Assessing the Response of Macroinvertebrate Communities to River Flow Dynamics in

the Sonoran Desert

by

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ABSTRACT

Climate change is causing hydrologic intensification globally by increasing both the frequency and magnitude of floods and droughts. While environmental variation is a key regulator at all levels of ecological organization, such changes to the hydrological cycle that are beyond the normal range of variability can have strong impacts on stream and riparian ecosystems within sensitive landscapes, such as the American Southwest. The main objective of this study was to investigate how anomalous hydrologic variability influences macroinvertebrate communities in desert streams. I studied seasonal changes in aquatic macroinvertebrate abundances in eleven streams that encompass a hydrologic gradient across Arizona's Sonoran Desert. This analysis was coupled with the quantification and assessment of stochastic hydrology to determine influences of flow regimes and discrete events on invertebrate community composition. I found high community variability within sites, illustrated by seasonal measures of beta diversity and nonmetric multidimensional scaling (NMDS) plots. I observed notable patterns of NMDS data points when invertebrate abundances were summarized by summer versus winter surveys. These results suggest that there is a difference within the communities between summer and winter seasons, irrespective of differences in site hydroclimate. Estimates of beta diversity were the best metric for summarizing and comparing diversity among sites, compared to richness difference and replacement. Seasonal measures of beta diversity either increased, decreased, or stayed constant across the study period, further demonstrating the high variation within and among study sites. Regime shifts, summarized by regime shift frequency (RSF) and mean net annual anomaly (NAA), and anomalous events, summarized by the power of blue noise (Maximum Blue Noise), were

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the best predictors of macroinvertebrate diversity, and thus should be more widely applied to ecological data. These results suggest that future studies of community composition in freshwater systems should focus on understanding the cause of variation in biodiversity gradients. This study highlights the importance of considering both flow regimes and discrete anomalous events when studying spatial and temporal variation in stream communities.

This is dedicated to my mom, Maria. Her constant words of encouragement and dedication to my thesis work were crucial for me and I absolutely could not have done it without her. I would also like to dedicate my thesis to my best friend and boyfriend of 7 years, Sergio. He helped me get through many difficult times in my graduate program and always pushed me to do my best. Lastly, I want to dedicate my work to my dog and best friend, Daisy. I wish she could have seen the day that I graduated with my master's degree. She helped me throughout my academic career by always being there for me and I know that she is tremendously proud of me.

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INTRODUCTION

Environmental variation regulates processes at all levels of ecological organization in streams (Roff 2002, Sabo and Post 2008) and supports diverse biological communities (Sousa 1979). An ecological disturbance in streams is an extreme and often sudden hydrologic event which renews limiting resources, clears space for recolonization, and promotes coexistence among species by disrupting competitive advantages of dominant taxa (McWethy et al. 2009, Sabo and Post 2008, Sousa 1979). However, large-scale disturbances (e.g., floods, excessive drying) cause significant mortality and alter rates of critical ecosystem processes (Grimm 1994). Sensitive ecosystems such as dryland rivers may become more vulnerable to environmental variation, as climate change continues to alter discharge variability across the globe (Seager et al. 2007).

Climate change is expected to increase drought frequency and severity as well as induce hydrologic regime shifts in the American Southwest (Dai 2010, Jaeger et al. 2014, Sponseller et al. 2010), where high-magnitude floods already occur in Arizona's Sonoran Desert (Baker 1977, Grimm and Fisher 1989). The Southwest has seen considerable warming (Karl et al. 2009, MacDonald 2010), with model predictions pointing toward a hotter and drier climate (IPCC 2007, Ye and Grimm 2013). Channel drying events in this region are projected to increase in frequency by 17% and duration by up to 15 days within the next 30 years (Jaeger et al. 2014). These extreme low flows result in channel fragmentation and loss, which isolates stream pools, concentrating predators (Boulton and Suter 1986) and increasing the likelihood of predation. These events can also shift flows from perennial to intermittent (Dai 2010, Jaeger et al. 2014), with consequences for population persistence and nutrient spiraling (Datry et al. 2016, Doretto et al. 2019,

Doretto et al. 2020). Floods are also increasing in both magnitude and frequency globally (Vander Vorste et al. 2021). Extreme high-flow events, capable of moving substrata, can displace or kill organisms (Sabo and Post 2008, Townsend et al. 1997) and reduce total invertebrate densities by as much as 98% (Boulton et al. 1992, Fisher et al. 1982).

While the matter of biodiversity response to climate-related disturbance is relevant to many biological systems (Kerr et al. 2015, Newbold 2018), it is particularly applicable in the context of river flooding and intermittency, as increases in floods and droughts continue to cause shifts in flow regimes (Vander Vorste et al. 2021). Flow regimes are characterized by the magnitude, frequency, duration, timing, and flashiness of a series of events over many years (Poff et al. 1997). They exert long-term pressure and may determine the degree of variation in species composition and local diversity. Because flow regimes are strongly associated with important environmental factors, such as habitat diversity, channel geomorphology, and biotic interactions, (Doretto et al. 2019), they are described as a "master variable" for rivers (Poff et al. 1997). With intensifying climate change (Durack et al. 2012, Krauss et al. 2010, Huntington 2006), changes in the predictability and seasonality of environmental fluctuations will affect ecosystems in ways that are less understood (Tonkin et al. 2017). Thus, it has become increasingly important to study these effects on susceptible communities by considering disturbance events, or short-term conditions, in conjunction with flow regimes, or long-term dynamics, when studying flow variability and community change in streams.

The effects of disturbance on community structure can be evaluated by quantifying beta diversity and its components among biological communities. Beta diversity is defined as the extent of variation in community composition (Whittaker 1960)

and essentially quantifies the number of unique species (those only found at one site)

between communities. Beta diversity describes how different communities are from one

another and is standardized across communities, making it a useful tool for comparing

diversity among sets of connected sites. The two components of beta diversity are

richness difference (difference in the number of species) and replacement, or turnover

(simultaneous gain and loss of species) (Legendre 2014). These indices can reveal

different aspects of ecosystem functioning and can be used to improve our understanding

of important geographical, ecological, and conservation issues, such as climate change

and community response to environmental gradients (Schmera et al. 2020). Factors such

as species dispersal strength and habitat connectivity, both of which are affected by

environmental variation, can affect richness difference and replacement (Heino 2013).

For example, species replacement can indicate environmental filtering and/or competition

(Leprieur et al. 2011), where higher replacement might show greater differences in

environmental conditions among neighboring sites (Gaston et al. 2007). Low dispersal

capacities may also result in increased beta diversity driven by replacement (Ruhi et al.

2017, Vanschoenwinkel et al. 2013). On the other hand, habitat capacity (the potential

number of individuals a site can hold) may increase richness differences among sites

(Dong et al. 2015, Ruhi et al. 2017). One might also expect higher richness difference in

areas that experienced the most severe past climate-related changes (Leprieur et al. 2009,

Leprieur et al. 2011, Baselga 2010), such as shifts in the flow regime or the increase in

frequency of extreme high- or low-flows (Dai 2010, Jaeger et al. 2014, Sponseller et al.

2010).

Because macroinvertebrates play important roles in many ecological processes, such as controlling biomass of primary producers, processing riparian litter, and nutrient cycling (Ramírez and Gutiérrez-Fonseca 2014), their abundance and diversity may be indicators of water quality and ecosystem health (Sharma and Rawat 2009). Thus, studying changes in macroinvertebrate assemblages can provide valuable information for river managers, enabling them to better understand how stream communities may shift in the future (Sabo et al. 2017, Tonkin et al. 2019). A recent study found that temporal taxonomic beta diversity of stream invertebrate communities increased with increasing number and duration of drying events within streams, largely due to replacement (Crabot et al. 2019). Richness difference did not vary with either increasing number or duration of drying events in that study. Similarly, another study found that beta diversity increased or remained stable in response to increased drying duration in benthic invertebrates (Stubbington et al. 2019). Community composition and diversity have also been shown to respond to environmental stochasticity across various community types. For example, one study found that plant community composition differed among sites with varying burn regimes, with declines in species richness in sites subjected to more frequent fires (Collins 2000). Another study of fish assemblages in a desert river found that richness difference was a greater contributor than replacement to beta diversity after anomalous droughts (Ruhi et al. 2014). In that study, fish abundance decreased after extreme droughts but increased after extreme floods. Both environmental regimes and extreme events play important roles in regulating community dynamics, yet the ecological responses to each are generally studied separately. Considering their combined effects on communities may provide insight to unexplored processes driving temporal variability.

In this study, I assessed how benthic invertebrate assemblages respond to hydrologic variability in streams of varying hydroclimates. I compared spatial and temporal patterns of beta diversity and its components, replacement and richness difference, for eleven Sonoran Desert streams. Replacement can imply environmental sorting by abiotic factors (Leprieur et al. 2011), whereas richness difference may reveal variation in habitat size and capacity (Dong et al. 2015). I hypothesized that temporal and spatial variation in invertebrate community composition is dependent on both flow regime and disturbances in desert streams. First, I predicted that both flow regime and disturbance events would be significant predictors of invertebrate beta diversity, due to their linked relationship to community dynamics. Second, I predicted that total beta diversity would be highest among sites of different geographic areas, compared to sites withing the same geographic area. I predicted that seasonality would be an important influence on beta diversity within sites. Lastly, I predicted that stream drying would increase beta diversity after rewetting—driven by replacement—in sites that experienced drying during the study period. I examined to what extent replacement and richness difference contribute to beta diversity across and within sites with varying flow regimes and disturbance frequencies. Because these data-exploration methods are widely relevant, this study provides necessary insight into the association between environmental regimes and anomalous events for other systems and communities.

METHODS

Study area

I studied eleven first- to third-order streams (headwaters) that span central and southern Arizona, USA (Table 1). This area has a hot, desert climate and encompasses a gradient in precipitation timing and hydrologic variation. Wet Beaver, Eagle, and San Francisco have cobble stream beds; Verde, Agua Fria, Sycamore, Babocomari, Santa Cruz, San Pedro, and Bonita have sand and gravel substrate; and Ramsey has mostly bedrock substrate. Intense monsoonal thunderstorms in the summer (July-September) dominate rainfall in southern (Babocomari, Ramsey, San Pedro, and Santa Cruz) and eastern Arizona (Bonita, Eagle, and San Francisco), with weak winter precipitation (November-April). Summer and winter precipitation evenly affect rainfall in Central Arizona (Agua Fria, Sycamore, Verde, and Wet Beaver). Sites were located near U.S. Geological Survey (USGS) discharge gauging stations.

Macroinvertebrate sampling

Sampling occurred quarterly in March, May, September, and December, bracketing winter and summer precipitation, beginning in March of 2016 and ending in May of 2017. I collected benthic invertebrate community samples from riffle habitats at each site using a Surber sampler ($31cm^2$, $500\mu m$ mesh). I took four samples per visit for each site and preserved them in 70% ethanol. I separated macroinvertebrates from plant and other materials found in the samples and individually counted and identified to family, apart from Acari, Collembola, Oligochaeta, and Ostracoda, which I identified to subclass. Due to intermittent flow, I could not collect invertebrates from Babocomari and

Sycamore on occasion, reducing the total number of surveys for these sites. Raw invertebrate abundance data for the 11 sites comprised a total of 63 samples with 83 families and 4 subclasses.

Changes in beta diversity and components to temporal and spatial variation

To test my first prediction that invertebrate diversity is influenced by flow regimes and anomalous events, I calculated beta diversity and its components for each site and between surveys. I calculated beta diversity with square-root transformed mean community abundance data and calculated replacement and richness difference using the quantitative form of Sørensen dissimilarity, the percent difference (Bray-Curtis) index with the 'beta.div.comp' function in the adespatial package (Legendre 2014). For sites with six surveys, I calculated five estimates of beta diversity, replacement and richness difference to evaluate differences between consecutive surveys. I also found total beta diversity, total replacement, and total richness difference for each site using the 'beta.div.comp' function which follows Legendre and De Cáceres (2013). I performed all statistical analyses in R version 3.6.1.

Relationship between beta diversity versus flow regimes and disturbance events

I examined twenty years of mean daily discharge (January 1st, 1997-December 31st, 2018) measured at USGS gauges to quantify flow regimes and flow anomalies for each site (June 6th, 1998 - April 15th, 2019 for Bonita Creek). I used Discrete Fast Fourier Transform (DFFT) to examine seasonal signals of hydrologic variation and quantify expected mean daily discharge (Sabo and Post 2008). I summarized two metrics this way

which I used as predictors of temporal variation of invertebrate beta diversity: flow-regime variability (σ_{hf}), and mean net annual anomaly (NAA), where σ_{hf} is the standard deviation of "catastrophic" events (Sabo and Post 2008). Therefore, σ_{hf} measures the frequency of extreme high-flow events relative to small variation from seasonal flow. NAA is the mean of the net annual anomalies across the twenty years of daily discharge data. It quantifies discharge variation within each site and describes mean anomalous high- and low-flows per year (Sabo et al. 2017). Since σ_{hf} measures variation across the entire (20-y) time series whereas NAA integrates the magnitude of annual departures from the DFFT signal (positive and negative), σ_{hf} and NAA are hence both flow regime metrics.

I used wavelets to quantify aspects of regime shifts between strings of high- and low-flow years. I used the wavelet power spectrum (using a Morlet mother wavelet) against a theoretical spectrum of blue noise, which characterizes negative autocorrelation, or significant shifts between strings of positive and negative anomalies (Sabo et al. 2019), using mean daily discharge from USGS stream gauges. I identified significant blue noise signals across temporal scales of 1-4 years in which I calculated a time series of annual power maxima (reflecting peak transition periods between wet and dry flow regimes). Using this time series, I identified significant peaks (Maximum Blue Noise), the number of these peaks (regime shift frequency, RSF) and the time in days since the last peak (Time Since). Maximum Blue Noise is a measure of shifts in flow regime between wet and dry within the last 20 years for each site, regime shift frequency (RSF) quantifies the number of times regimes have shifted, and time since the last maximum blue noise (Time Since) measures the number of days between the last regime shift and the time of

sampling. RSF is hence a flow regime metric, whereas Time Since and Maximum Blue Noise (within the survey period) are event-based metrics.

I used two sets of multiple linear regression models to evaluate how flow regime variability (σ_{hf}, NAA, and RSF) and disturbance events (Maximum Blue Noise and Time Since) correlate with each measure of diversity. I ran the first set of models against the highest observed beta diversity and its associated components across surveys for each site. These models consisted of NAA, σ_{hf}, and RSF. I ran the second set of models against seasonal measurements of beta diversity and its components and consisted of Maximum Blue Noise and Time Since. For all linear models, I arcsine transformed measurements of beta diversity, richness difference, and replacement. I used Akaike's Information Criterion for small sample size (AICc) to compare relative support among models using multi-model inference.

Comparing temporal macroinvertebrate abundances across study sites

I conducted a nonmetric multidimensional scaling (NMDS) ordination to compare Bray-Curtis dissimilarities among surveys for each site. I evaluated the fit of the ordination via ordination stress, where stress less than or near 0.1 corresponds to good fit and near or above 0.2 has potential to be misleading (Dexter et al. 2018). Stress for untransformed dissimilarities for ordination plots of all surveys across sites was 0.1411 with three dimensions. Stress for combined survey abundances was 0.1162, 0.1748 for pre versus post summer and winter, and 4.378e-05 for combined summer versus winter surveys, with two dimensions. I also used site geography to group sites into south, east, and central site locations, as shown in Table 1.

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RESULTS

Changes in beta diversity and components to temporal and spatial variation

Beta diversity differed significantly among sites (ANOVA, $F_{10,41} = 3.503$, $p =$ 0.002084), while there were no significant site effects on richness difference (ANOVA, $F_{10,41} = 1.015$, $p = 0.4481$) or replacement (ANOVA, $F_{10,41} = 0.6503$, $p = 0.7622$). For all sites, excluding Sycamore, beta diversity either began lower and then increased over the study period or began higher and then dropped below the first measured beta diversity (Figure 1). This could indicate variation in community response to disturbance among sites. There was also no significant effect of site location on beta diversity (ANOVA, $F_{2,42} = 1.80$, $p > .05$), richness difference (ANOVA, $F_{2,42} = 1.014$, $p > .05$), or replacement (ANOVA, $F_{2,42} = 0.731$, $p > .05$). Total beta diversity was highest in two central sites: Sycamore and Agua Fria (Figure 2). Sycamore also had the highest total richness difference, while Agua Fria had the highest total replacement, of all sites.

Relationship between beta diversity and mean net annual anomaly, flow-regime variability, and regime shift frequency

Maximum beta diversity, richness difference, and replacement were equally well predicted by NAA, σ_{hf}, and RSF across sites (Table 2). All single-predictor models were well supported (ΔAICc < 2) for beta diversity and its components, with the RSF-only model being the best supported across beta diversity and richness difference. The NAA-only model was best supported across the replacement diversity metric. RSF had the highest predictor weight across beta diversity and richness difference, while NAA had the highest predictor weight for replacement, which suggests that RSF and NAA are most

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important in predicting beta diversity and its components, compared to σ_{hf} (Table 3). For beta diversity and richness difference, NAA had the second highest predictor weight, followed by σ_{hf}, while for replacement, RSF had the second highest variable weight, followed by σ_{hf}. However, all predictor weights for beta diversity, richness difference, and replacement fell between 0.27 and 0.53, which indicates low probability that the predictors are components of the best model and is likely due to low model weights. Overall, these models revealed that RSF and NAA are significant predictors of beta diversity, richness difference, and replacement.

Relationship between beta diversity, Maximum Blue Noise and Time Since

Seasonal measures of beta diversity, richness difference, and replacement varied within and across sites (Figure 1). Maximum Blue Noise-only models were best supported across all diversity metrics, while Time Since-only models were supported for richness difference and replacement only (Table 4). Model weights for beta diversity and richness difference with Maximum Blue Noise as the only predictor was 0.665 and 0.588, respectively, indicating reasonable relative probability that these are the best models. The model weight for replacement with the Maximum Blue Noise-only model was 0.451, which indicates relatively low probability that this is the best model. These models showed that Maximum Blue Noise is a significant predictor of beta diversity, while there is less certainty for richness difference and replacement.

Maximum Blue Noise had the highest predictor weight across all diversity metrics. (Table 5). This suggests that Maximum Blue Noise is the most important predictor of beta diversity and its components, when compared to Time Since. The

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predictor weight for Maximum Blue Noise was 0.889 for beta diversity, 0.775 for richness difference and 0.591 for replacement. This indicates high probability that Maximum Blue Noise is a component of the best beta diversity model and moderate to low probability that it is a component of the best richness difference and replacement models. Predictor weights for Time Since were between 0.34 and 0.55, indicating low probability that it is a component of the best models. These predictor weights show that Maximum Blue Noise is a significant predictor variable in these models and that there is a relatively high probability that it is a component of the best model.

Comparing temporal macroinvertebrate abundances across study sites

Plots of the NMDS axes were examined for any clustering of the data. Notable clusters of axis data points were not observed for ordinations of seasonal mean abundances, combined survey mean abundances, or combined before and after data (Figure 3). However, there were clusters observed for the summer versus winter survey data (Figure 4). This reveals that while there is no significant difference among the macroinvertebrate communities across sites, surveys, or before versus after seasonal disturbances, there is a difference in community composition between the winter and summer seasons.

DISCUSSION

The effects of disturbance in shaping biodiversity have been a central focus of ecological theories for decades (Sousa 1979, Lake 2003). Previous studies have focused on organismal response to gradual changes due to climate change (Jentsch et al. 2009) or

on singular anomalous events (Bokhorst et al. 2011, Buckley and Huey 2016); however, climate change is also causing extreme annual variation in precipitation associated with alterations between droughts and unusually heavy rains (Kozlovsky et al. 2018). Because of this, I hypothesized that both flow regimes and anomalous events would be important predictors of beta diversity. I also hypothesized that total beta diversity would differ with respect to site location, I would find significant patterns of seasonal beta diversity within sites, and that I would observe an increase in beta diversity after stream drying, driven by the replacement of taxa. I also examined to what extent spatial and temporal estimates of replacement and richness difference contribute to beta diversity in streams with varying hydroclimates. Seasonal measures of beta diversity either increased, decreased, or remained constant throughout the study period and temporal measures of beta diversity demonstrated the high variation within and among study sites. Flow regimes summarized by NAA and RSF, and anomalous events summarized by Maximum Blue Noise, were the best predictors of macroinvertebrate diversity. NMDS ordinations also illustrated the high amount of community variation within sites of seasonal macroinvertebrate abundances, combined seasonal abundances, and combined pre versus post summer and winter seasonal abundances. Here, I highlight the importance of considering both flow regimes and anomalous events when studying spatial and temporal variation in desert stream communities.

Effects of anomalous events and flow regime on benthic community diversity

Macroinvertebrate communities became more diverse over the course of the study period in about half of the sites, while the other half became less diverse. This indicates

that these sites are more distinct from one another than initially predicted. This could also indicate different patterns of recovery and/or seasonality in these sites. Future studies should focus on understanding the cause of variation among nearby sites. Beta diversity at the Sycamore site remained especially high throughout the study period, where it had the highest total beta diversity and total richness difference among the sites. Sycamore maintained high beta diversity after intermittency for the fall and winter of 2016, which is consistent with finding from other studies (Crabot et al. 2019, Stubbington et al. 2019). This high beta diversity was driven by an increase of replacement during the spring of 2017 and was possibly due to the presence of refugia which allowed resistant taxa to persist (Wood and Petts, 1999) and shorter-term stream drying in comparison to droughts that occur over several years which have larger negative impacts on benthic communities (Herbst et al. 2019). Similarly, Babocomari is missing a survey for the fall of 2016, in which beta diversity dropped by nearly 50% between the summer and the winter of that year. These results are consistent with other studies on the general effects of stream drying on macroinvertebrate diversity (Bodana et al. 2006, Herbst et al. 2019). Surprisingly, richness difference was highest directly after stream flows resumed, which could be due to aerial invertebrate dispersal (Crabot et al. 2019).

There is a general trend of higher total richness difference relative to total replacement among sites. These results suggests that richness difference is a greater contributor to total beta diversity than replacement and that temporal variation in community composition is mostly driven by changes in the number of species and less by changes in species identity. This ratio of richness difference to replacement implies that variation within sites is mostly due to ecological processes, such as changes in habitat

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size and capacity (Legendre 2014) and less due to environmental filtering by abiotic factors (Leprieur et al. 2011). This also implies that these sites are more susceptible to discharge variation, like those that come with stochastic floods and droughts. These results suggest that future studies of community composition in streams should focus on understanding the cause of variation in biodiversity gradients. Understanding how richness difference and replacement contribute to community composition over time could help conservation managers identify sites that may have a disproportionately high effect on metacommunity dynamics and to prioritize conservation actions in those sites (Ruhi et al. 2017).

Anomalous events, summarized by NAA and RSF, and regime shifts, summarized by Maximum Blue Noise, were the best predictors of macroinvertebrate diversity. Sabo et al. 2017 describes NAA as a "high-level" predictor and is a compact metric of hydrologic variance. It essentially describes anomalous wetness or dryness and is important because its various components quantify events that comprise the timing, magnitude, frequency, and duration of annual hydrographs and abnormal departures (Sabo et al. 2017), all of which describe a flow regime. These results demonstrate that these sites are significantly affected by anomalous high- and low-flows and that NAA is an important descriptor of discharge variance and predictor of diversity that should be more widely applied to community composition data. Estimating RSF and Maximum Blue Noise are novel approaches which characterize shifts between positive and negative anomalies. RSF is a regime-based metric which measures the number of high- and low-flow transitions in a given time series. RSF was also shown to be an important predictor of beta diversity and richness difference, likely due to flow regimes being strongly associated with important

environmental factors (Doretto et al. 2019). This indicates that beta diversity and richness difference are significantly affected by the frequency of regime shifts. Maximum Blue Noise is an event-based metric which reveals transitions between high- and low-flow regimes. Its significance in predicting beta diversity supports the concept that anomalous events are important to consider when studying spatial and temporal diversity, which are known to affect communities (McWethy et al. 2009, Sabo and Post 2008, Sousa 1979). Based on my results, RSF and Maximum Blue Noise should also be adopted as frequently used metrics, as they are useful tools for quantifying regime shifts in ecological systems.

CONCLUSION

Anthropogenic activity is causing non-stationarity in environmental conditions and climate warming, which has led to modified long-term regime averages and more intense disturbance events (Kozlovsky et al. 2018, Poff 2018). Thus, new methods that quantify these sources of variation are key in order for ecological models to adapt along with the adapting biodiversity. This paper presents methods that allow for quantification of both long-term environmental regimes and seasonal sources of variation from time series data. I used these methods to estimate variation in community composition of 11 desert stream communities. The results of this study demonstrate the importance of considering both flow regimes and disturbance events when studying variation in stream and river systems. Understanding how community diversity is likely to respond to future changes in flow regime and disturbance magnitude or frequency should also prove useful for river managers in the conservation of freshwater ecosystems (Tonkin et al. 2019).

Because the hypotheses being evaluated are broadly applicable, this study will also

provide insight into the association between flow regimes and discrete events in other

systems and biological communities.

REFERENCES

Baker, V. R. 1977. Stream-channel response to floods, with examples from central Texas. Geological Society of America Bulletin 88:1057–1071.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19:134–143.

Bokhorst, S., J. W. Bjerke, L. E. Street, T. V. Callaghan, and G. K. Phoenix. 2011. Impacts of multiple extreme winter warming events on sub-Arctic heathland: phenology, reproduction, growth, and CO2 flux responses. Global Change Biology 17:2817–2830.

Boulton, A. J., and P. J. Suter. 1986. Ecology of Temporary Streams—an Australian Perspective. Limnology in Australia:313–327.

Boulton, A. J., C. G. Peterson, N. B. Grimm, and S. G. Fisher. 1992. Stability of an Aquatic Macroinvertebrate Community in a Multiyear Hydrologic Disturbance Regime. Ecology 73:2192–2207.

Buckley, L. B., and R. B. Huey. 2016. How Extreme Temperatures Impact Organisms and the Evolution of their Thermal Tolerance. Integrative and Comparative Biology 56:98–109.

Collins, S. L. 2000. Disturbance Frequency and Community Stability in Native Tallgrass Prairie. The American Naturalist 155:311–325.

Crabot, J., J. Heino, B. Launay, and T. Datry. 2019. Drying determines the temporal dynamics of stream invertebrate structural and functional beta diversity. Ecography 43:620–635.

Dai, A. 2010. Drought under global warming: a review. WIREs Climate Change 2:45–65.

Datry, T., H. Pella, C. Leigh, N. Bonada, and B. Hugueny. 2016. A landscape approach to advance intermittent river ecology. Freshwater Biology 61:1200–1213.

Dong, X., R. Muneepeerakul, J. D. Olden, and D. A. Lytle. 2015. The effect of spatial configuration of habitat capacity on β diversity. Ecosphere 6.

Doretto, A., E. Piano, and C. E. Larson. 2020. The River Continuum Concept: lessons from the past and perspectives for the future. Canadian Journal of Fisheries and Aquatic Sciences 77:1853–1864.

Doretto, A., F. Bona, E. Falasco, D. Morandini, E. Piano, and S. Fenoglio. 2019. Stay with the flow: How macroinvertebrate communities recover during the rewetting

phase in Alpine streams affected by an exceptional drought. River Research and Applications 36:91–101.

Durack, P. J., S. E. Wijffels, and R. J. Matear. 2012. Ocean Salinities Reveal Strong Global Water Cycle Intensification During 1950 to 2000. Science 336:455–458.

Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal Succession in a Desert Stream Ecosystem Following Flash Flooding. Ecological Monographs 52:93–110.

Gaston, K. J., R. G. Davies, C. D. Orme, V. A. Olson, G. H. Thomas, T.-S. Ding, P. C. Rasmussen, J. J. Lennon, P. M. Bennett, I. P. F. Owens, and T. M. Blackburn. 2007. Spatial turnover in the global avifauna. Proceedings of the Royal Society B: Biological Sciences 274:1567–1574.

Grimm, N. B. 1994. Disturbance, succession and ecosystem processes in streams: a case study from the desert. Pages 93–112 in Aquatic ecology: scale, pattern, and process. Essay Blackwell Science Publications Oxford, England.

Grimm, N. B., and S. G. Fisher. 1989. Stability of Periphyton and Macroinvertebrates to Disturbance by Flash Floods in a Desert Stream. Journal of the North American Benthological Society 8:293–307.

Heino, J. 2013. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. Biological Reviews 88:166–178.

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 64:886–902.

Huntington, T. G. 2006. Evidence for intensification of the global water cycle: Review and synthesis. Journal of Hydrology 319:83–95.

Jaeger, K. L., J. D. Olden, and N. A. Pelland. 2014. Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. Proceedings of the National Academy of Sciences 111:13894–13899.

Jentsch, A., J. Kreyling, J. Boettcher-Treschkow, and C. Beierkuhnlein. 2009. Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. Global Change Biology 15:837–849.

Karl, T. R., J. M. Melillo, and T. C. Peterson, editors. 2009. Global climate change impacts in the United States: a state of knowledge report from the U.S. Global Change Research Program. Cambridge Univ. Press Cambridge, NY.

Kerr, J. T., A. Pindar, P. Galpern, L. Packer, S. G. Potts, S. M. Roberts, P. Rasmont, O. Schweiger, S. R. Colla, L. L. Richardson, D. L. Wagner, L. F. Gall, D. S. Sikes, and A. Pantoja. 2015. Climate change impacts on bumblebees converge across continents. Science 349:177–180.

Kozlovsky, D. Y., C. L. Branch, A. M. Pitera, and V. V. Pravosudov. 2018. Fluctuations in annual climatic extremes are associated with reproductive variation in resident mountain chickadees. Royal Society Open Science 5:171604.

Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, J. Pöyry, K. M. Raatikainen, A. Sang, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology Letters 13:597–605.

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

Legendre, P. 2014. Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography 23:1324–1334.

Legendre, P., and M. De Cáceres. 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecology Letters 16:951–963.

Leprieur, F., J. D. Olden, S. Lek, and S. Brosse. 2009. Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. Journal of Biogeography 36:1899–1912.

Leprieur, F., P. A. Tedesco, B. Hugueny, O. Beauchard, H. H. Dürr, S. Brosse, and T. Oberdorff. 2011. Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. Ecology Letters 14:325–334.

MacDonald, G. M. 2010. Water, climate change, and sustainability in the southwest. Proceedings of the National Academy of Sciences 107:21256–21262.

McWethy, D. B., C. Whitlock, J. M. Wilmshurst, M. S. McGlone, and X. Li. 2009. Rapid deforestation of South Island, New Zealand, by early Polynesian fires. The Holocene 19:883–897.

Newbold, T. 2018. Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. Proceedings of the Royal Society B: Biological Sciences 285:20180792.

Poff, N. L. 2018. Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world. Freshwater Biology 63:1011–1021.

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: A paradigm for river conservation and restoration. BioScience 47:769–784.

Ramírez, A., and P. E. Gutiérrez-Fonseca. 2014. Functional feeding groups of aquatic insect families in Latin America: a critical analysis and review of existing literature. Revista de Biología Tropical 62:155.

Roff, D. A. 2002. Life history evolution. Sinauer Associates Sunderland, MA.

Ruhí, A., E. Chappuis, D. Escoriza, M. Jover, J. Sala, D. Boix, S. Gascón, and E. Gacia. 2014. Environmental filtering determines community patterns in temporary wetlands: a multi-taxon approach. Hydrobiologia 723:25–39.

Ruhí, A., T. Datry, and J. L. Sabo. 2017. Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. Conservation Biology 31:1459–1468.

Sabo, J. L., A. Ruhi, G. W. Holtgrieve, V. Elliott, M. E. Arias, P. B. Ngor, T. A. Räsänen, and S. Nam. 2017. Designing river flows to improve food security futures in the Lower Mekong Basin. Science 358.

Sabo, J. L., Tamara Harms, and A. Ruhi. Quantifying hydrologic regime shifts on ecological time scales using wavelets. AGU Fall Meeting 2019. AGU, 2019.

Sabo, J. L., and D. M. Post. 2008. Quantifying periodic, stochastic, and catastrophic environmental variation. Ecological Monographs 78:19–40.

Schmera, D., J. Podani, and P. Legendre. 2020. What do beta diversity components reveal from presence-absence community data? Let us connect every indicator to an indicandum! Ecological Indicators 117:106540.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H.-P. Huang, N. Harnik, A. Leetmaa, N.-C. Lau, C. Li, J. Velez, and N. Naik. 2007. Model Projections of an Imminent Transition to a More Arid Climate in Southwestern North America. Science 316:1181–1184.

Sharma, R. C., and J. S. Rawat. 2009. Monitoring of aquatic macroinvertebrates as bioindicator for assessing the health of wetlands: A case study in the Central Himalayas, India. Ecological Indicators 9:118–128.

Solomon, S. 2007. IPCC (2007): Climate change the physical science basis. *in* AGU Fall Meeting Abstracts. essay.

Sousa, W. P. 1979. Disturbance in Marine Intertidal Boulder Fields: The Nonequilibrium Maintenance of Species Diversity. Ecology 60:1225.

Sponseller, R. A., N. B. Grimm, A. J. Boulton, and J. L. Sabo. 2010. Responses of macroinvertebrate communities to long-term flow variability in a Sonoran Desert stream. Global Change Biology 16:2891–2900.

Stubbington, R., R. Sarremejane, and T. Datry. 2019. Alpha and beta diversity of connected benthic–subsurface invertebrate communities respond to drying in dynamic river ecosystems. Ecography 42:2060–2073.

Tonkin, J. D., M. T. Bogan, N. Bonada, B. Rios-Touma, and D. A. Lytle. 2017. Seasonality and predictability shape temporal species diversity. Ecology 98:1201–1216.

Tonkin, J. D., N. L. R. Poff, N. R. Bond, A. Horne, D. M. Merritt, L. V. Reynolds, J. D. Olden, A. Ruhi, and D. A. Lytle. 2019. Prepare river ecosystems for an uncertain future. Nature 570:301–303.

Townsend, C. R., M. R. Scarsbrook, and S. Dolédec. 1997. Quantifying Disturbance in Streams: Alternative Measures of Disturbance in Relation to Macroinvertebrate Species Traits and Species Richness. Journal of the North American Benthological Society 16:531–544.

Vander Vorste, R., R. Stubbington, V. Acuña, M. T. Bogan, N. Bonada, N. Cid, T. Datry, R. Storey, P. J. Wood, and A. Ruhí. 2021. Climatic aridity increases temporal nestedness of invertebrate communities in naturally drying rivers. Ecography 44:860–869.

Vanschoenwinkel, B., F. Buschke, and L. Brendonck. 2013. Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity. Ecology 94:2547–2557.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:407–407.

Wood, P. J., and G. E. Petts. 1999. The influence of drought on chalk stream macroinvertebrates. Hydrological Processes 13:387–399.

Ye, L., and N. B. Grimm. 2013. Modelling potential impacts of climate change on water and nitrate export from a mid-sized, semiarid watershed in the US Southwest. Climatic Change 120:419–431.

APPENDIX A

TABLES AND FIGURES

Table 1. Study site information, watershed characteristics, flow-regime variability (σ_{hf}), mean net annual anomaly (NAA), and highest Maximum Blue Noise observed during the study period.

Site name	USGS gage number	Number of surveys	Site location	Watershed area (ha)	Mean discharge (m^3/s)	σ_{hf}	NAA	Max blue noise
Agua Fria	09512500	6	Central	151,514	0.402	3.28	0.042	26.90
Babocomari	09471380	5	South	40,844	0.104	4.01	-8.09	26.13
Bonita	09447800	6	East	78,218	0.130	2.19	0.097	26.90
Eagle	09447000	6	East	161,097	1.24	0.56	0.051	24.60
Ramsey	09470750	6	South	1,064	0.016	5.74	7.412	75.90
San Francisco	09444500	6	East	716,391	4.61	0.49	0.059	413.9
San Pedro	09471000	6	South	319,605	0.893	1.15	0.050	242.0
Santa Cruz	09480500	6	South	138,046	0.229	5.64	-0.01	135.2
Sycamore	09510200	4	Central	42,476	0.461	5.19	0.359	163.3
Verde	09503700	6	Central	649,310	0.964	0.65	0.005	47.49
Wet Beaver	09505200	6	Central	28,749	0.697	0.93	0.039	47.18

Table 2. Linear regression models of metrics summarizing variation across sites in macroinvertebrate diversity. All diversity metrics were arcsine transformed and represent the highest beta diversity with its associated components measured at each site. Models were composed of mean net annual anomaly magnitude (NAA), flow-regime variability (σ_{hf}), and regime-shift frequency (RSF). Best supported models (ΔAICc < 2) are bolded.

K = number of predictors +2

exp(-0.5*Δ) = model likelihood

ω_i = model weight

Diversity metric	Model	K	AICc	ΔAICc	exp(-0.5*Δ)	ω_i
Beta diversity	**RSF**	**3**	**- 1.865**	**0.000**	**1.000**	**0.454**
	NAA	**3**	**-0.572**	**1.293**	**0.524**	**0.238**
	σ_{hf}	**3**	**- 0.362**	**1.503**	**0.472**	**0.214**
	σ_{hf}+ RSF	4	3.027	4.892	0.087	0.039
	NAA + RSF	4	3.320	5.185	0.075	0.034
	σ_{hf} + NAA	4	4.406	6.271	0.043	0.020
	σ_{hf} + NAA + RSF	5	10.26	12.12	0.002	0.001
Richness difference	**RSF**	**3**	**18.49**	**0.000**	**1.000**	**0.362**
	NAA	**3**	**18.92**	**0.426**	**0.808**	**0.292**
	σ_{hf}	**3**	**19.17**	**0.678**	**0.713**	**0.258**
	NAA + RSF	4	22.97	4.477	0.107	0.039
	σ_{hf} + RSF	4	23.66	5.165	0.076	0.027
	σ_{hf} + NAA	4	24.15	5.658	0.059	0.021
	σ_{hf} + NAA + RSF	5	30.28	11.79	0.003	0.001
Replacement	**NAA**	**3**	**11.11**	**0.000**	**1.000**	**0.397**
	RSF	**3**	**11.92**	**0.812**	**0.666**	**0.265**
	σ_{hf}	**3**	**12.01**	**0.902**	**0.637**	**0.253**
	NAA + RSF	4	15.90	4.793	0.091	0.036
	σ_{hf} + NAA	4	16.34	5.225	0.073	0.029
	σ_{hf} + RSF	4	17.15	6.042	0.049	0.019
	σ_{hf} + NAA + RSF	5	23.23	12.12	0.002	0.001

Table 3. Variable weights of flow-regime variability (σ_{hf}), mean net annual anomaly (NAA), and regime shift frequency (RSF) for the eleven sites. Diversity metrics are the same as those shown in Table 2. The predictor variables with the highest weights are bolded.

ω_j = variable weight

Diversity metric	Predictor variable	ω_j
Beta diversity	σ_{hf}	0.274
	NAA	0.293
	RSF	**0.528**
Richness difference	σ_{hf}	0.307
	NAA	0.353
	RSF	**0.429**
Replacement	σ_{hf}	0.302
	NAA	**0.463**
	RSF	0.321

Table 4. Linear regression models of metrics summarizing seasonal variation in macroinvertebrate diversity. All diversity metrics were arcsine transformed and represent seasonal measures of beta diversity, richness difference, and replacement across sites. Models were composed of Maximum Blue Noise and time since last maximum blue noise in days (Time Since). Best supported models (ΔAICc < 2) are bolded.

K = number of predictors +2

exp(-0.5*Δ) = model likelihood

ω_i = model weight

Diversity metric	Model	K	AICc	ΔAICc	exp(-0.5*Δ)	ω_i
Beta diversity	**Max blue noise**	**3**	**-9.053**	**0.000**	**1.000**	**0.665**
	Max blue noise + Time Since	4	-6.881	2.172	0.338	0.224
	Time Since	3	-5.471	3.582	0.167	0.111
Richness difference	**Max blue noise**	**3**	**29.40**	**0.000**	**1.000**	**0.588**
	Time Since	**3**	**31.32**	**1.923**	**0.382**	**0.225**
	Max blue noise + Time Since	4	31.70	2.296	0.317	0.187
Replacement	**Max blue noise**	**3**	**4.400**	**0.000**	**1.000**	**0.451**
	Time Since	**3**	**4.597**	**0.197**	**0.906**	**0.409**
	Max blue noise + Time Since	4	6.739	2.338	0.311	0.140

Table 5. Variable weights of Maximum Blue Noise and time since last maximum blue noise in days (Time Since) across seasons for the eleven sites. Diversity metrics are the same as those shown in Table 4. The predictor variables with the highest weights are bolded.

ω_j = variable weight

Diversity metric	Predictor variable	ω_j
Beta diversity	**Maximum Blue Noise**	**0.889**
	Time Since	0.335
Richness difference	**Maximum Blue Noise**	**0.775**
	Time Since	0.412
Replacement	**Maximum Blue Noise**	**0.591**
	Time Since	0.549
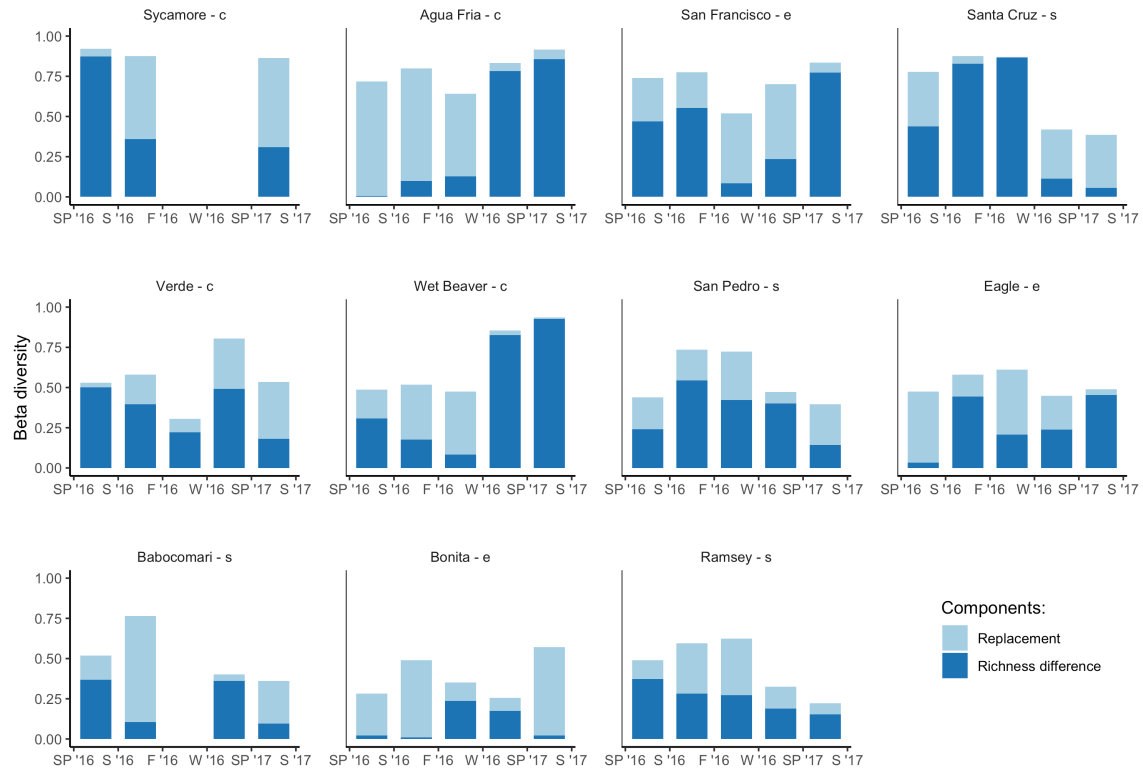
Figure 1. Seasonal observations of square root transformed beta diversity, richness difference, and replacement across sites. Missing values are from missing macroinvertebrate surveys due to intermittency. Richness difference and replacement sum to beta diversity and are calculated for each survey. Sites are ordered from highest to lowest total beta diversity. Letters next to each site name correspond to site location (c = central, e = east, s = south).

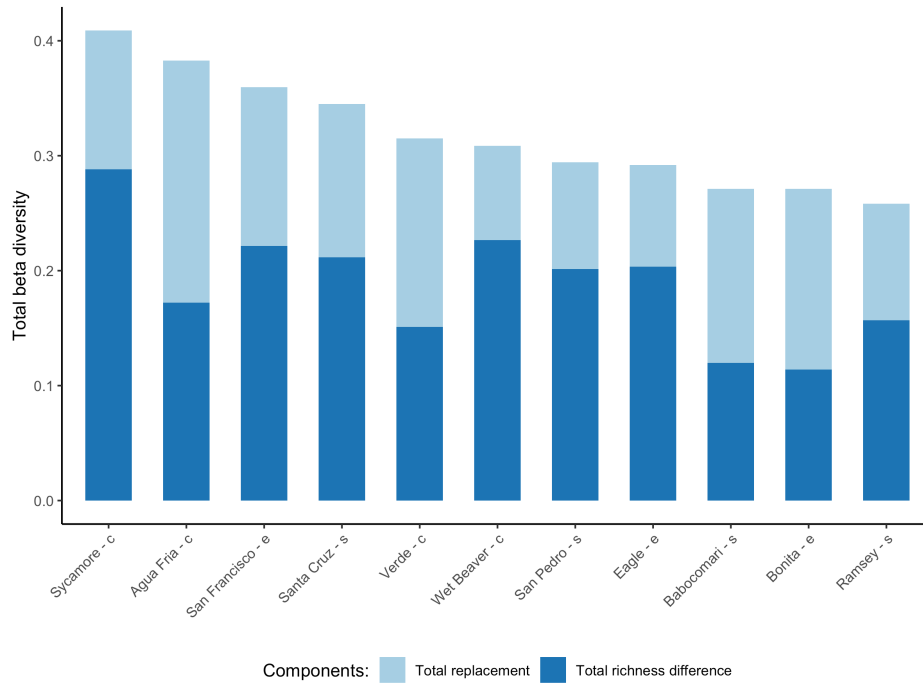SP = spring, S = summer, F = fall, W = winter

Figure 2. Total values of square root transformed beta diversity, richness difference, and replacement across all sites. Total richness difference and replacement sum to total beta diversity. Sites are ordered from highest to lowest total beta diversity. Letters next to each site name correspond to site location (c = central, e = east, s = south).
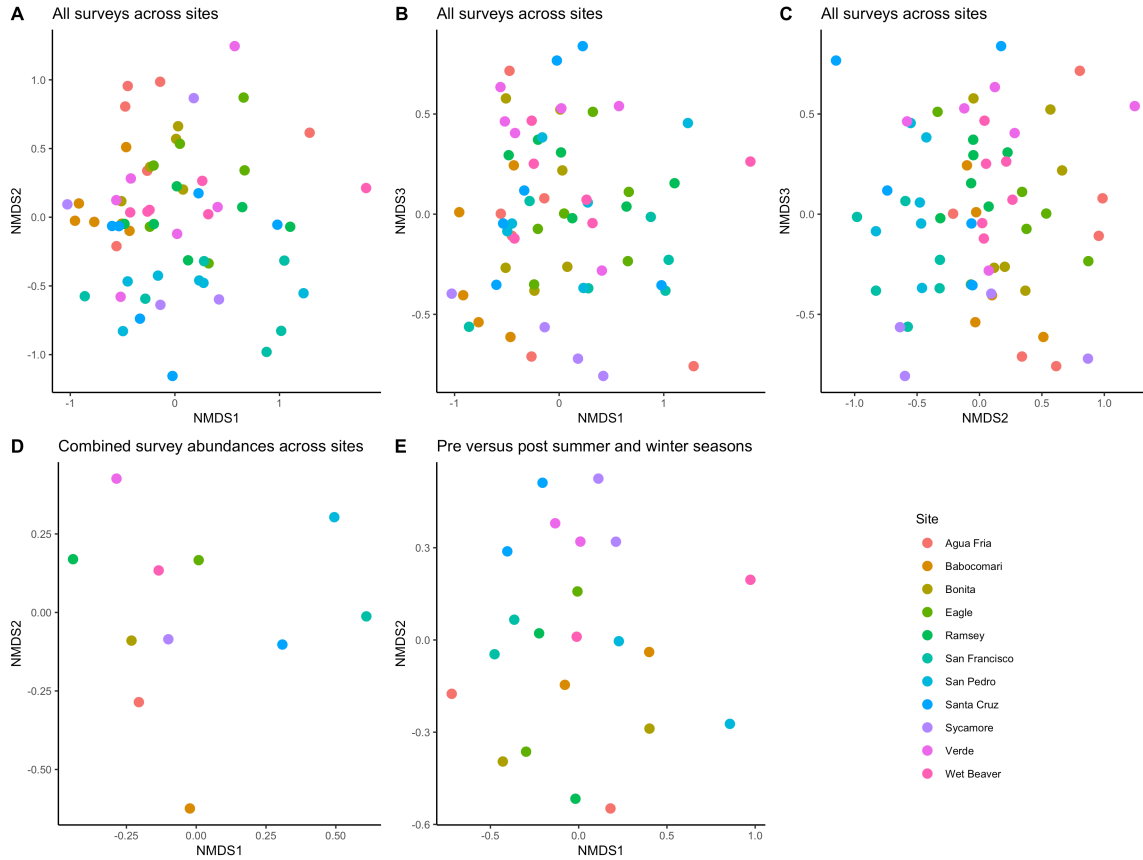
Figure 3. Nonmetric multidimensional scaling (NMDS) plots based on untransformed seasonal macroinvertebrate abundances across all sites (A-C), untransformed abundances summed across surveys for each site (D), and untransformed abundances summed between alternating surveys for each site (E). Stress for plots A-C, D, and E are 0.1411, 0.1162, and 0.1748, respectively.
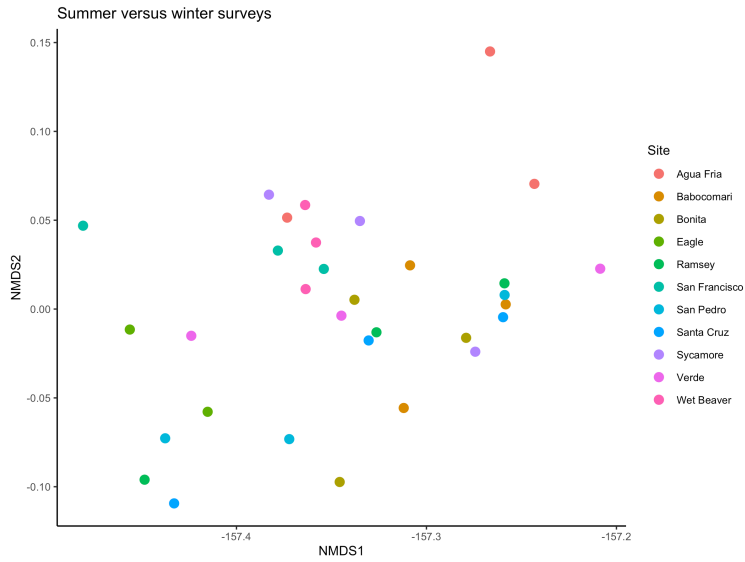
Figure 4. Nonmetric multidimensional scaling (NMDS) plot of untransformed summed macroinvertebrate abundances for one winter and two summer surveys. Stress = 4.378e-05.