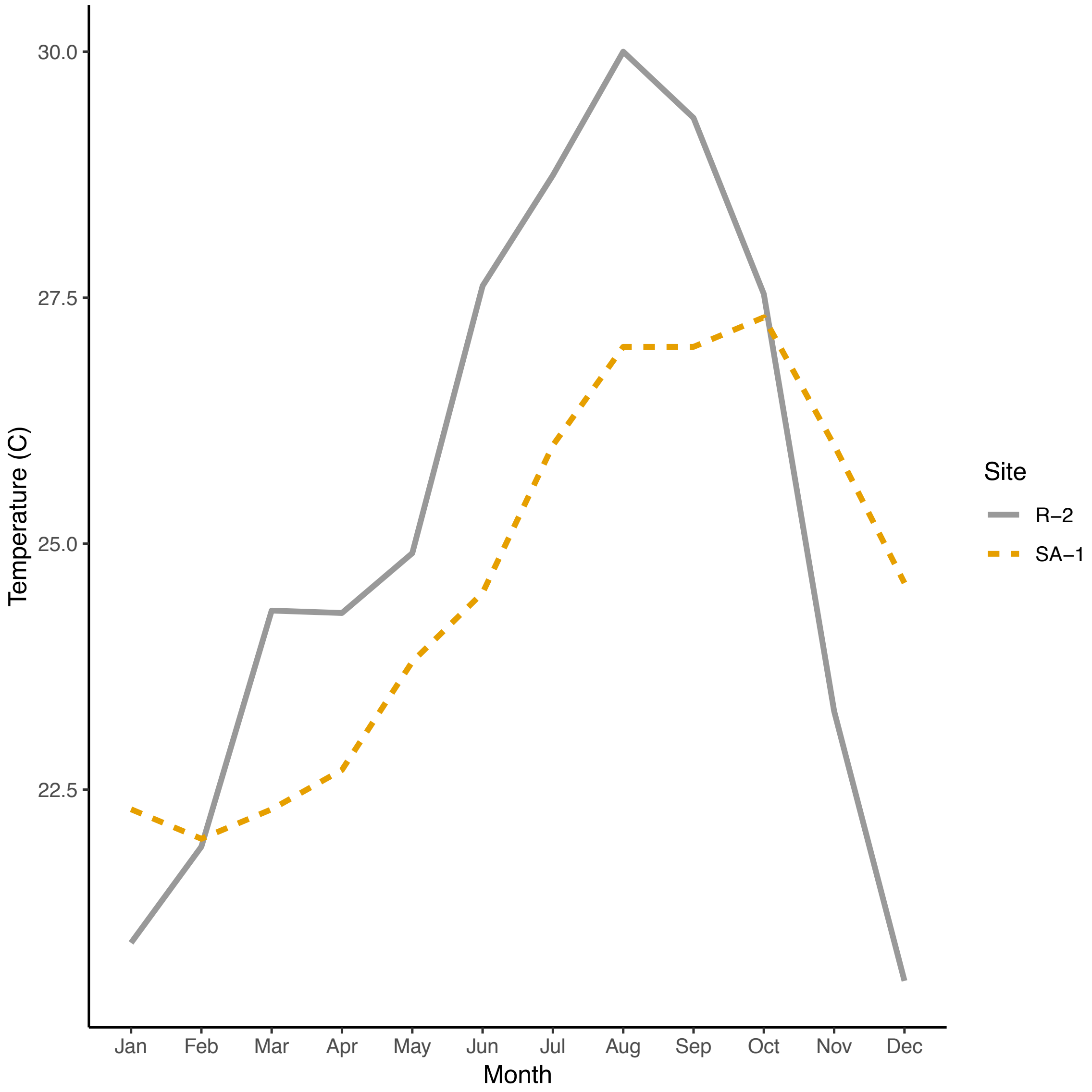


Figure 3.4. Monthly average temperatures for sites downstream of the Rialto (R2) and RIX (SA1) outflows in 2016.

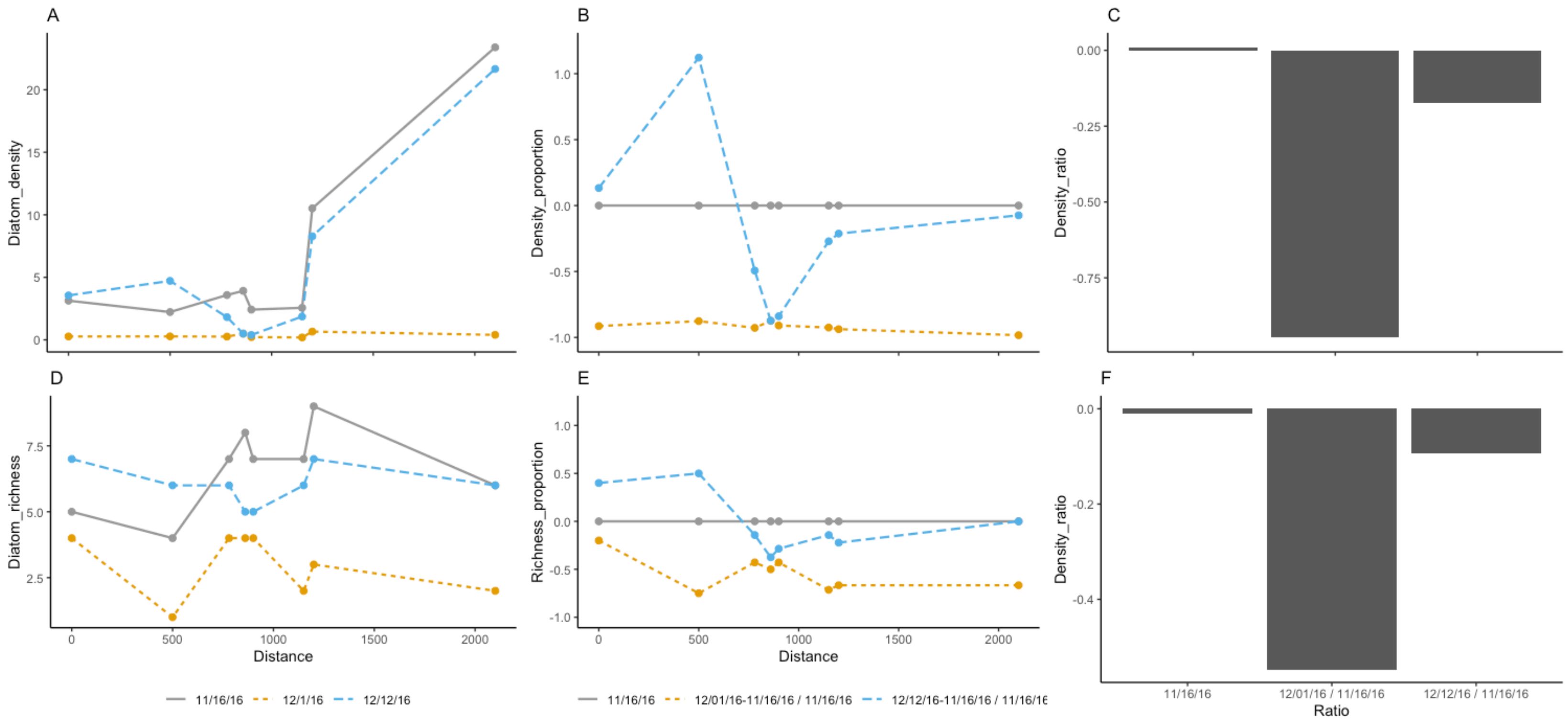


Figure 3.5. Diatom density (A) and richness (D) during the study period in the Santa Ana River. Diatom density and richness were plotted against the distance from the most upstream sampling site (R1). Points in the line graphs are the sampling locations shown in Figure 1. Samples taken on November 16, 2016, were taken immediately before a flow shutdown by the RIX WWTP, while samples from December 1, 2016, and December 12, 2016, were taken approximately two and four weeks afterward, respectively. Proportions of diatom density and richness were calculated with respect to the communities sampled before the flow shutdown on November 16, 2016 (B and E). Proportions are presented for each site, as are averages across all sites sampled (C and F).

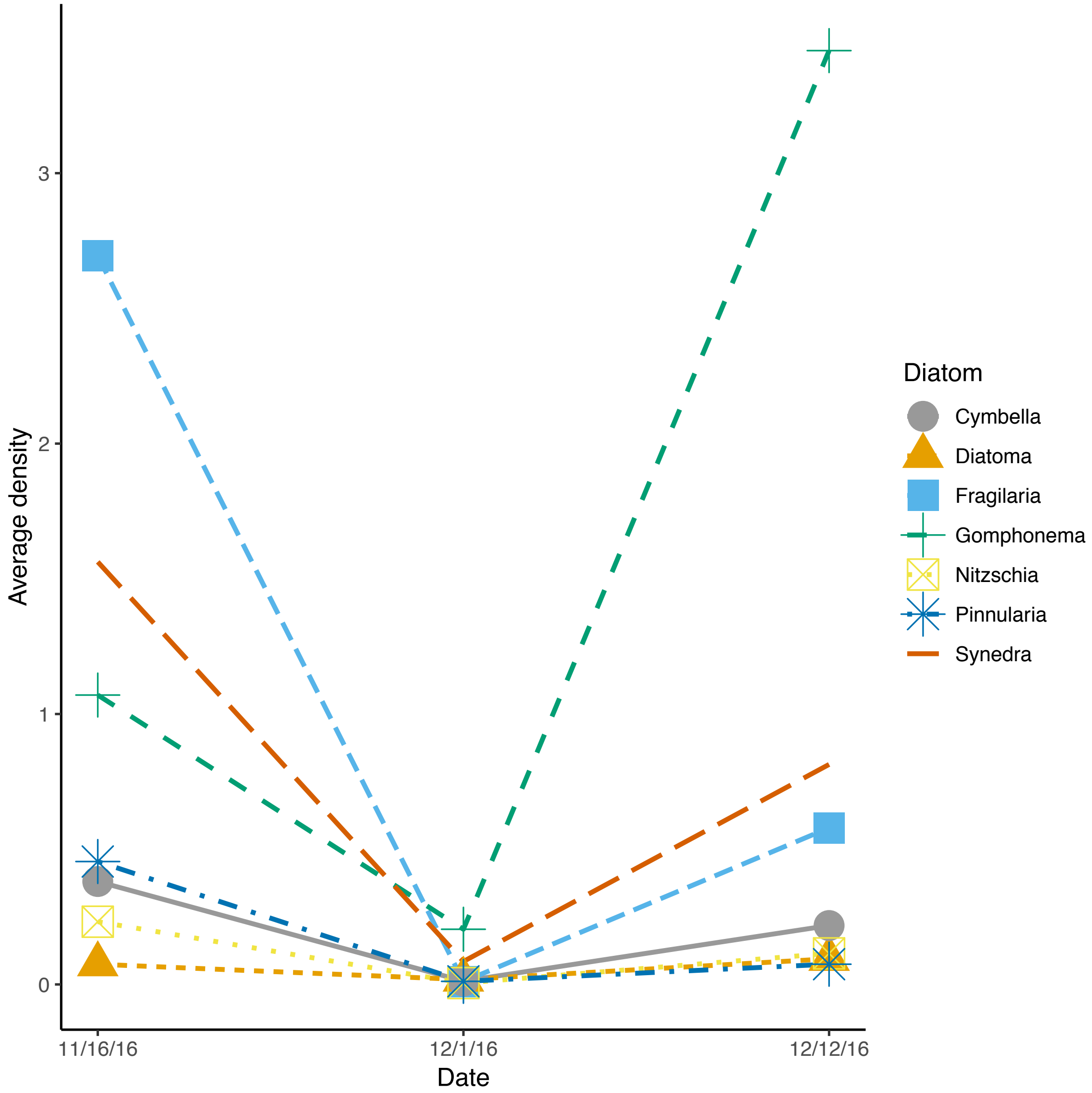


Figure 3.6. The density of each diatom genus was summed across all sites for each sampling date: November 16, 2016 (1), December 1, 2016 (2), and December 12, 2016 (3).

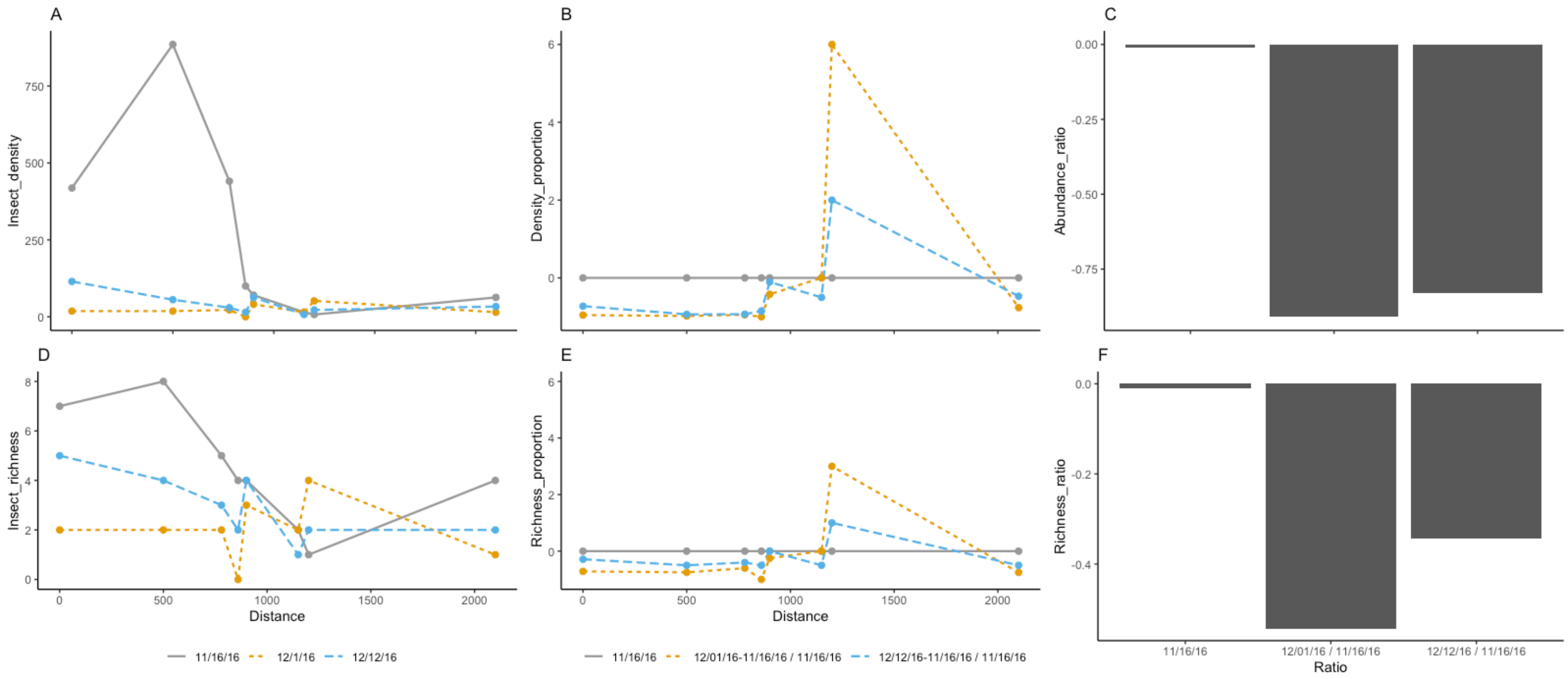


Figure 3.7. This figure protrays similar relationships to those mentioned in Figure 3.6, except with insect abundance and richness.

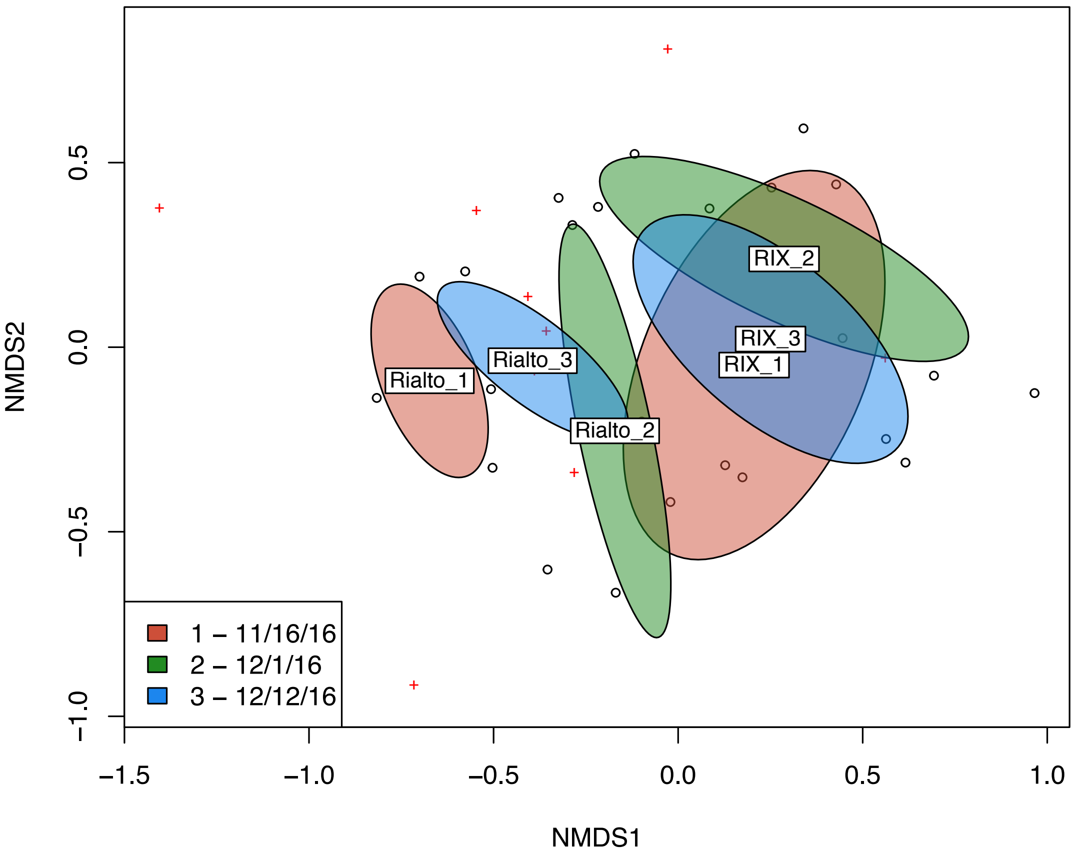


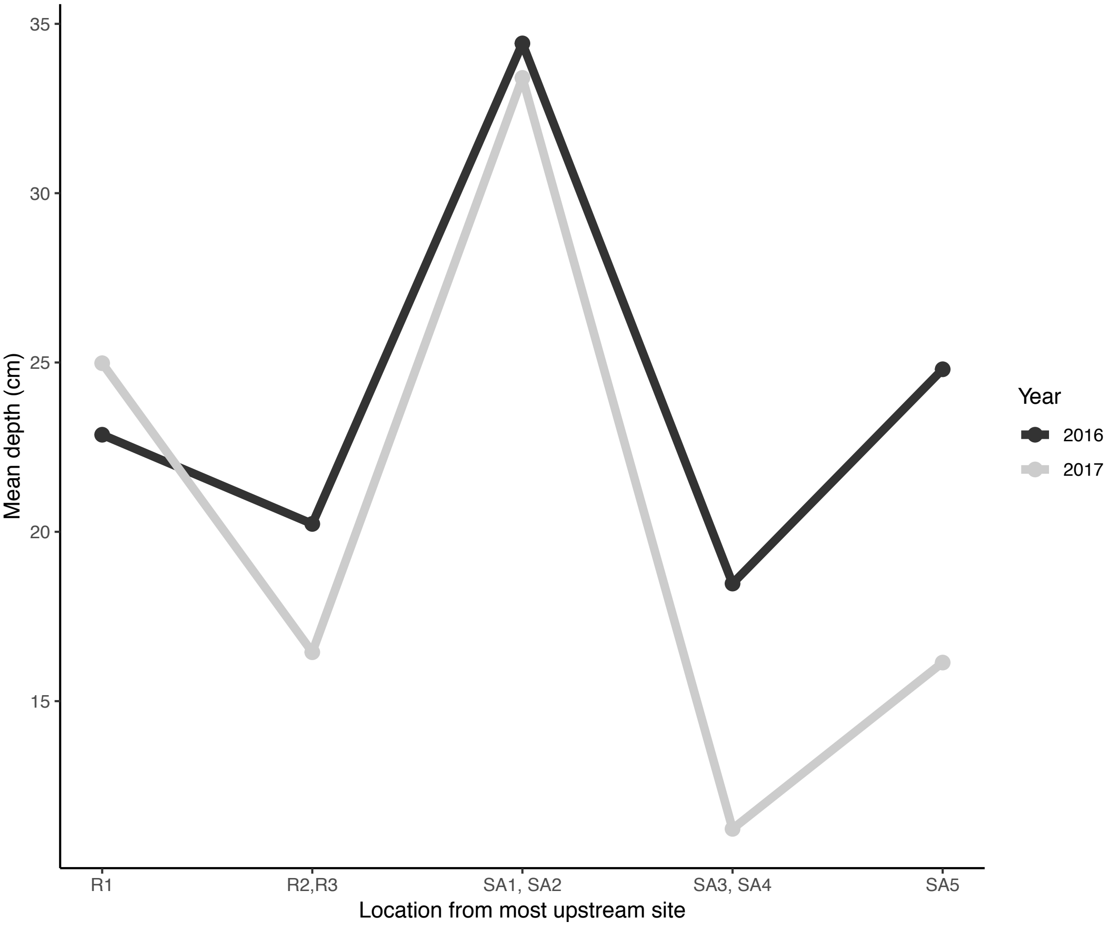
Figure 3.8. NMDS ordination of BMI community composition during each sampling event, separated by location (Rialto channel vs. channel below RIX outflow). Numbers 1, 2, and 3, and colors red, green, and blue represent the timing of the sampling event. BMI data are shown grouped among sites. Ellipses are drawn around the centroids of each community.

Tables

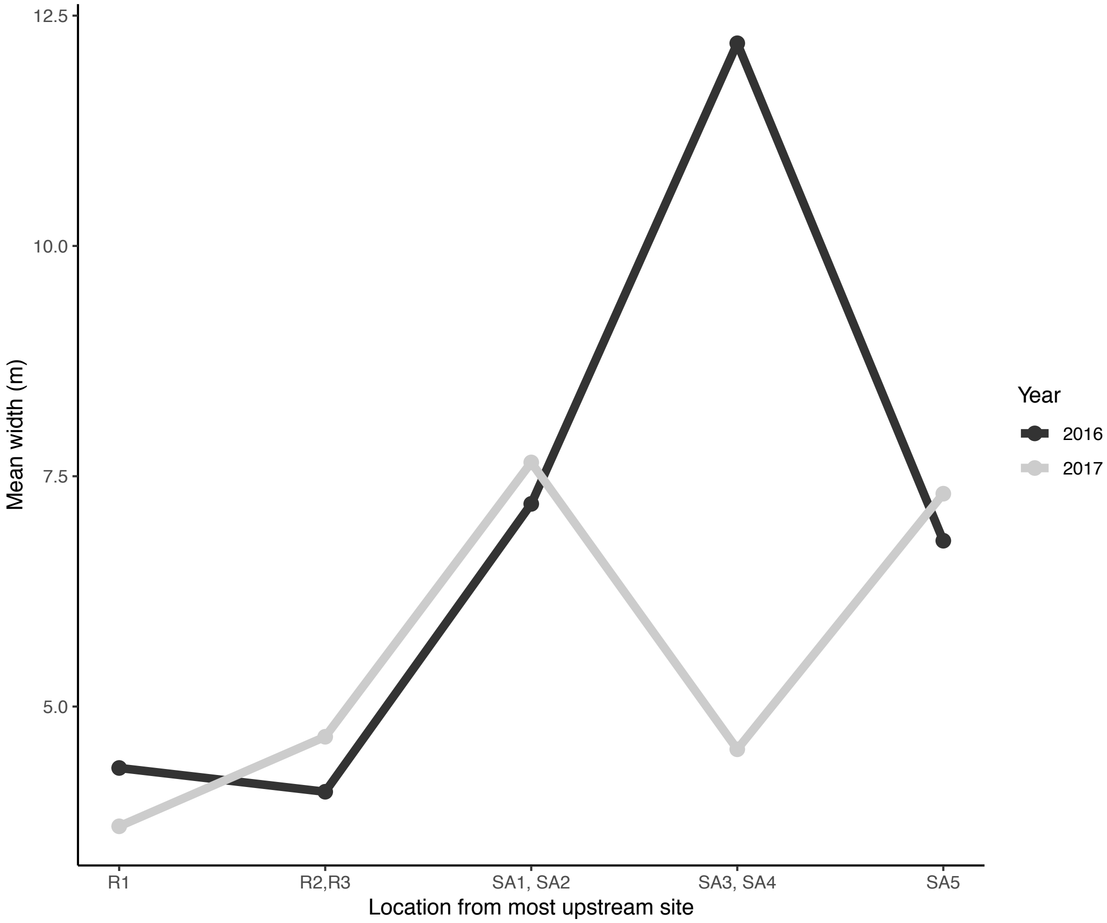
Table 3.3. GLMs used with abundance and richness as outcome variables. GLM models used to explain variations in stream diatoms and BMIs through space and time. Several different spatial groupings of diatoms and BMIs were used to determine which spatial scale was most influential in explaining community responses. Spatial groupings included no spatial factors, SA1-4 and SA-5, SA1-3 and SA4-5, SA1-2 and SA3-5, SA1 and SA2-5, above/below RIX (Rialto channel as one group, and every site below RIX as one group), and each site as its own group (SA-1, SA-2, SA-3, SA-4, and SA-5). Sites in Rialto channel (R-1, R-2, and R-3) were considered their own factor and are not reflected in the model output (they were the factor level among the spatial groupings chosen as the baseline). Models are ranked according to AICc values.

Model	*Model predictors*	*df*	*ΔAICc*	*weight*
Diatom density	11/16/16, 12/01/16, 12/12/16, SA1-3, SA4-5	6	0.0	0.9910
	11/16/16, 12/01/16, 12/12/16, SA1, SA-2, SA-3, SA-4, SA-5	9	11.4	0.0034
	11/16/16, 12/01/16, 12/12/16, SA1-2, SA3-5	6	11.9	0.0026
	11/16/16, 12/01/16, 12/12/16, SA1-4, SA-5	6	12.2	0.0023
	11/16/16, 12/01/16, 12/12/16	4	14.8	0.001
	11/16/16, 12/01/16, 12/12/16, above/below RIX	5	17.7	0.001
	11/16/16, 12/01/16, 12/12/16, SA-1, SA2-5	6	20.0	0.001
Diatom richness	11/16/16, 12/01/16, 12/12/16	4	0.0	0.719
	11/16/16, 12/01/16, 12/12/16, above/below RIX	5	2.9	0.165
	11/16/16, 12/01/16, 12/12/16, SA1-4, SA-5	6	6.2	0.033
	11/16/16, 12/01/16, 12/12/16, SA-1, SA2-5	6	6.5	0.028
	11/16/16, 12/01/16, 12/12/16, SA1-2, SA3-5	6	6.5	0.027
	11/16/16, 12/01/16, 12/12/16, SA1-3, SA4-5	6	6.5	0.027
	11/16/16, 12/01/16, 12/12/16, SA1, SA-2, SA-3, SA-4, SA-5	9	19.6	0.001
Insect density	11/16/16, 12/01/16, 12/12/16, above/below RIX	5	0.0	0.4833
	11/16/16, 12/01/16, 12/12/16, SA-1, SA2-5	6	2.0	0.1774
	11/16/16, 12/01/16, 12/12/16, SA1-2, SA3-5	6	3.2	0.0990
	11/16/16, 12/01/16, 12/12/16, SA1-3, SA4-5	6	3.5	0.0857
	11/16/16, 12/01/16, 12/12/16, SA1-4, SA-5	6	3.6	0.0806
	11/16/16, 12/01/16, 12/12/16	4	3.8	0.0723
	11/16/16, 12/01/16, 12/12/16, SA1, SA-2, SA-3, SA-4, SA-5	9	11.3	0.0017
Insect richness	11/16/16, 12/01/16, 12/12/16, above/below RIX	5	0.0	0.492
	11/16/16, 12/01/16, 12/12/16	4	2.6	0.133
	11/16/16, 12/01/16, 12/12/16, SA1-2, SA3-5	6	2.8	0.119
	11/16/16, 12/01/16, 12/12/16, SA-1, SA2-5	6	3.3	0.092
	11/16/16, 12/01/16, 12/12/16, SA1-3, SA4-5	6	3.6	0.082
	11/16/16, 12/01/16, 12/12/16, SA1-4, SA-5	6	3.6	0.081
	11/16/16, 12/01/16, 12/12/16, SA1, SA-2, SA-3, SA-4, SA-5	9	14.8	0.001

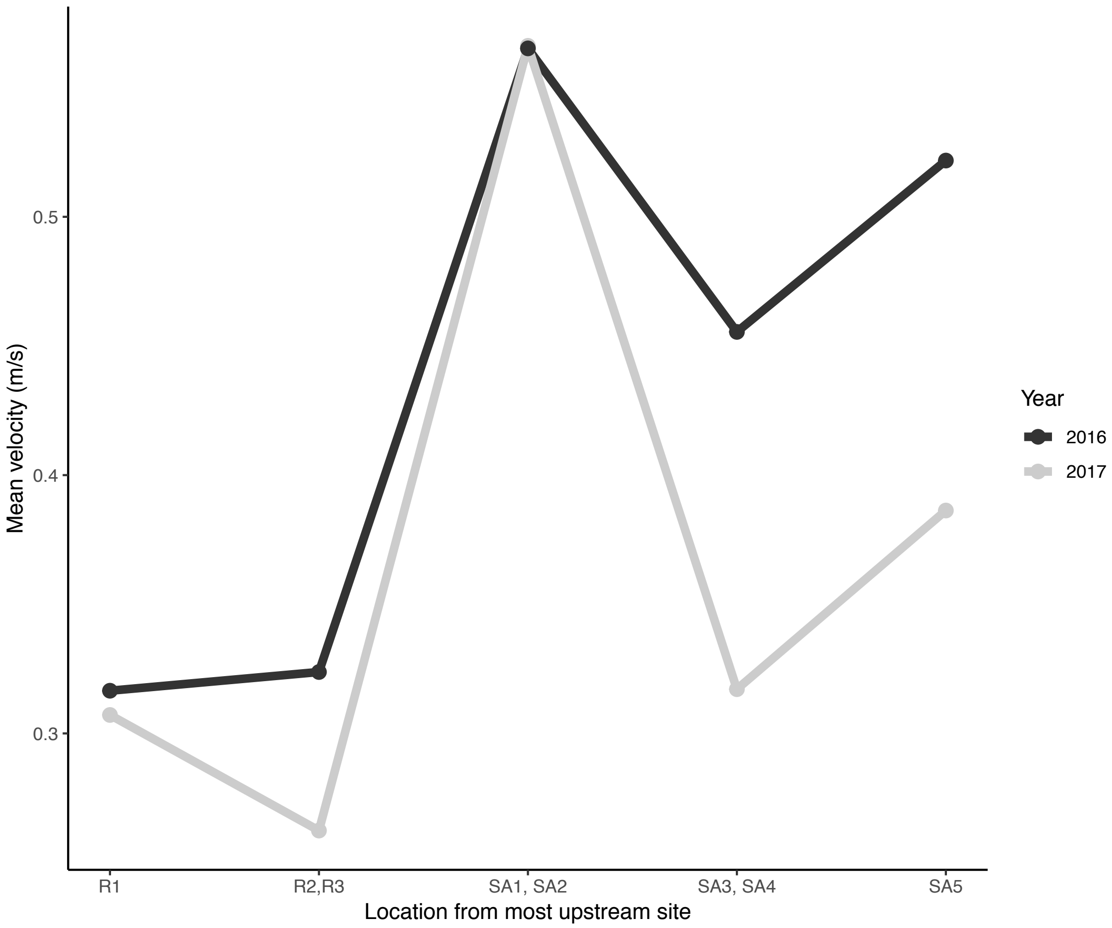
Supplemental Figures



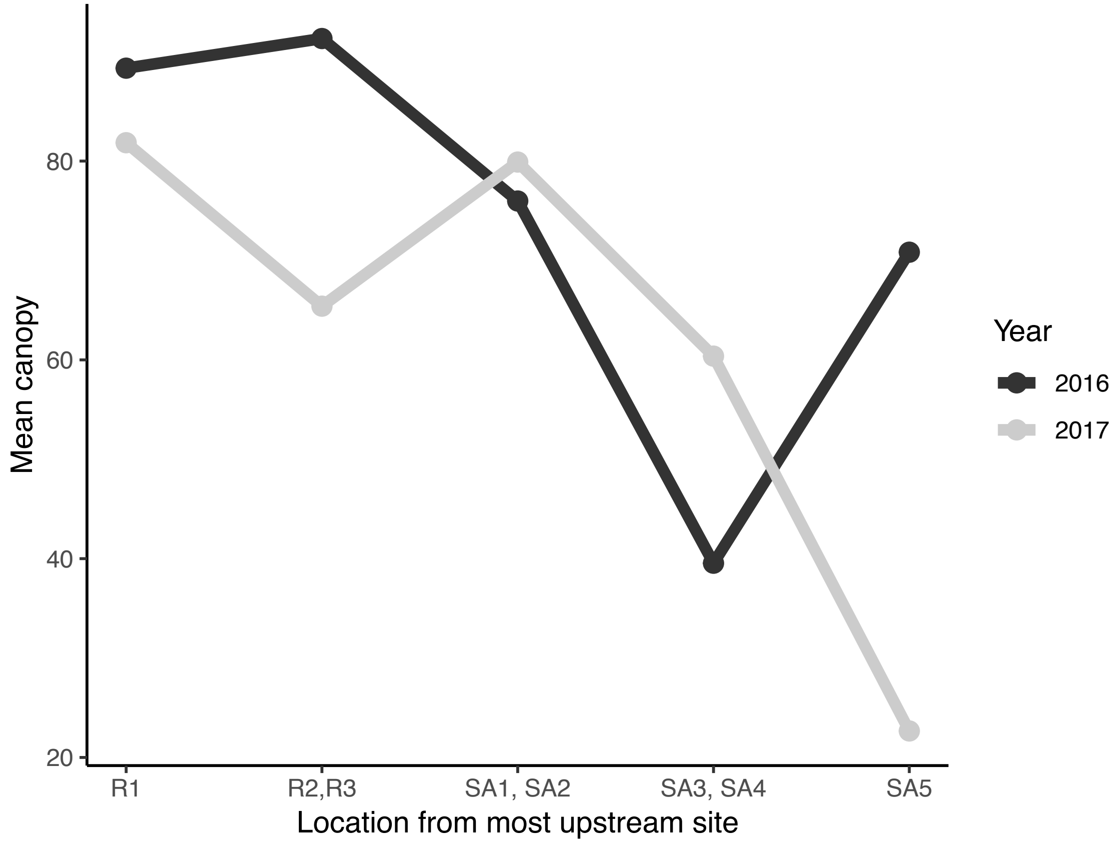
Supplemental Figure 3.9. Mean depth measured during fish surveys by USGS during September 2016 and 2017. Some sampling site locations are combined since USGS conducted their study at a slightly different spatial scale.



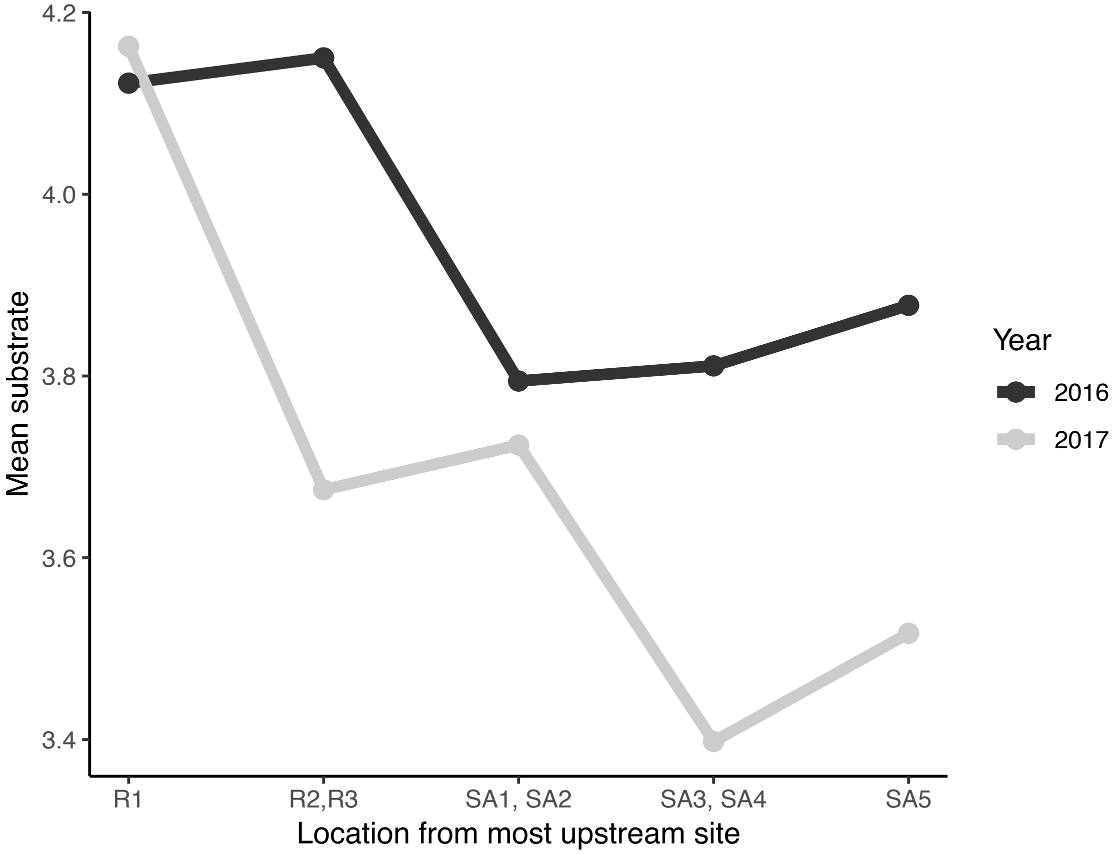
Supplemental Figure 3.10. Mean wetted channel width measured during fish surveys by USGS during September 2016 and 2017. Some sampling site locations are combined since USGS conducted their study at a slightly different spatial scale.



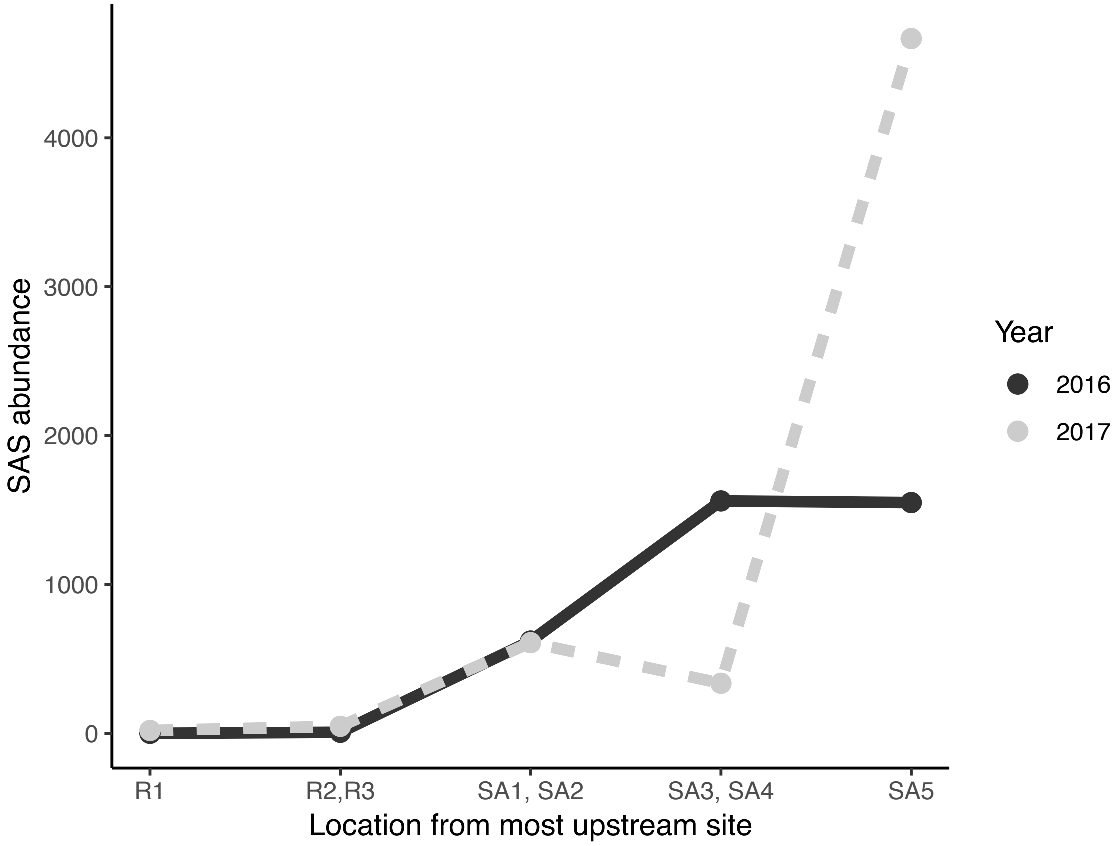
Supplemental Figure 3.3. Mean water velocity measured during fish surveys by USGS during September 2016 and 2017. Some sampling site locations are combined since USGS conducted their study at a slightly different spatial scale.



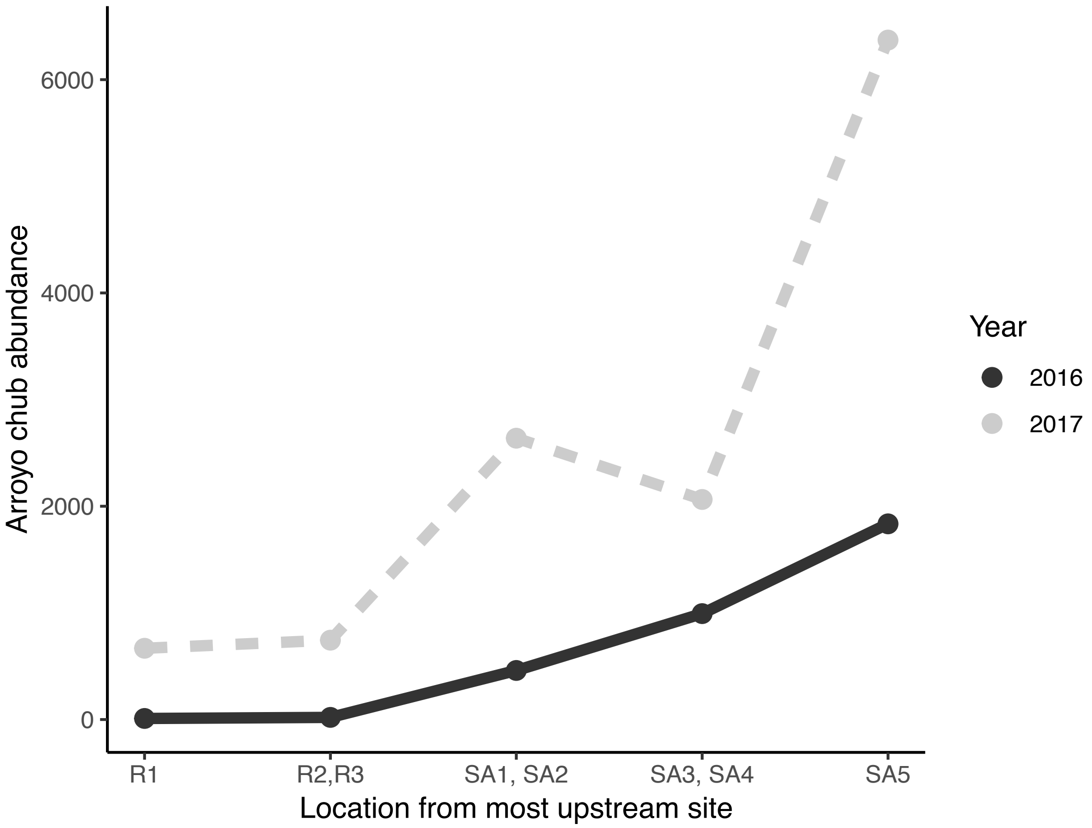
Supplemental Figure 3.4. Mean canopy cover measured with a spherical densitometer during fish surveys by USGS during September 2016 and 2017. Some sampling site locations are combined since USGS conducted their study at a slightly different spatial scale.



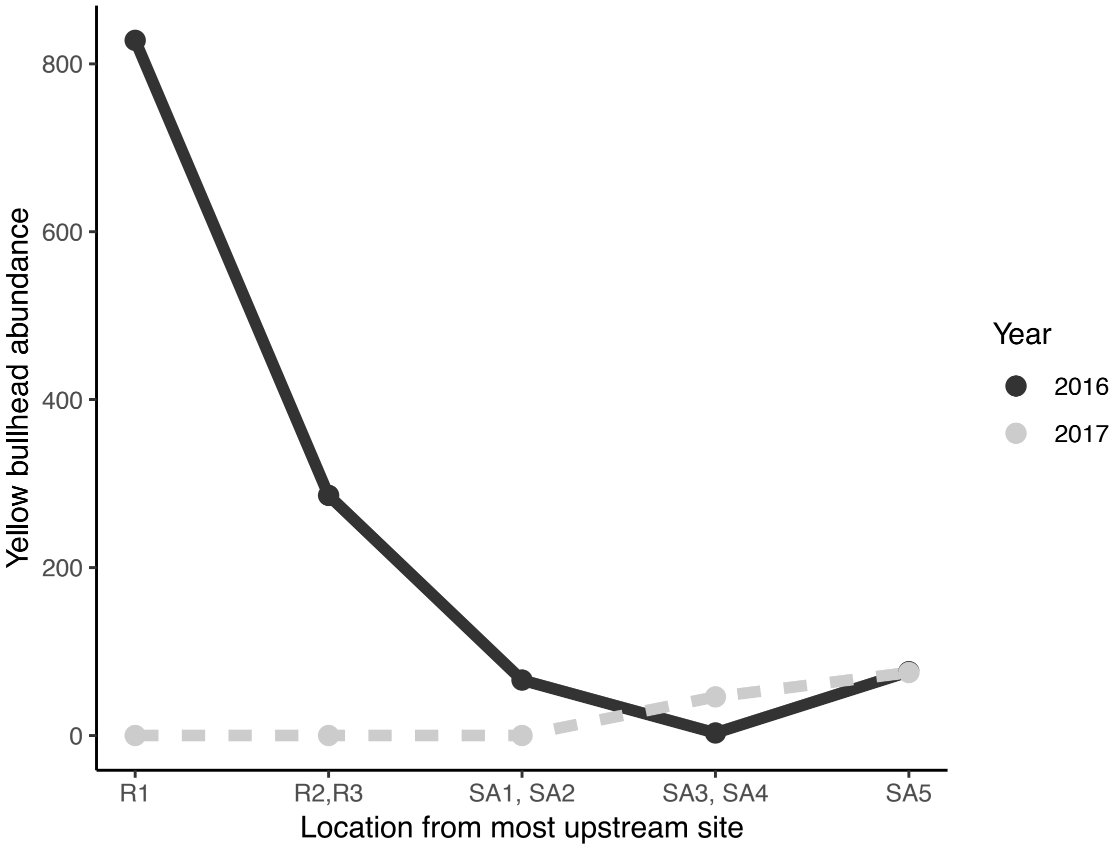
Supplemental Figure 3.5. Mean channel substrate measured during fish surveys by USGS during September 2016 and 2017. Some sampling site locations are combined since USGS conducted their study at a slightly different spatial scale.



Supplemental Figure 3.6. Santa Ana Sucker abundance measured during fish surveys by USGS during September 2016 and 2017. Some sampling site locations are combined since USGS conducted their study at a slightly different spatial scale. Abundance was estimated from either a snorkel survey, electrofishing, or seining event depending on the condition of in-stream environment during sampling.



Supplemental Figure 3.7. Arroyo chub abundance measured during fish surveys by USGS during September 2016 and 2017. Some sampling site locations are combined since USGS conducted their study at a slightly different spatial scale. Abundance was estimated from either a snorkel survey, electrofishing, or seining event depending on the condition of in-stream environment during sampling.



Supplemental Figure 3.8. Yellow bullhead abundance measured during fish surveys by USGS during September 2016 and 2017. Some sampling site locations are combined since USGS conducted their study at a slightly different spatial scale. Abundance was estimated from either a snorkel survey, electrofishing, or seining event depending on the condition of in-stream environment during sampling.

Conclusions

Freshwater benthic communities are strongly regulated in both diversity and abundance by the flow regime (Poff and Zimmerman 2010). However, identifying the spatial and temporal scales at which communities are structured by the hydrograph is a fundamental issue in freshwater conservation and ecology (Anderson et al. 2006, Palmer and Ruhí 2019). In this dissertation, I have investigated how flow variability structures the freshwater benthic community at multiple spatial and temporal scales with studies in natural and urban environments and through big data analysis. The studies outlined here contribute to a growing body of work that suggests that benthic macroinvertebrate communities have a strong affinity with background flow conditions and tend to have distributions that reflect the heterogeneity in the flow regimes that they have experienced in the recent past (Lytle and Poff 2004, Davis et al. 2013, Greenwood and Booker 2014). As water resources in California become increasingly contested and variable due to climate change (Swain et al. 2018), it is vital to understand the hydrologic threshold of imperiled freshwater communities in order to preserve thriving, complex food webs in river systems.

The outlined chapters of this dissertation share the theme of seeking to understand the interplay of time, space, and flow-dependent environmental conditions on driving the persistence of aquatic communities. In chapter one, I described how aquatic insect communities can resist flow perturbation without significant losses in abundance until the surface flow is lost, regardless of species identity. In chapter two, I demonstrated that certain aspects of the hydrograph (zero-flow days, flow variability) and spatial metrics, such as drainage density, significantly explain turnover in benthic macroinvertebrate communities at large spatial scales and long temporal scales, compared to local environmental variables. Finally, in chapter three, I documented the extent to which urban river flow shutdowns and storm runoff events alter the diversity and abundance of benthic macroinvertebrates and diatoms, showing that, while macroinvertebrates were able to somewhat resist extreme flow variations, diatoms were resilient in recolonizing after high losses in genus identity and abundance.

The conservation of riverine biodiversity has been hampered by a lack of understanding of the spatial and temporal scales at which disturbances operate in structuring communities, especially in relation to flow regimes. The studies outlined here add to a growing library of evidence which suggests that researchers have been conducting experiments on a scale that is too small and have not considered the effects of temporal change in their efforts to understand the relationship between community persistence and disturbance. I hope that my work here will spur more research into understanding how disturbances in riverine systems can structure communities across even larger gradients.

References

Anderson, K. E., A. J. Paul, E. McCauley, L. J. Jackson, J. R. Post, and R. M. Nisbet. 2006. Instream Flow Needs in Streams and Rivers: The Importance of Understanding Ecological Dynamics. Frontiers in Ecology and the Environment 4:309–318.

Davis, J. M., C. V. Baxter, E. J. Rosi-Marshall, J. L. Pierce, and B. T. Crosby. 2013. Anticipating Stream Ecosystem Responses to Climate Change: Toward Predictions that Incorporate Effects Via Land–Water Linkages. Ecosystems 16:909–922.

Greenwood, M. J., and D. J. Booker. 2014. The influence of antecedent floods on aquatic invertebrate diversity, abundance and community composition. Ecohydrology 8:188–203.

Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. Trends in Ecology & Evolution 19:94–100.

Palmer, M., and A. Ruhí. 2019. Linkages between flow regime, biota, and ecosystem processes: Implications for river restoration. Science 365:eaaw2087–15.

Poff, N. L., and J. K. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshwater Biology 55:194–205.

Swain, D. L., B. Langenbrunner, J. D. Neelin, and A. Hall. 2018. Increasing precipitation volatility in twenty-first- century California. Nature Climate Change 8:1–10.