Food Webs Across the Stream-Riparian Boundary:

Disentangling the Influence of Hydrologic Variability and Resource Dynamics

by

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ABSTRACT

Spatial and temporal patterns of biodiversity are shaped, in part, by the resources available to biota, the efficiency of resource transfer through the food web, and variation in environmental conditions. Stream and riparian zones are dynamic systems connected through reciprocal resource exchange and shaped by floods, droughts, and long-term patterns in the quantity, timing, and variability of streamflow (flow regime). The interdependent nature of the stream-riparian ecosystem defies the scope of any single discipline, requiring novel approaches to untangle the controls on ecological processes. In this dissertation, I explored multiple mechanisms through which streamflow and energy flow pathways maintain the community and trophic dynamics of desert stream and riparian food webs. I conducted seasonal sampling of Arizona streams on a gradient of flow regime variability to capture fluctuations in aquatic communities and ecosystem production. I found that flow regime shapes fish community structure and the trajectory of community response following short-term flow events by constraining the life history traits of communities, which fluctuate in prevalence following discrete events. Streamflow may additionally constrain the efficiency of energy flow from primary producers to consumers. I estimated annual food web efficiency and found that efficiency decreased with higher temperature and more variable flow regime. Surprisingly, fish production was not related to the rate of aquatic primary production. To understand the origin of resources supporting aquatic and riparian food webs, I studied the contribution of aquatic and terrestrial primary production to consumers in both habitats. I demonstrated that emergent insects “recycled” terrestrial primary production back to the riparian zone, reducing the proportion of aquatic primary production in emergent insect

biomass and riparian predator diet. To expand the concept of stream and riparian zones as an integrated ecosystem connected by resource cycling through the food web, I introduced a quantitative framework describing reciprocal interconnections across spatial boundaries and demonstrated strong aquatic-riparian interdependencies along an Arizona river. In this dissertation, I develop a novel perspective on the stream-riparian ecosystem as an intertwined food web, which may be vulnerable to unforeseen impacts of global change if not considered in the context of streamflow and resource dynamics.

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CHAPTER 1

INTRODUCTION

Ecosystems are studied at the scale and scope required to discern patterns and processes over a finite range of observations. Although it is inherently necessary to bound systems for observational or experimental analysis, ecological processes occur over spatial and temporal scales that defy convenient definitions—such as a forest, field, or stream (Post et al. 2007a). The exchange of nutrients, detritus, and organisms across spatial boundaries (resource subsidies) frequently alters consumer population and trophic dynamics, and ecosystem nutrient and energy budgets, obfuscating the distinction between individual ecosystems (Polis et al. 1997). Temporal instability in environmental conditions actuates variation in community structure over time (Menge and Sutherland 1987), influencing the effects of locally produced and cross-boundary resources on ecological processes (Nakano and Murakami 2001, Marcarelli et al. 2020).

In the stream-riparian ecosystem, spatial and temporal patterns in trophic interactions and community structure are driven by hydrologic variability and resource dynamics, integrating two physically distinct habitats. Streamflow is a master variable in flowing waters that shapes and maintains biodiversity, productivity, and trophic interactions (Power et al. 1995). Over many years, the magnitude, timing, frequency, duration, and variability of streamflow constitutes the flow regime; which regulates channel geomorphology, succession, productivity, and biodiversity of both active channels and riparian floodplains (Poff et al. 1997). Dynamic cycles of floods and droughts maintain the natural community structure of riparian plant communities, which provide habitat and services for animals (Merritt and Bateman 2012, Lytle et al. 2017). Flow regimes exert long-term evolutionary pressure on the behavioral, morphological, and reproductive adaptations of aquatic and riparian biota (Lytle and Poff 2004), and constrain the distribution of species within a watershed according to life history traits (Poff 1997). Highly variable flow regimes shorten food chain length and select for small-bodied taxa, potentially reducing the productivity of upper trophic levels, while more stable regimes promote longer food chains with long-lived, large-bodied species (Sabo et al. 2010a, Mims and Olden 2013).

At shorter time scales, floods and droughts are discrete flow events that restructure community composition. Floods scour the stream channel, removing sedentary organisms and primary producers (Grimm and Fisher 1989) and initiate new trajectories of primary and secondary production (Fisher et al. 1982, Bernhardt et al. 2018), while low flows reduce habitat size and quality (Lake 2003, Matthews and Marsh-Matthews 2003). Despite an extensive body of literature, ecological response to flow has typically been studied at either the short-term event scale, or the long-term scale characterized by regimes, yielding continued debate on the definition and role of disturbance in ecology (Resh et al. 1988, Poff 1992, Fox 2013). Developing a greater understanding of the interconnected mechanisms through which flow variability shapes aquatic ecosystems requires expanding the scope of hydrologic constraints used in ecological models to simultaneously examine multiple temporal scales.

Uniting the constraints imposed by hydrologic variation on community structure and trophic dynamics with cross-boundary resource exchange provides a novel approach to integrate the ecological processes of aquatic and riparian ecosystems. Bidirectional, reciprocal, exchange of resources between streams and riparian zones can initiate cascading trophic interactions that are perpetuated back-and-forth and sustain the biodiversity of both (Nakano and Murakami 2001, Baxter et al. 2005). However, research on cross-boundary resource subsidies has historically been narrow in scope, taking either an ecosystem ecology approach of studying fluxes and budgets of energy and nutrients (Fisher and Likens 1973, Minshall 1978) or a food web approach focused on populations and trophic dynamics (Nakano et al. 1999, Sabo and Power 2002a, Marcarelli et al. 2011). Flow events and seasonality influence the quantity, quality, and habitat of origin of resources supporting consumers over time. Thus, it is necessary to jointly apply ecosystem and food web approaches to evaluate the multiple spatial and temporal scales sustaining ecosystem functions—within and across spatial boundaries.

Freshwater and riparian ecosystems support a large portion of global biodiversity, despite occupying only a small fraction of the landscape, but are facing myriad threats, including climate change, streamflow alteration, and physical modification (Vörösmarty et al. 2010, Poff et al. 2011, Reid et al. 2019). Interactions across the stream-riparian boundary add additional complexity to predicting ecosystem response to global change because alterations in one habitat can have unforeseen consequences in linked but distal systems (Larsen et al. 2016, Gounand et al. 2018). Adapting ecological research to a nonstationary climate with uncertain future conditions necessitates uniting the scopes of traditional disciplines over spatial and temporal scales.

SCALE AND SCOPE

In this dissertation, I evaluate the interconnections between environmental and ecological patterns across scales in streams and riparian zones in the American Southwest. In four chapters, I apply concepts from the fields of community, food web, and ecosystem ecology to demonstrate how the effects of hydrologic variability and resource dynamics on distinct ecological processes can reverberate through multiple pathways, uniting stream and riparian zones as one integrated ecosystem.

Chapter 2 examines how temporal fluctuations in fish community structure and directional response to discrete, unpredictable flow events are contextually dependent on the long-term flow regime due to ecological filtering of life history strategies. Fish can be placed on a triangular continuum of life history strategies according to tradeoffs in adaptive traits that are favored in more stable, variable, or seasonal environments (Winemiller and Rose 1992). The distribution of strategies within a community can be predicted by patterns of hydrologic variability (Olden and Kennard 2010) and may additionally influence short-term changes in community composition. I used two years of quarterly estimates of fish populations in nine streams across Arizona to calculate community structure, the distribution of life history strategies, and how each varied over time relative to flow regime and in response to discrete flow events.

Chapter 3 explores ecological efficiency in riverine ecosystems and evaluates the mechanisms through which flow regime and other hypothesized constraints influence the transfer of energy from primary producers to consumers. While resource availability, disturbance, biotic interactions, and efficiency of energy transfer through food webs are known drivers of the production of consumer biomass (Lindeman 1942, Resh et al. 1988, Hairston and Hairston 1993), food web efficiency remains mostly unstudied in the field. Using the same set of streams as in Chapter 2, I applied an ecosystem ecology approach by measuring rates of primary and secondary production to estimate food web efficiency—defined as the rate of fish secondary production relative to aquatic gross primary production. I then explored relationships between food web efficiency and hypothesized constraints that have been documented in experimental settings – nutrient availably, food chain length, and temperature (Dickman et al. 2008, Barneche et al. 2021). I additionally investigated the untested effect of flow regime on food web efficiency in riverine ecosystems.

Chapter 4 investigates reciprocal resource exchange between streams and riparian zones, expanding on the traditional concept of a resource subsidy to trace "recycled" terrestrial primary production consumed by aquatic invertebrates back to riparian predators. Aquatic primary production is a high-quality resource that contains essential fatty acids and may be consumed by aquatic biota preferentially over externally produced plant detritus (Marcarelli et al. 2011, Brett et al. 2017). Many larval invertebrates consume a mixture of aquatic and terrestrial primary production, and emergent adults recycle some portion of terrestrially produced resources back to the riparian zone (Kraus and Vonesh 2012). The flux of emergent invertebrates is therefore not a homogenous resource for riparian predators and may contain different portions of aquatic and terrestrial production. I measured the flux of aquatic-to-riparian, riparian-to-aquatic, and recycled terrestrial resources at two rivers to evaluate temporal changes in quantity and quality of resources available to consumers. I further calculated the contribution of locally produced and cross-boundary primary production to consumer diet and explored the potential for preferential resource consumption by both aquatic and riparian consumers.

Chapter 5 develops and tests a novel quantitative framework for describing reciprocal reliance on cross-boundary resources in spatially distinct habitats—establishing the concept of an integrated ecosystem. I calculated dietary sources of aquatic and riparian consumers on a Wild and Scenic designated river in Arizona to determine how cross-boundary resources reciprocally sustain both ecosystem compartments and cycle up the food web to indirectly support upper trophic level consumers. This framework for measuring the extent of reciprocal inter-reliance between spatially distinct food webs has broad applicability to diverse ecosystems that almost universally exchange resources across permeable boundaries.

In Chapter 6, I summarize the main findings of this dissertation, synthesize the results, and discuss their implications for stream-riparian ecosystems facing mounting pressure from global change as well as the potential for application in the broader field of ecology.

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CHAPTER 2

FLOW VARIATION AT MULTIPLE SCALES FILTERS FISH LIFE HISTORIES AND CONSTRAINS COMMUNITY DIVERSITY IN DESERT STREAMS

ABSTRACT

Environmental regimes shape communities by selecting for adaptive life histories, behaviors, and morphologies. In turn, at ecological timescales, discrete extreme events may still cause short-term changes in composition and structure via mortality and recolonization of the species pool. Here, we illustrate how short-term variation in desert stream fish communities following floods and droughts depends on the context of the long-term flow regime through ecological filtering of life history strategies. Using quarterly measures of fish populations in streams spanning a gradient of precipitation variability in Arizona, USA, we quantified temporal change in community composition and life history strategies. In streams with highly variable flow regimes, fish communities were less diverse, fluctuation in species richness was the principle mechanism of temporal change in diversity, and communities were dominated by opportunistic life history strategies. Conversely, relatively stable flow regimes resulted in more diverse communities with greater species replacement and dominance of periodic and equilibrium strategies. The effects of anomalous high- and low-flow events were also modified by strong dependence on flow regime. Diversity in streams with more stable flow regimes was lower following large floods than after seasons without floods, whereas diversity was independent of high-flow events in streams with flashier flow regimes. Likewise, community life-history composition was more dependent on antecedent

anomalous events in stable compared to more temporally variable regimes. These findings indicate that anomalous events are a second-level filter nested within the disturbance regime. We additionally show that temporal variation in community composition depends on event magnitude in context of the long-term regime, suggesting that ongoing changes to global environmental regimes will likely drive new patterns of community response to extreme events.

INTRODUCTION

Temporal fluctuations in environmental conditions regulate the structure of communities and their variability over time (Menge and Sutherland 1987, Tilman 1996). Punctuated, extreme environmental events that alter community composition and abundance account for much of the dynamic nature of biotic communities (Connell 1978, Sousa 1979). Over longer timescales, spatial and temporal patterns in the type, frequency, intensity, timing, and spatial extent of extreme events constitute environmental regimes (Sabo and Post 2008, Grimm et al. 2017). Regimes control community stability and resilience (Connell and Sousa 1983), and select for adaptive life history strategies that shape patterns of community succession (*sensu* Grime 1977). Community-level responses to extreme events are often challenging to predict because these two timescales (i.e., event and regime) are largely studied independently (Datry et al. 2017, Vander Vorste et al. 2021). However, these scales interact to shape the trajectory of post-event community dynamics. For example, drought universally increases tree mortality, but impacts on growth and recruitment are biome-dependent (McDowell et al. 2020), and higher atmospheric CO_2 raises the likelihood that overfishing disturbances will cause state changes in coral reefs (Anthony et al. 2011). Understanding such context dependencies could help identify scenarios where the effects of a particular extreme event could be dampened—or conversely, particularly harmful.

Long-term data could be analyzed to develop ecological theory describing context dependency of community response to events on regimes. Plant communities in tallgrass prairies differ in composition between habitats with distinct burn regimes, with communities subject to frequent fires experiencing lower year-to-year variation (Collins 2000). Using the same data, it would be possible to ask: does community succession following a fire differ in recovery rate, assemblage composition, or species replacement between burn regimes? The effects of discrete events may also compound to amplify differences between environmental regimes. Urban parks have lower species richness than non-urban preserves – regime – but have greater increase in richness in a wet year following a dry year than non-urban communities – event contextualized by regime (Wheeler et al. 2021).

In the ecological literature, disturbance is defined as a discrete event that disrupts ecosystem, organism, resource, substrate, or physical environmental conditions, allowing for colonization by new individuals (Sousa 1984). However, this definition of disturbance is dependent on the magnitude of biotic or physical responses, making an exact threshold difficult to identify. In contrast, the residual between observed and expected environmental conditions with respect to long-term patterns provides a quantitative and unitless measure of an anomalous event. By focusing on residual variation, anomaly magnitude statistically defines the extremity of an event without depending on ecological response in a unique system (Sabo and Post 2008). For many ecological processes, timing is critical, and anomalies capture unpredictable timing and magnitude of events. The distribution of anomalies over a longer timescale constitutes a composite signature of the timing, magnitude, and frequency of a series of events – the regime (Sabo and Post 2008). While the roles of disturbances and environmental regimes in shaping biotic communities are well documented, the two are rarely considered together and have not been mechanistically linked to patterns of community change over time.

Events and Regimes in Riverine Ecosystems

In streams and rivers, flow regimes are characterized by the magnitude, timing, and variability of flow over many years (Poff et al. 1997). Flow regimes exert evolutionary pressure on organismal life history and morphological traits (Lytle and Poff 2004), maintain native community assemblages (Bunn and Arthington 2002), shape trophic interactions (Sabo et al. 2010a), and mediate temporal variation in community structure (Tonkin et al. 2017). At shorter timescales, anomalous hydrologic events such as floods and drought disrupt biotic and abiotic processes (Resh et al. 1988). Floods physically alter habitat and remove organisms (Grimm and Fisher 1989), while prolonged low flows cause habitat loss and mortality (Lake 2003, Matthews and Marsh-Matthews 2003). These discrete events influence survivorship and recruitment, and temporarily alter community composition by selecting for species that can persist following an event of a given magnitude or timing relative to sensitive life stages and development. The two timescales of flow variability have sometimes been conflated and have generated a rich debate on what is a disturbance, and if it can be predictable (Resh et al. 1988, Poff 1992).

Here, we explore the hypothesis that the ecological consequences of disturbance events are dependent on the evolutionary context created by regimes.

Ecological filters are environmental or habitat characteristics that influence the likelihood of a species persisting in a local community due to their morphological and life history traits. Environmental variability may filter organismal life history traits through tradeoffs between adaptation to regimes and responses to extreme events. The composition of life history traits in riverine communities are therefore constrained by flow regime, which acts as an environmental filter by influencing physical and chemical attributes of habitats (Poff 1997). When regimes are characterized by environmental variation with predictable frequency and magnitude, life history traits that are synchronous with the regime are favored, such as concurrent invertebrate diapause to survive predictable droughts (Lytle 2001). Alternatively, communities filtered by unpredictable regimes are expected to experience less change over time and contain species with asynchronous life history traits favoring bet-hedging strategies, illustrated by increased asynchrony in hatching of some invertebrate populations in more variable flood regimes (Lytle and Poff 2004, Tonkin et al. 2017). Adaptation to unpredictable events in stable flow regimes may impose a high cost relative to the benefit on evolutionary timescales, thus communities in these environments may have a greater response to unpredictable events at ecological timescales.

Three life history strategies of freshwater fish represent a triangular continuum of tradeoffs in adaptive traits; opportunistic strategists are favored in unpredictable environments, periodic strategists in seasonally variable but predictable environments, and equilibrium strategists in stable environments with abundant resources (Winemiller and Rose 1992, Winemiller 2005). Distribution of freshwater fish life history strategies are predictably filtered by gradients in hydrologic variability (Olden and Kennard 2010) and anthropogenic changes to flow regime (Mims and Olden 2013). We propose that local species pools at one time point reflect both long-term environmental regime and recent events, while temporal patterns of taxonomic diversity are a function of hierarchical filtering of life histories (Figure 1).

Here, we assessed the relative effects of flow regime and hydrologic events on fish communities in Sonoran Desert streams to determine if temporal community variation and response to events are dependence on the context of regimes. We compared temporal patterns in beta diversity and its components: replacement (simultaneous species gain and loss) and richness difference (patterns of nestedness caused by differences in species richness and abundance), which quantify the magnitude and pathways driving spatial or temporal community variation (Legendre 2014, Ruhí et al. 2017). Species replacement can indicate environmental filtering by abiotic factors (Leprieur et al. 2011), while richness difference might reflect changes in habitat capacity and configuration (Dong et al. 2015). We hypothesized that temporal variation in community composition is dependent on flow regime due to filtering of life history strategies. Additionally, dynamic interplay between the intensity of discrete hydrologic events and the periodic nature of regimes further filters life history strategies at seasonal timescales to constrain the magnitude and mechanisms of short-term variation in community composition. Although this study focuses on floods and droughts, and the flow regimes in which these events occur, our hypotheses around the interaction between regimes and discrete events are broadly applicable to other biotic communities and could help clarify long-standing uncertainty surrounding the role of disturbance in ecology (Fox 2013, Huston 2014, Jentsch and White 2019).

METHODS

We studied nine streams that encompassed a gradient of seasonality in precipitation and resulting streamflow regimes across Arizona, USA (Appendix A: Figure S1). Precipitation in southern and eastern Arizona predominantly occurs in the summer months (July-September) during short, intense monsoonal storms. Central Arizona receives about half of its annual precipitation in the winter from frontal storms and generally has a weaker monsoon (Sheppard et al. 2002). Sites were located near US Geological Survey (USGS) gaging stations, and upstream of major human development (Appendix A: Table S1). Annual average precipitation at sample sites ranged from 350 to 456 mm/yr and average temperature from 14.54 to 20.42 °C (Appendix A: Table S2; www.worldclim.org).

Fish populations at each site were surveyed approximately quarterly for two years to capture biologically relevant changes in environmental conditions: after winter storms, before summer low-flow and monsoons, after monsoons, and before winter storms. We established permanent 100-m reaches containing both riffle and pool habitats for fish sampling at each site. We used 6-mm mesh nets to block the top and bottom of the reach and conducted three-pass depletion backpack electrofishing (Model LR-24 Electrofisher, Smith- Root, Vancouver, Washington, USA) and identified each fish to species. Intermittent flow (Sycamore Creek) and floods reduced the total number of surveys for some sites (Appendix A: Table S1). We used the *FSA* package (Ogle et al. 2020) to calculate population size for each species with k-pass depletion using maximum weighted likelihood estimation (Carle and Strub 1978). All statistical analyses were conducted in R (R Core Team 2019).

To quantify long-term flow regimes and flow anomalies during the study period, we analyzed 20 years of mean daily discharge (01/01/1997/ – 12/31/2018) collected by the USGS at each site (06/06/1998 – 04/15/2019 for one site [Bonita]). We used the Discrete Fast Fourier Transform (DFFT) following Sabo and Post (2008) to extract seasonal signals of hydrologic variation from the frequency domain of the time series and quantify expected mean daily discharge, accounting for seasonality. Daily flow observations were converted to standardized residuals (observed – expected) to quantify flow anomaly. We then summarized three metrics that described 1) flow regime variability (high-flow sigma – σ_{hf}), 2) low-flow events (LSAM), and 3) high-flow events (HSAM) using the *discharge* package (Shah and Ruhi 2019), and used these as predictors of temporal variation in fish diversity. σ_{hf} is calculated as the standard deviation of "catastrophic" events, defined as discharge anomalies exceeding predicted discharge by more than two standard deviations (Sabo and Post 2008). σ_{hf} thus quantifies the prevalence of extreme high-flow events relative to small discrepancies from seasonal flows. We identified the lowest and highest flow spectral anomaly magnitude (LSAM and HSAM, respectively) that occurred between consecutive surveys and in the three months preceding the first survey to quantify both the magnitude of extreme flow events and seasons with flows within the expected range (Figure 2).

Diversity Analysis

To test our hypothesis that flow regime filters local species pools and drives community change over time, we calculated average abundance-weighted taxonomic diversity (Shannon–Weaver) and beta diversity for each site. We calculated beta diversity with square-root-transformed population estimates and partitioned beta diversity into replacement and richness difference components using Podani family, Bray-Curtis indices with the '*beta.div.comp*' function in the *adespatial* package (Legendre 2014). Beta diversity over the two-year study evaluates heterogeneity of community composition over time and the components of change driving this variation; change in the identity of species (replacement) or change in the number of species (richness-difference). We used linear regressions to assess how flow regime variability (σ_{hf}) correlates with each measure of diversity.

We assessed our hypothesis that community response to anomalous events depends on flow regime using seasonal measures of Shannon diversity, Bray-Curtis dissimilarity, replacement, and richness difference. Bray-Curtis dissimilarity ranges from 0-1 and is the sum of replacement and richness difference between seasons. Communities at consecutive surveys that have identical population size and composition have a dissimilarity value of 0 and a complete change in composition would result in a value of 1. For sites with eight surveys, we calculated eight values of Shannon diversity and seven measures of dissimilarity, replacement, and richness difference to quantify change between consecutive surveys. We compared a set of six models for each measure of diversity, constructed to test the effects of flow regime, anomaly magnitude, and their interaction while reducing model complexity. Fixed effects in each model were: 1) null,

2) high-flow anomaly (HSAM), 3) low-flow anomaly (LSAM), 4) regime variability (σ_{hf}), 5) HSAM + σ_{hf} + HSAM • σ_{hf}, 6) LSAM + σ_{hf} + LSAM • σ_{hf}. All models included site as a random effect and compound symmetry correlation structure of variances arising from repeated measures over time. All flow variables were mean centered and standardized prior to analysis and tested for collinearity. All correlation coefficients were < 0.7 with VIF values < 2. We used Akaike's Information Criterion for small sample size (AICc) to compare relative support between models using a multi-model inference framework. This approach allowed us to assess the relative effects of flow regime, flow anomalies, and the contextual dependence of event magnitude within a regime on intra-annual variation in fish diversity.

Life History Analysis

We analyzed life history traits to assess how fish community diversity and seasonal changes in composition might arise from interaction between flow regime and anomalous events. We obtained life history and ecological traits for all 15 species observed in this study from multiple sources (Mims et al. 2010, Giam and Olden 2016, Kominoski et al. 2018) and selected a subset of 10 traits relevant to life history strategies (Winemiller and Rose 1992): maximum total body length (cm), age at maturation (years), aspect ratio (of the caudal fin), longevity (years), egg size of fully yolked ovarian oocytes (mm), fecundity (total number of eggs or offspring per female per spawning season), spawning frequency (categorized as single or multiple), parental care (scale 0-4, Winemiller 1989), trophic guild (herbivore, omnivore, invertivore, invertivore/piscivore, and piscivore), and water column position (benthic or non-benthic).

We evaluated the contribution of each life history trait to the total species pool observed at each site over the duration of the study to test the hypothesis that regimes selectively filter for specific traits. We mean centered and scaled all continuous traits, then multiplied the species x trait matrix and a site x species matrix containing the presence or absence of all species observed at each site over the study period, creating a matrix of trait abundance in each regional species pool. Categorical trait abundances were averaged to determine proportional abundance (0-1) for each trait state per site (Hale et al. 2015). We then used Gower's distance to calculate the distance between each site pair in multidimensional trait space followed by distance-based redundancy analysis (db-RDA) to assess the relationships between functional trait composition at each site and potential environmental predictors. Characteristics of aquatic habitat that are known to affect community dynamics, flow regime (σ_{hf}), watershed area (ha), and average annual discharge (m^3/s), were considered as environmental predictors. Similar to redundancy analysis, db-RDA is a constrained ordination but can be used with distance or dissimilarity matrices (Legendre and Andersson 1999). We used the '*envfit*' function from the *vegan* package (Oksanen et al. 2019) to test correlation between ordination axes and functional traits.

For each site, we also calculated the distribution of life history strategies in the fish community following the triangular continuum model of Winemiller and Rose (1992) that describes opportunistic, periodic, and equilibrium strategies. The model differentiates species along three axes: 1) ln(age at maturation +1), 2) ln(fecundity), and 3) juvenile investment, calculated as ln(egg size +1) + ln(parental care +1) (Winemiller 1989). Instead of assigning species to one life history classification, we placed species on the three-axis continuum and calculated their relative affinity to each strategy using ordination techniques (Olden and Kennard 2010). First, we computed synthetic endpoint values for each strategy: opportunistic (minimum age at maturation, minimum fecundity, and minimum juvenile investment), periodic (maximum age at maturation, maximum fecundity, and minimum juvenile investment), and equilibrium (maximum age at maturation, mean fecundity, and maximum juvenile investment) based on the range of values in our species list. We then calculated the Euclidean distance between each species and the three endpoints, normalized the values between 0 and 1, and subtracted the value from one so that larger values denote greater association with a life history strategy (Appendix A: Figure S2). We multiplied the resulting species x life history strategy matrix by the site x species presence-absence matrix and calculated the proportional contribution of each life history strategy to the regional species pools. We ran a second db-RDA with proportional contributions of life history strategies for each site and the same set of environmental constraints to determine if life history strategy analysis explains more of the variation between sites given the environmental factors.

Finally, we used linear mixed-effects models to evaluate how flow events affect the proportional contribution of life history strategies in a fish community at one time point and if this effect is dependent on flow regime. We fit the same set of candidate models with combinations of metrics describing flow regime and events as in the previously described analysis of diversity. To calculate the seasonal distribution of life history strategies, we followed the same methods as for the db-RDA but used square-root-transformed seasonal abundance data. Proportional contribution of each strategy (opportunistic, periodic, and equilibrium) was used as a response variable for the set of six mixed-effects models. One site (Sycamore Creek) was removed from seasonal life history strategy analysis because only one species was observed.

RESULTS

Flow Regime Influence on Fish Diversity

Flow regime was a significant predictor of average taxonomic diversity within the two-year dataset. Flow regime also predicted the mechanisms of change in community composition over time, but not the magnitude of change. Specifically, average taxonomic diversity (Shannon diversity) was negatively correlated with long-term flow variation, measured by σ_{hf} (Figure 3). Average beta diversity was not correlated with σ_{hf} ($p = 0.258$); however, both the replacement and richness difference components of beta diversity were significantly correlated with σ_{hf} (Figure 3). Replacement was negatively correlated with σ_{hf}, indicating relatively greater change in community composition over time in streams with more stable flow regimes. Richness difference was positively correlated with σ_{hf}, with less temporal variation in the number of species and abundance of fish in more stable flow regimes than variable regimes. The ratio of replacement to richness difference was also negatively correlated with σ_{hf}, revealing that, independent of magnitude, beta diversity is driven by richness difference in sites with variable flow regimes and is more strongly influenced by replacement in more stable regimes.

Seasonal Variation in Fish Diversity

Seasonal measures of taxonomic diversity, dissimilarity, replacement, and richness difference between consecutive seasons varied within and between sites (Figure 4). All supported models of diversity metrics contained σ_{hf} as a predictor, and the interaction of flow regime with seasonal flow anomaly (HSAM or LSAM) was included in the supported set of models for three of the four response variables. Seasonal variation in Shannon diversity was predicted by the σ_{hf}-only model and an interaction model (σ_{hf}-HSAM). Community dissimilarity and replacement between seasons were best predicted by the σ_{hf}-only and the σ_{hf}-LSAM interaction models. When supported, models with interaction terms always had greater predictive power (marginal R^2) than σ_{hf}-only models (Table 1).

These interactions revealed that an anomalous flow event of the same magnitude drives different responses of Shannon diversity, dissimilarity, and replacement depending on local flow regime (Figure 5A). For example, Shannon diversity was influenced by anomalous flow events in streams with relatively stable flow regimes (predicted range 0.36-1.33), but was independent of antecedent high- or low-flow anomalies in flashier regimes (predicted range 0.22-0.32). Richness difference was only correlated with σ_{hf} (Table 1). Because the sum of replacement and richness difference equals dissimilarity, the three response variables are not independent (Appendix A: Table S3). However, the relative contributions of replacement and richness difference illustrate the mechanisms driving community change over time.

Community Life History

Distance-based redundancy analysis of life history trait composition of the fish community at each site was significant overall (ANOVA, $F_{3,5} = 1.960$, $p = 0.04$), and the environmental predictors explained 54% of observed variation in traits across sites. VIF values for all predictors (σ_{hf}, watershed area, and average annual discharge) were < 3. However, only the first axis (p = 0.038) and its associated environmental constraint, σ_{hf} (p= 0.006) which explained 37.2% of total between-site variation captured by the ordination, were significantly correlated with the composition of life history traits of species assemblages over the study period (Appendix A: Table S4). This suggests flow regime is more dominant in filtering life history traits of a local species pool than average annual discharge or watershed area. Of the 10 life history traits considered, only longevity, spawning frequency, omnivorous trophic guild, and vertical position in the water column were significantly correlated with the RDA (p < 0.05; Appendix A: Figure S3; Appendix A: Table S5).

Redundancy analysis of the proportional contribution of each life history strategy to the species pool observed at each site over the study was more strongly correlated with the environmental constraints (ANOVA, $F_{3,5}$ = 7.062, p = 0.012) than when considering each functional trait individually, explaining 80.9% of observed variation. Like life history trait distribution, only the first axis was significant (p = 0.009) and σ_{hf} was the only significant environmental constraint (p = 0.002), explaining 75.9% of variation captured by the ordination (Appendix A: Table S4). The proportional contribution of all three life history strategies was also significantly correlated with the first axis of the db-RDA (p < 0.001; Appendix A: Figure S3; Appendix A: Table S6), suggesting that differences in life history strategy composition corresponded with changes in flow regime.

Seasonal Life History Strategies

The proportional contribution of life history strategies to seasonal variation in fish communities changed between sites and over time within sites (Appendix A: Figure S4). Like models of seasonal fish diversity, σ_{hf} was included in all supported models (Table 2). Flow regime (σ_{hf}) and the interaction of σ_{hf} and LSAM were included in supported models for the contribution of opportunistic and periodic strategies to seasonal patterns of life history strategy composition. These results indicate that the proportional contribution of opportunistic and periodic strategies to a fish community in a highly variable flow regime change little following low-flow events (Figure 5B). Conversely, in low variability flow regimes, the percent contribution of the opportunistic strategy is predicted to increase following more extreme low-flow events, while the contribution of the periodic strategy is predicted to decrease (Figure 5B). σ_{hf} was the only supported predictor for the relative contribution of the equilibrium strategy. The contribution of the three life history strategies to a community are relative proportions and therefore non-independent responses, but together these patterns illustrate the how flow regime, flow anomalies, and their interaction result in directional changes in the composition of communities.

DISCUSSION

The role of disturbance events in shaping community structure on short timescales has long been a central tenet of ecological theory (Sousa 1979), but increasingly altered environmental regimes have prompted the necessity for new approaches to classic models (Poff 2018). Here, we demonstrate that seasonal changes in fish community structure and life history strategy composition in response to anomalous events is bounded by the ecological limits imposed by the flow regime. Over the two-year study period, average fish community diversity, patterns of species change over time, and the distribution of life history strategies were linearly correlated with flow regime variability, supporting the concept that flow regime is an ecological filter that shapes the regional species pool. Flow regime also influenced the effect of anomalous flow events on seasonal measures of diversity and components of beta diversity between seasons, suggesting support for the hypothesis that variation in community structure is contextually dependent on flow regime. The proportional distribution of life history strategies within a community at the seasonal timescale was similarly contingent on flow regime, illustrating the mechanism by which regimes filter life history strategies and anomalous events act as a second-level filter on a subset of life histories.

Environmental Drivers of Temporal Variation in Species Diversity

Fish communities are less diverse and more variable in composition over time in ecosystems with more variable flow regimes (Taylor et al. 2006). We found that taxonomic diversity and replacement are inversely correlated with flow regime variability, indicating reduced diversity of species available for replacement in more variable regimes drives this diversity-flow relationship. Flow regime and beta diversity were not correlated. However, we found that temporal variation in community composition is driven by change in species identity in highly variable flow regimes and variation in the number of species in low variability regimes, illustrated by the negative correlation of the ratio of replacement to richness difference with regime variability. A stronger understanding of how replacement and richness difference contribute to temporal variability in community composition could aid in locating priority sites for conservation by identifying unique assemblages, independent of species-richness (Ruhí et al. 2017). We demonstrate that considering local flow regime could further inform expected patterns of community variability.

Life history theory additionally identifies strategies adapted to the environment through demographic patterns and can help predict community response to changes in management or environmental conditions (Winemiller 2005). We found that environmental constraints, primarily flow regime, explained significant variation in longevity and spawning frequency, functional traits that describe demographic processes, across communities. However, flow regime was a stronger predictor of the distribution of life history strategies. These results demonstrate that life history strategy metrics are responsive to environmental conditions and communities are increasingly dominated by periodic and equilibrium strategies in more stable regimes. Communities downstream of dams, where flows are artificially stable, show similar patterns of relatively abundant equilibrium strategists and loss of opportunists (Mims and Olden 2013). Together with the results that Shannon diversity, replacement, and richness difference are correlated with flow regime, these findings support our hypothesis that flow regime filters life history strategies to determine how community composition changes over time.

Extreme flow events can reset communities by initiating successional trajectories of species abundance, diversity of life history traits, and food web dynamics (Power et al. 2013). Most studies of temporal change in community composition consider either environmental disturbances or differences in flow regime (reviewed in Lake 2003, Death

2010, Poff and Zimmerman 2010). We found that considering both better explains observed variation in communities over time. While mostly illustrative given the limited sample size of this study, we demonstrate that seasonal values of Shannon diversity, dissimilarity and replacement between seasons, and the relative proportion of opportunistic and periodic life history strategies depended on both the magnitude of recent anomalous flow events and flow regime. This suggests that anomalous events act on a set of life history traits filtered by the long-term flow regime and thus affect different short-term, regime-dependent responses.

In highly variable flow regimes, community dissimilarity was predicted to be greatest following seasons without large low-flow anomalies. Life history theory suggests the dominant contribution of opportunistic strategies to these communities, defined by short generation times, rapid population growth under favorable conditions, and resilience to high-magnitude events, drive this trend. Opportunists can additionally quickly recolonize vacated habitat and increase population size, leading to high richness difference. This interpretation is supported by low Shannon diversity and communities dominated by opportunistic strategies in highly variable streams in all seasons, regardless of antecedent flow conditions. In contrast, streams with relatively stable flows may change more in composition, decrease in diversity, and increase in prevalence of opportunistic strategies following extreme low-flows, suggesting the regime has not filtered the species pool to just drought tolerant species and low-flows are a second-level filter. Applying trait-based approaches to determine flow-ecology relationships can help identify how changes in flow affect ecosystem function and facilitate conservation (Aspin et al. 2019).

Incorporating flow metrics across temporal scales will further improve assessments of the threats or benefits posed by anomalous flow events.

Beyond Disturbance

Like ecological communities, ecological theory must, itself, adapt to and embrace a future defined by intensifying extremes and a nonstationary climate (Poff 2018). This transition requires a quantitative framework for integrating event-based analysis with long-term environmental change. Our results provide a foundation for building such an integrative framework. Flow variability determines many aspects of community structure in riverine ecosystems, but natural flows have been heavily modified by direct and indirect anthropogenic pressures globally (Sabo et al. 2010b, Vörösmarty et al. 2010). Here we demonstrate how community response to anomalous events depends on the context of flow regime. Understanding how the components of beta diversity and community life history strategies are likely to respond to future alterations in flow regime and event magnitude will facilitate the conservation of freshwater biodiversity. Alterations to baseflow and timing of high-flow events are likely to increase the extinction risk for native fish species, but decrease the risk for non-natives across the American Southwest (Ruhí et al. 2016b). Management strategies to conserve biodiversity in the future will need to consider not only the established effects of regime alterations, but also how changes in regimes will reshape ecological response to extreme events (Horne et al. 2019).

Although we have used streams and rivers to illustrate how environmental regimes interact with anomalous events to drive temporal variation in biotic communities, these principles can be flexibly extended to other ecosystems. Rising temperatures and changes in precipitation regime have filtered the community composition of Sonoran Desert winter annual plants over the last 25 years, such that the timing and abundance of precipitation events now trigger different responses in community composition than historically observed (Kimball et al. 2010). Temperate forests exhibit characteristic trajectories following disturbances that occur with predictable frequency (Runkle 1985). However, changing nutrient, temperature, and precipitation regimes will likely alter community composition following disturbances, filtering recovering communities, and may initiate novel successional pathways (Anderson-Teixeira et al. 2013). In annual plants, temperate forests, and desert fish, community life history composition is filtered by long-term environmental regime to maximize population growth based on demographic constraints. Discrete, anomalous events act on this filtered community to initiate a response characterized by the available set of life histories.

Extreme events and regimes are environmental filters acting on biotic communities at different timescales to shape patterns of biodiversity. Our findings additionally suggest that it is not sufficient to only project how changes in regime or event magnitude may affect biodiversity, but it is also necessary to consider how novel regimes may cause different, and potentially unexpected, environment-ecology relationships across localities (Bruckerhoff et al. 2019). The role of environmental regimes in mediating the effects of extreme events on biotic communities through filtering of life history strategies should be further explored to better understand current patterns of biodiversity and community response to a changing climate.

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Table 1: Linear regression models of metrics summarizing seasonal variation in fish community diversity. Each row describes one model with marginal (m) and conditional (c) R^2, and standardized beta for all fixed effects. Supported models (ΔAICc < 2) are bolded. All models included site as a random effect with compound symmetry correlation structure. The null model without hydrologic covariates was never supported and is not listed.

Diversity metric	R^2_m	R^2_c	AICc	ΔAICc	σ_{hf}	PSAM	NSAM	PSAM • σ_{hf}	NSAM • σ_{hf}
Shannon div.									
	0.384	**0.521**	**39.655**	**0.000**	**-0.257**	**-**	**-**	**-**	**-**
	0.410	**0.534**	**41.613**	**1.958**	**-0.215**	**-0.163**	**-**	**0.107**	**-**
	0.393	0.537	43.193	3.538	-0.261	-	0.027	-	-0.050
	0.016	0.498	47.520	7.865	-	-0.049	-	-	-
	0.000	0.513	49.019	9.364	-	-	0.002	-	-
Dissimilarity									
	0.153	**0.265**	**-10.054**	**0.000**	**0.091**	**-**	**-**	**-**	**-**
	0.216	**0.414**	**-8.671**	**1.383**	**0.120**	**-**	**0.010**	**-**	**0.042**
	0.020	0.258	-6.47	3.584	-	0.030	-	-	-
	0.173	0.271	-6.211	3.843	0.071	0.077	-	-0.053	-
	0.021	0.379	-6.01	4.044	-	-	0.033	-	-
Replacement									
	0.153	**0.154**	**-61.793**	**0.000**	**-0.022**	**-**	**0.014**	**-**	**0.026**
	0.073	**0.076**	**-60.340**	**1.453**	**-0.040**	**-**	-	-	-
	0.140	0.141	-57.629	4.164	-	-	0.057	-	-
	0.064	0.065	-57.153	4.607	-0.043	0.035	-	-0.025	-
	0.092	0.105	-55.845	5.948	-	-0.041	-	-	-
Rich. diff.									
	0.257	**0.421**	**1.157**	**0.00**	**0.144**	**-**	**-**	**-**	**-**
	0.292	0.518	3.379	2.222	0.189	-	0.059	-	0.006
	0.059	0.442	3.406	2.249	-	0.062	-	-	-
	0.282	0.474	4.183	3.026	0.116	0.073	-	-0.022	-
	0.030	0.559	6.022	4.865	-	-	0.050	-	-

Table 2: Candidate models for seasonal proportional contribution of life history strategies to communities. Each row is one model with standardized beta given for all fixed effects and supported models (AICc < 2) are bolded. Model structure is the same as in Table 1.

Life history strategy (%)	R^2_m	R^2_c	AICc	ΔAICc	σ_{hf}	PSAM	NSAM	PSAM • σ_{hf}	NSAM • σ_{hf}
Opportunistic									
	0.461	**0.815**	**-159.529**	**0.000**	**0.093**	**-**	**-**	**-**	**-**
	0.469	**0.831**	**-159.122**	**0.407**	**0.085**	**-**	**-0.018**	**-**	**0.021**
	0.461	0.818	-155.991	3.538	0.095	-0.018	-	0.016	-
	0.000	0.807	-153.56	5.969	-	0.004	-	-	-
	0.000	0.809	-153.405	6.124	-	-	-0.001	-	-
Periodic									
	0.465	**0.791**	**-223.723**	**0.000**	**-0.043**	**-**	**0.013**	**-**	**-0.014**
	0.437	**0.761**	**-222.615**	**1.108**	**-0.048**	**-**	**-**	**-**	**-**
	0.442	0.763	-218.184	5.539	-0.048	0.003	-	-0.005	-
	0.004	0.748	-216.77	6.953	-	-0.004	-	-	-
	0.000	0.752	-216.221	7.502	-	-	0.002	-	-
Equilibrium									
	0.376	**0.831**	**-241.076**	**0.000**	**-0.044**	**-**	**-**	**-**	**-**
	0.390	0.840	-238.996	2.080	-0.047	0.014	-	-0.011	-
	0.383	0.836	-237.747	3.329	-0.042	-	0.005	-	-0.006
	0.000	0.829	-236.526	4.550	-	0.000	-	-	-
	0.000	0.828	-236.522	4.554	-	-	0.000	-	-

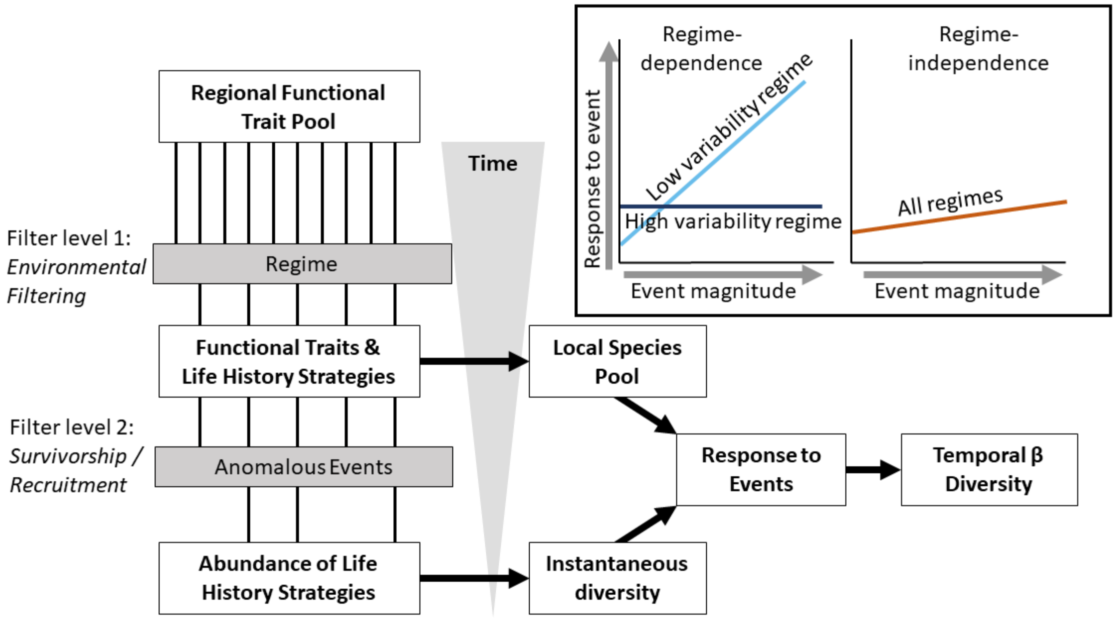

Figure 1: Conceptual diagram illustrating our hypothesis on discrete events acting as a nested filter within the disturbance regime to select for compatible life history strategies—shaping community responses to individual events and resulting patterns of temporal β diversity. Inset: predicted community response to anomalous events given regime-dependence and independence.

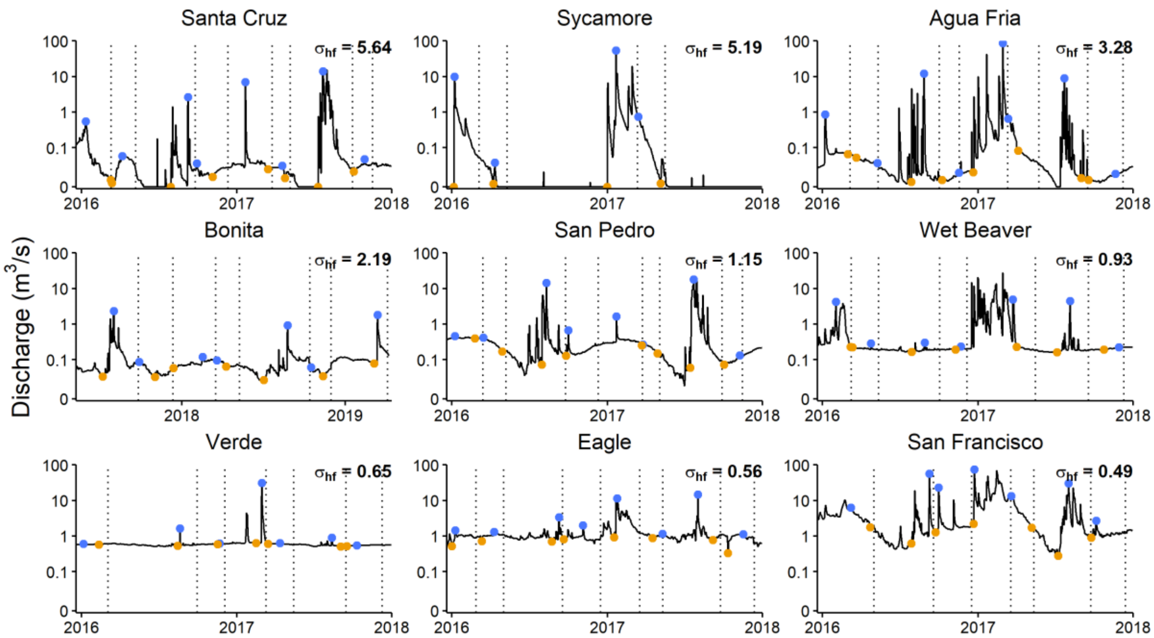

Figure 2: Discharge over the study period at nine study sites in Arizona, USA, ordered from most variable to most stable flow regime (high to low σ_{hf}). Dots indicate the highest (blue) and lowest (yellow) flow anomaly magnitude (HSAM and LSAM, respectively) between consecutive surveys (survey dates indicated by dotted lines) or in the preceding season.

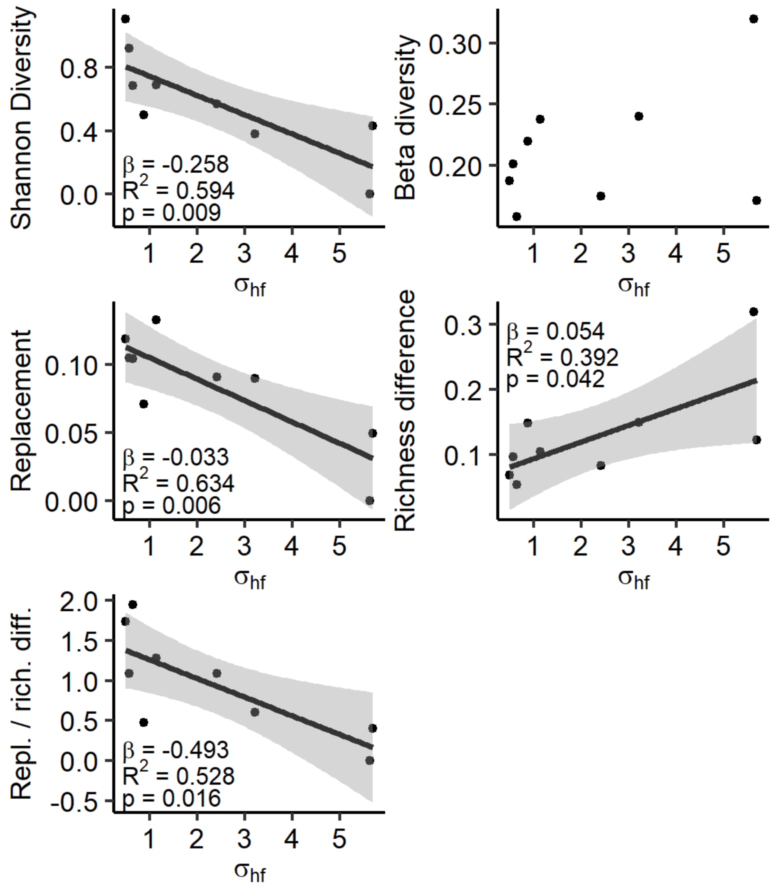

Figure 3: Mean values of taxonomic diversity, temporal beta diversity and its components (replacement and richness difference), and the ratio of replacement to richness difference over two years of quarterly sampling. Each point represents one site. Best-fit line, standard error band, standardized beta estimate, and R^2 are shown for significant relationships ($p < 0.05$).

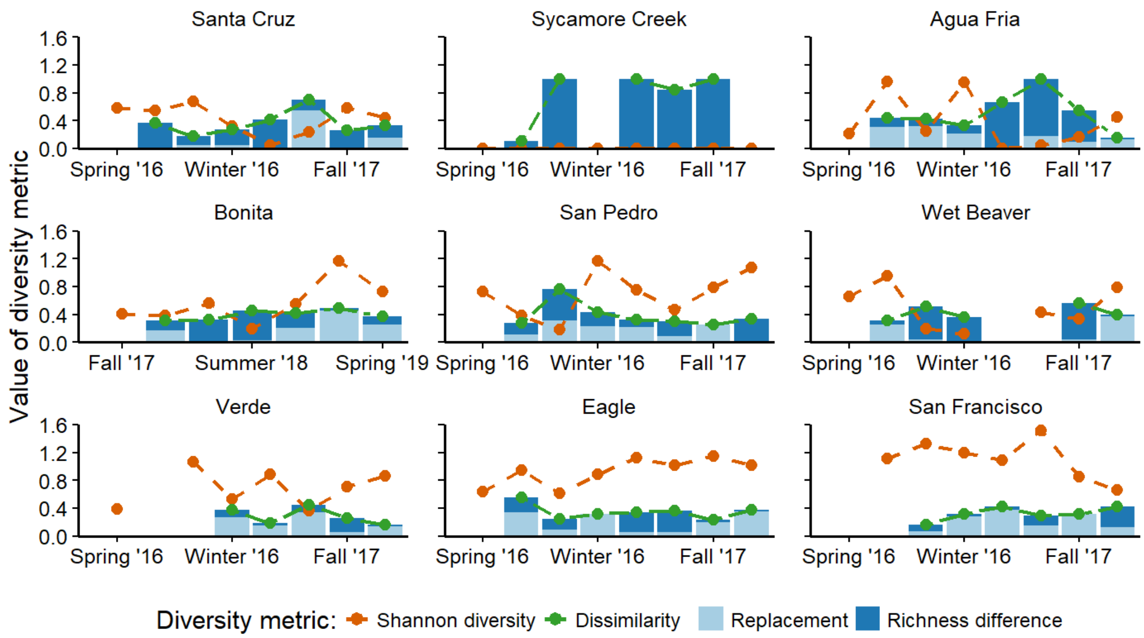

Figure 4: Seasonal observations of four measures of taxonomic diversity. Missing values of Shannon diversity are from missed fish surveys. Dissimilarity, replacement, and richness difference are calculated between consecutive surveys. Sites are ordered from high to low σ_{hf}.

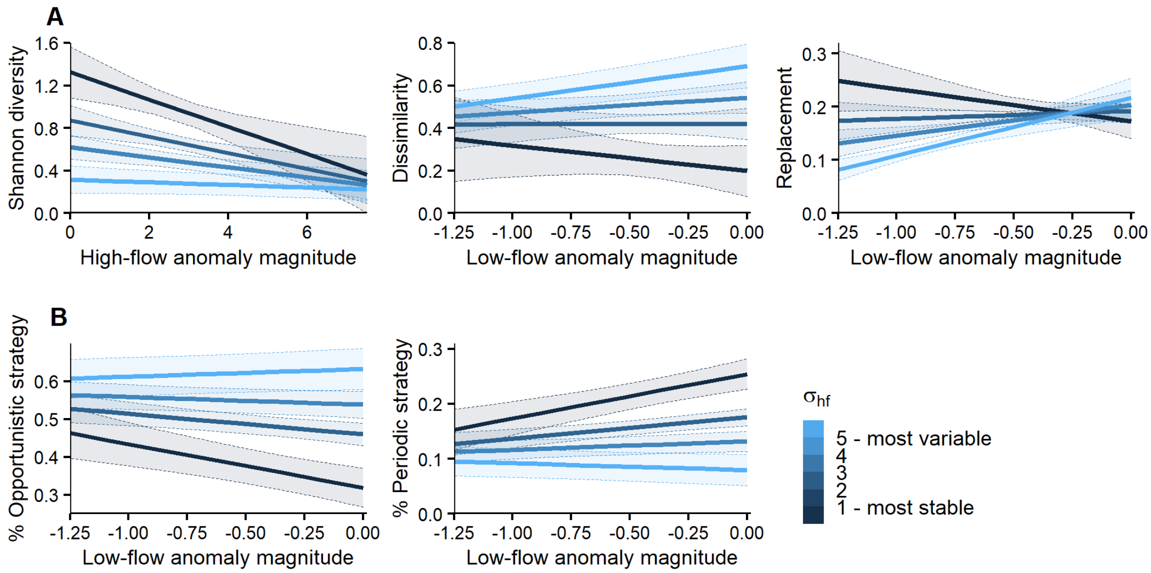

Figure 5: Predicted values of three measures of fish diversity (A) and contributions of life history strategies to communities (B) following seasonal flow anomalies across a gradient of magnitudes. Predictions are from linear regression models with interaction terms between flow regime and flow anomalies (Table 1 [A] and Table 2 [B]). Values of flow regime variability (σ_{hf}) and flow anomalies span those observed in the 9 study sites (Appendix A: Table S2). More positive high-flow and more negative low-flow anomalies are higher intensity events. Bands indicate standard error.

CHAPTER 3

DISTURBANCE REGIME SHAPES ECOLOGICAL EFFICIENCY BY DECOUPLING PRIMARY AND SECONDARY PRODUCTION IN DESERT RIVERS

ABSTRACT

The production of consumer biomass and number of trophic levels supported by an ecosystem depend in part on rates of primary production, disturbance, predator-prey interactions, and the efficiency of energy flow through food webs. Of these factors, food web efficiency (FWE) has been among the most difficult to quantify empirically. Thus, both the drivers and consequences of variation in FWE remain largely unstudied in the field. We estimated FWE across gradients of flow regime variability, resource availability, and trophic structure in nine desert streams. FWE was estimated as fish community production relative to gross primary production (GPP) at an annual timescale and was based on quarterly observations of fish biomass and stream metabolism. Fish production ranged from 0.02 to 0.50 g C $m^{-2}yr^{-1}$, FWE ranged from $9.5 \cdot 10^{-5}$ to $1.8 \cdot 10^{-2}$, and both decreased with greater flow regime variability and increasing temperature. In contrast to mesocosm experiments, efficiency in these food webs was not correlated with algal nitrogen or phosphorus ratios, nor food chain length. Further, GPP was not related to flow regime or rate of fish production, indicating disturbance regime did not mediate production through indirect bottom-up metabolic pathways. Estimates of FWE from streams subject to disturbance by floods and drought indicated that flow regime decouples energy flow from primary producers to consumers, and more strongly

influences the efficiency of fish production than previously hypothesized factors, such as top-down and bottom-up biotic interactions, resource quality, and food chain length.

INTRODUCTION

Productivity is a fundamental function of ecosystems that supports services including carbon storage and food supply. Accordingly, ecology and fisheries research over decades has documented patterns of production and energy flow through food webs (Odum 1957, Waters et al. 1990, Randall et al. 1995). The productive capacity of upper trophic levels is constrained by the efficiency of energy transfer from primary producers to consumers, which in turn limits total food chain length (FCL; Elton 1927, Lindeman 1942). Fish are top consumers in many freshwater ecosystems, and thus production of fish biomass reflects biotic and abiotic processes throughout the ecosystem, including resource availability and environmental conditions (Waters 1977, Valentine-Rose et al. 2011, Dolbeth et al. 2012). Freshwater fish production and standing biomass consequently have implications for the provisioning of protein in human diets (Funge-Smith and Bennett 2019), conservation of charismatic species (Vander Zanden et al. 2003), and energy flow through ecosystems (Hairston and Hairston 1993). Despite enduring interest in trophic dynamics and secondary production of streams and rivers (Tank et al. 2010, Dolbeth et al. 2012), their constraints remain uncertain due to complex interactions between primary production, energy transfer efficiency, and consumer production.

Food web efficiency (FWE), the proportion of energy fixed by primary producers that is transferred to the top consumers of an ecosystem, can be constrained by top-down and bottom-up trophic forces (Rand and Stewart 1998). In aquatic ecosystems, the identity and trophic position of top consumers, resource quality, and temperature may regulate FWE (also termed food chain efficiency in experimental settings; Dickman et al. 2008, Rock et al. 2016, Barneche et al. 2021). While FWE can determine ecosystem FCL; (Lindeman 1942, Hutchinson 1959), the inverse, where the number of trophic levels constrains FWE due to top-down pressure shaping prey abundance, behavior, and community composition, has also been hypothesized (Hairston and Hairston 1993) and experimentally documented (Dickman et al. 2008, Degerman et al. 2018).

Bottom-up forces limit the production and diversity of upper trophic levels through the regulation of resources available to support primary consumers (Hutchinson 1959, Schoener 1989). *In situ* fixation of carbon dioxide (CO_2) to organic C (gross primary production [GPP]) and the breakdown of organic C to CO_2 (ecosystem respiration [ER]) are the primary processes of ecosystem metabolism in streams and rivers. Resources that cross the aquatic-terrestrial boundary can also contribute substantially to the production of aquatic consumers (Wipfli and Baxter 2010). These externally produced (allochthonous) resources are not captured in measures of aquatic GPP, but contribute to ER such that the ratio of GPP:ER reflects the relative importance of heterotrophic respiration of these allochthonous inputs to river metabolism (Tank et al. 2010). The balance of GPP and ER, or net ecosystem production (NEP), indicates the difference between rates of locally produced (autochthonous) C sources and respiratory loss of C from any source (Chapin et al. 2006). Aquatic food webs heavily supported by terrestrial resources may have greater than expected secondary production relative to GPP (Rüegg et al. 2021), and consequently, higher FWE (Lefébure et al. 2013). Rising global temperatures may also affect energetic efficiency by accelerating ER relative to GPP through increased rates of organismal metabolism and decomposition (Gillooly et al. 2001, Barneche et al. 2021).

In aquatic ecosystems, nutrient supply often constrains primary production (Grimm and Fisher 1986, Sterner et al. 1997). Nutrient content of primary producers may also limit bottom-up energy transfer efficiency when nitrogen (N) and/or phosphorus (P) are limiting relative to consumer nutritional requirements (Sterner and Hessen 1994, Elser et al. 2000), thus altering the availability of resources and energetic transfer efficiency at multiple trophic levels. Primary producer quality, based on C:N and C:P, persists through multiple trophic levels to limit FWE in mesocosms (Rowland et al. 2015). However, while FCL, temperature, and nutrient ratios constrain FWE in experimental environments; these hypotheses may not hold in field conditions where uncontrolled, confounding effects can decouple production and energy transfer between trophic levels.

Flow regime, defined by the timing, intensity, and predictability of disturbances over time, constrains FCL and community dynamics in rivers (McHugh et al. 2010, Sabo et al. 2010a). More variable flow regimes reduce the strength of top-down biotic interactions, promote shorter food chains (Resh et al. 1988, Sabo et al. 2010a), and select for small species occupying lower trophic positions via environmental filtering of large-bodied, long-lived taxa (Fisher and Gray 1983, Poff 1997, Mims and Olden 2013). Fish at lower trophic positions tend to have greater rates of production on average (Rypel and David 2017). However, disturbance can decrease standing biomass of fish and invertebrates, reduce predator body size, and lessen top-down trophic pressure by altering the composition of the invertebrate community (food source for fish), resulting in lower consumption efficiency, and thus decouple fish production from production at lower trophic levels (Jellyman et al. 2014, Jellyman and McIntosh 2020). In contrast to fish, aquatic primary producers may be less susceptible to highly variable flow regimes, maintaining high rates of primary production (Busch and Fisher 1981, Fisher et al. 1982) and returning to pre-flood levels of standing stock in days to weeks (Grimm and Fisher 1989). Flow regime variability may therefore affect FWE through constraints on FCL, rates of secondary production, and consumption efficiency, and by shaping community structure.

Despite longstanding theory describing the central role of efficiency in influencing food webs and the examination of hypothesized mechanisms in mesocosms, lack of *in situ* observations has limited the applicability of this theory. Fish secondary production has been used to measure the response of fisheries to environmental and anthropogenic changes (Dolbeth et al. 2012, Layman and Rypel 2020), but community-level fish production has rarely been linked to primary production in a single study. Here, we simultaneously measured ecosystem metabolism and secondary production of fish communities as the basis for estimates of FWE in nine desert rivers. First, we examined the hypotheses that nutrient content of primary producers, temperature, FCL, and flow regime constrain FWE. Additionally, we explored the hypotheses that environmental constraints on FWE are mediated by indirect bottom-up metabolic pathways (Bernhardt et al. 2018, Rüegg et al. 2021) or exert top-down pressure by controlling secondary production (Hairston et al. 1960). Global alterations to streamflow, nutrient, and metabolic regimes underscore the need to understand the mechanisms influencing energy flows through aquatic food webs. Our objective in this study is to relate environmental conditions with patterns of resource availability and secondary production to explain potential mechanisms underlying the trophic dynamics of desert rivers.

METHODS

Site Description

We conducted our study in nine 1st- to 3rd-order streams across Arizona, USA, in the semi-arid Sonoran Desert. Sites were selected to span a seasonal precipitation gradient. Sites in central Arizona were dominated by strong Pacific winter precipitation driven by frontal storms, and by a weak summer monsoon. In contrast, sites in southern and eastern Arizona had weak winter and strong monsoonal precipitation (concentrated in July-September). All sites were located upstream of major human settlements, were relatively unaffected by streamflow regulation (upstream of large dams), and in close proximity (<10% change in drainage area) to US Geological Service (USGS) gaging stations.

We conducted quarterly surveys of fish production, stream metabolism, and metrics of hypothesized drivers of FCE to capture variation in flow and environmental conditions. All nine streams were studied from spring 2016 – winter 2017 (8 surveys). We continued monitoring five of these sites until spring 2019 (13 surveys total), but at one of these sites fish were only sampled from fall 2017 – spring 2019. Stream drying and high-flow conditions precluded us from conducting the full number of surveys at all sites (Appendix B: Table S1). All sampling was conducted within 100-m reaches representative of each site that were revisited for each survey.

Flow Regime

We characterized the disturbance regime as variability in low- and high-flow anomalies in the river discharge record of each site. We obtained 20 years of mean daily discharge data (1/1/1997 to 31/12/2017) from the USGS gaging stations closest to our sampling sites (Appendix B: Table S1). These dates were chosen to contain the most recent 20 years that did not extend past the study period of any study site. Stochasticity in hydrologic regimes was characterized via spectral methods with the Discrete Fast Fourier Transform (DFFT) to describe interannual variability in extreme flow events (Sabo and Post 2008). DFFT was selected because of its utility in identifying the periodic (seasonal) and stochastic (interannual) components of long-term variations in discharge, which can be important drivers of aquatic community composition (Ruhí et al. 2015). We used variation in extreme high-flow events (σ_{hf}) as the measure of flow regime variability, which was calculated as the standard deviation of positive flow anomalies greater than two standard deviations above the detrended long-term average, using the *discharge* package (Shah and Ruhi 2019) in R (version 3.6.1, R Core Team 2019). All additional analyses were conducted in R.

Ecosystem Metabolism

Whole-stream metabolism was modeled from diurnal variation in dissolved oxygen (DO) concentration, light, and water temperature (Odum 1956). During surveys, we deployed two optical DO sensors (ProODO, YSI, Yellow Springs, Ohio) and two photosynthetically active radiation (PAR) loggers (Odyssey®, Christchurch, New Zealand) at the upstream and downstream ends of the study reach for one to four days, with occasional extended sensor deployment of up to two weeks. Sensors recorded DO, water temperature, and barometric pressure at 10-min intervals and PAR at 5-min intervals. We measured wetted width and made at least 10 cross-sectional depth measurements at the top, middle, and bottom of the reach.

We estimated GPP and ER from diel variation in oxygen production and consumption based on the model:

$$\frac{dDO}{dt} = \frac{GPP+ER}{z} + K(DO_{sat} - DO)$$

where $\frac{dDO}{dt}$ is the rate of change in DO, GPP and ER are the rates of photosynthetic production and metabolic respiration of O_2, respectively, z is reach-averaged water depth, and $K(DO_{sat}\text{-}DO)$ is the net volume of water-atmospheric oxygen exchange, defined by the gas exchange rate coefficient (K). Parameters were estimated using a Bayesian state-space model implemented by the R package *streamMetabolizer* (Appling et al. 2017). To reduce the possibility of equifinality in parameter estimates, we pooled estimates of K across binned values of stream discharge, a parameter closely correlated with physical gas exchange. We ran three Markov Chain Monte Carlo (MCMC) chains, saving 18,000 samples from the posterior distribution after parameters converged. Model convergence was verified using the Gelman-Rubin statistic. R^2 between measured DO and modeled DO was calculated to evaluate model fit, and we eliminated parameter estimates from further analysis when this value was < 0.75. Estimates of GPP and ER from the two monitoring locations were averaged for each site, and GPP and ER were converted from units of oxygen (g O_2 $m^{-2}d^{-1}$) to units of carbon (g C $m^{-2}d^{-1}$) using a photosynthetic quotient of 1.2 and a respiratory quotient of 0.85 on molar quantities, following Bott (2007).

Fish Production

We blocked the upstream and downstream ends of the study reaches with 6-mm mesh nets and used three-pass depletion backpack electrofishing (Model LR-24 Electrofisher, Smith- Root, Vancouver, Washington, USA) to quantitatively sample fish populations. All captured fish were anaesthetized with tricaine methanosulphate (MS-222), identified to species, weighed (nearest g), measured (fork length; nearest mm), and released after recovery. We assumed fish abundance and biomass was zero when streams were dry during a survey period. Weights for small individuals of four species of fish (red shiner [*Cyprinella lutrensis*], western mosquitofish [*Gambusia affinis*], longfin dace [*Agosia chrysogaster*], and green sunfish [*Lepomis cyanellus*]) that could not be accurately measured in the field were calculated using species-specific length-weight regressions based on data from specimens stored in the laboratory. We calculated population estimates based on k-pass removal data for all species at each survey using the *FSA* package (Ogle et al. 2020).

We divided our study into three years that roughly corresponded with 2016, 2017, and 2018, with surveys conducted in the spring of the following year included in both years to capture a full year of fish production. For example, year 1 spanned spring 2016 – spring 2017 (5 surveys), with spring 2017 included in both year 1 and year 2. If a survey for the second spring was not conducted, then production for that year was calculated on 4 surveys. We calculated the weighted mean annual biomass for each species observed at a site to account for the number of days between surveys, following Newman and Martin (1983). We calculated annual secondary production using an allometric equation of P/B for rivers (Randall et al. 1995), using the average weight of each species in the sampled population:

$$\log(P) = 0.51 - 0.33 \cdot \log(W) + 0.89 \cdot \log(B)$$

Where P = production (kg ha^{-1} yr^{-1}), W = mean weight (g), and B = average annual biomass (kg ha^{-1}). Production and biomass of freshwater fish scale nearly linearly (Downing and Plante 1993, Hatton et al. 2015), producing robust estimates of secondary productivity (Randall and Minns 2000, Rypel and David 2017). Estimates of secondary production for all species found at a site during each study year were summed for annual measures of community-level secondary production.

Food Chain Length and Nutrient Analysis

We estimated FCL for each site and season from analysis of $\delta^{15}N$ of stream biota. During each survey in the first two years of the study (2016 and 2017), we collected three replicate samples of filamentous algae, up to three individuals of each fish species present, and larval mayflies using kick nets. Mayflies were kept alive for at least 6 hours to clear their guts, and all samples were kept on ice in the field, frozen until analysis, and identified to family in the lab (Appendix B: Table S2). Mayflies were not collected and analyzed for stable isotopes at all surveys, and consumer trophic position could only be calculated for one survey at Bonita Creek, and 4-8 surveys at all other sites (Appendix B: Table S2). Algae were washed with deionized water and visually inspected for any debris before processing, dorsal muscle tissue was excised from fish for analysis, and mayflies were pooled to reach minimum weight for analysis. All samples were dried at 60°C for 48 hours and ground to a homogenous powder. Three replicates of algae and up to three replicates of mayflies and each fish species were analyzed for N content and $\delta^{15}N$ with a Costech 4010 elemental analyzer coupled to a Thermo Scientifc Delta V isotope ratio mass spectrometer. Phosphorus content of plant tissues was measured as total dissolved phosphorus following persulfate digestion, using the molybdate blue method (Murphy and Riley 1962) on a Smartchem autoanalyzer (limit of quantitation = 0.6 µg P/L).

We calculated trophic position (TP) for each fish as the difference in $\delta^{15}N$ between the fish and the isotopic baseline following standard convention:

$$TP = [(\delta^{15}N_{fish} - \delta^{15}N_{baseline}) / \Delta] + 2$$

We assumed a trophic enrichment factor (Δ) of 3.4 (Post 2002a) and used mayflies of the family *Baetidae* as the $\delta^{15}N_{baseline}$. Baetid mayflies were abundant at most surveys, and estimation of FCL based on widely distributed primary consumers as the $\delta^{15}N$ baseline has been well documented to reflect trophic structure in lotic ecosystems (Kristensen et al. 2016, Sabo et al. 2018). Trophic position for each fish species at a site was averaged for each year of the study, and the greatest observed value for resident species (observed in more than one survey) was assigned as the average annual FCL.

Data Analysis

To explore the relationships between flow regime, nutrients, light, and ecological efficiency, we calculated food web efficiency as the ratio of the annual rate of fish community secondary production to the annual rate of aquatic GPP.

$$FWE = \frac{\text{secondary production (grams C } \text{yr}^{-1}\text{)}}{\text{mean daily GPP (g C } \text{d}^{-1}\text{)} \bullet 365}$$

Annual estimates of mean daily GPP, ER, and standard deviations were made from 1000 bootstrapped samples of daily estimates stratified across all surveys with metabolism data for a year. Our calculations of fish secondary production were converted from grams wet mass to grams C by assuming fish are 25% dry mass (Hartman and Brandt 1995) and 46% of dry mass is C (Sterner and George 2000).

We used Spearman rank correlations to examine relationships between measures of ecosystem metabolism, fish secondary production, and FWE and metrics of hypothesized constraints including disturbance regime, resource availability, and temperature for each year. Because of the small sample size and changes in the identity and number of sites in each study year, we did not evaluate statistical significance based on p value and instead report Spearman rank correlation (ρ) and interpret $\rho > 0.3$ as suggestive of correlation if the pattern occurred for more than one year. Within-site interannual variation in FWE relative to nutrient availability, FCL, and temperature was assessed with ANOVA tests.

RESULTS

Annual estimates of stream metabolism varied across sites but were relatively consistent within each site between years (Figure 1 A-D). Average annual GPP ranged from 16–786 g C $m^{-2}yr^{-1}$, ER from -90 – -907 g C $m^{-2}yr^{-1}$, NEP from -512–78 g C $m^{-2}yr^{-1}$, and GPP:ER from 0.06–1.86. FCL spanned 1.5 trophic levels (2.3–3.9) with high interannual variability in some sites (Figure 1 E). Annual fish production varied from 0.02–0.50 g C $m^{-2}yr^{-1}$ across sites and was more variable in time than metabolism (Figure

1 F). FWE ranged from $9.5•10^{-5}$–$1.8•10^{-2}$, where one site was an outlier with markedly higher efficiency (Figure 1 G).

We tested hypotheses that FWE is constrained by resource quality, FCL, and temperature, which have been supported in experimental food chains, and the additional hypothesis that disturbance regime is a control on efficiency in riverine ecosystems (Figure 2, Table 1). We found that, across sites, annual FWE was negatively correlated with average water temperature and σ_{hf}, with lower efficiency in warm, highly variable flow regimes. Temperature and σ_{hf} were correlated in two of the three study years (Appendix B: Figure S1) and thus the effects of the two variables cannot be considered fully independently. In contrast to experimental studies, FWE was not correlated with either algal C:N (range 11.7-18.2) or C:P (range 202.3-660.3), nor with average FCL across sites. However, for the seven sites with two years of FCL data, FWE within each site was significantly higher in the year with greater FCL (df = 1, F = 7.9, p = 0.03; Figure 3). Additionally, within sites, average annual water temperature was also correlated with FWE, with lower efficiency in warmer years (df = 1, F = 81.8, $p < 0.001$). Within-site variation in annual average algae C:N (df = 1, F = 0.9, p = 0.39) and C:P (df = 1, F = 0.6, p = 0.45) were not associated with FWE.

We additionally explored the mechanisms through which the same set of hypothesized constraints (resource quality, FCL, temperature, and flow regime) may act on FWE through indirect bottom-up effects on ecosystem metabolism, and top-down forces on secondary production. Aquatic primary production, GPP, was not correlated with algal nutrient ratios, FCL, or streamflow variability, but was positively related to temperature (Figure 4; Table 1). Fish secondary production was more closely associated with environmental conditions than either FWE or GPP (Figure 5; Table 1). Fish secondary production was negatively correlated with temperature and flow regime variability for all three years of the study. Secondary production was also positively correlated with FCL in both study years with available data, but exhibited no consistent correlations with algae C:N or C:P. We further explored the relationship between secondary production and metrics of ecosystem metabolism, GPP, ER, NEP, and GPP:ER, to assess support for environmental conditions indirectly mediating trophic dynamics through metabolic pathways. Secondary production was not associated with GPP or ER, but was negatively correlated with NEP for all three years and GPP:ER for the second two years of the study (Figure 5; Table 1), illuminating a potential mechanism relating resource availability to consumer dynamics.

DISCUSSION

Production of consumer biomass is constrained by the efficiency of energy flow from primary producers to upper trophic levels. In experiments, the efficiency of this energy transfer has been linked to ecological theory on nutrient ratios of primary producers, FCL, and temperature (Dickman et al. 2008, Faithfull et al. 2015, Rowland et al. 2015, Rock et al. 2016, Barneche et al. 2021). We tested these mechanisms *in situ*, where stream food webs are additionally subject to disturbance due to floods and droughts, to prompt further research and comparative analysis. Here, we observed negative relationships between annual rates of fish production and food web efficiency with temperature and flow regime variability, suggesting that the production of fish biomass is driven by environmental conditions and not the rate of aquatic primary production.

Production and Efficiency in Streams

Observed estimates of ecosystem metabolism, secondary production, and FWE in desert streams were similar to previously published values. Seasonal measures of average daily GPP (range 0.00–4.65 g C $m^{-2}d^{-1}$) encompassed the range observed for a well-studied desert stream (0.9–3.9 g C $m^{-2}d^{-}1$; Grimm 1987). Estimates of annual fish production (1.7–43.4 g $m^{-2}yr^{-1}$; reported as g C in previous analyses) generally fell in the first quartile of observations from 55 rivers across the globe (range 2.6–280 g $m^{-2}yr^{-1}$; Randall et al. 1995) but spanned the range from similar size streams in the Appalachian mountains (Myers et al. 2018). Few estimates of food web efficiency in rivers are available, but can be calculated for the Colorado River based on values of GPP and fish production published in Hall et al. (2015) and Cross et al. (2013). Using these studies, food web efficiency in the Colorado River ranged from $6.2 \cdot 10^{-4}$–$4.3 \cdot 10^{-3}$, while we observed values from $2.8 \cdot 10^{-5}$–$1.6 \cdot 10^{-2}$.

As with all field studies, several potential sources of error should be considered when interpreting these results. One limitation is that ecosystem metabolism was measured at discrete times throughout the year, occasionally with only a few days of observations in each season and some missing seasons due to stream intermittence or site inaccessibility (Appendix B: Table S1). However, our sampling dates were designed to monitor periods before and after biologically relevant seasonal change and incorporate seasons expected to capture the full range of ecosystem metabolism. Strong coherence in metabolism metrics among years within sites indicates the measured values are representative of each site. Our calculations of fish secondary production also relied on modeled relationships between production and biomass. This is a common method and is strongly correlated with other methods of calculating secondary production (Downing and Plante 1993, Rypel and David 2017), but may be less precise than direct measures of secondary production (Hayes et al. 2007). Finally, the identity of fish species and community composition varied between sites and over time within sites. The identity of predators in a system can influence ecological efficiencies through body stoichiometry, foraging preferences, and changes in FCL (Rock et al. 2016). However, this study was designed to capture stochasticity in natural conditions and document production and ecological efficiency across time and rivers, including the inherent community variability.

Linking Ecological Efficiency and Environmental Constraints

Temperature and flow regime variability were negatively related to FWE, situating these variables as preeminent environmental constraints on trophic dynamics in riverine ecosystems. Temperature increases the energetic cost of growth and may decrease trophic efficiency, with the magnitude of effects depending on organismal mass and ontogeny (Barneche and Allen 2018). Our finding that FWE was negatively corelated with temperature across sites is potentially confounded by the positive correlation between temperature and flow regime variability (Appendix B: Figure S1). However, because flow regime can structure species functional and taxonomic composition (Lamouroux et al. 2002), and temperature has species-dependent effects on rates of production (Rypel and David 2017), predicting effects of temperature on trophic efficiency in streams may be improved when considered in the context of flow regime. Significant within-site decreases in efficiency in warmer years also suggests evidence for direct effects of temperature on FWE, potentially resulting from increased metabolic rates (Gillooly et al.

2001). Higher temperatures generally increase GPP over short timescales (Padfield et al. 2017), but also accelerate organic C loss through respiration at each trophic level, with potential for microbial respiration to substantially reduce NEP available to consumers (Yvon-Durocher et al. 2012, Follstad Shah et al. 2017). Hence, a warming climate may increase the ratio of primary production that is respired relative to production of consumer biomass, decreasing FWE (Barneche et al. 2021).

In contrast to our predictions based on experimental studies, primary producer quality, as C:N and C:P, was not associated with FWE in desert rivers, either across sites or within sites over time. Additionally, algal nutrient ratios were not correlated with GPP, which is consistent with experimental observations (Mulholland et al. 1995), nor the rate of fish secondary production. The lack of consistent relationships between resource quality and GPP, fish secondary production, or FWE indicates that other environmental factors are stronger constraints on consumer trophic dynamics in rivers.

If FCL influences food web efficiency across rivers, it would support the top-down hypothesis of trophic dynamics, where top predators induce consistent and predictable responses at lower trophic levels (Hairston et al. 1960). While strong top-down trophic pressures exist in rivers (Power 1990), we did not observe a relationship between variation in top trophic position and FWE across sites. Instead, FCL was positively correlated with fish production, likely because streams that support piscivores, the top trophic level at some sites, must produce sufficient biomass of smaller fish. We did, however, find that in sites with two years of data, FWE was consistently higher in the year where food chain length was greatest. These findings contrast results from two- or three-trophic-level experiments, where longer food chains had lower efficiency (Dickman et al. 2008). This suggests that differences in conditions between sites, such as flow regime, are strong controls on trophic efficiency, obscuring generalizable trends with FCL. While not addressed directly here, greater abundance of invertebrate prey items can increase production of fish biomass and lengthen food chains through altered patterns of omnivory (Jellyman et al. 2014, Ruhí et al. 2016a). Higher rates of fish production, with coincident dietary shifts to greater invertebrate consumption, could potentially increase FCL and the efficiency of fish production if GPP does not also increase with fish production. The absence of relationships between GPP and FCL or fish production suggests a decoupling of both top-down control on primary producers (*sensu* Hairston et al. 1960) and bottom-up limitation by aquatic primary production on trophic dynamics in these streams.

While neither NEP nor GPP:ER are direct measures of organic C accumulation or terrestrial resources available to consumers, greater values indicate shifts from dominant contribution of allochthonous to autochthonous sources in stream metabolism (Chapin et al. 2006, Tank et al. 2010, Brett et al. 2017). These metrics revealed that fish production increased in more heterotrophic streams (low GPP:ER) with less potential for accumulation of autochthonous C (low NEP), suggesting support of fish production by allochthonous resources. Terrestrial primary production contributes 25% or more of resources in fish diet in another AZ river (Baruch et al. *in press*) and it is possible that the fish in the current study are more reliant on allochthonous resources in streams with low GPP. This conclusion is supported by findings from a large-scale mesocosm experiment where greater inputs of terrestrial matter increased FWE due to elevated rates of bacterial production relative to aquatic primary production (Lefébure et al. 2013).

The availability of ecosystem metabolism data is rapidly increasing and could be paired with existing datasets on fish communities to evaluate broad-scale patterns of FWE. Here, we define FWE relative to aquatic primary production, and not total basal resource availability (Rand and Stewart 1998). Aquatic GPP is an efficient metric to use in the denominator of efficiency calculations because other metrics that are proxies for the availability of both aquatic and terrestrial resources, such as ER, only reflect the portion of primary and microbial production that are respired. Further, FWE based on aquatic GPP can help increase understanding of carbon sequestration, pollutant accumulation, and fate of long-chain polyunsaturated fatty acids and other essential biomolecules produced by aquatic primary producers (Downing and Plante 1993, Cabana G. and Rasmussen J. B. 1994, Gladyshev et al. 2009). Future studies using dietary or stable isotope analysis may help resolve the origin of primary production supporting consumers.

Flow Regime Disconnects Top-Down and Bottom-Up Forces

The observed negative correlation between food web efficiency and flow regime variability complements previous findings of limitation of FCL by streamflow variability (Post 2002b, Sabo et al. 2010a) and implies that the ecological efficiency of fish biomass production is also impeded by unpredictable flow regimes. These findings do not support the hypothesis that consumer communities are directly structured by the primary components of ecosystem metabolism (GPP and ER) and are only indirectly shaped by the environmental constraints of flow regime as mediated through bottom-up metabolic pathways (Bernhardt et al. 2018, Rüegg et al. 2021). Instead, we found that flow regime variability appeared to constrain FWE through restricting fish secondary production.

Frequent disturbances in streams limit strong predator-prey interactions compared to infrequently disturbed streams, lakes, or experimental food chains (Resh et al. 1988, Jellyman and McIntosh 2020). Desert streams generally have high rates of primary production, which recovers quickly following a disturbance (Fisher et al. 1982). In contrast, streamflow variability structures fish communities and selects for species with life history strategies compatible with the local regime (Mims and Olden 2013). Because large-bodied, long-lived organisms are less resilient to extreme events than small-bodied organisms (Pimm 1984), disturbance regime may structure both secondary production and trophic efficiency. We can then hypothesize that, in highly disturbed aquatic ecosystems, primary production does not drive secondary production because fish communities are more strongly influenced by disturbance than the rate of primary production. The differential responses of fish and primary producers to highly variable flow regimes on an annual timescale can additionally prevent top-down control of primary production that has been observed under more stable environmental conditions (i.e., Hairston et al. 1960, Power 1990). Hence, flow regime may decouple the links in the classic Eltonian food pyramid, where a relatively predictable portion of energy is transferred from one level to the next.

While primary producers do ultimately limit trophic dynamics of food webs, the strength of bottom-up and top-down forces are affected by myriad factors (Power 1992). Hypothesized constraints on food webs could therefore induce differential, regime-dependent, responses in communities shaped by long-term patterns of disturbance. Thus, across streams on a gradient of disturbance regime variability, mechanisms such as FCL, resource quality, and resource quantity may have little predictive power of FWE, but could structure temporal dynamics of food webs at a single site—providing a mechanistic explanation for the lack of positive effects of resource availability on FCL found by McHugh et al. (2010) and Sabo et al. (2010). These conclusions highlight the dearth of empirical studies on spatial or temporal variation in trophic efficiency and the roles of top-down versus bottom-up forces in food webs, and emphasize that *in situ* studies reveal additional mechanisms, such as disturbance regime, not discernable from mesocosms or single-site observations.

Conclusions

Documentation of fish community secondary production in streams and rivers is rare (Rypel and David 2017), but is recognized as an underused tool in assessing ecosystem restoration efforts (Layman and Rypel 2020). Further integrating measures of primary production with secondary production in field conditions may be additionally informative for managing and monitoring freshwater ecosystems. As technological and modeling advances have facilitated large-scale studies of ecosystem metabolism (Appling et al. 2018), there is increasing capacity and interest in understanding energy flow from primary production to consumers (Rüegg et al. 2021). Here, we demonstrated how simultaneous monitoring of metabolic regimes and community secondary production can be implemented to study interactions between potential controls on food web dynamics in natural systems. The emergent property of FWE arises from biotic and abiotic processes at all levels of the ecosystem, highlighting its potential to reassess classic theories on food webs and understand ecosystem function as aquatic ecosystems face increasing anthropogenic pressure. Climate change and river degradation are altering riverine community structure, flow regimes, and nutrient cycles (Palmer and Ruhí 2019). We found that rising temperatures may decrease FWE. Additionally, energy flow from primary producers to consumers and the strength of biotic interactions on energy transfer may be decoupled by the effects of flow regime, further suggesting that modifications to river ecosystems may produce complicated antagonistic effects on fish production. Increased comprehension of ecological efficiencies opens the opportunity to understand not just how individual consumers, populations, or biogeochemical processes are affected by global change, but how each response propagates through food webs.

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Table 1: Spearman's rank correlation between food web efficiency (FWE), annual gross primary production (GPP) and fish secondary production with hypothesized constraints for each study year. Components of ecosystem metabolism (GPP, ecosystem respiration [ER], NEP, and GPP:ER) were not correlated with FWE because efficiency is calculated relative to GPP. Correlation coefficients are bolded when ρ > 0.3.

	Algae C:N	Algae C:P	FCL	Temp (C)	σ_{hf}	GPP	ER	NEP	GPP:ER
				Food web efficiency					
Year 1	-0.047	-0.167	0.048	**-0.667**	-0.240	–	–	–	–
Year 2	-0.033	0.083	0.167	**-0.467**	**-0.483**	–	–	–	–
Year 3	–	–	–	**-0.700**	**-0.800**	–	–	–	–
				Annual GPP					
Year 1	0	0.267	0.190	**0.300**	0.017	–	–	–	–
Year 2	-0.133	0.05	**0.452**	**0.383**	0.283	–	–	–	–
Year 3	–	–	–	**0.900**	**0.400**	–	–	–	–
				Fish secondary production					
Year 1	-0.214	**0.381**	**0.881**	**-0.571**	**-0.357**	0.167	**-0.690**	**-0.738**	-0.261
Year 2	-0.150	0.083	**0.476**	**-0.383**	**-0.517**	-0.167	-0.067	**-0.383**	**-0.433**
Year 3	–	–	–	**-0.700**	**-0.800**	**-0.600**	0.200	**-0.600**	**-0.700**

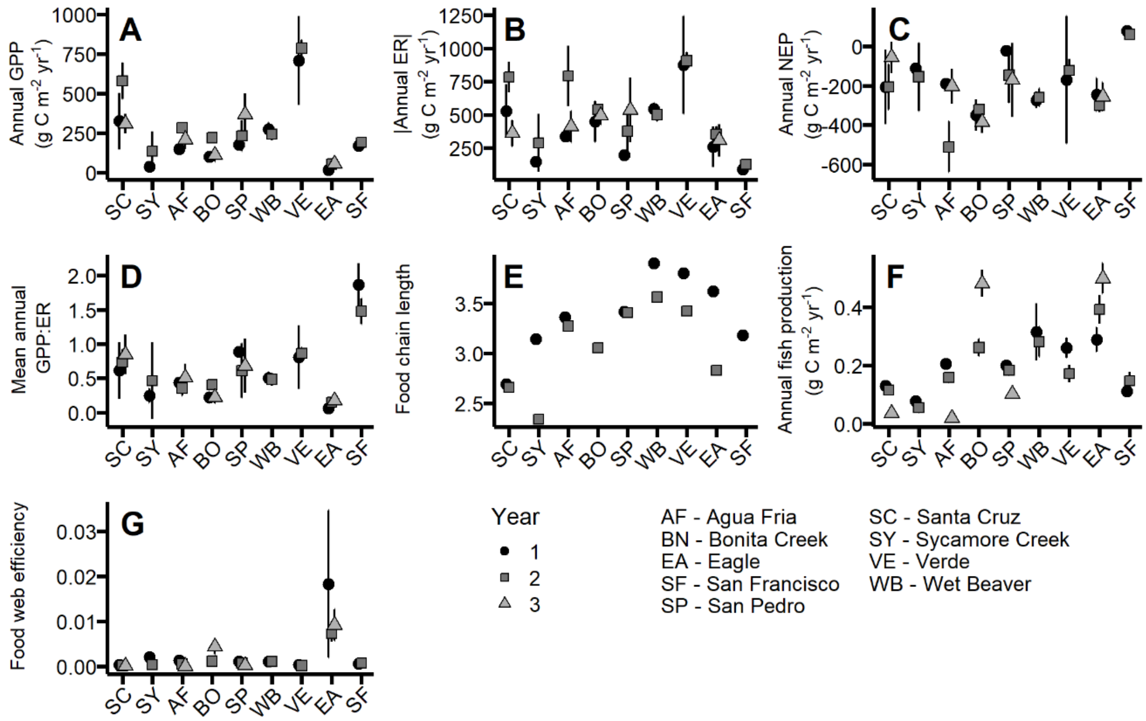

Figure 1: Annual estimates of ecosystem metabolism metrics (A-D), food chain length (E), fish community secondary production (F), and food web efficiency (G) at nine streams and rivers. Sites are arranged from high to low flow regime variability (σ_{hf}). Not all sites were sampled in each of the study years (Appendix B: Table S1).

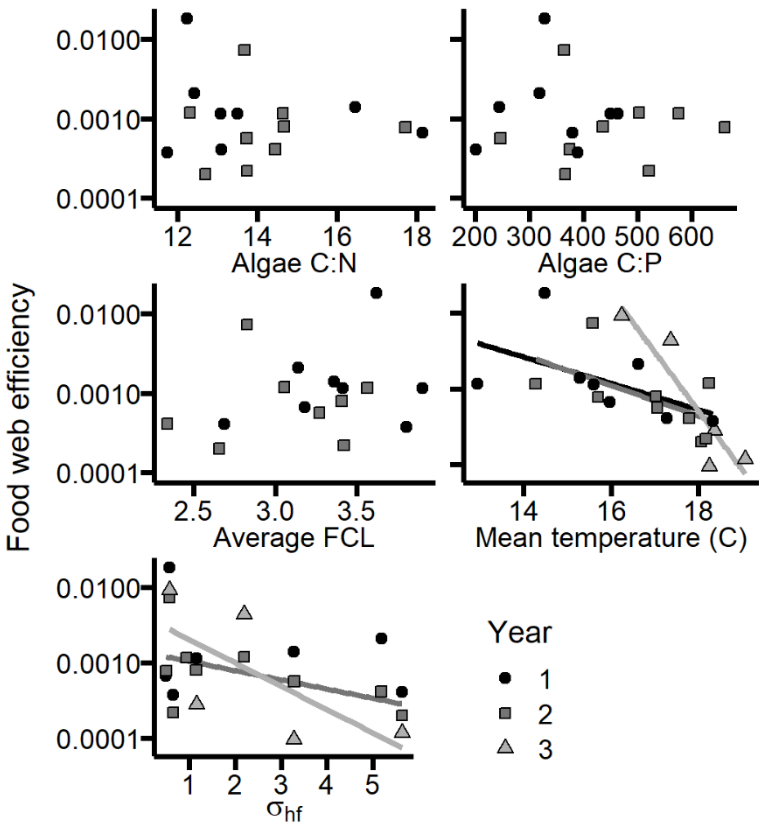

Figure 2: Relationships between food web efficiency (fish secondary production / annual GPP) and hypothesized constraints. Best fit lines are drawn when Spearman ρ > 0.3.

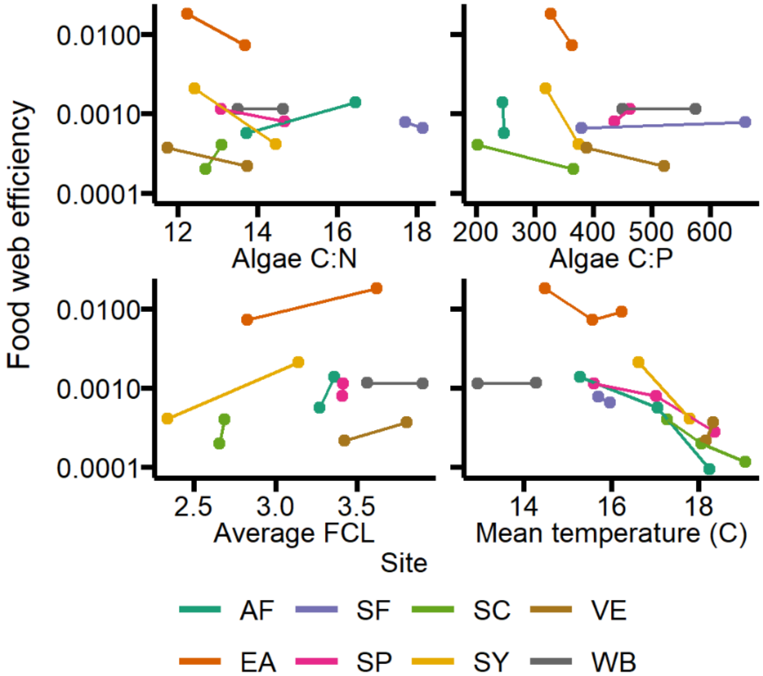

Figure 3: Within-site difference in food web efficiency between consecutive years.

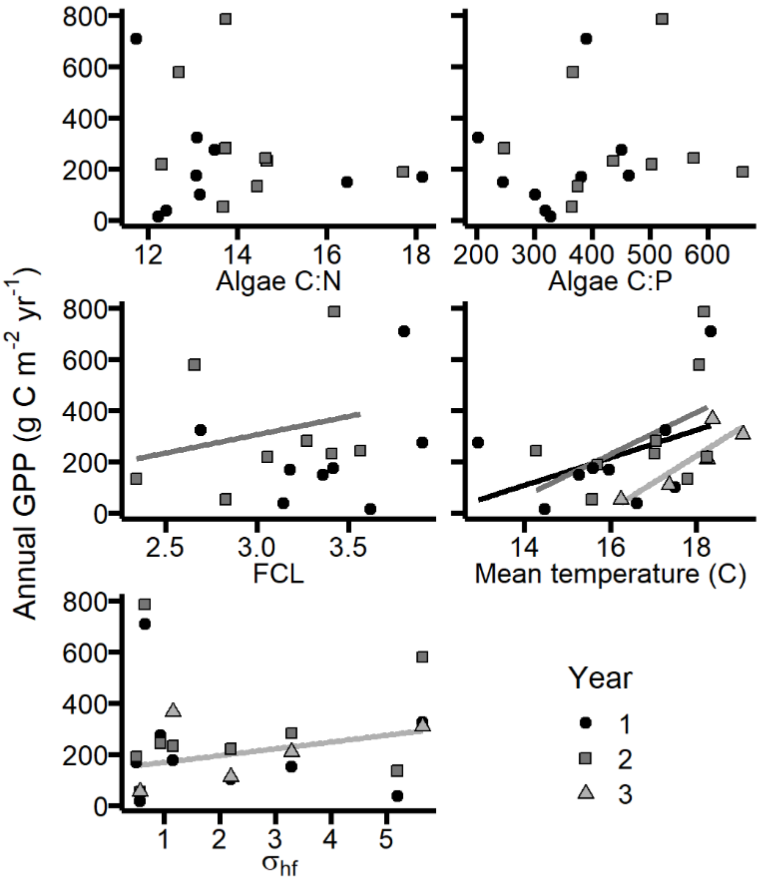

Figure 4: Relationships between estimates of annual gross primary production (GPP) and environmental conditions to explore bottom-up constraints on food web efficiency. Best fit lines are drawn when Spearman ρ > 0.3.

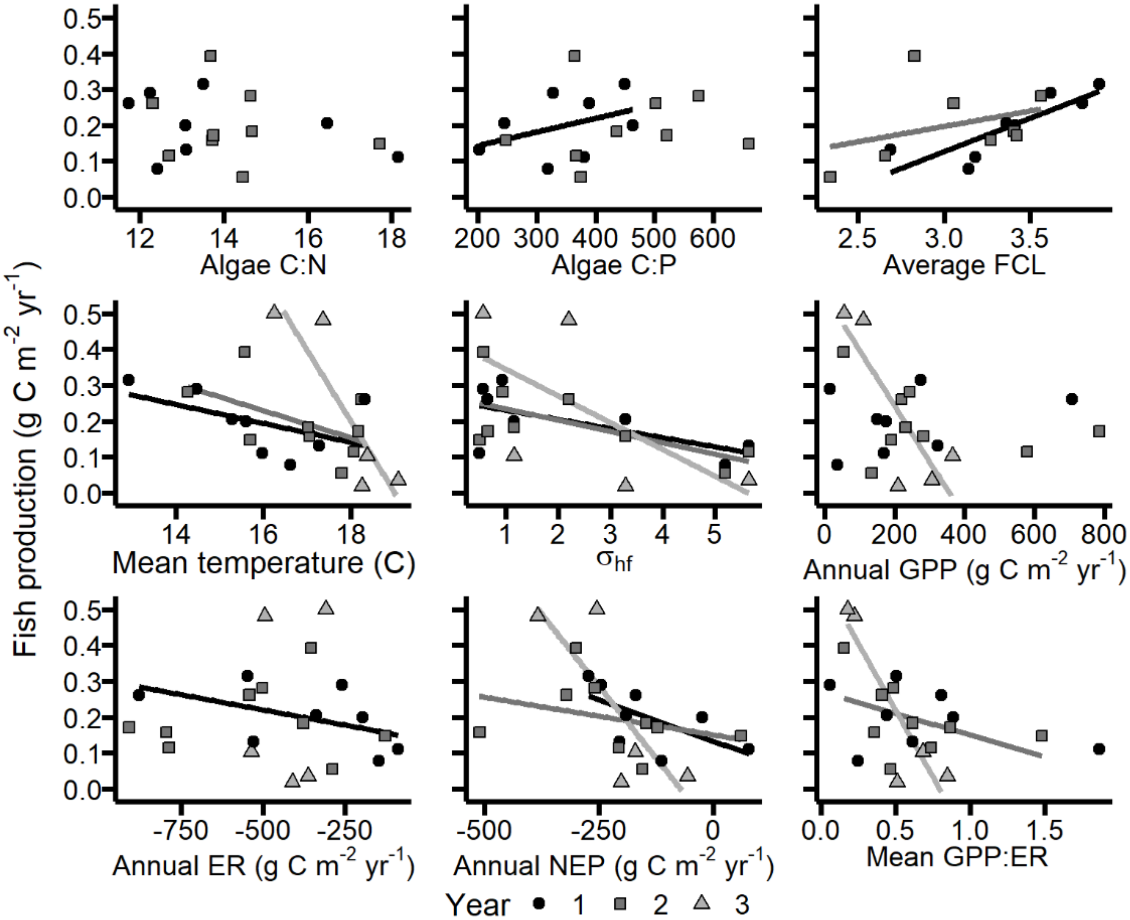

Figure 5: Relationships between annual fish community secondary production and hypothesized constraints over three years. Best fit lines are drawn when Spearman ρ > 0.3.

CHAPTER 4

THERE AND BACK AGAIN: RESOURCE RECYCLING BY EMERGENT INSECTS DECREASES AQUATIC ENERGY FLUX TO RIPARIAN PREDATORS

ABSTRACT

The study of resource exchange across the aquatic-riparian boundary largely focuses on the quantity of cross-boundary resource flux to establish ecosystem nutrient budgets, or their influence on population and trophic dynamics. What remains largely unexplored is how resources derived from primary production in one system may cycle back and forth across spatial boundaries after they are first consumed. Aquatic insects that assimilate terrestrial resources and emerge as winged adults recycle terrestrial primary production back to the habitat of origin, and thus, are not a homogenous cross-boundary resource. In this study, we measured the flux of aquatic-to-riparian, riparian-to-aquatic, and recycled terrestrial resources at two rivers over multiple seasons. We evaluated how the contribution of aquatic and terrestrial primary production to aquatic insect and riparian predator diets varied in response to resource availability. Reliance on cross-boundary resources was remarkably stable over time for consumers in both ecosystems, despite large changes in the flux of detritus to rivers and the relative abundance of emergent insects. Cross-boundary resource use was also notably consistent between sites and with previous studies, suggesting consumers may preferentially select prey to achieve specific nutrient targets, regardless of prey abundance. Estimates of riparian predator reliance on the aquatic ecosystem differed substantially depending on whether resource recycling was considered. On average, spiders received over half their diet from emergent

insects, but only 34–42% from aquatic primary production. Lizard diet contained approximately 27% aquatic insects, with less than 20% of resources consumed originating from aquatic primary production. Discerning between the origin of prey consumed and the original sources of primary production contributing to these resources will facilitate predictions of how the quantity and quality of cross-boundary resources contribute to consumer dynamics in stream-riparian ecosystems.

INTRODUCTION

Resource exchange across ecosystem boundaries is ubiquitous, but is particularly well documented between aquatic and riparian ecosystems (Polis et al. 1997). Nutrient and energy transfers between streams and riparian zones occur predominantly in the form of plant detritus and terrestrial invertebrates passively falling into streams, and aquatic insects emerging from the water as winged adults (Vannote et al. 1980, Polis et al. 1997), reciprocally linking stream and riparian food webs (Nakano and Murakami 2001, Baxter et al. 2005). Yet the study of resource exchange tends to focus on either the quantity of resource flux and contributions to ecosystem energy and nutrient budgets (Fisher and Likens 1973, Jackson and Fisher 1986), or on the organisms that directly consume the resources, and resulting population and trophic dynamics (Nakano et al. 1999, Sabo and Power 2002b). However, the nutritional content of resources consumed by organisms can cycle through the food web to indirectly affect higher trophic level predators (Malzahn et al. 2007) and initiate cross-boundary trophic cascades (Sitters et al. 2015). Untangling the extent of aquatic-riparian linkages therefore requires new approaches to merge resource fluxes and budgets with energy and nutrient flow through sequential trophic interactions.

The distinction between consumption of locally produced primary production, internal resources, and cross-boundary sources of primary production, external resources, is necessary to consider in linked stream-riparian ecosystems where the quantity and quality of resources available to consumers significantly affect population and ecosystem dynamics (Bartels et al. 2012). In freshwaters, primary consumers tend to rely on resources of higher quality, regardless of origin or relative abundance (Marcarelli et al. 2011). Consumers require a certain balance of nutrients and energy to survive, grow, and reproduce, and can optimize the identity and quantity of ingested resources by preferential selection to reach these targets (Raubenheimer and Simpson 1993). If consumers preferentially select for or against resources based on nutritional quality to achieve a nutritional target, spatial and temporal patterns of cross-boundary resource use may be more consistent than expected based on abundance.

Algae are high-quality food resources (e.g. low carbon to nitrogen and phosphorus ratios) relative to the wood and leaf detritus that dominate terrestrial-to-aquatic flux in small, shaded streams (Cross et al. 2005), and may therefore be selected for and support a high proportion of aquatic invertebrate production relative to availability (McCutchan and Lewis 2002). Riparian predators may preferentially consume emergent insects because they contain elevated concentrations of essential long-chain polyunsaturated fatty acids, which are high quality biomolecules produced by algae and absent in most terrestrial plants (Martin-Creuzburg et al. 2017). Omega-3 polyunsaturated fatty acid content is high in emergent insects and is a better indicator of terrestrial invertivore growth and condition than resource abundance (Twining et al. 2016). The mechanisms shaping resource use by consumers are significant to conservation and management of coupled stream-riparian ecosystems because global stressors are altering riparian plant community composition, the timing and abundance of invertebrate emergence, and aquatic to riparian pollutant transport (Merritt and Poff 2010, Larsen et al. 2016, Kraus 2019).

Many aquatic insect taxa rely on aquatic primary production (grazers), but collector-gatherer and filter-feeding taxa integrate both aquatic production and terrestrial plant detritus (Merritt and Cummins 1996). Larval aquatic insects that consume external resources and emerge from the stream as adults "recycle" some portion of terrestrial-originated primary production back to the system of origin (Kraus and Vonesh 2012). Few field studies have directly addressed resource recycling through emergent insects (but see Scharnweber et al. 2014, Jonsson and Stenroth 2016, Kautza and Sullivan 2016), and the contribution of these recycled resources to riparian predator diet has not been quantified.

Significantly for riparian predators, the recycling of terrestrial primary production decreases the magnitude of algae-derived resources in emergent insect flux relative to the quantity expected if emergent insects are considered a homogenous resource subsidy. The measured strength of aquatic-riparian linkages may then depend on the approach used to calculate the linkage, either as the flux and consumption of emergent insects, or the contribution of aquatic and terrestrial primary production to emergent insect flux and riparian predator diet. Thus, the recycling of terrestrial primary production through streams obfuscates the term "resource subsidy", defined as nutrients, detritus, and organisms crossing a spatial boundary (*sensu* Polis et al. 1997), suggesting the need for a new approach to cross-boundary resource dynamics. Here, we illustrate that the approach used to evaluate resource flux or use by consumers can strongly affect the interpretation of aquatic-riparian linkage strength, which may have implications for policy and management of freshwater ecosystems (Muehlbauer et al. 2019).

Synthesizing temporal patterns of bidirectional resource exchange, resource abundance and quality, and consumer reliance on cross-boundary resources is necessary to better understand ecosystem and trophic dynamics (Subalusky and Post 2019). Here, we studied two rivers in Arizona, USA for 16 months to quantify seasonal variation in reciprocal resource flux, the relative availability of internal and external resources, and the pools of primary production supporting aquatic insects and riparian predators. Rivers in the desert Southwest have a year-round growing season for aquatic invertebrates and elevated rates of insect emergence due to high temperatures and flood-adapted species with short generation times (Jackson and Fisher 1986), allowing for continuous measures of emergence. We used emergence traps to quantify aquatic-to-riparian insect flux, pitfall traps to assess the relative abundance of potential riparian invertebrate prey items, and pan traps to measure riparian-to-aquatic detritus flux. Additionally, we used stable isotope analysis to estimate the dietary contribution of external resources to aquatic insects and two abundant riparian predators, and the proportional contribution of recycled resources to the flux of emergent insect biomass and riparian predator diet.

To explore the flow of nutrients and energy through the aquatic-riparian food web more fully, we asked three broad questions: 1) how does temporal variation in the diet of aquatic insects and riparian predators relate to the flux, relative availability, and quality of external resources? 2) To what extent do recycled riparian resources contribute to cross-boundary resource flux and the diets of riparian predators? 3) How does recycling affect measured aquatic-riparian linkage strength? By conducting a temporal and longitudinal study, we endeavored to assess how resource quantity and quality influence consumer selection of prey items and resulting dietary reliance on aquatic versus terrestrial primary production.

METHODS

Site Description

Field sampling took place between March 2018 and June 2019 at the Agua Fria and San Pedro rivers in Arizona, USA (Table 1), which are characterized by an arid climate (mean temperature = 17.2 and 17.6 ºC, respectively) and seasonal rainfall occurring in summer and winter. We studied a 250-m stretch of river at each site that included several riffles, pools, and runs, and a 10-m wide band of riparian habitat on each side. Riparian overstory vegetation was dominated by cottonwood (*Populus fremontii*) and willow (*Salix goodingii*) at both sites and we measured average summer canopy cover using a concave spherical densitometer. During the study period, average daily discharge was 0.53 $m^3 s^{-1}$ (range 0–37.38 $m^3 s^{-1}$) at Agua Fria and 0.36 $m^3 s^{-1}$ (range 0.01–16.40 $m^3 s^{-1}$) at San Pedro, measured at US Geological Survey stream gauges near each site (Table 1). Although there was no measurable flow at the Agua Fria gauge for 16 days in summer 2018, the entire study reach remained connected.

Resource Flux and Prey Abundance

To measure aquatic-to-riparian resource flux, we sampled emergent aquatic insects monthly at each site using pyramidal floating emergence traps with 0.36 m^2 surface area, adapted from Cadmus *et al.* (2016). Traps were constructed with white No-See-Um mesh fabric (Rockywoods Fabric Co. Loveland, CO, USA) to effectively capture small-bodied invertebrates. Invertebrates were collected in a sample bottle attached to the top of the trap. We deployed eight traps for 48 hours throughout the reach, placed in proportion to the abundance of primary habitat types (pools, riffles, and runs). Monsoons in August and October 2018 at Agua Fria and July 2018 at San Pedro destroyed emergence trap samples for these months. We counted and identified all emergence trap samples (following Merritt and Cummins 1996), and dried each sample sorted by family to obtain dry mass (DM; nearest 0.01 mg) of invertebrates collected in each trap. We calculated the rate (number m^{-2} d^{-1}) and biomass (mg m^{-2} d^{-1}) of aquatic-to-riparian invertebrate flux for each month and quantified annual emergence as the average daily number and biomass of emergent insects from July 2018–June 2019 multiplied by 365.

We measured riparian-to-aquatic flux using eight floating pan traps (0.21 m^2) spaced evenly throughout the reach. Traps were shallow plastic trays filled with 3-4 cm of water and several drops of surfactant, anchored along alternating sides of the riverbank. We deployed pan traps for 48 hours, collected all organic matter and froze the samples. We were unable to collect pan trap samples in October–December 2018 and June 2019 at both sites, and August 2018 at Agua Fria and July 2018 at San Pedro. In the lab, we isolated all plant materials from each trap, dried samples for at least 48 hours at 60 ºC, and recorded dry mass.

To quantify the relative abundance of riparian prey items for lizards and spiders, we sampled ground-dwelling riparian arthropods monthly from December 2018–June 2019 using pitfall traps constructed from 16 oz cups filled with approximately 5 cm of water and a drop of surfactant. We deployed eight traps 1 m from the stream and eight traps 10 m from the stream, bordering the riparian-upland interface. Traps were collected after 48 hours and samples were stored in 70% ethanol. We identified pitfall trap samples to order and counted all macroinvertebrates. We calculated the abundance of riparian invertebrates for each month as the average number of invertebrates per trap, including both the 1-m and 10-m traps.

Stable Isotope Sample Collection and Analysis

For our analysis of riparian predator diet, we selected the ornate tree lizard (*Urosaurus ornatus*) and thin-legged wolf spider (*Pardosa* sp.) as abundant, generalist riparian predators that are known to integrate aquatic and terrestrial resources (Baruch et al. *in press*). *U. ornatus* is found in riparian zones throughout the southwestern USA and is primarily arboreal or semiarboreal, inhabiting rocky outcroppings in the absence of trees (Dunham 1981). Individuals in this study had an average snout-vent length of 45.4 ± 4.6 mm and mass of 3.0 ± 0.9 g. *U. ornatus* hibernate during winter months and were collected within 10 m of the water's edge from March–June. We collected blood samples from four individual lizards per month and centrifuged the samples to separate plasma from red blood cells. We selected lizard plasma for stable isotope analysis because it has a fast tissue turnover time, allowing for measurement of short-term dietary shifts (Vander Zanden et al. 2015).

Pardosa are a genus of small, ground-dwelling spiders in the Lycosidae family that actively forage in the riparian zone (Martin Nyffeler 1999). Because the quantity of emergent insects available to predators attenuates rapidly in the riparian zone

(Muehlbauer et al. 2014), we sampled *Pardosa* spiders within 1 m of the water to capture a maximum estimate of aquatic insect consumption. Spiders were hand collected from January–June 2019 and kept alive in individual containers for several hours to allow gut clearance, then frozen.

To isolate the baseline isotopic signatures of primary producers in 2019, we collected detrital (January and February) and fresh (March-June) leaves from cottonwood trees and fresh Bermuda grass leaves (all months), which have C3 and C4 photosynthetic pathways, respectively. C3 and C4 photosynthetic pathways produce distinct ratios of carbon stable isotopes ($\delta^{13}C$) and have seasonal changes in abundance and contribution to consumer diet in arid ecosystems (Warne et al. 2010b). We used fresh leaves instead of stream-conditioned vegetation because conditioned detritus is colonized by bacteria, fungi, and other heterotrophic organisms that alter isotope ratios (Finlay 2001). We collected samples of filamentous algae from throughout the study reach to quantify aquatic primary producer stable isotope and nutrient ratios. Additionally, we collected crickets of the genera *Gryllus* and *Nemobiinae* as representative, generalist invertebrate herbivores. All samples were stored on ice in the field then frozen.

In the lab, we washed leaves and algae with deionized water and algae were visually inspected for and cleaned of debris and calcium carbonate deposits. Four replicates of each primary producer were then processed individually. We selected three of the most abundant emergent insect families to include in stable isotope analysis as potential food sources for riparian predators: Chironomidae (midges) are a diverse family of dipterans with predatory and non-predatory species, Simuliidae (blackflies) are filter feeders that integrate both aquatic and riparian resources, and mayflies of the family Baeitidae are collector-gatherers and scrapers (Merritt and Cummins 1996), and were assumed to feed exclusively on aquatic primary producers. We conducted stable isotope analysis on three replicate samples of each of the three selected invertebrate families, when available, for each site visit. Replicates were composed of pooled samples of invertebrates from distinct locations throughout the reach and contained at least 3 and up to 40 individuals to reach target weight for analysis. By pooling several individuals within each sample and analyzing samples from different locations, we aimed to quantify the isotopic signatures representative of the dominant taxa of emergent insects at each month, capturing potential changes in species composition within each family over time. We analyzed four whole spiders, two males and two females, individually to capture variation in riparian invertebrate predator diet.

We dried plant and invertebrate samples at 60 ºC for 48 hours, then ground samples to a fine powder with a mortar and pestle before stable isotope analysis. For lizard isotope analysis, we pipetted 15 μL of plasma directly into tin capsules, which were dried at 60 ºC for 24 hours, then closed. All samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ isotopes with a Thermo Scientific Delta V mass spectrometer connected to a Costech 4010 elemental analyzer at the University of New Mexico Center for Stable Isotopes. Stable isotope ratios are expressed in δ notation relative to the international standards, Pee Dee belemnite limestone for C and atmospheric N.

Stable Isotope Mixing Models

We estimated dietary proportions of consumer food sources with a Bayesian mixing-model framework using MixSIAR (Stock and Semmens 2016, Stock et al. 2018) in R (R

Core Team 2019). These models incorporate variability in the isotope input data and uncertainty in trophic enrichment factors to estimate likely ranges of consumer diet (Parnell et al. 2010). We selected the widely used trophic enrichment factors (TEFs), 0.39 ± 1.3‰ for $\delta^{13}C$ and 3.4 ± 0.98‰ for $\delta^{15}N$, published by Post (2002). Although estimates from mixing models may be affected by variability in enrichment factors (Bond and Diamond 2011), these values have been found to be generally applicable and yield robust results in aquatic and riparian food web studies (Paetzold et al. 2005, Ruhí et al. 2016, Baruch et al. *in press*). Additionally, published fractionation factors for lizard plasma, -0.5 ‰ for $\delta^{13}C$ and 2.7‰ for $\delta^{15}N$ (Warne et al. 2010a, Warne and Wolf 2021), are similar to the values used here and fall within the range of uncertainty accounted for by the mixing models. Stable isotope ratios of consumer tissue reflect the isotopic signature of food sources integrated over the time period the tissue was synthesized (Vander Zanden et al. 2015). Tissue turnover time for lizard plasma is approximately 20 days for ^{15}N (Warne and Wolf 2021) and 25 days for ^{13}C (Warne et al. 2010a). Predatory invertebrates may also approach the isotopic values of their prey within 21 days (Ostrom et al. 1997). Our estimates of lizard and spider diet should therefore reflect the food sources assimilated by the sample population between our monthly sampling.

An additional strength of using a Bayesian mixing model framework is the ability to include information from other data sources as informative prior distributions (Moore and Semmens 2008). We used estimates of lizard and spider diet sources at another river in Arizona (Baruch et al. *in press*) to construct a prior distribution for each predator, scaling the Dirichlet hyperparameters of the prior distribution to create an informative prior with the same weight as an "uninformative" generalist prior (Stock et al. 2018). We retained the uninformative prior for estimates of aquatic insect diets. Riparian predator diets were estimated using Baetidae, Chironomidae, and Simuliidae as potential emergent insect sources, when available, and tree leaves and Bermuda grass corrected with 2xTEFs (following Phillips et al. 2014) to represent the isotopic signatures of riparian invertebrates feeding exclusively on C3 and C4 plants, respectively. We ran separate mixing models for each consumer taxa and site every month and verified model convergence on the posterior distribution using Geweke and Gelman-Rubin tests (Stock and Semmens 2016).

Periphyton is a primary food source for herbivorous aquatic invertebrates (Feminella and Hawkins 1995), but could not be collected consistently during the study. However, herbivorous invertebrates are often used to represent the isotopic baseline of the aquatic food web instead of filamentous algae or periphyton because they represent the aquatic primary production assimilated by primary consumers. (Vander Zanden and Rasmussen 1999, Finlay 2001). We estimated the isotopic signature of aquatic primary producers by subtracting one TEF from the isotopic ratios of Baetid mayflies. Baetid mayflies feed primarily on aquatic primary producers, but may consume small quantities of terrestrial resources (Chessman et al. 2009), introducing a potential source of error in the mixing models. Chironomidae and Simuliidae diets were calculated using the estimated aquatic baseline, tree leaves, and Bermuda grass. We ran an additional set of models for Chironomidae and Simuliidae diets using algae isotope ratios instead of the baseline calculated from Baetid mayflies to validate our assumption that mayflies were a more accurate representation of the aquatic primary producers assimilated by invertebrates.

These models had poorer convergence based on Geweke and Gelman-Rubin tests and we therefore used model results with the Baetid aquatic baseline in all further analyses.

Chironomidae (Chiro.) and Simuliidae (Simu.) external resource use was calculated as the sum of tree leaves and Bermuda grass in diet estimates. To quantify the cycling of recycled resources, we attributed the estimated proportion of aquatic and terrestrial primary production in the diet of each invertebrate prey taxa to predator diet relative to the consumption of each prey source. Total terrestrial primary production in riparian predator diet was then calculated as:

$$\Sigma\ (\mathit{diet\%\ riparian\ inverts} + \mathit{diet\%\ Chiro.} \cdot \mathit{Chiro.\ \%terrestrial} + \mathit{diet\%\ Simu.} \cdot \mathit{Simu.\ \%\ terrestrial})$$

Recycled resources in riparian predator diet were calculated as:

$$\Sigma\ (\mathit{diet\%\ Chiro.} \cdot \mathit{Chiro.\ \%\ terrestrial} + \mathit{diet\%\ Simu.} \cdot \mathit{Simu.\ \%\ terrestrial})$$

Data Analysis

We visually assessed temporal trends in resource flux and use by consumers to describe dietary patterns from January–June 2019. To assess potential interactions between resource quantity and quality, we used C:N of primary producers and invertebrates as one measure of nutritional value. We averaged C:N values of each producer and consumer group across the two sites within each month. We used one-way ANOVAs to test if the nutritional value of primary producers, based on C:N, changed over time and if invertebrate consumers were homeostatic in their nutritional composition, or adapted in response to resource stoichiometry.

RESULTS

Cross-Boundary Resource Flux and Resource Recycling

Aquatic insect emergence was continuous throughout the year, with strong fall and spring peaks at Agua Fria and muted peaks in spring and early summer at San Pedro (Figure 1 A, B). Average flux of emergent insects differed between the two rivers, with greater annual number and biomass at Agua Fria than at San Pedro (Figure 1 C, D; Table 2). Invertebrate emergence was dominated primarily by Chironomidae, and the three invertebrate taxa used to calculate resource recycling composed 69% of annual emergent biomass, averaged over both sites (Table 2). Average daily flux of riparian plant detritus to each river for the months with available data was 0.61 ± 0.54 g m^{-2} at Agua Fria and 1.37 ± 1.50 g m^{-2} at San Pedro.

The contributions of aquatic and terrestrial primary production to Chironomidae and Simuliidae diet were relatively consistent over time and between sites (Figure 2 A, B). However, the relative proportion of total emergent insect biomass derived from terrestrial primary production varied over time at both sites, decreasing from the winter to spring months at San Pedro (Figure 2 C). When considering just Baetidae, Chironomidae, and Simuliidae, 7.1 and 2.4 g m^{-2} of aquatic primary production was exported to the riparian zone over six months, and 5.7 and 0.6 g m^{-2} of terrestrial primary production was recycled at Agua Fria and San Pedro, respectively. Thus, only 55% of emergent insect dry mass at Agua Fria, and 80% at San Pedro were derived from aquatic primary production on average.

Riparian Predator Resource Use

Spiders caught within 1 m of the water exhibited little variation in resource use over time (Figure 3 A, B). On average, 34% and 42% of spider diet originated from aquatic primary production at Agua Fria and San Pedro, respectively (Figure 3 C, D). However, emergent aquatic insects constituted 54% and 57% of spider diet at the two sites. The difference between aquatic primary production and aquatic insects in spider diet reveals that, on average across both sites, 15-20% of spider diet came from terrestrial primary production that was recycled through the stream by emergent aquatic insects (Figure 3 C, D). Lizards exhibited similar patterns of temporally consistent resource use (Figure 4 A, B). Aquatic primary production composed 18% and 20% of average resource use by lizards at Agua Fria and San Pedro, respectively, while emergent aquatic insects constituted 28% and 26% of lizard prey at the two rivers. Consequently, on average, recycled terrestrial primary production provided 7-9% of the resources in lizard diet across both sites (Figure 4 C, D).

Consumer Diet: Resource Quantity and Quality

The flux of riparian plant detritus into the rivers varied over time, with spring peaks at both sites and an early fall peak at Agua Fria (Figure 1 E). However, terrestrial resource use by aquatic insects did not exhibit a visual relationship with detritus input. Calculated as the ratio of the average number of emergent insects m^{-2} day^{-1} to average number of riparian invertebrates per pitfall trap, the relative availability of aquatic insects declined from December through June (Figure 5). Over this time, the abundance of riparian invertebrates increased, except after a hard frost at San Pedro in February that reduced riparian invertebrate abundance. The number of emergent insects showed little directional change, except for peaks in emergence in April at Agua Fria and March at San Pedro. However, the proportion of emergent insects in spider and lizard diets was nearly equal at the two sites, even though the total abundance and relative availability of emergent insects was consistently higher at Agua Fria.

Using C:N as an indicator of resource quality (Elser et al. 2000), we found that variation in primary producer quality depended on the ecosystem of origin (Figure 6 A). C:N of cottonwood leaves changed significantly during the study period (df = 5, F = 23.0, $p < 0.001$) from high C:N in January and February when only detrital leaves were available, to low C:N in March when fresh leaves were the youngest. Bermuda grass also exhibited temporal variation in C:N (df = 5, F = 13.5, $p < 0.001$), but was highest in the summer instead of winter. In contrast, algal C:N did not change significantly over the study (df = 5, F = 0.5, p = 0.80). Temporal change in cricket C:N followed the same pattern as cottonwood leaves, exhibiting significant change over time (df = 5, F = 3.3, p = 0.02; Figure 6 B). Emergent aquatic insects as a group (Baetidae, Chironomidae, and Simuliidae) and spiders, which receive a large portion of their diet from aquatic primary production, did not significantly change in C:N stoichiometry over the study (df = 5, F = 1.8, p = 0.11; df = 5, F = 0.7, p = 0.61, respectively).

DISCUSSION

Interconnections between adjacent ecosystems have been studied for decades (Polis et al. 1997, Baxter et al. 2005), but the transformations that cross-boundary resources undergo after they are first consumed have been largely ignored. In this study, we found that the contribution of externally produced primary production to aquatic insect and riparian predator diet remained relatively constant over time, and that recycled resources formed a sizable component of aquatic-to-riparian flux. With these results, we examined the implications of two approaches to measuring aquatic-riparian linkage: the much-applied “uni-directional” approach that considers emergent insects to be a uniform cross-boundary aquatic resource, and a second approach that acknowledges and quantifies recycling of terrestrial primary production by insects. Resources that cross a boundary may cross back again, and this recycling has important implications for our interpretation of the coupling of food webs in aquatic and terrestrial realms. The greater the recycling—in both realms—the more tightly coupled and more singular the ecosystem.

Following the flux of resources consumed by aquatic insects revealed that not all emergent insect biomass is equivalent. Emergence of aquatic insects at Agua Fria (17.2 g DM $m^{-2}yr^{-1}$) was significantly higher than the literature-derived average (4.1 ± 1.9 g DM $m^{-2}yr^{-1}$; Gladyshev et al. 2009), while emergence at San Pedro was about average (4.7 g DM $m^{-2}yr^{-1}$). However, the flux of aquatic-to-riparian emergent insect biomass was diluted by terrestrially derived resources. Averaged over both rivers, aquatic primary production contributed just over 60% of total emergent insect biomass of the three families considered for dietary analysis, with terrestrial primary production accounting for the balance.

Independent evaluation of the contributions of aquatic insects and aquatic primary production to riparian predator diet revealed that the two approaches to measuring cross-boundary resource reliance are not equivalent due to terrestrial primary production being recycled through emergent insects and unaccounted for in the “uni-directional” approach.

For example, Lycosid spiders are commonly used in stable isotope studies of aquatic-riparian food web linkage, with average consumption of aquatic resources ranging from approximately 45-55% (Collier et al. 2002, Paetzold et al. 2005, Krell et al. 2015, Stenroth et al. 2015). In this study, we found average spider reliance on cross-boundary resources was slightly higher than most previously reported averages when measured as consumption of aquatic insects (56%), but was lower when measured as the dietary proportion originating from aquatic primary production (38%). The discrepancy between approaches to calculating resource exchange illustrates that in future research, employing language that explicitly defines resource use based on origin (aquatic versus terrestrial invertebrates) or original resource pool (internal versus external primary production) will provide more accurate estimates of true resource transfer and cross-boundary mutual dependencies.

This finding has significant implications for inferences drawn from the assumption that emergent insects are a homogenous resource flux. A global meta-analysis of resource use across the freshwater-terrestrial interface found that on average, cross-boundary resources composed 39% of consumer carbon, with no significant difference between aquatic and terrestrial animals (Bartels et al. 2012). In the current study, average cross-boundary resource use was 43% if emergent insects are considered a homogenous resource to riparian predators. However, this average drops to 37% when quantifying external contribution as aquatic primary production instead of total aquatic insects in consumer diet. In application, the concept of resource recycling could help generate more precise syntheses of literature derived-values that may not be consistent in methods used to calculate cross-boundary resources. Understanding recycling not only allows us to measure individual fluxes more accurately, but by acknowledging recycling we can also measure ecosystem coupling more effectively (see Baruch et al. *in press*).

Surprisingly, we observed little change over time in the diets of both aquatic insects and riparian predators, suggesting these consumers may be selecting resources to achieve nutritional targets (Marcarelli et al. 2011). We observed that riparian lizards, *U. ornatus*, and spiders, *Pardosa* sp., maintained relatively consistent dietary proportions of aquatic and riparian invertebrates throughout the study, independent of emergent insect relative or absolute abundance. Interestingly, we also found that both lizards and spiders had nearly equal reliance on aquatic insects between the two sites, despite large differences in the relative abundance of aquatic prey items (Figure 5), indicating that these predators may preferentially select for taxon-specific intake targets of aquatic and riparian prey. This interpretation is additionally supported by the result that, although temporal change in spider C:N was not significant, spider C:N consistently had intermediate values between aquatic insects and temporally variable cricket C:N (Figure 6). If spider nutrient requirements are imbalanced with their prey, altered nutrient excretion and predation rates can perpetuate through the food web and alter nutrient flux back to the aquatic system (Sitters et al. 2015). Thus, ecosystem changes that limit predators' capacity to balance among aquatic and terrestrial prey could have reverberating effects on whole system nutrient cycling.

Aquatic insect diet also exhibited remarkably little temporal variation in aquatic versus terrestrial-derived foods, despite changes in the influx and C:N of terrestrial detritus. This suggests the observed taxa may select for relatively consistent proportions of aquatic and terrestrial resources regardless of abundance or nutrient ratios and are able to post-ingestively regulate nutrient acquisition. Terrestrial resources are frequently considered lower quality than aquatic primary production, and suboptimal primary producer nutrient ratios can reduce growth efficiency (Elser et al. 2000, Cross et al. 2005). However, nutrient ratios are not strictly equivalent to resource quality, and insects can select for specific resources to achieve a nutritional target instead of maximizing nutrient intake (Raubenheimer and Simpson 2004). For example, long-chain polyunsaturated fatty acids are not captured in measurements of C:N, but selection for these biomolecules could contribute to the observed consistency in aquatic insect reliance on aquatic primary production. Previous studies on resource cycling found chironomids obtained approximately 25-50% of their diet from riparian sources (Scharnweber et al. 2014, Kautza and Sullivan 2016). Here we found similar ratios of external resource reliance by chironomids (average 45 ± 7%), which may indicate conserved nutritional targets of this taxon that are achieved by preferential resource selection, thus regulating the availability of fatty acids and other aquatic-derived resources to riparian consumers.

Like all field studies, care is required when interpreting these results. Consumer diets were estimated using stable isotope analysis, with considerable uncertainty around mean values. Potential sources of error in these estimates include using a primary consumer to represent the aquatic primary producer baseline, uncertainty in trophic enrichment factors, and a relatively small group of consumers analyzed. Additionally, inference about preferential consumption is based on the observation of low variation in internal and external resource use by consumers over time relative to our measures of resource availability. We were not able to measure the availability of aquatic primary production for aquatic consumers, and therefore cannot conclude that the relative abundance of external resources changed over time. More detailed dietary analysis and manipulative feeding experiments would be necessary to reduce the uncertainty of consumer resource use and to directly test for preferential consumption.

Increased understanding of resource selection and cross-boundary recycling could provide novel insight for establishing priority conservation locations and strategies. Aquatic invertebrates primarily supported by aquatic primary production and their predators can have higher mercury content due to methylation in stream channels and uptake by periphyton than consumers more heavily dependent on terrestrially derived resources (Jardine et al. 2012). Riparian predators with a greater reliance on emergent insects also have higher concentrations of polychlorinated biphenyls (PCBs; Walters et al. 2008). From these studies, we can extrapolate that riparian predators with greater reliance on aquatic primary production will have higher exposure to aquatic contaminants. Further, if the relative proportion of recycled primary production in emergent insect biomass varies over time, as observed at one of our sites, exposure levels may also vary, even if predators select for a constant dietary proportion of emergent insects. Alternatively, emergent insects are often considered a homogenous group with high levels of polyunsaturated fatty acids that are highly beneficial to riparian consumers (Gladyshev et al. 2009, Twining et al. 2016). Changes in the sources of primary production supporting aquatic consumers and the flux of emergent insects due to land use change, altered hydrology, and other global stressors (Larsen et al. 2016) could alter the availability of these essential biomolecules to riparian and migratory species of special concern. Only by considering the contributions of recycled resources to cross-boundary resource exchange and temporal variation in resource use, availability, and quality will it be possible to apply and adapt current understandings of aquatic-riparian food web linkages in the context of global change.

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Table 1: Site characteristics.

	Catchment area (km^2)	Mean width (m) Average	Range	Canopy cover (%)	Coordinates	USGS gauge #
Agua Fria	1,360	3.0	2.1–3.9	44	34°19'3.81"N, 112° 4'23.97"W	9512500
San Pedro	3,028	7.2	5.2–8.0	61	31°36'19.96"N, 110° 9'12.24"W	9471000

Table 2: Annual abundance and dry mass (DM) of all emergent invertebrates, Chironomidae (Chiro., the most abundant family), and the three families used in calculations of resource recycling (Baetidae, Chironomidae, and Simuliidae) at two rivers from July 2018-June 2019. Parentheses indicate percentage of the full community.

	Emergence (# $m^{-2}yr^{-1}$) •10,000	DM (g $m^{-2}yr^{-1}$)	Chiro (# $m^{-2}yr^{-1}$) •10,000	Chiro DM (g $m^{-2}yr^{-1}$)	3 families (# $m^{-2}yr^{-1}$) •10,000	3 families DM (g $m^{-2}yr^{-1}$)
Agua Fria	17.0	17.2	14.5 (86%)	9.0 (53%)	15.7 (92%)	12.7 (74%)
San Pedro	3.8	4.7	2.8 (72%)	1.2 (25%)	3.3 (86%)	3.0 (63%)

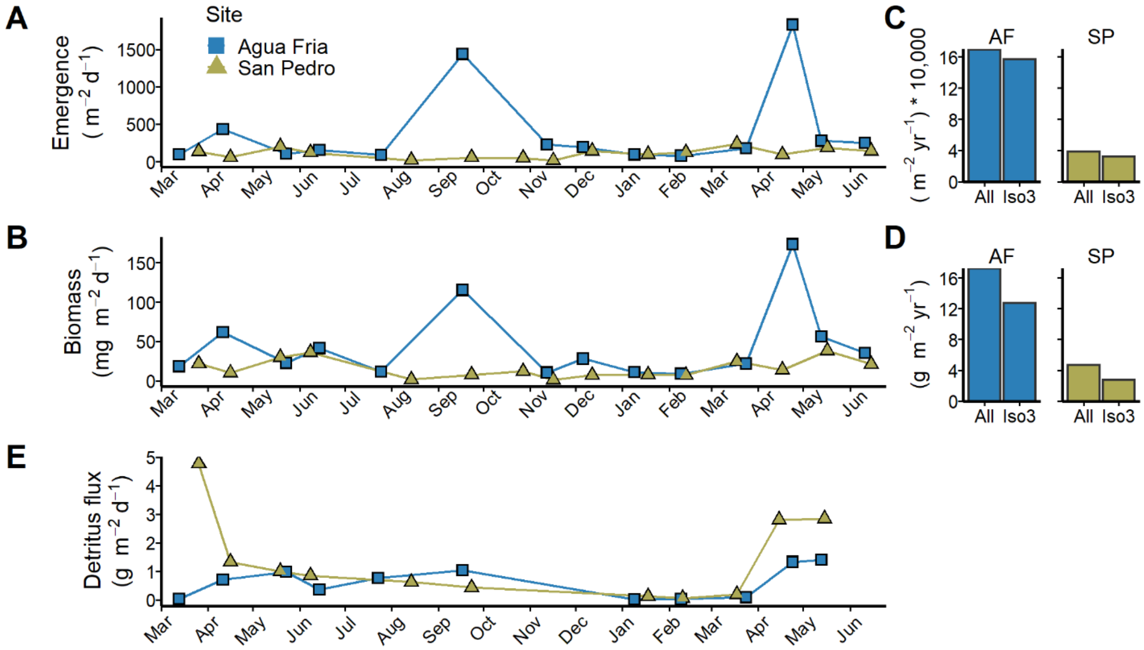

Figure 1: Monthly aquatic invertebrate emergence rate (A) and biomass flux (B), and riparian to aquatic flux of plant detritus (E) at two rivers from March 2018-June 2019. Total annual number (C) and biomass (D) of emergent invertebrates (July 2018-June 2019) for all emergent invertebrates (All) and the three families in stable isotope analysis (Iso3).

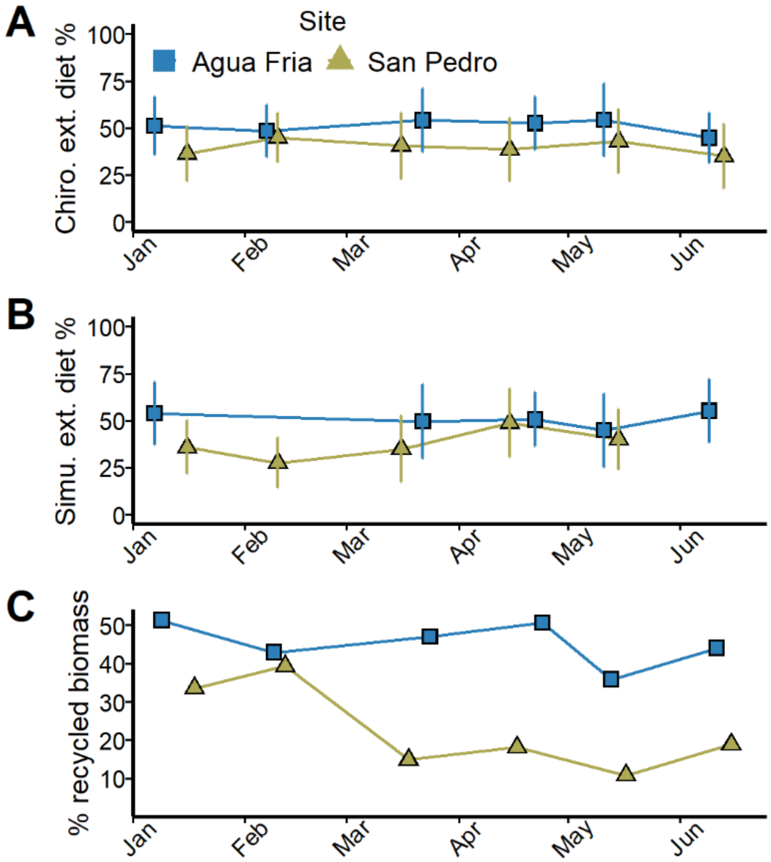

Figure 2: Monthly estimates of terrestrial resource contribution (ext. diet %) to emergent chironomid (A) and simuliid (B) diet at two rivers. (C) Percent of emergent invertebrate biomass from recycled resources for three families (Baetidae, Chironomidae, and Simuliidae).

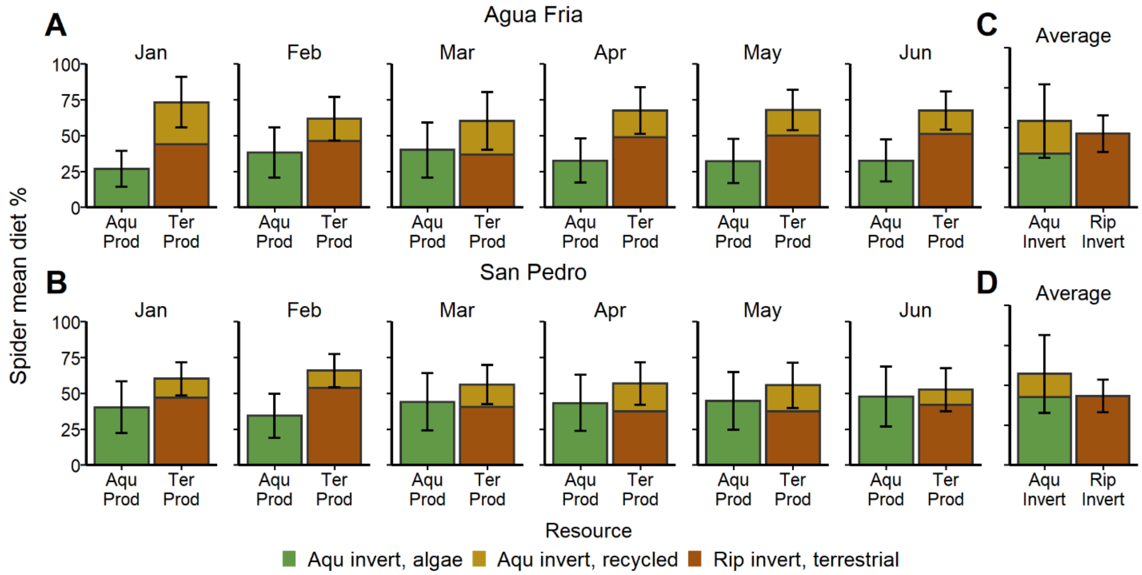

Figure 3: Estimated dietary proportion of spider (*Pardosa* sp.) diet originating from aquatic and terrestrial primary production at two rivers from January-June 2019 (A, B) and average dietary contributions of aquatic and riparian invertebrates (C, D). Error bars indicate standard deviation of model estimates.

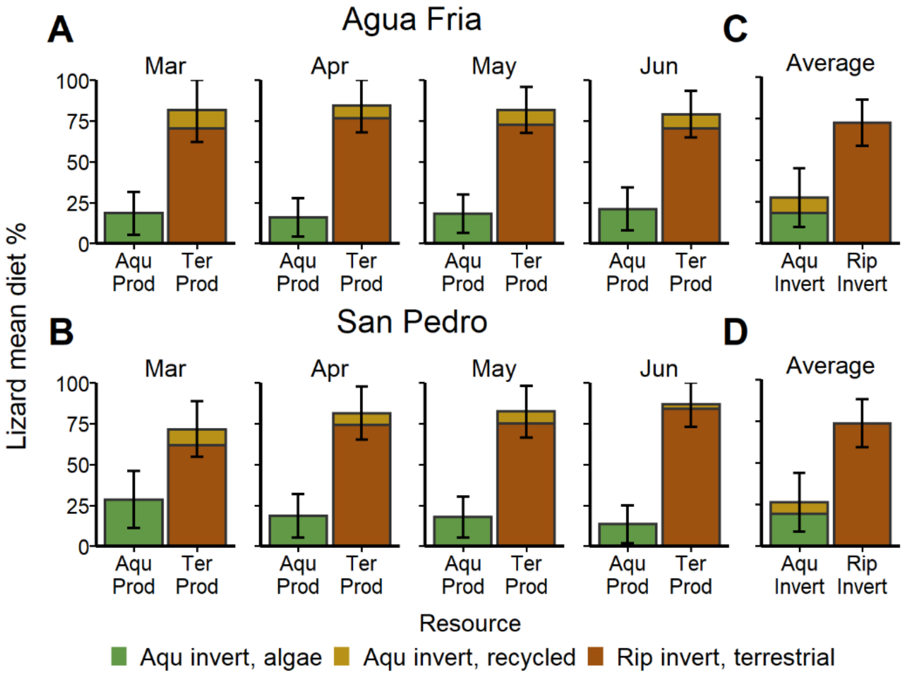

Figure 4: Estimated dietary proportion of riparian lizard (*Urosaurus ornatus*) diet originating from aquatic and terrestrial primary production from March-June 2019 (A, B) and average dietary contributions of aquatic and riparian invertebrates (C, D). Error bars indicate standard deviation of model estimates.

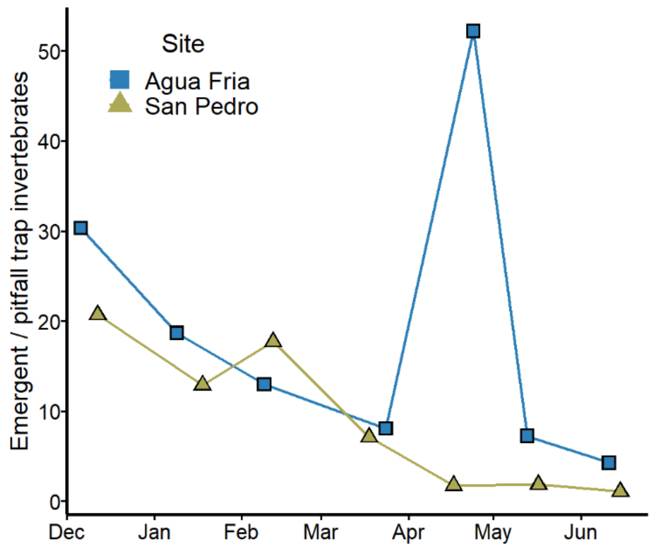

Figure 5: Relative availability of emergent invertebrates, measured as the ratio of the number of emergent invertebrates $m^{-2}day^{-1}$ to average number of riparian invertebrates per pitfall trap.

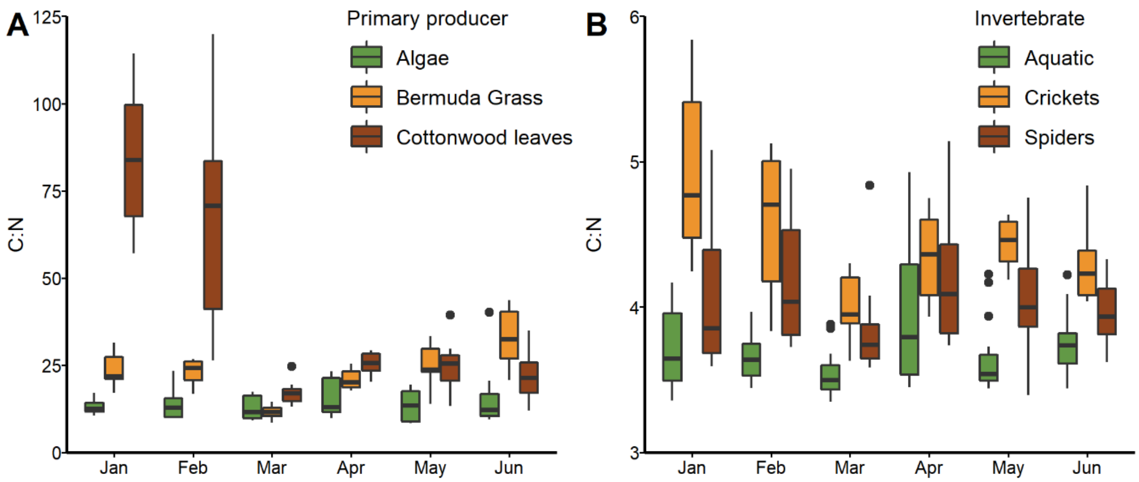

Figure 6: Resource quality of primary producers (A) and invertebrates (B), measured as C:N.

CHAPTER 5

INTEGRATED ECOSYSTEMS:

LINKING FOOD WEBS THROUGH RECIPROCAL RESOURCE RELIANCE

ABSTRACT

Ecosystems are defined, studied, and managed according to boundaries constructed to conceptualize patterns of interest at a certain scale and scope. The distinction between ecosystems becomes obscured when resources from multiple origins cross porous boundaries and are assimilated into food webs through repeated trophic transfers. Ecosystem compartments can define bounded localities in a heterogeneous landscape that simultaneously retain and exchange energy in the form of organic matter. Here we developed and tested a framework to quantify reciprocal reliance on cross-boundary resource exchange and calculate the contribution of primary production from adjacent ecosystem compartments cycling through food webs to support consumers at different trophic levels. Under this framework, an integrated ecosystem can be measured and designated when the boundary between spatially distinct compartments is permeable and the bidirectional exchange of resources contributes significantly to sustaining both food webs. Using a desert river and riparian zone as a case study, we demonstrate that resources exchanged across the aquatic-riparian boundary cycle through multiple trophic levels. Further, predators on both sides of the boundary were supported by externally produced resources to a similar extent, indicating this is a tightly integrated river-riparian ecosystem and that changes to either compartment will substantially impact the other. Using published data on lake ecosystems, we demonstrated that benthic and pelagic

ecosystem compartments are likely not fully integrated, but differences between lakes could be used to test ecological hypotheses. Finally, we discuss how the integrated ecosystem framework could be applied in urban-preserve and field-forest ecosystems to address a broad range of ecological concepts. Because few systems function in complete isolation, this novel approach has application to research and management strategies globally as ecosystems continue to face novel pressures that precipitate cascading ecological repercussions well beyond a bounded system of focus.

INTRODUCTION

The ecosystem concept proposed by Tansley (1935) – which defines an ecosystem as the organisms and the physical and environmental factors with which they interact – provides a useful and practical framework for many ecological studies. However, while ecological processes integrate biological and environmental factors across multiple geographic and temporal scales, conceptualizing an ecosystem necessitates spatially bounding the system of interest (Post et al. 2007a). The failure to properly define the extent of an ecosystem, or recognize the importance of interactions within and between ecosystems, can limit effectiveness of environmental management strategies. Therefore, environmental research and policies should recognize and quantify interconnections between ecosystems and their discrete habitats, such as fields and forests, parks and surrounding urban development, and streams as a gradient of aquatic-riparian-upland interactions. Expanding our conceptual understanding of how systems interact across boundaries could have profound implications for improving our understanding of ecosystem function and developing wholistic environmental management practices that transcend individual ecosystems (Muehlbauer et al. 2019).

Nutrients, detritus, and organisms that cross a spatial boundary may provide resource subsidies to the recipient ecosystem, and contribute significantly to nutrient cycling, species distribution, and trophic dynamics (Polis et al. 1997). Resource subsidies have been extensively documented in relationship to populations, communities, trophic interactions, and total system budgets and fluxes (Marcarelli et al. 2011). Reciprocal resource exchange between adjacent habitats may initiate trophic cascades and precipitate indirect effects in both habitats (Nakano and Murakami 2001, Baxter et al. 2005), prompting the question: how can one objectively define where one ecosystem ends and another begins (Sabo and Hagen 2012, Muehlbauer et al. 2014)?

When an ecosystem receives resource subsidies, the resulting transfers of energy and trophic cascades may not be wholly self-contained, leading to the cycling of resources both within the system and laterally back to the donor system. For example, freshwater invertebrates are often subsidized by riparian organic matter. Thus, a portion of the biomass of emergent adults that are consumed or die in the riparian zone recycles these resources back to their original system (Scharnweber et al. 2014, Jonsson and Stenroth 2016). Consumers may also forage across habitats to transport resources across spatial boundaries, which then cycle through subsequent trophic transfers (Vander Zanden and Vadeboncoeur 2002, Gounand et al. 2018).

In lakes, benthic and pelagic food webs were historically considered discrete compartments of primary and secondary production, but have undergone a paradigm shift in recent decades as new methods of measuring interconnections between the two have refocused attention on the whole-lake ecosystem (Vadeboncoeur et al. 2002, Reynolds 2008). The permeability of the river-riparian boundary has also been widely documented and theoretical advances have proposed studying these ecosystems through the lens of cross-ecosystem resource exchange (Soininen et al. 2015). However, the cycling of resources through repeated trophic transfers, and the reciprocal and inter-reliant nature of spatially distinct food webs have not been specifically addressed in a quantitative framework.

How resources with discrete origins move through food webs to support consumers at all trophic levels is universally important along ecosystem boundaries. Yet delineating these complex pathways is difficult and remains understudied. In this paper, we develop a novel quantitative method to describe cross-boundary resource use and explore this framework and its potential management applications using a river-riparian ecosystem. We then apply these methods to an existing dataset of lake food webs and discuss two examples of terrestrial ecosystems to demonstrate the broad applicability of our concept of the integrated ecosystem that traces the flow of resources across boundaries through the lens of consumer use.

The Integrated Ecosystem

Rooted in the concept of donor controlled trophic dynamics (Polis and Strong 1996), the term ‘resource subsidy’ has been adapted to describe directional and terminal cross-boundary movement of a resource to a consumer and subsequent changes in predator-prey dynamics (Polis et al. 1997). Over a heterogeneous landscape, boundaries differentiate ecosystem compartments that exchange and internally cycle energy and nutrients. In ecosystems where resources continually cycle within and between compartments, the term 'subsidy' does not consider the reality that many organisms are composed of contributions from multiple compartments. Shifting the focus from the flux of resources to the consumers that integrate them creates a more comprehensive understanding of resource dynamics across multiple trophic transfers and compartments. Here we propose the terms internal resources and external resources to replace the general term resource subsidy, where internal and external are defined relative to the consumer. Prey items from any trophic level are considered as vectors that transport resources derived from primary production to their consumers. Using this perspective, the diet of a consumer can be divided into the fraction originating from internally produced resources (ι) and externally produced resources (ε). For a consumer with n prey items:

$$\iota = \%\text{prey}_1 \text{ in diet} \cdot \text{prey}_1\,\iota + \%\text{prey}_2 \text{ in diet} \cdot \text{prey}_2\,\iota + \ldots + \%\text{prey}_n \text{ in diet} \cdot \text{prey}_n\,\iota$$

$$\varepsilon = \%\text{prey}_1 \text{ in diet} \cdot \text{prey}_1\,\varepsilon + \%\text{prey}_2 \text{ in diet} \cdot \text{prey}_2\,\varepsilon + \ldots + \%\text{prey}_n \text{ in diet} \cdot \text{prey}_n\,\varepsilon$$

Propagating ι and ε through consecutive trophic transfers can trace the flow of cross-boundary resources and determine the original resource pools supporting consumers that integrate primary production from multiple ecosystem compartments (Figure 1).

By conceptualizing resource exchange from the standpoint of consumers, it is possible to quantify the degree of independence or inter-reliance between trophic dynamics of adjacent ecosystem compartments. An integrated ecosystem is defined by the extent to which the boundary between spatially distinct ecosystem compartments is permeable to the bidirectional flow and cycling of resources, and formed when consumers in both are reciprocally reliant on external resources that cycle through consecutive trophic transfers. Here, we propose three metrics of an integrated ecosystem that can be empirically evaluated using measures of consumer ι and ε. These metrics summarize trophic interactions where external resources are passed from one consumer to another, with all consumers used in these calculations assimilating both internal and external resources. Resources are defined here as organic material consumed by an organism, but this term could be applied to specific nutrients, elements, or other material that can be traced across trophic transfers. There are few examples where ecosystem or habitat peripheries function as a hard barrier, and thus the principles of the integrated ecosystem could be applied widely to better understand the interactions between ecosystem compartments that are often studied in isolation.

Cycling efficiency (*C*) quantifies the extent to which external resources cycle up the food web to indirectly support upper trophic levels. *C* is defined as a pairwise comparison between the ε of all consumers assimilating both internal and external resources within one ecosystem compartment; where i = 1 to n consumers, and j = 1 to m prey items for consumer i.

$$C = \sum_{i=1}^{n} \left(\sum_{j=1}^{m} \left(\frac{\varepsilon_i}{\varepsilon_j} \right) / m \right) / n$$

C = 1 indicates external resources support all consumers equally, instead of only supporting production at specific trophic levels. When *C* > 1, upper trophic level consumers are more reliant on external resources than the average of their prey items and could be caused by differences in abundance of potential prey items, or preferential consumption of prey with high ε. When *C* is between 0.75 and 1.25, on average, at least 75% of external resources consumed by prey items are cycling up to support the next trophic level and predators are consuming no more than 25% more external resources than their average prey. As defined here, *C* calculates the reliance on external resources of consumers relative to their likely prey items instead of the ecological efficiency of resource transfer, which would require measures of biomass or production, and is therefore sensitive to selective feeding by consumers. By not accounting for proportional contributions of prey to consumer diet, *C* reflects the actual contribution of cross-boundary resources to multiple trophic levels. For example, C << 1 would support the hypothesis that external resources are a terminal subsidy for lower trophic levels. Given sufficient data on prey abundance and consumer diet, this definition could be expanded to inform hypotheses on preferential prey consumption and determine the trophic efficiency of external resource transfers.

Reciprocity (*R*) quantifies the similarity in ε, regardless of magnitude, between consumers in two different ecosystem compartments, and is defined by the ratio of the average ε of consumers in ecosystem compartments x and y.

$$R = \frac{min(\bar{\varepsilon}_x, \bar{\varepsilon}_y)}{max(\bar{\varepsilon}_x, \bar{\varepsilon}_y)}$$

A ratio of 1 indicates reciprocal resource reliance, or equal reliance on external resources by consumers in both compartments. As *R* decreases from 1, the compartment with the lower mean is progressively less reliant on resources from its neighbor than the inverse, or is effectively being subsidized by the adjacent compartment. If more than two compartments contribute to an ecosystem, *R* is calculated pairwise such that $\bar{\varepsilon}_x$ only includes resources from compartment y and vice versa.

Integration (*I*) is a complementary metric to *R* and describes how evenly consumers are reliant on internal and external resources, accounting for the magnitude of each. *I* is defined by the proximity of consumers in ecosystem compartments x and y to equal reliance on internal and external resources, or the evenness of the average ε and ι in an ecosystem.

$$I = 2 \cdot \left(\bar{\varepsilon}_x \cdot \bar{\iota}_x + \bar{\varepsilon}_y \cdot \bar{\iota}_y\right)$$

I is bounded from 0-1, where 1 is equal use of internal and external resources in both compartments (ι = 0.5 & ε = 0.5) and 0 is complete reliance on either internal or external resources (ι = 1 & ε = 0 or ι = 0 & ε = 1). $I > 0.75$ indicates that, on average, consumers assimilate between 25 and 75% of their resources from external sources, suggesting external resources contribute significantly to the trophic dynamics of both compartments. If more than two compartments are considered, ε is the sum of resource use from all external compartments.

Ecosystem integration is quantified by *C*, *R*, and *I*, with values closer to 1 indicating stronger interdependencies. An integrated ecosystem is therefore defined on a relative scale of these metrics, where *C* describes external resource use between trophic levels within a compartment, *R* the ratio of ε between compartments independent of ε magnitude, and *I* the parity of ε and ι within and across compartments. We stipulate that *C* must only be evaluated for one ecosystem compartment to assess ecosystem integration. If compartments exhibit reciprocal resource reliance and evenly integrate internal and external resources ($R \approx 1$ & $I \approx 1$), then high *C* in one compartment is sufficient to indicate that decoupling resource exchange could alter trophic dynamics in a cascade of cross-boundary interactions (see Fausch et al. 2010). The theoretical perfectly integrated ecosystem is fully mixed, such that any boundary between compartments is permeable to the flow of resources, and resources from both compartments contribute equally to all consumers that are not fully reliant on internal resources; or where *C*, *R*, and *I* all equal 1. If *C*, *R*, and *I* all equal 0, then a hard boundary between compartments prevents any resource exchange. Most ecosystems will fall between these extremes.

We tested the integrated ecosystem concept in two freshwater ecosystems to evaluate the interconnection between spatially distinct food webs. Using the *C*, *R*, and *I* metrics, we quantify how external primary production indirectly supports upper trophic levels, whether one compartment is disproportionately reliant on resources from the other, and how evenly consumers rely on internal and external resources. Understanding the pathways through which resources with different origins support consumers can help identify significant trophic pathways, imbalances and interdependencies in resource flow, and vulnerabilities to future change. This set of unitless metrics can quantifiably compare the permeability of ecosystem boundaries and the inter-reliance of coupled food webs across space, time, and published studies and be applied broadly to improve our understanding and management of ecosystems; the majority of which do not fall neatly into the traditional bounded ecosystem concept.

METHODS

River – Riparian Case Study

Study Sites

To test the integrated ecosystem concept, we focused on the Verde River in Arizona, USA, a perennial river without major impoundments, but steadily declining baseflows from water withdrawal and climate change (Paretti et al. 2018). This type of flow modification is characteristic of free-flowing rivers globally and is important to consider when establishing reference conditions or assumptions for management strategies (Poff 2018). We sampled three sites within (Beasley Flat and Childs) and below (Sheep Bridge) federally designated Scenic and Wild reaches. Sites are characterized by cottonwood gallery and willow forest with mesquite uplands (described in Cubley et al. 2020).

Field Methods

We sampled representative components of the aquatic and riparian food webs at each study site in June 2018. For the aquatic food web, we collected larvae of emergent invertebrates representing different functional feeding groups from riffle and pool habitats and several of the most common species of fish using backpack and boat mounted electrofishing and seining (Table 1). For the riparian food web, we collected insects, spiders, and lizards as representative consumers and fresh leaves from the dominant species of trees, grasses, and wetland plants (Table 1). We collected all riparian samples, with the exception of spiders, within 10 m of the river because aquatic resource flux declines rapidly with increasing distance from the water (Muehlbauer et al. 2014). Spiders were collected within 1 m of the river to capture high aquatic subsidy contribution to a riparian predator. We preserved all samples (fish, invertebrates, lizards, and leaves) in 70% ethanol in the field (Appendix C).

Laboratory Methods and Stable Isotope Analysis

We identified invertebrates in the lab to the lowest taxonomic level possible (genus or species) and processed four individual samples of each plant and invertebrate taxon and eight samples of each species of fish, lizard, and spider per site. We analyzed samples for stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). Stable isotopes are used to quantify organismal trophic position and identify the original resource pool supporting consumers (Post 2002a). Stable isotope analysis is especially powerful for quantifying energy flow through food webs because it measures the resources assimilated by organism, not the gross resources that are ingested (Bearhop et al. 2004). We used the *MixSIAR* package (Stock et al. 2018) to determine relative dietary contributions of food sources to consumers using stable isotope Bayesian mixing models, then calculated proportional contributions of aquatic and riparian primary production to consumer diet. Details on laboratory analysis and isotope mixing models are provided in Appendix C. We selected the widely used trophic enrichment factors (TEFs) published by Post (2002), $\Delta^{15}N = 3.4 \pm 0.98‰$ and $\Delta^{13}C = 0.39 \pm 1.3‰$, to use in mixing models for all consumers. However, many other estimates of TEFs exist in the literature and mixing models can be sensitive to uncertainty in trophic enrichment (Bond and Diamond 2011, Phillips et al. 2014). We validated that our estimated dietary proportions and conclusions drawn from calculations of the integrated ecosystem metrics were robust to model assumptions by running all models and subsequent analyses with a range of alternative TEF values (Appendix D).

Resource Cycling

We built aquatic and riparian food webs from the bottom up to determine the proportion of each original resource pool supporting consumers (Appendix C). For example, for caddisflies and blackflies, the dietary contributions of riparian plants (from

MixSIAR models) were summed to determine ε. Damselfly diet was calculated using mayflies, blackflies, and caddisflies as representative potential prey items. The total aquatic resource contribution to damselfly diet (ι) was calculated as: *% mayfly in diet · mayfly ι + % caddisfly in diet · caddisfly ι + % blackfly in diet · blackfly ι*. We averaged all results from stable isotope mixing models and resource cycles across the three sites for each taxon to conceptualize the Verde River aquatic-riparian food web. All analyses were conducted in R (R Core Team 2019).

Lake Case Study

To demonstrate the applicability of the integrated ecosystem framework to existing data, we considered a study of resource use by organisms in four low-productivity lakes on the Wisconsin-Michigan border with a range of dissolved organic carbon (DOC), resulting in a gradient of light penetration depth (Solomon et al. 2011). In summary, stable isotopes of C, N, and H were used to quantify the contributions of benthic, pelagic, and terrestrial primary production to benthic consumers (zoobenthos) and pelagic consumers (zooplankton and fishes). See Solomon et al. (2011) for full methods.

Using median estimates of benthic, pelagic, and terrestrial resource use by consumer groups, we calculated *C*, *R*, and *I* for each lake. Traditional models of lake ecosystems emphasize the paradigm of pelagic primary production as the base of higher trophic levels (Hairston and Hairston 1993). We therefore considered both benthic and terrestrial resources as external for pelagic consumers and calculated *C* within the pelagic compartment for both types of external resources individually. We considered pelagic and terrestrial resources as external for benthic consumers. We calculated *R* between the benthic and pelagic ecosystem compartments without including terrestrial production as an external resource to examine the extent to which production from each of these compartments is complementary in supporting consumers in the other.

RESULTS

River – Riparian Case Study

External resources contributed significantly to diets of consumers on the Verde River (Figure 2, Table 1). External riparian resources composed nearly half the diet of filter feeding aquatic invertebrates and 50% for a generalist benthic-feeding fish. A predatory aquatic invertebrate and four predatory fish received over one quarter of their diet from external resources. Riparian predators were more variable, with spiders living directly on the riverbank consuming more external aquatic resources (36% of diet) than lizards living dispersed in the riparian zone (22% of diet). These results agree with a global analysis of published data finding that consumers in both lotic and riparian zones are composed of ~39% external resources (Bartels et al. 2012).

Prey items that are vectors of resources from multiple resource pools can further tie together aquatic and riparian food webs when they move between compartments. We found emergent aquatic invertebrates recycled riparian-originated resources through the river and back to riparian predators (Figure 3). These recycled resources contributed 15.8% (sd = 10.2%) of wolf spider diet (24.6% of total ι) and 8.5% (sd = 6.3%) of ornate tree lizard diet (10.9 % of total ι).

The Verde River integrated ecosystem

We used these results to demonstrate the applicability of the integrated ecosystem concept and test the hypothesis that trophic dynamics of the Verde River aquatic-riparian zone are integrated through reciprocal resource reliance. Ecosystem integration was evaluated using nine consumers that assimilated internal and external resources; blackflies (BF), caddisflies (CF), damselflies (DF), red shiner (RS), green sunfish (GS), smallmouth bass (SB), largemouth bass (LB), ornate tree lizards (TL), and wolf spiders (WS). *C* in the aquatic compartment summarized four sets predator-prey interactions (n = 4) and was close to one, indicating that external primary production indirectly contributed to the diets of upper trophic levels through efficient resource cycling, with marginally higher external resource reliance by lower trophic levels.

$$C = \left(\left(\frac{RS}{BF} + \frac{RS}{CF} + \frac{RS}{DF}\right) / 3 + \left(\frac{GS}{BF} + \frac{GS}{CF} + \frac{GS}{DF} + \frac{GS}{RS}\right) / 4 + \left(\frac{SB}{BF} + \frac{SB}{CF} + \frac{SB}{DF} + \frac{SB}{RS}\right) / 4 + \left(\frac{LB}{BF} + \frac{LB}{CF} + \frac{LB}{DF} + \frac{LB}{RS} + \frac{LB}{GS} + \frac{LB}{SB}\right) / 6\right) / 4 = (2.215/3 + 3.377/4 + 3.237/4 + 4.795/6)/4 = 0.798$$

Denoting the aquatic system as compartment x, and the riparian system as compartment y;

$\bar{\varepsilon}_x$, $\bar{\iota}_x$ = mean [LB (ε = 0.28, ι = 0.72), SB (ε = 0.30, ι = 0.60), GS (ε = 0.31, ι = 0.69), RS (ε = 0.30, ι = 0.60), DF (ε = 0.29, ι = 0.71), BF (ε = 0.45, ι = 0.55), CF (ε = 0.50, ι = 0.50)] : $\bar{\varepsilon}_x$ = 0.35, $\bar{\iota}_x$ = 0.65

$\bar{\varepsilon}_y$, $\bar{\iota}_y$ = mean [Tree Lizard (ε = 0.22, ι = 0.78), Wolf Spider (ε = 0.36, ι = 0.64)] : $\bar{\varepsilon}_y$ = 0.29, $\bar{\iota}_y$ = 0.71

On average, diets of aquatic and riparian predators were 35% and 29% external, respectively. While riparian primary production contributed more on average to aquatic consumers than aquatic primary production contributed to riparian consumers, the reciprocity ratio ($R = \frac{0.29}{0.35} = 0.829$) was close to one, suggesting minimal deviation from reciprocal resource reliance. Finally, generalist predators in the aquatic-riparian ecosystem were highly reliant on both internal and external resources ($I = 2 \cdot (0.35 \cdot 0.65 + 0.29 \cdot 0.71) = 0.867$.

Lake Case Study

The contribution of benthic, pelagic, and terrestrial resources to lake consumers varied between ecosystem compartments and across lakes (Figure 4; Solomon et al. 2011). Original analysis of the stable isotope ratios determined that terrestrial primary production contributed half or more of the resources used by a majority of the consumer groups considered. Pelagic resources contributed more to consumers in the pelagic compartment (zooplankton and fish), while benthic resource use was higher in zoobenthos but had the greatest contribution to fish. In support of the hypothesis that higher DOC and lower light penetration reduce primary production and internal resource use (Ask et al. 2009), terrestrial resource use tended to increase along the light extinction gradient (Solomon et al. 2011).

Expanding on the previous analysis, we found that cycling, reciprocity, and integration yielded distinct patterns between lakes that agreed with the results of Solomon et al. (2011) and quantified how resource reliance changed over the light extinction gradient (Table 2). Generally, benthic production use did not flow to fish through the prey items considered here (C > 1), but was used more extensively by upper trophic levels. In all but one lake, benthic and pelagic resources were not reciprocally consumed by the opposite ecosystem compartment (R < 1), with pelagic consumers disproportionately reliant on benthic production. Finally, the evenness of resource use from internal and external sources (I) decreased with increasing light extinction as reliance on terrestrial production increased. However, uncertainty in estimates of resource use from stable isotope analysis was high and our analysis was based on median estimates of resource use. Our results are therefore used as illustrative examples and not for quantitatively testing hypotheses. See Appendix E for full calculations of C, R, and I at each lake.

DISCUSSION

Ecosystems are constrained by basic physical principles. Therefore, the movement of resources across spatial boundaries is neither unidirectional nor terminal. Early studies on the movement of resources between ecosystems revealed direct and indirect effects through top-down and bottom-up pathways so that compartments may be nearly isolated or thoroughly mixed (Polis et al. 1997). The reciprocal nature of resource exchange can further link and stabilize both food webs (Nakano and Murakami 2001). Adapting food web, and indeed any ecological discipline, to the Anthropocene requires quantifiably applying these concepts to heterogeneous systems where processes in one compartment may be integrated across spatial boundaries with another, such that a perturbation to one can have unforeseen, cascading repercussions.

The concept of resource subsidies as a field of study designates resources as either autochthonous (not crossing a boundary) or allochthonous (crossing a boundary) and tends to only follow external resources to the consumer that first uses them. When considering prey items as vectors transferring resources to a consumer instead of a homogenous subsidy, the distinction becomes less clear. As shown here, many prey items used by consumers are composed of nutrients and materials that do not fall neatly into either of these categories. The integrated ecosystem concept extends the paradigm of resource subsidies and provides a framework for quantifying the assimilation of resources by consumers to calculate the extent to which two ecosystem compartments are functionally independent or inter-reliant.

The growing field of metaecosystem ecology also connects spatially distinct ecosystems through the reciprocal movement of nutrients and organisms (Soininen et al. 2015, Gounand et al. 2018). The integrated ecosystem framework is a complementary method for understanding spatially explicit resource exchange but only considers the flow of resources assimilated by consumers and therefore does not rely on quantifying resource flux, nor make assumptions about resource quantity or quality affecting resource use. Further growth of the integrated ecosystem framework could be applied to evaluate ecosystem dynamics over both space and time. Temporal variability in the magnitude and effects of resource exchange on biotic interactions may maintain diverse trophic interactions and communities (Marcarelli et al. 2020). Cycling efficiency, reciprocity, and integration can describe both average ecosystem integration over time or space, or potentially clarify how seasonal and spatial variations in trophic interactions and resource flow support species diversity and ecosystem stability. These metrics further allow for direct testing of hypotheses relating to ecosystem response to global change, such as food web rewiring resulting from alterations to species' behavior and distribution (Bartley et al. 2019).

Application to the Verde River

Observing a fully integrated ecosystem where *C*, *R*, and *I* all equal 1 is unlikely. However, we illustrate that the aquatic-riparian transition on the Verde River is a permeable boundary characterized by quantifiable, bidirectional resource exchange. Further, high cycling efficiency, near-reciprocal resource reliance, and integration approaching an even distribution in these compartments describe a tightly integrated ecosystem. A significant challenge in this study, as in most analyses using stable isotope analysis to attribute diet source in aquatic ecosystems (Brett et al. 2017), was isolating the isotopic signature of aquatic primary producers and determining the enrichment fractionation between trophic levels. We found that our results are robust to variation in the isotopic baseline of the aquatic food web and that using a general TEF did not affect our conclusion that altering resource cycles within, or exchange between compartments would likely affect the trophic dynamics of both (Appendix D).

The Verde River is threatened by reduced baseflows, increased flow intermittency and flow regime alterations due to climate change, water diversions, and groundwater withdrawal (Paretti et al. 2018). These changes are likely to alter community composition of aquatic invertebrates, distribution and composition of fish species, and shift the structure of riparian vegetation from native trees to non-native plant species (Paretti et al. 2018). The results presented here can be used to expand the scope of previous studies to consider indirect effects of projected changes in each of these communities on the integrated Verde River ecosystem. For example, reducing streamflow or groundwater levels can shift riparian forests dominated by native deciduous trees to shrub-dominated and sometimes non-native vegetation (Merritt and Poff 2010, Stromberg et al. 2010), altering resource input to streams with implications for aquatic invertebrate production and community composition that could cascade through both aquatic and riparian communities. This phenomenon could have further-reaching consequences as migratory neotropical birds and butterflies are abundant, but transient, residents of the Verde River, and may affect systems far beyond that observed in this and other integrated ecosystems.

Resource use in Lakes

In contrast to the Verde River, most of the lakes examined were not highly interdependent, with values of C, R, and I far from 1. However, analyzing the individual components of the integrated ecosystem framework allows us to untangle some of the complex pathways through which external resources support upper trophic levels. Because these lakes have low rates of primary production, many consumers were disproportionately reliant on terrestrial resources (Carpenter et al. 2005). Interestingly, cycling of terrestrial resources was not far from 1 for most lakes, showing these resources supported all consumers to a similar extent. The high values for cycling of benthic resources agree with the observations by Solomon et al. (2011) that fish likely feed on zoobenthos more highly reliant on benthic resources than those considered in this study. Low reciprocity in most of the lakes can largely be attributed to the heavy reliance of fish on benthic primary production while pelagic use by zoobenthos was minimal. This result quantifiably demonstrates that pelagic primary production is not the most significant base of these lake's food webs (Vadeboncoeur et al. 2002).

Here, integration specifically quantifies the magnitude of the imbalance between internal and external resources in lake ecosystems. Although not statistically tested, higher values of integration in lakes with lower light penetration support the hypothesis that DOC limits energy mobilization in unproductive lakes (Ask et al. 2009), increasing reliance on terrestrial resources. Given more precise estimates of resource use and a wider range of potential prey items for fish, the values of C, R, and I could be used in a traditional hypothesis-testing framework to address the DOC-light hypothesis explicitly. The similarity between our results and those of Solomon et al. (2011) demonstrate the ability of this framework to describe significant pathways of resource flow that have not previously been summarized in quantitative metrics.

Broader Applications

The movement of resources across boundaries and subsequent food web responses have been extensively studied in aquatic ecosystems. However, the exchange of resources between adjacent ecosystem compartments is ubiquitous (Polis et al. 1997) and thus the concept of an integrated ecosystem can be applied in diverse ecotones. Here we discuss two examples of how the integrated ecosystem concept could apply to terrestrial ecosystems to address a broader range of ecological questions. As urban areas continue to expand, anthropogenic food resources are increasingly subsidizing urban-adapted wildlife (Fischer et al. 2012). Some carnivores cannot directly consume anthropogenic foods, but high resource availability increases the density of their prey items, which cycle these resources up the food web (Fischer et al. 2012) and may be preyed upon by non-urban consumers crossing the urban boundary.

In a study of coyotes living in urban areas, and natural preserves, Newsome et al. (2015) used stable isotopes to determine the prevalence of anthropogenic resources in coyote diet. The authors found that prey items available to coyotes, including squirrels, domestic cats, and rodents, varied widely in their use of anthropogenic resources. For coyotes living in natural preserves, anthropogenic resources may be external, while the same resources may be considered internal for coyotes living in the urban matrix. The integrated ecosystem concept can be logically applied to quantify the flow and cycling of anthropogenic resources in the urban-natural preserve ecosystem. Here, cycling can assess if coyotes preferentially consume prey that have a diet higher in natural resources relative to all potential prey (low C for preserve, and high C for urban coyotes). If consumers from multiple trophic levels were considered, C would also describe if anthropogenic resources supported all levels of the food web evenly and if this pattern differed between urban and preserve ecosystem compartment. Newsome et al. (2015) found preserve coyotes use a lower proportion of external anthropogenic resources than urban residents used external natural resources, suggesting a reciprocity ratio of less than one. This metric would quantify an uneven exchange of resources contributing to the urban ecosystem food web, with a greater input by natural compartments. Integration would further describe the inter-reliance between preserve and urban food webs on cross-boundary resources. As an integrated urban ecosystem, preserves and other sources of natural food would provide resources to support urban wildlife, while natural ecosystem compartments would be equally reliant on anthropogenic resources supplementing local production—creating two co-dependent ecosystem compartments. However, urban ecosystems are more open than most natural systems, importing most food resources from 100s or 1000s of miles away. Although urban consumers may continue to draw on resources from natural sources, consumers in natural compartments may become more reliant on novel food sources if the natural environment degrades (Poessel et al. 2017).

Old fields and forests form a mosaic of discrete ecosystem compartments in the northeastern United States where edge structure can mediate the interaction between the two (Cadenasso and Pickett 2001). Seeds and seedlings of forest plants that blow and establish in fields are preyed upon by many field-dwelling herbivores (Ostfeld et al. 1997). Herbivores also cross the field-forest boundary to forage within the forest. In forests with experimentally thinned edges, some herbivores forage more extensively within the forest compartment, increasing the contribution of forest resources to external consumers (Cadenasso and Pickett 2000). These external resources may cycle through the field food web as herbivores are consumed by predators. Within the forest, external resources may come from forest predators consuming field herbivores and seeds dispersing from fields, with more seeds crossing the boundary and dispersing further into forests with thinned edges (Cadenasso and Pickett 2001).

The integrated ecosystem framework can be applied here to quantify cross-boundary resource reliance of field and forest food webs to inform ecological theory and management of edge structure. Applying the framework would require dietary analysis of a wide range of consumers in the field-forest ecosystem, with consumers assigned to the ecosystem compartment where they primarily reside. Cycling efficiency would therefore describe how variation in edge structure drives change in the flow of external resources up the food web. Reciprocity could determine the compartment most reliant on external resources, and if changes to edge structure alters the magnitude or direction of imbalance. Integration would be calculated using average internal and external resource use of both compartments and assess the proximity of all consumers to equal use of field and forest resources. Both *R* and *I* could be applied using just herbivores that are likely to consume both field and forest resources. Edge structure is an important control of resource flow across heterogenous landscapes (Cadenasso et al. 2004). Quantifying the components of an integrated ecosystem would further determine how the effects of edge structure on resource use can propagate through adjacent food webs.

CONCLUSIONS

Considering multiple habitat types in ecosystem or species management plans is not a new concept. However, a simple, quantitative framework for describing cross-boundary interactions does not currently exist. Each component of the integrated ecosystem concept could be applied individually or together by decision makers to sustainably manage ecosystems. Cycling efficiency can demonstrate indirect external resource reliance of a consumer of interest, while reciprocity and integration could establish baseline measures of food web interactions threatened by anthropogenic pressures. For example, a native fish may receive significant dietary contributions from riparian detrital input both directly, and indirectly through aquatic invertebrates (Pusey and Arthington 2003). Integrated ecosystem management would consider the extent to which conservation plans for this species must protect riparian vegetation. Alternatively, agriculture may alter emergent aquatic invertebrate communities that support riparian birds (Stenroth et al. 2015). An integrated ecosystem approach to riparian bird conservation would therefore quantify this reliance on aquatic resources and inform management of the streamflow regime and water quality needed to sustain invertebrate populations.

As climate change, land use change, and modifications to hydrologic cycles alter organismal phenology, physiology, and trophic interactions, natural patterns of resource exchange between ecosystems are shifting (Larsen et al. 2016). If inter-reliant ecosystems are studied or managed individually, it will not be possible to predict how alterations to one may have cascading cross-boundary repercussions. The integrated ecosystem concept can be used to predict potential disconnects in resource flow and provide evidence for or against independent management of ecosystems. Applying knowledge of integrated ecosystems will be facilitated by interdisciplinary thinking, drawing together ecological, physical, and conservation science to understand the natural functioning of ecosystems, threats to these dynamic processes, and how we can manage and restore existing, or design novel systems using ecological principles.

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Table 1: List of species collected on the Verde River, external resource use, and trophic position

Sample type	Sites collected	Common name	Species	Diet % from external resources (ε)	Trophic position
Basal resource	All	Gooding's willow	*Salix gooddingii*	NA	1
	All	Fremont cottonwood	*Populus fremontii*	NA	1
	All	Tamarisk/saltcedar	*Tamarix ramosissima*	NA	1
	All	Giant reed	*Arundo donax*	NA	1
	All	Bermuda grass	*Cynodon dactylon*	NA	1
Riparian insect	Beasley	Ant	*Dorymyrmex bicolor*	NA	2
	Childs & Sheep	Ant	*Formica gnava*	NA	2
	All	Carolina ground cricket	*Eunemobius carolinus*	NA	2
	All	spur-throat grasshopper	*Melanoplus* sp.	NA	2
Riparian Predator	All	Thin-legged Wolf Spider	*Pardosa* sp.	ε = 35.9%, sd = 15.6%	3.69
	All	Ornate Tree Lizard	*Urosaurus ornatus*	ε = 22.0%, sd = 10.9%	3.30
Aquatic insect	All	Mayfly	*Baetis* sp.	NA	2
	All	Caddisfly	*Hydropsyche* sp.	ε = 49.7%, sd = 14.2%	2
	All	Black Fly	*Simulium* sp.	ε = 44.9%, sd = 12.6%	2
	All	Damselfly	*Hetaerina* sp.	ε = 29.4%, sd = 14.5%	2.65
Fish	All	Red Shiner	*Cyprinella lutrensis*	ε = 29.7% sd = 13.0%	3.53
	Childs & Sheep	Common Carp	*Cyprinus carpio*	ε = 50.2% sd = 15.3%	2.90
	All	Green Sunfish	*Lepomis cyanellus*	ε = 31.2% sd = 12.0%	3.61
	Beasley & Sheep	Smallmouth x Redeye Bass	*Micropterus dolomieu* x *coosae*	ε = 29.9% sd = 11.0%	3.80
	Beasley & Childs	Largemouth Bass	*Micropterus salmoides*	ε = 27.6% sd = 9.8%	3.92

Table 2: Components of the integrated ecosystem framework for lakes on a light extinction gradient

	Crampton	Peter	Paul	Tuesday
Light Extinction (k_D/m)	0.58	0.86	0.96	1.37
Cycling Benthic	2.114	2.873	0.644	1.996
Cycling Terrestrial	1.032	0.637	0.967	0.744
Reciprocity	0.226	0.194	0.993	0.318
Integration	0.791	0.691	0.609	0.443

Notes: Light extinction and estimates of resource use are from Solomon et al. 2011. Increasing light extinction indicates a faster rate of light attenuation with depth.

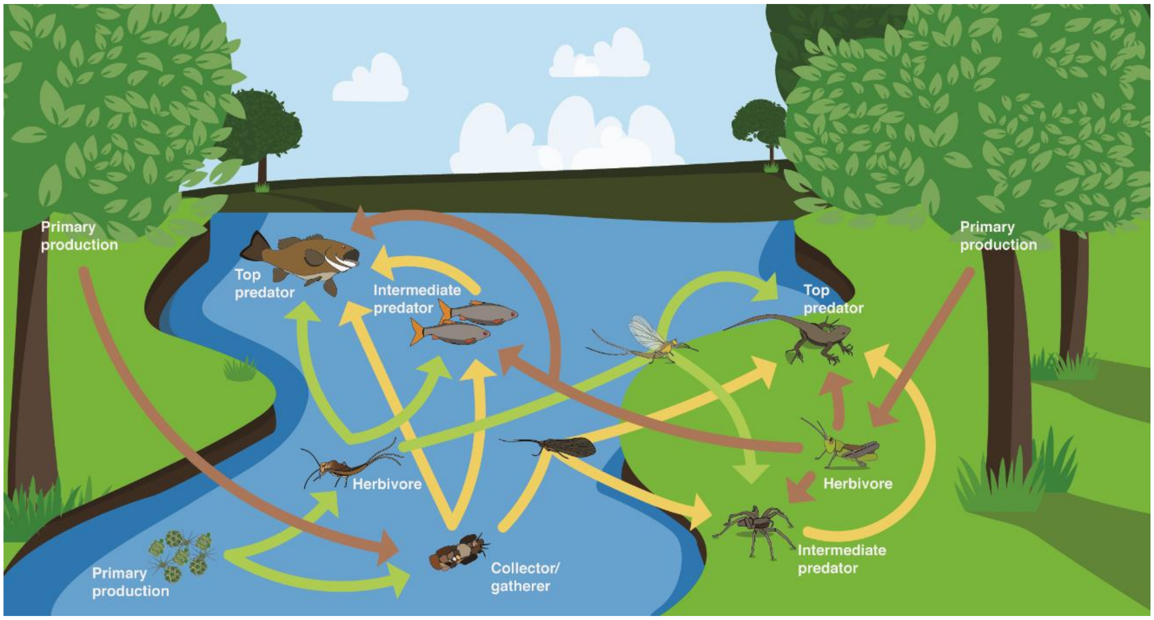

Figure 1: Resources that move between adjacent ecosystem compartments cycle through multiple trophic transfers and may be recycled back to the original compartment. Here, a model stream and riparian zone illustrate resource movement through an integrated ecosystem. Green and brown arrows indicate the transfer of resources originating from aquatic and riparian primary production, respectively, while yellow arrows are a mix of the two. Resources are designated as internal (green for aquatic consumers, brown for riparian consumers) or external (brown for aquatic consumers, green for riparian consumers) relative to the consumer, not the prey item.

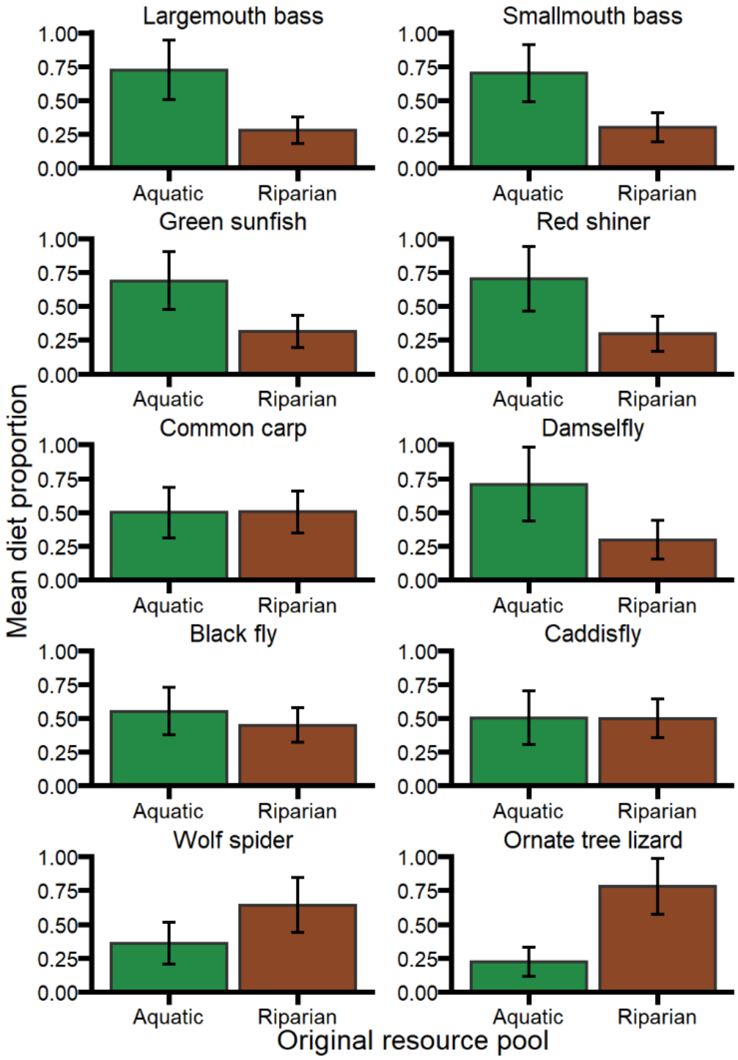

Figure 2: Dietary proportions of resources originating from aquatic and riparian primary producers for consumers in the Verde River ecosystem.

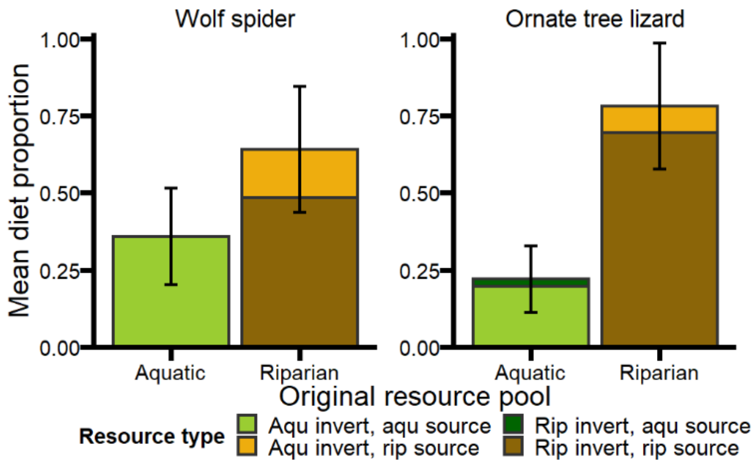

Figure 3: Riparian primary production is recycled back to riparian consumers through emergent aquatic invertebrates. Source indicates original resource pool.

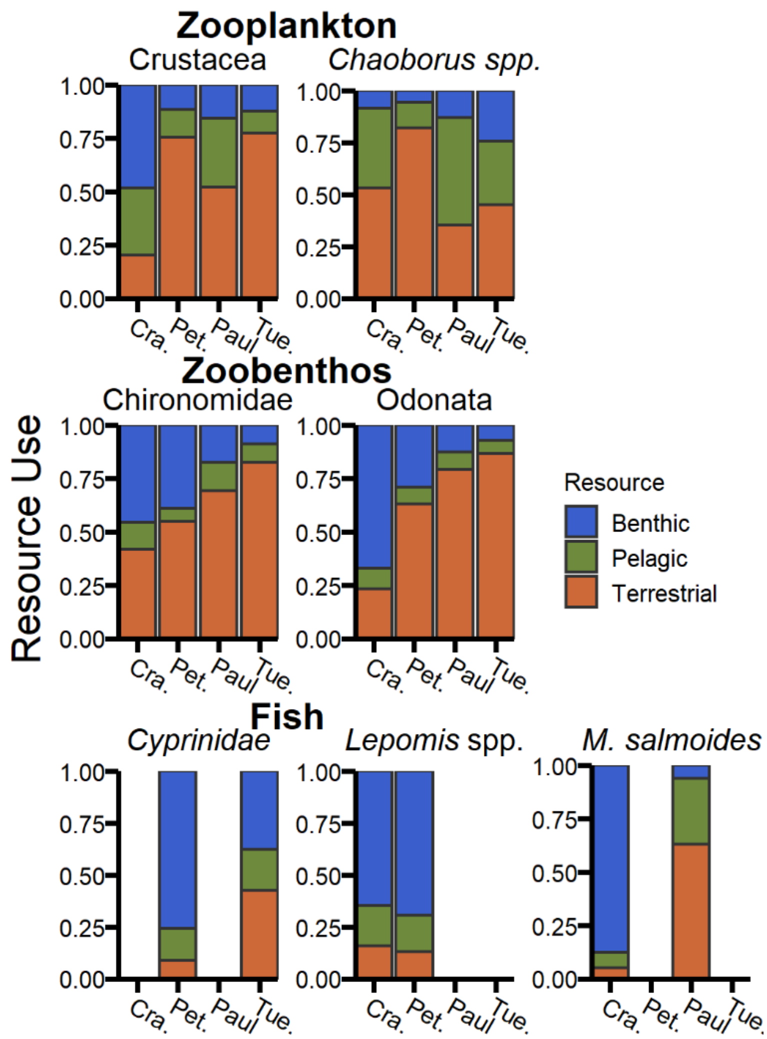

Figure 4: Median estimates of resource use for consumer groups representing benthic (Zoobenthos) and pelagic (Zooplankton and Fish) ecosystem compartments in four lakes. Lakes are arranged from low to high light extinction. Data from Solomon et al. 2011.

CHAPTER 6

CONCLUDING REMARKS

In this dissertation, I explored the community and trophic dynamics of coupled stream-riparian ecosystems to identify the energy flow pathways and environmental regimes that maintain biodiversity. By conducting observations across spatial and temporal scales, I documented how ecosystem processes that are often studied independently are interconnected through direct and indirect interactions. In these concluding sections, I review the central research findings from each chapter, highlight themes and mechanisms uniting this body of work, discuss implications for conservation and the field of ecology, and identify future research directions.

FLOW REGIME OVER SPACE AND TIME

The effects of disturbance on communities is a fundamental theme of ecological research (Connell 1978, Sousa 1979), yet the role of disturbance regime in shaping response and recovery from a discrete event is greatly understudied. In Chapter 2, I examined how fluctuations in fish communities following floods and droughts depend on the composition of life history strategies in the local species pool, and how these life history strategies are selected for by the long-term flow regime via ecological filtering. Relatively stable flow regimes fostered diverse communities dominated by periodic and equilibrium life history strategies. In these streams, unpredictable low-flow events displaced species that were less resilient to drought, facilitating replacement by new species from the local pool with greater affinity for opportunistic strategies. Communities filtered by highly variable regimes were less diverse and supported communities with predominantly opportunistic life history strategies. Thus, temporal variation in community composition was driven by changes in the number and abundance of species due to limited availability of different species for replacement. These communities exhibited lower change in species composition and negligible variation in life history strategy distribution following low-flow events. The results of this study support the hypothesis that the magnitude and mechanisms of variation in community composition following a discrete flow event depends on the context of long-term flow regime due to ecological filtering of life history strategies at both the event and regime timescales.

Over spatial scales from watersheds to continents, communities in highly variable flow regimes are dominated by small-bodied species with opportunistic life history strategies and shorter food chains (Chapter 2, Poff 1997, Olden and Kennard 2010). These ecological parameters imposed by flow regimes may additionally influence the efficiency of energy transfer through the food web, which influences the productivity of upper trophic levels (Elton 1927, Lindeman 1942, Hairston and Hairston 1993). While several constraints on ecological efficiency have been documented in mesocosms, including food chain length (FCL), nutrient content of primary producers, and temperature (Dickman et al. 2008, Faithfull et al. 2015, Rowland et al. 2015, Rock et al. 2016, Barneche et al. 2021), *in situ* studies are needed to assess the additional effect of flow regime in rivers. In Chapter 3, I examined the potential for plant nutrient content, temperature, FCL, and flow regime to constrain food web efficiency, (FWE) and whether these controls are mediated by top-down or bottom-up trophic pathways. I found that temperature and flow regime variability were both negatively associated with FWE, but primary producer nutrient content and FCL did not constrain efficiency when considered across streams on a gradient of streamflow variability. However, when comparing within-site variation over time, FWE was negatively correlated with temperature and positively correlated with FCL. Gross primary production (GPP) was independent of both flow regime and fish production, indicating that flow regime controls transfer efficiency through constraints on fish community production instead of availability of locally produced resources.

As demonstrated in Chapter 2, flow regime is a dominant force in structuring both the composition of fish species and the life history strategies employed by that community. Rates of secondary production and the influence of temperature on production are species specific (Rypel and David 2017), suggesting that environmental constraints on FWE are contextually dependent on the flow regime that has filtered the life history strategies of the community. These results support the hypothesis that energy flow and community structure in rivers are structured by flow regime, not the availability of local food resources (McHugh et al. 2010, Sabo et al. 2010a). Further, by simultaneously measuring GPP and fish production, I demonstrated that variation in flow regime across rivers decouples the observed strength of top-down and bottom-up trophic pressures that are characteristic of streams with predictable flows and studies conducted at a single site (Hairston et al. 1960, Resh et al. 1988, Power 1990).

TROPHIC DYNAMICS OF THE INTEGRATED STREAM-RIPARIAN ECOSYSTEM

Trophic dynamics and ecosystem processes of streams and their riparian zones are tightly integrated through the reciprocal exchange of resources (Baxter et al. 2005). The influence of flow regime on community taxonomic and functional composition (Chapter 2), and energy flow through food webs (Chapter 3) further suggests that hydrologic variability shapes complex ecological interactions that may perpetuate across the stream-riparian boundary. Terrestrial inputs of invertebrates to streams influence fish distribution (Kawaguchi et al. 2003) and reduce predatory pressure on aquatic invertebrates (Nakano et al. 1999, Baxter et al. 2004). Likewise, emergent aquatic insects contribute to the diets, distribution, and abundance of riparian consumers, including spiders (Sanzone et al. 2003), lizards (Sabo and Power 2002a, 2002b), and birds (Nakano and Murakami 2001). The energetic and nutrient contributions of externally produced resources can additionally augment ecosystem resource availability (Fisher and Likens 1973, Minshall 1978, Jackson and Fisher 1986). However, most studies on stream-riparian linkages have not addressed the cycling of cross-boundary resources through the food web and the potential implications for consumer resource selection.

In Chapter 4, I applied approaches from organismal, food web, and ecosystem ecology to expand the scope of classic studies that described cross-boundary resource fluxes and biotic interactions in discipline-specific terms – population dynamics, trophic pathways, or carbon and nutrient budgets (Marcarelli et al. 2011). Emergent insects that consume terrestrial primary production recycle some of these resources back to the riparian zone (Kraus and Vonesh 2012). By tracing the flow of resources from aquatic and terrestrial primary producers, I found that cross-boundary primary production contributes substantially to the diets of aquatic and riparian consumers. Significantly, recycled primary production comprised a portion of riparian predator diet that would be considered an aquatic resource if only tracing the origin of prey items. This finding demonstrates that the strength of aquatic-riparian linkages depends on the method used to calculate the contribution of aquatic resources to riparian consumer diet. If emergent insects are considered a homogenous cross-boundary resource, riparian consumer reliance on the aquatic ecosystem compartment may be substantially higher than if calculated as the consumption of aquatic primary production. Further, aquatic primary production supported just over 60% of the cross-boundary flux of energy and nutrients transferred by the emergent insect taxa considered for analysis.

The mechanisms and consequences of external resource flux and consumption can be further explained by exploring variation in resource quantity and quality. Nutritional benefits of available resources can be greater determinants of resource use by consumers than resource abundance (Marcarelli et al. 2011). Higher quality resources at the base of the food web can affect trophic dynamics across multiple trophic levels by increasing the efficiency of trophic transfers and condition of upper trophic level consumers (Malzahn et al. 2007, Rowland et al. 2015), and potentially initiating cross-boundary feedback loops (Sitters et al. 2015). However, I found that aquatic primary producer quality, measured as C:N and C:P ratios, in riverine ecosystems was not a strong predictor of fish production rates or FWE (Chapter 3). Exploring the dietary contributions of aquatic and terrestrial primary production to aquatic insects revealed that insects were remarkably consistent in diet source over time and between two rivers, despite seasonal changes in the input and C:N of terrestrial plant detritus (Chapter 4). Aquatic insects also had constant C:N over time. These findings suggest that some taxa may preferentially consume resources to achieve nutritional targets independent of N and P content (Raubenheimer and Simpson 1993). Consistent nutritional content of aquatic insects may then reduce the influence of primary producer nutrient ratios on upper trophic levels, suggesting a potential explanation for the lack of observed relationships between algae nutrient ratios and FWE.

In the final research chapter of this dissertation (Chapter 5), I developed the integrated ecosystem concept, a novel framework to quantitatively evaluate reciprocal reliance on cross-boundary resources in spatially distinct ecosystem compartments. I demonstrated the applicability of the framework using field data from a desert river and riparian zone and a previously published data set. While tested in aquatic and riparian systems, the integrated ecosystem concept could be applied to diverse habitats that exchange resources across a porous boundary, a nearly ubiquitous feature of ecosystems that are bounded for the purpose of scientific investigation. This novel framework allows for robust hypothesis testing and comparisons over space and time of cross-boundary trophic interactions that have previously only been measured as taxa-specific dietary proportions. It further quantifies the cycling of external resources to indirectly support upper trophic levels, opening avenues to explore multi-trophic level effects of resource quantity and quality.

FUTURE PERSPECTIVES

Synthesizing the mechanistic processes relating environmental constraints to the maintenance of stream and riparian ecosystems requires understanding interactions between ecosystem processes across spatial and temporal scales, and across levels of biological organization. Anthropogenic climate change is driving changes in both river flow regimes and extreme flow events globally (Gudmundsson et al. 2021). These changes compound effects of widespread flow alterations from land use, dams, and water withdrawal, which are among the most significant threats to global freshwater biodiversity (Vörösmarty et al. 2010, Tickner et al. 2020). Global changes are leading to non-stationarity in hydrologic, temperature and nutrient regimes, signifying that relationships between historical reference conditions and ecological responses may not hold true in the future, requiring the development of process-based understandings of ecological relationships to environmental conditions (Poff 2018).

The development of environmental flows designed to support ecosystem function and achieve specific outcomes by retaining ecologically significant components of the hydrograph has been significant for freshwater conservation, and is a rapidly evolving field (Poff et al. 2010, Yarnell et al. 2020). Establishing flow targets and identifying appropriate ecosystem functions to support biological processes requires understanding how changes to any one ecological or environmental variable can initiate a cascade of repercussions within and across the stream-riparian boundary. In this dissertation, I demonstrate how hydrologic variability shapes community structure and energy flow from primary producers to upper trophic levels, which are supported by cross-boundary resources cycling through multiple trophic transfers – reciprocally linking aquatic and riparian food webs. These apparently distinct processes are often studied independently, but, when considered as a whole, illustrate mechanistic pathways that may help inform strategies to preserve essential ecosystem functions in a changing world.

Based on my dissertation research, I propose that fish secondary production and food web efficiency are strong process-based metrics that can be applied to further develop ecological theory and conservation strategies, and are most relevant when paired with consideration of how flow regime filters local species pools and shapes the trajectory of community response to anomalous flow events. Additionally, I suggest that achieving conservation goals for fish and riparian predators requires greater understanding of how resource quality and quantity influence resource cycling through distinct trophic pathways to support all levels of the food web.

Collaboration across research specialties is growing and is increasingly recognized as necessary to address ecological questions outside the scale and scope of traditional disciplines and bounded ecosystems (Post et al. 2007a, Rüegg et al. 2021). However, further work is needed to develop robust ecological theory applicable to the conservation and management of stream-riparian ecosystems in a time of non-stationary environmental conditions. Specifically, temporal studies that use repeated measures, and ideally long-term data, could substantially further the development of flow-ecology relationships through mechanistic explanations of demographic processes, but are greatly underrepresented in the literature (Wheeler et al. 2018). Long-term research could expand on the 2-3 years of data in this dissertation and reveal how top-down versus bottom-up trophic forces vary across flow regimes by observing temporal variation within sites (Chapter 3). However, even long-term ecological studies are negligible on evolutionary time scales. Incorporating metrics of both discrete disturbances and disturbance regime in ecological models accounts for the evolutionary mechanisms that have been selected for by regimes to shape variation in community structure at the scale of ecological studies (Chapter 2). This approach may improve the ability to predict future patterns of biodiversity over models using single timescale hydrologic metrics (Ruhí et al. 2016b, Horne et al. 2019).

Expanding studies on community structure and trophic dynamics across spatial scales is also necessary to capture stochasticity in biological and environmental events. In Chapter 4, patterns of resource use and exchange across the aquatic-riparian boundary exhibited different trends at two rivers, urging caution when drawing conclusions based on one study site: a frequent practice in studies of cross-boundary linkages. Additionally, this dissertation research was conducted on desert streams with relatively uniform climates. Further work in temperate, tropical, and tundra streams is necessary to examine how temperature and seasonality influence flow-ecology and trophic dynamic relationships.

Finally, the diets of emergent aquatic insects and contribution of aquatic primary production to riparian consumers can have significant implications for riparian food webs (Chapter 4). Aquatic primary producers synthesize essential long-chain polyunsaturated fatty acids that are absent in most terrestrial plants and increase the health of riparian consumers when available in the form of emergent aquatic insects (Twining et al. 2016, Martin-Creuzburg et al. 2017). Flow regime filters the life history and feeding strategies of aquatic invertebrate (Vannote et al. 1980, Schriever et al. 2015) and fish communities (Chapter 2). Regimes that select for insects that are more heavily reliant on external resources may export lower quantities of long-chain polyunsaturated fatty acids. It is therefore necessary to consider how flow regime may drive patterns of resource recycling to inform estimates of aquatic primary production contribution to riparian consumers. While this concept was illustrated through the proxy of consumer diet sources in this dissertation, future research should directly measure how resource recycling affects the quality of emergent insects as potential prey items. In-depth analysis of insect fatty acid content, macronutrient ratios, and elemental stoichiometry, could reveal how flow regime, rates of aquatic primary production, or other environmental constraints affect riparian consumer population size, body condition, or reproductive success. Application of the integrated ecosystems framework (Chapter 5) to quantifiably compare cross-boundary food web linkages across space and time could identify important resource pathways and changes in trophic dynamics. Together, this information could inform conservation efforts by identifying riparian locations likely to have greater success in supporting species of concern, migratory populations, and strong aquatic-riparian linkage.

In this dissertation, I demonstrate that hydrologic variability and trophic dynamics inexorably link aquatic and riparian food webs such that neither can be considered independently. Collectively, this body of research begins to untangle the environmental and biotic controls on ecological processes of the stream-riparian ecosystem. Developing greater understanding of the mechanisms that connect disparate processes, from consumer resource selection to ecosystem metabolism, requires expanding the scale and scope of ecological studies. Only by continuing to resolve the process-based relationships integrating ecosystem function across traditional spatial and disciplinary boundaries will it be possible to apply relevant ecological theory and conservation strategies in the context of global change.

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APPENDIX A

CHAPTER 2 SUPPLEMENTARY TABLES AND FIGURES

Table S1: Study site information.

Site name	Abr.	Map #	USGS gage #	Sampling period	# of surveys	Reason for missing surveys
Agua Fria	AF	1	09512500	Spring 2016 – Winter 2017	8	NA
Bonita Creek	BO	2	09447800	Fall 2017 – Spring 2019	7	Fish were not sampled Summer 2017
Eagle	EA	3	09447000	Spring 2016 – Winter 2017	8	NA
San Francisco	SF	4	09444500	Summer 2016 – Winter 2017	7	Water too high for fish sampling Spring 2016
San Pedro	SP	5	09471000	Spring 2016 – Winter 2017	8	NA
Santa Cruz	SC	6	09480500	Spring 2016 – Winter 2017	8	NA
Sycamore Creek	SY	7	09510200	Spring 2016 – Winter 2017	4	Stream dry Fall and Winter 2016 and Fall and Winter 2017
Verde	VE	8	09503700	Spring 2016 – Winter 2017	7	Storm prevented sampling Summer 2016
Wet Beaver	WB		09505200	Spring 2016 – Winter 2017	7	Water too high for fish sampling Spring 2017

Table S2: Watershed characteristics, flow regime variability (σ_{hf}), and observed range of high-flow and low-flow seasonal anomalies (HSAM and LSAM, respectively) during the study duration.

Site	Watershed area (ha)	Avg. disch. (m^3/s)	Avg. precip. (mm)	Avg. temp. (C)	σ_{hf}	HSAM		LSAM	
						Min	Max	Min	Max
Agua Fria	136,001	0.403	447	17.17	3.212	-0.050	5.443	-0.655	-0.050
Bonita	81,322	0.125	350	17.35	2.223	-0.450	2.105	-0.877	-0.305
Eagle	160,995	1.223	374	16.63	0.568	0.085	0.760	-0.295	-0.002
San Francisco	708,351	4.491	350	17.42	0.494	0.071	0.890	-0.357	0.088
San Pedro	302,849	0.888	350	17.57	1.137	-0.095	1.595	-0.883	0.028
Santa Cruz	138,980	0.230	456	17.69	5.680	0.080	9.731	-1.778	0.297
Sycamore	28,018	0.452	426	20.42	5.627	-0.838	8.554	-1.890	-0.516
Verde	643,947	0.956	397	14.54	0.643	-0.021	1.181	-0.064	-0.014
Wet Beaver	29,748	0.675	445	15.89	0.868	0.012	1.230	-0.462	-0.040

Table S3: Pearson correlation coefficients for four measures of taxonomic diversity

	Shannon Diversity	Dissimilarity	Replacement	Richness difference
Shannon Diversity	–	–	–	–
Dissimilarity	-0.54	–	–	–
Replacement	0.39	-0.03	–	–
Richness difference	-0.66	0.85	-0.55	–

Table S4: Permutational test for significance of environmental constraints for db-RDA analyses on site functional trait composition and proportional contribution of each life history strategy. Total inertia (explained variation) was 0.734 for the life history trait ordination and 0.862 for the life history strategy ordination.

		Life History Traits		Life History Strategies	
	Df	Sum of Squares	p-value	Sum of Squares	p-value
σ_{hf}	**1**	**0.273**	**0.006**	**0.654**	**0.002**
Watershed Area	1	0.046	0.678	0.026	0.456
Average annual discharge	1	0.078	0.354	0.017	0.487
Residual	5	0.337		0.165	

Table S5: Correlation of life history traits with db-RDA using envfit analysis to determine the strength of the correlation between functional traits and the first two axes of the RDA. Only the first axis (CAP1) was significant in the RDA. Abbreviations for significant variables correspond with Figure S3.

	Abr.	CAP1	CAP2	R^2	p
Maximum total body length		0.674	0.739	0.615	0.058
Aspect ratio		-1.000	-0.005	0.127	0.657
Age at maturation		0.999	0.045	0.395	0.229
Longevity	LONG	**0.700**	**0.714**	**0.765**	**0.014**
Fecundity		0.158	0.987	0.577	0.084
Egg rize		0.738	-0.675	0.170	0.585
Parental care		0.998	-0.056	0.339	0.283
Spawning frequency: single	SPAWNFREQ_1	**1.000**	**0.010**	**0.920**	**0.001**
Spawning frequency: multiple	SPAWNFREQ_MULT	**-0.99995**	**-0.01033**	**0.9201**	**0.0005**
Trophic guild: herbivore		0.74588	-0.66608	0.6328	0.0547
Trophic guild: omnivore	TROPHICG_OMN	**-0.90251**	**0.43066**	**0.8093**	**0.0037**
Trophic guild: invertivore		-0.66022	-0.75107	0.5732	0.0684
Trophic guild: invertivore/piscivore		0.90387	0.4278	0.5721	0.0846
Trophic guild: piscivore		0.9954	-0.0958	0.6302	0.0685
Vertical position: benthic	VERTP_BEN	**0.93915**	**-0.3435**	**0.7002**	**0.0295**
Vertical position: non-benthic	VERTP_NON	**-0.93915**	**0.3435**	**0.7002**	**0.0295**

Table S6: Correlation of life history strategies with db-RDA using envfit analysis to determine the strength of the correlation between the proportional contribution of life history strategies to species assemblages and the first two axes of the RDA. Only the first axis (CAP1) was significant in the RDA.

	Abr.	CAP1	CAP2	R^2	p
% Opportunistic	**OPPp**	**-1.000**	**0.008**	**1.000**	**< 0.001**
% Periodic	**PERp**	**0.974**	**0.226**	**0.990**	**< 0.001**
% Equilibrium	**EQUp**	**0.945**	**-0.328**	**0.986**	**< 0.001**

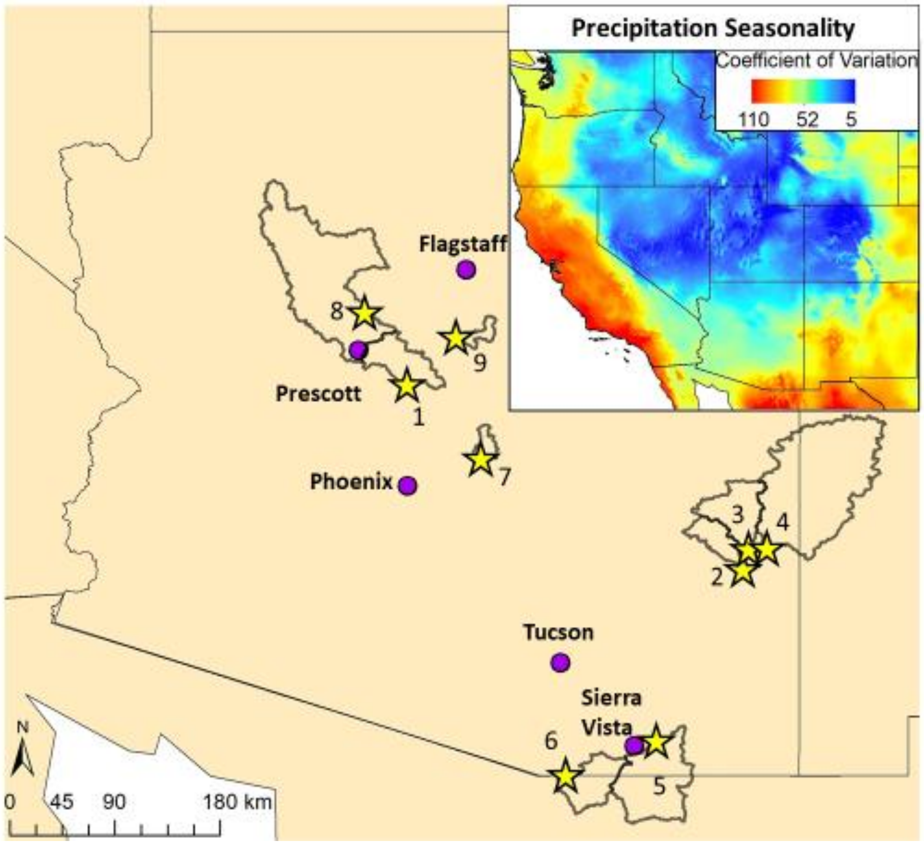
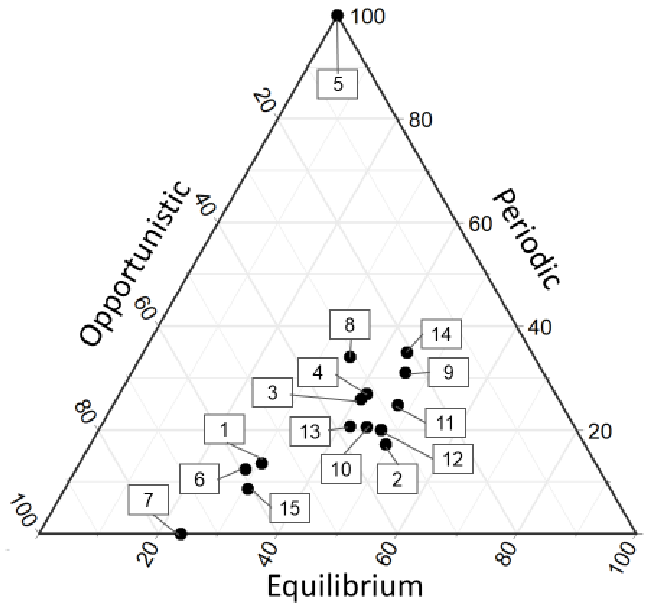


Figure S1: Study sites (yellow stars) spanned a range of watershed area (watersheds outlined in black) and a precipitation gradient in AZ. See Table 1 for site names. Inset shows precipitation seasonality (coefficient of variation). Watersheds were delineated using the National Hydrography Dataset Plus (Moore et al. 2019). Precipitation data from worldclim.org.



1	Longfin dace	*Agosia chrysogaster*
2	Yellow bullhead	*Ameiurus natalis*
3	Desert sucker	*Catostomus clarkii*
4	Sonora sucker	*Catostomus insignis*
5	Common carp	*Cyprinus carpio*
6	Red shiner	*Cyprinella lutrensis*
7	Western mosquitofish	*Gambusia affinis*
8	Roundtail chub	*Gila robusta*
9	Channel catfish	*Ictalurus punctatus*
10	Green sunfish	*Lepomis cyanellus*
11	Smallmouth bass	*Micropterus dolomieu*
12	Rainbow trout	*Oncorhynchus mykiss*
13	Fathead minnow	*Pimephales promelas*
14	Flathead catfish	*Pylodictis olivaris*
15	Speckled dace	*Rhinichthys osculus*

Figure S2: Relative affinity of all species observed to each life history strategy of the three-axis continuum (Winemiller and Rose 1992).

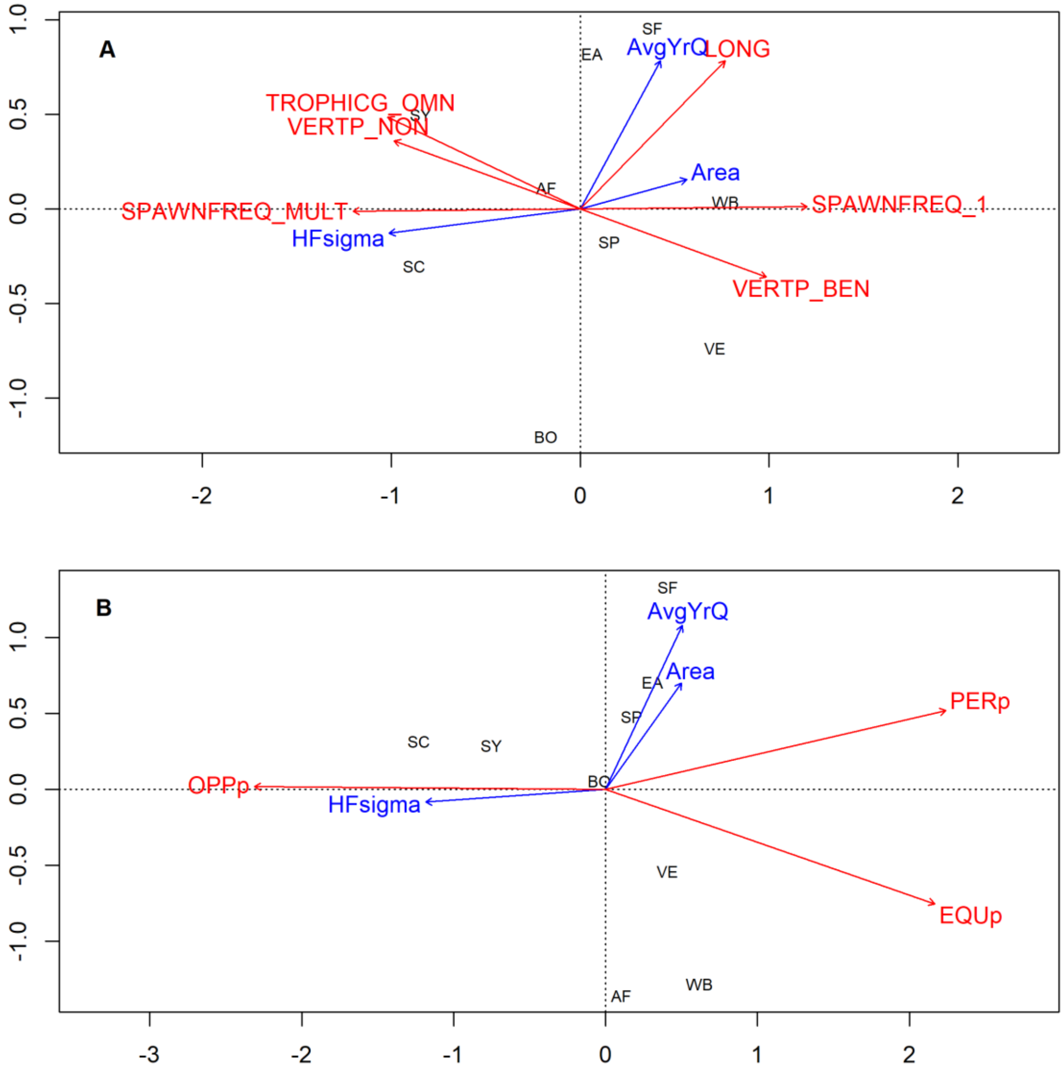


Figure S3: distance-based RDA (db-RDA) results with environmental constraints (blue) and significantly correlated life history traits (A) and relative proportion of life history strategies (B). σ_{hf} was the only environmental variable significantly correlated with either db- RDA. Abbreviations of site names (black), and life history traits and life history strategies (red) correspond with names in tables S1, S5, and S6, respectively.

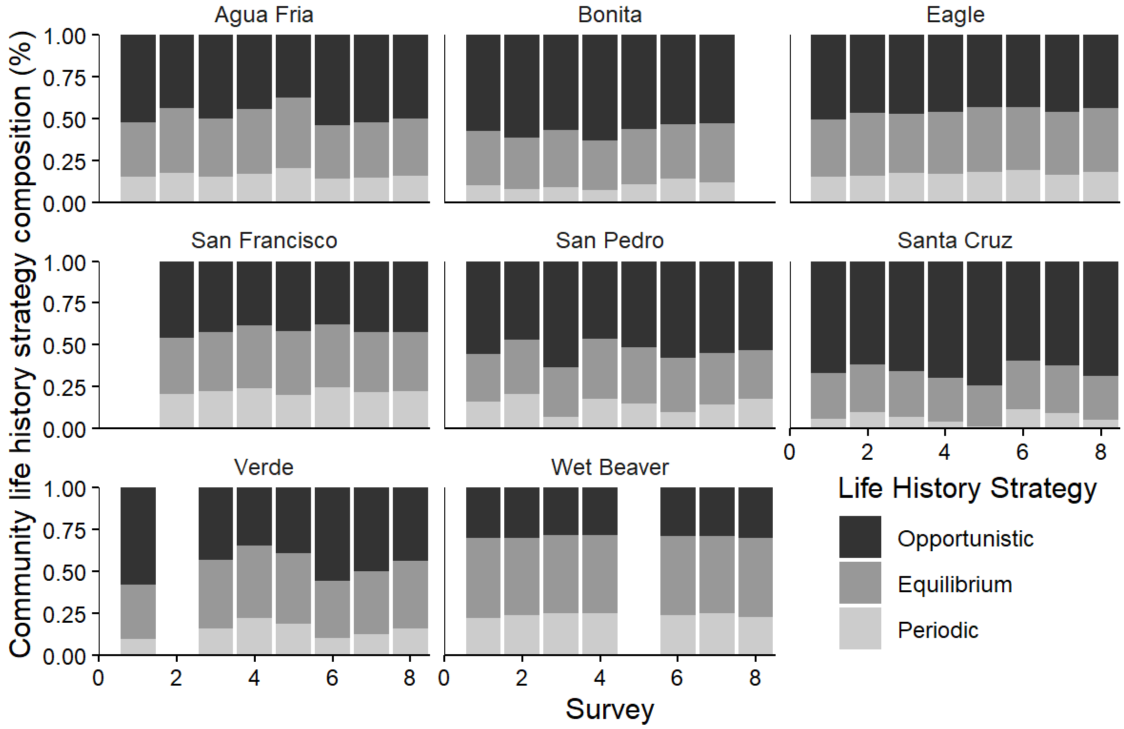


Figure S4: Proportional contributions of each life history strategy to fish communities. Sycamore Creek was excluded because only one species was observed.

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APPENDIX B

CHAPTER 3 SUPPLEMENTARY TABLES AND FIGURES

Table S1: Study site and sampling period information

Site name	USGS gage #	Watershed area (km^2)	Study period	# fish surveys	Missing data
Agua Fria	09512500	1360	Spring 2016 – Spring 2019	13	Metabolism: Fall and winter 2016, spring and winter 2018
Bonita Creek	09447800	813	Spring 2016 – Spring 2019	7	Metabolism: Winter 2016 and winter 2017 Fish: Spring 2016 – summer 2017
Eagle	09447000	1610	Spring 2016 – Spring 2019	13	Metabolism: Spring and fall 2016
San Francisco	09444500	7083	Summer 2016 – Winter 2017	7	Fish: Spring 2016
San Pedro	09471000	3028	Spring 2016 – Spring 2019	13	Metabolism: Winter 2018
Santa Cruz	09480500	1390	Spring 2016 – Spring 2019	13	Metabolism: Summer 2016, winter 2018
Sycamore Creek	09510200	280	Spring 2016 – Winter 2017	8	Metabolism: Summer – winter 2016, fall and winter 2017
Verde	09503700	6439	Spring 2016 – Winter 2017	7	Metabolism: Summer 2016 Fish: Summer 2016
Wet Beaver	09505200	297	Spring 2016 – Winter 2017	7	Metabolism: Summer 2016 Fish: Spring 2017

When streams were dry, ecosystem metabolism was not measured, and fish abundance and biomass were assumed to be zero.

Table S2: Invertebrates used to calculate isotopic baseline for food chain length (FCL)

Site	*Baetidae* family	# of surveys with FCL
Agua Fria	*Baetis, Procleon*	7
Bonita Creek	*Baetis, Procleon*	1
Eagle	*Baetis*	6
San Francisco	*Baetis*	4
San Pedro	*Baetis, Procleon*	5
Santa Cruz	*Baetis, Procleon*	8
Sycamore Creek	*Fallceon, Procleon*	4
Verde	*Baetis, Fallceon*	7
Wet Beaver	*Baetis*	8

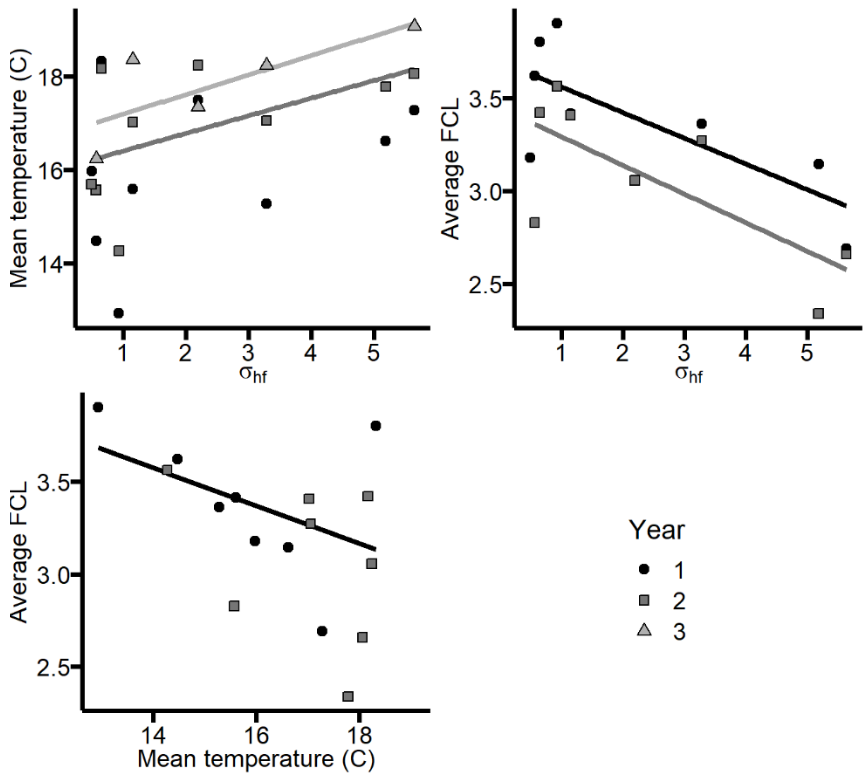

Figure S1: Relationships among hypothesized constraints that were correlated with food web efficiency either across sites or within sites between years. Spearman ρ of relationships for years 1-3 of the study were, respectively; mean temperature – σ_{hf} (0.250, 0.500, 0.700), average FCL– σ_{hf} (-0.548, -0.571, NA), and average FCL – mean temperature (-0.476, -0.286, NA). Best fit lines are drawn when ρ > 0.3.

APPENDIX C

CHAPTER 5 STABLE ISOTOPE METHODS

STABLE ISOTOPE ASSUMPTIONS

In food web analyses, the stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are used to quantify organismal trophic position and identify the original resource pools supporting consumers (Layman et al. 2012). Isotope ratios are measured in percent per million (‰) relative to a standard value and expressed as the δ value. $\delta^{13}C$ is measured relative to carbonate rock from the Pee Dee Belemnite formation and $\delta^{15}N$ is measured relative to atmospheric air (Hershey et al. 2017). Stable isotope ratios of C tend to be distinct for terrestrial and aquatic plants, with $\delta^{13}C$ of aquatic plants typically depleted relative to the atmosphere and terrestrial plants (Finlay 2001). Stable isotope ratios in consumers integrate diet source over longer periods of time than stomach content analysis (Tieszen et al. 1983), and can be used to quantify terrestrial or aquatic origins of carbon in consumer tissues (Layman et al. 2012, Kautza and Sullivan 2016).

Preserving tissues can modify the stable isotope composition of samples. The effects of preservation in ethanol vary by species, tissue, and protein and lipid content, but generally cause enrichment of $\delta^{13}C$ through hydrolysis of lipids, which are rich in C and have a high C:N ratio, and has more variable and often minimal effects on $\delta^{15}N$ (Sweeting et al. 2004, Kelly et al. 2006, Vizza et al. 2013). Freezing samples is the most common method of preservation, but also alters stable isotope ratios (Feuchtmayr and Grey 2003, Barrow et al. 2008), and this modification may not be significantly different than the effects of preservation in ethanol (Syväranta et al. 2011). Preserving our samples in ethanol may have introduced error into our diet source estimates; however, this preservation method was necessary for our field collection and all our samples were preserved the same way. Given the uncertainty surrounding the magnitude of modification to isotope ratios resulting from ethanol preservation and the fact that freezing may also alter isotopic composition, we did not apply corrections to the isotope ratios of our samples.

An additional potential source of error in our stable isotope analysis stems from the presence of lipids in biological tissues. Lipids are more depleted in ^{13}C than other macromolecules due to fractionation during lipid synthesis (DeNiro and Epstein 1977), and lipid correction through models or chemical extraction can be used to account for differential fractionation in lipid-rich tissues (Post et al. 2007b). However, lipid correction does not account for the contribution of lipids routed to consumers through diet and may therefore bias the calculation of diet sources when using ^{13}C (Arostegui et al. 2019). A recent review of published studies using stable isotope mixing models for diet reconstruction found little consistency between studies on when or how lipid corrections were applied (Arostegui et al. 2019). Lipid correction may be necessary when samples have high lipid content, but C:N ratios < 3.5 for aquatic and < 4 for terrestrial animals indicate corrections are not necessary (Post et al. 2007b, Logan et al. 2008). All but four of our fish samples had C:N ratios < 3.5 (max 3.7), all lizards had C:N < 4, and all invertebrates had C:N <5, another suggested cutoff for lipid corrections (Arostegui et al. 2019). Additionally, lipid correction through chemical extraction or normalization based on C:N enriches samples in ^{13}C, which is similar to the effect of preserving samples in ethanol (Sweeting et al. 2004, Post et al. 2007b). We therefore concluded neither mathematical nor additional chemical lipid corrections were necessary for our analysis.

Algae and other aquatic primary producers were scarce during our sampling and were not collected consistently across all sites. However, using measured stable isotope values of aquatic primary producers as endpoints for mixing models can be problematic because it is often not possible to collect periphyton in streams, which is a primary food source for herbivorous invertebrates (Minshall 1978, Feminella and Hawkins 1995). Additionally, invertebrates may selectively feed on the algal component of periphyton (Rezanka and Hershey 2003, McNeely et al. 2006, Chessman et al. 2009), which is difficult to isolate for isotopic analysis but forms the base of many freshwater food webs (Finlay 2001). Aquatic herbivores are often used in stable isotope mixing models as the aquatic baseline instead of aquatic primary producers because they represent the primary production that is assimilated into the food web and made available to predators, and may more accurately represent the baseline of the aquatic food web (Vander Zanden and Rasmussen 1999, Finlay 2001, Olsson et al. 2009, Erdozain et al. 2019).

We estimated aquatic primary producer (algae hereafter) $\delta^{13}C$ and $\delta^{15}N$ by subtracting one trophic enrichment factor (TEF) from the isotopic signature of Baetidae *Baetis*, a genus of herbivorous collector – gatherer and scraper mayflies (Merritt and Cummins 1996). Using herbivores to infer stable isotope values of algae introduces several sources of potential error, including uncertainty in TEFs, potential ingestion of riparian derived organic matter, and selective grazing on some algal taxa by the selected herbivore. However, because we were not able to consistently collect aquatic primary producers across all sites, we believe using the mayfly Baetidae *Baetis* as a proxy is a robust method of estimating the isotopic signatures of the aquatic primary producers contributing to invertebrate production. Opposed to riparian vegetation, algae and herbivore $\delta^{13}C$ are highly variable between locations due to differences in growth form, dissolved CO_2 concentration, flow velocity, and photosynthetic fractionation (Finlay 2001, 2004), making it impractical to compare values between our study sites or with literature values. Instead, we tested the sensitivity of our results to a range of TEFs and report how changing these assumptions propagated through estimates of dietary ratios and the metrics of the integrated ecosystem (Appendix D). Our analysis found that small changes to the aquatic isotopic baseline resulting from the application of different TEFs did not significantly change the study results.

STABLE ISOTOPE LABORATORY AND STATISTICAL METHODS

We excised dorsal muscle from fish and muscle from the base of tails from lizards for stable isotope analysis. Whole invertebrates and plant leaves were processed individually, except for small insect taxa where several individuals were aggregated to reach target weight for analysis. Samples were rinsed in deionized water, dried at 60°C for 48 hours, ground finely using a mortar and pestle, and weighed into tin capsules. Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a Costech 4010 elemental analyzer coupled to a Thermo

Scientifc Delta V isotope ratio mass spectrometer at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM).

We used fresh leaves from riparian plants to isolate the isotopic signature of riparian energy supporting both the riparian and aquatic food webs instead of using stream conditioned detritus for the aquatic food web, which can have altered isotopic ratios due to decomposition and the presence of microorganisms (Finlay 2001, Kautza and Sullivan 2016). Isotopic signatures for leaves of the three species of trees clustered together and were not significantly different (Hotelling's T^2 test**)** and were combined as one resource for all mixing models (Phillips et al. 2005, Stock et al. 2018). All analyses were conducted in R (R Core Team 2019).

We used the Bayesian mixing model package MixSIAR (Stock and Semmens 2016) to calculate the relative dietary contributions of food sources to consumers. MixSIAR integrates uncertainty in resources and TEF values to estimate probability distributions of consumer dietary proportions using Markov chain Monte Carlo (MCMC) methods. Models were run with a chain length of at least 300,000 and were assessed for convergence using Gelman-Rubin and Geweke tests. One model was run for each consumer taxa at each of the three sites using all potential prey items as sources in the mixing models (Table S1). Mixing models were not run for mayflies (assumed to consume only aquatic primary producers) nor riparian insects (assumed to only consume riparian primary producers). Standard deviations from the output of the mixing models were propagated when building resource cycles to account four uncertainty in estimates in both the prey and predator's diets.

We calculated trophic position for each predator using the difference in $\delta^{15}N$ between the predator and the baseline invertebrate based on standard convention (Vander Zanden and Rasmussen 1999, Post 2002a):

$$TP = [(\delta^{15}N_{Predator} - \delta^{15}N_{baseline}) / 3.4] + 2$$

Blackflies were used as the baseline for aquatic predators because they integrate both aquatic and riparian primary producers and have been shown to be useful for trophic baseline identification (Kristensen et al. 2016). Blackflies do not represent the dominant pathway of riparian resources to the diet of riparian predators and therefore would not be an appropriate baseline. We used mayflies and grasshoppers as the baselines for riparian predators and weighted TP by the proportional contribution of aquatic and riparian (respectively) resources to predator diet. Grasshoppers were selected as the riparian baseline because they had the lowest $\delta^{15}N$ of any invertebrate analyzed. TP for all insects, other than damselflies, which are predatory (Merritt and Cummins 1996), was assumed to be two.

Resource Cycling Methods

Output from MixSIAR models provide a mean estimate and standard deviation for the percent contribution to total diet of each resource that was included in the model for each taxon. To calculate resource cycling of aquatic and riparian primary production, we first calculated the proportional contributions of internal and external primary production (ι and ε, respectively) to the diets of primary consumers. We assumed that the diet of herbivorous invertebrates (all riparian insects and mayflies) was 100% internal primary production. Blackflies and caddisflies are both collector-filterers (Merritt and Cummins 1996) and potential resources included both aquatic and riparian primary producers (Table S1). ι for blackflies and caddisflies was calculated as % algae in total diet and ε was calculated as the sum of the proportional contribution of each riparian primary producer to the total diet.

Damselflies were the only strict primary predator and we assumed mayflies, blackflies and caddisflies were representative potential prey items. Damselfly ι was calculated as: %mayfly in diet * mayfly ι + % caddisfly in diet * caddisfly ι + % blackfly in diet * blackfly ι. Damselfly ε was calculated as: % caddisfly in diet * caddisfly ε + % blackfly in diet * blackfly ε.

The contribution of internal and external resources to all other consumers was then calculated using these invertebrates and primary producers as potential prey items when appropriate and adding lower trophic level predators as prey items for larger predators (see Table S1 for prey items considered for each consumer).

Table S1: Sources in stable isotope mixing models for consumers

Consumer	Dietary Sources
Caddisflies	Tree leaves, Giant reed, Bermuda grass, Algae
Blackflies	Tree leaves, Giant reed, Bermuda grass, Algae
Damselflies	Caddisflies, Blackflies, Mayflies
Red Shiner	Caddisflies, Blackflies, Mayflies, Damselflies
Common Carp	Caddisflies, Blackflies, Mayflies, Damselflies, Tree leaves, Giant reed, Bermuda grass, Algae
Green Sunfish	Caddisflies, Blackflies, Mayflies, Damselflies, Red Shiner
Smallmouth Bass	Caddisflies, Blackflies, Mayflies, Damselflies, Red Shiner
Largemouth Bass	Caddisflies, Blackflies, Mayflies, Damselflies, Red Shiner, Green Sunfish, Smallmouth Bass
Wolf Spider	Caddisflies, Blackflies, Mayflies, Damselflies, Ants, Crickets, Grasshoppers
Ornate Tree Lizard	Caddisflies, Blackflies, Mayflies, Damselflies, Ants, Crickets, Grasshoppers, Wolf Spiders

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APPENDIX D

CHAPTER 5 MIXING MODEL SENSITIVITY ANALYSIS

TROPHIC ENRICHMENT FACTOR SENSITIVITY ANALYSIS

Background and Methods

Stable isotope ratios of $\delta^{15}N$ in animal tissues are enriched relative to their food sources on average by 3–4‰, while $\delta^{13}C$ exhibits lower rates of enrichment of 0-1‰ (DeNiro and Epstein 1981, Peterson and Fry 1987, Post 2002a). These trophic enrichment factors (TEFs) for C ($\Delta^{13}C$) and N ($\Delta^{15}N$) are used in mixing models to determine the relative contributions of resources to consumer diet (Hershey et al. 2017). However, TEF values can vary based on consumer identity, tissue analyzed, and consumer diet (McCutchan et al. 2003), such that there is currently no consistent method for identifying the most accurate TEFs for field studies where consumers incorporate a range of food sources (Martínez Del Rio et al. 2009, Bunn et al. 2013). For example, TEF values for tropical freshwater invertebrates are highly variable between taxa and trophic guild, and can fall outside the range of commonly used TEFs (de Carvalho et al. 2015). Uncertainty in TEFs is inherent in all stable isotope mixing models and can affect model results (Bond and Diamond 2011, Phillips et al. 2014). To address these limitations, modern Bayesian mixing models incorporate uncertainty in TEFs and are robust to the fact that TEFs are not static numbers (Moore and Semmens 2008, Layman et al. 2012, Stock et al. 2018). We used the TEF values published by Post (2002), $\Delta^{15}N = 3.4 \pm 0.98$‰ and $\Delta^{13}C = 0.39 \pm 1.3$‰, for all mixing models and results reported in this study. We additionally assessed the sensitivity of our results to uncertainty in TEFs by running all models again with a second commonly used, generic set of TEFs (McCutchan et al. 2003), and with taxa-specific TEF values from the literature. We used the results of these additional models to calculate each metric of the integrated ecosystem framework (cycling efficiency, reciprocity, and integration) under several alternative scenarios to validate that the framework is robust to uncertainty that is inherent to field studies and stable isotope mixing models.

First, we varied the TEF values of the aquatic herbivores while holding the TEF values of predators constant to specifically test the effects of model assumptions for baseline trophic transfers and uncertainty stemming from the use of herbivorous mayflies to infer isotopic ratios of algae. We used three TEF values to calculate the isotopic signature of algae and the diet sources of two herbivorous invertebrates, blackflies and caddisflies. The first alternative set of TEF values we tested was from another widely cited review that found average aquatic consumer $\Delta^{15}N = 2.3 \pm 1.6$‰ and $\Delta^{13}C = 0.4 \pm 1.2$‰ (McCutchan et al. 2003). The second alternative used TEF values from a global literature review of aquatic consumer diet-tissue fractionation, which found $\Delta^{15}N = 1.4 \pm 1.4$‰ for algae to herbivorous invertebrates (Bunn et al. 2013). We used this value because it is one of the lower estimates of nitrogen enrichment factors and is specific to herbivorous aquatic invertebrates. Additionally, the large SD incorporates the high amount of uncertainty in $\delta^{15}N$ enrichment factors, which informs the MixSIAR model. $\Delta^{13}C$ is often found to range between 0 and 1‰ (Peterson and Fry 1987) , although negative enrichment values have been observed for some tropical aquatic invertebrate taxa (de Carvalho et al. 2015). We therefore used $\Delta^{13}C = 0 \pm 1.4$‰ with the $\Delta^{15}N$ from Bunn *et al.* (2013) to test the effects of TEFs significantly lower than those in our original models

(Post 2002a). We used the three estimates of aquatic invertebrate dietary sources from mixing models using Post (2002), McCutchan *et al.* (2003) and Bunn *et al.* (2013) TEFs to calculate the contribution of aquatic and riparian primary production to the diets of predators, using the Post (2002) TEFs for all predator-prey enrichment factors. Changing the TEF between plants and aquatic herbivores and holding all other TEFs constant effectively shifts the isotopic baseline of the food web. If the mixing models or metrics developed in this paper were highly sensitive to variability in the baseline isotopic signature, this would be expected to significantly alter our conclusions.

Second, we assessed the sensitivity of our results to uncertainty in enrichment factors for upper trophic level consumers using TEF values from the literature that were specific to each predator. For fish, we used values found by Bunn *et al.* (2013) for predatory fish ($\Delta^{15}N = 1.9 \pm 1.6$‰) as one of the lower published $\Delta^{15}N$ values and $\Delta^{13}C = 0 \pm 1.4$‰. For spiders, we used TEF values from a feeding experiment using the same genus of spiders we collected (Lycosidae *Pardosa*) that were fed high or very high quality diets ($\Delta^{15}N = 2.29 \pm 0.5$ and $\Delta^{13}C = 0.37 \pm 0.37$; Oelbermann and Scheu 2002). We used a species-specific TEF for the lizard used in our study (*Urosaurus ornatus*) from a diet-switching experiment ($\Delta^{15}N = 0.7 \pm 0.4$ and $\Delta^{13}C = 1.2 \pm 0.4$; Lattanzio and Miles 2016). To fully assess the effects of uncertainty in diet-tissue enrichment at multiple trophic levels, we calculated consumer resource use and the metrics of the integrated ecosystem framework using each combination of TEF values for aquatic invertebrates and the taxa-specific TEF values for predators. Between the two tests, we calculated six estimates of resource use for each predator and six values of each metric of the integrated ecosystem concept.

Results and Discussion

Changing the trophic enrichment factor between plants and aquatic herbivores and propagating the three estimates of resource use up the food web had minimal effect on the resources supporting predators (Table S1). The maximum difference in average external resource use (ε) in the diet of a herbivorous invertebrate between the three TEF values tested was 5.3% between the Post (2002) and Bunn *et al.* (2013) estimates for caddisflies, which is within the range of error for each estimate. The effects of different plant-aquatic herbivore TEF values were negligible for predators when holing predator TEF constant (Table S1). Similarly, cycling efficiency (*C*), reciprocity (*R),* and integration (*I*) were almost unchanged in this trial (Table S2). These results indicate that a) model results are robust to uncertainty in TEF between primary producers and herbivores, b) using mayflies to infer the isotopic signature of algae is robust to potential errors introduces by not directly measuring the algae directly, and c) minor changes in the original resource pool supporting consumers has little influence on the integrated ecosystem metrics.

Applying taxa-specific TEF values for each consumer in the food web had a larger effect on calculated resource use than adjusting primary consumer TEFs alone (Table S3). For example, lizard ε changed from 22.0% when using Post (2002) TEFs to 34.7% when using taxa-specific values for both aquatic invertebrates (Bunn *et al.* 2013) and lizards

(Lattanzio and Miles 2016). However, the lower original estimate is within one standard deviation of the mean estimated from taxa-specific enrichment values. While we found that choice of TEF does affect estimates of consumer diet, the differences were generally minimal. Because there is such high variability in TEF values between closely related taxa, and even within the same species (Vanderklift and Ponsard 2003, Martínez Del Rio et al. 2009, Bunn et al. 2013, de Carvalho et al. 2015), we conclude that applying a single, widely used TEF in our mixing models yielded results that were not meaningfully different than taxa-specific TEF values and did not significantly alter the conclusions of this study.

The metrics of the integrated ecosystem were also found to be robust to uncertainty in isotopic mixing models (Table S2). Estimates of fish and invertebrate dietary ratios were minimally affected by the use of taxa-specific TEFs relative to general TEF values. As a result, cycling efficiency, calculated for the aquatic food web, was consistently close to 0.8 in each trial (Table S2). Similarly, integration had little variation between the six trials, showing that uncertainty in enrichment factors did not greatly affect the evenness of internal and external resource use in each ecosystem compartment. The reciprocity ratio was found to be more sensitive to variation in estimates of consumer diet (Table S2). This change is from an increase in the average estimated ε by riparian predators when using taxa-specific TEFs, resulting in relatively higher reliance on external resources by riparian predators than the average of aquatic predators. These results indicate that R is the most sensitive metric to small variations in estimates of consumer diet. However, all three metrics are > 0.75 for each of the six methods tested and it is therefore unlikely that the assumptions used in this study significantly altered the conclusion that the aquatic and riparian compartments of the Verde River form an integrated ecosystem.

Table S1: Sensitivity analysis of consumer resource use to the trophic enrichment factor (TEF) between primary producers and aquatic herbivores. TEF values for upper trophic level consumers were from Post (2002) for all models. Diet % from external resources (ε) and standard deviation (sd) are shown for each plant-herbivore TEF.

Consumer group	Common name	Species	Post 2002	McCutchan et al. 2003	Bunn et al. 2013
Riparian Predator	Thin-legged Wolf Spider	*Pardosa* sp.	ε = 35.9% sd =15.6 %	ε = 35.8% sd = 15.6%	ε = 36.4% sd = 15.7%
	Ornate Tree Lizard	*Urosaurus ornatus*	ε = 22.0% sd = 10.9%	ε = 21.8% sd = 10.9%	ε = 22.2% sd = 10.9%
Aquatic insect	Caddisfly	*Hydropsyche* sp.	ε = 49.7% sd = 14.2%	ε = 53.0% sd = 16.1%	ε = 49.3% sd = 16.8%
	Black Fly	*Simulium* sp.	ε = 44.9% sd = 12.6%	ε = 41.9% sd = 12.7%	ε = 39.6% sd = 13.1%
	Damselfly	*Hetaerina* sp.	ε = 29.4% sd = 14.5%	ε = 29.8% sd = 14.2%	ε = 29.4% sd = 13.4%
Fish	Red Shiner	*Cyprinella lutrensis*	ε = 29.7% sd = 13.0%	ε = 30.3% sd = 13.7%	ε = 28.8% sd = 13.0%
	Common Carp	*Cyprinus carpio*	ε = 50.2% sd = 15.3%	ε = 51.9% sd = 16.3%	ε = 50.3% sd = 15.8%
	Green Sunfish	*Lepomis cyanellus*	ε = 31.2% sd = 12.0%	ε = 31.6% sd = 12.5%	ε = 30.0% sd = 11.9%
	Smallmouth x Redeye Bass	*Micropterus dolomieu* x *coosae*	ε = 29.9% sd = 11.0%	ε = 31.8% sd = 12.3%	ε = 30.7& sd = 11.9%
	Largemouth Bass	*Micropterus salmoides*	ε = 27.6% sd = 9.8%	ε = 25.1% sd = 8.9%	ε = 24.0% sd = 8.4%

Table S2: Metrics of the integrated ecosystem calculated with different combinations of plant-aquatic herbivore TEFs and prey-predator TEFs. Results calculated with Post (2002) TEF values for both herbivores and predators are used in this study.

	Predator TEF from Post (2002)			Taxa-specific predator TEF		
Metric	Post 2002	McCutchan et al. 2003	Bunn et al. 2013	Post 2002	McCutchan et al. 2003	Bunn et al. 2013
Cycling efficiency	0.798	0.793	0.789	0.816	0.812	0.816
Reciprocity	0.829	0.828	0.898	0.926	0.940	0.878
Integration	0.867	0.864	0.852	0.926	0.924	0.918

Table S3: Resource use for consumers calculated using taxa-specific TEF values for upper trophic level consumers (riparian predators and fish) paired with three combinations of TEF values for aquatic herbivores. Diet % from external resources (ε) and standard deviation (sd) are shown for each plant-herbivore TEF.

Consumer group	Common name	Species	Post 2002	McCutchan et al. 2003	Bunn et al. 2013
Riparian Predator	Thin-legged Wolf Spider	*Pardosa* sp.	ε = 41.3% sd = 17.7%	ε = 40.8% sd = 17.4%	ε = 41.6% sd = 17.5%
	Ornate Tree Lizard	*Urosaurus ornatus*	ε = 34.5% sd = 14.1%	ε = 33.9% sd = 13.9%	ε = 34.7% sd = 14.1%
Fish	Red Shiner	*Cyprinella lutrensis*	ε = 20.5% sd = 14.7%	ε = 31.3% sd = 15.2%	ε = 30.0% sd = 14.5%
	Common Carp	*Cyprinus carpio*	ε = 50.8% sd = 17.0%%	ε = 51.7% sd = 17.6%	ε = 50.3% sd = 17.1%
	Green Sunfish	*Lepomis cyanellus*	ε = 31.4% sd = 11.9%	ε = 32.1% sd = 12.5%	ε = 30.7% sd = 11.9%
	Smallmouth x Redeye Bass	*Micropterus dolomieu* x *coosae*	ε = 30.1% sd = 11.6%	ε = 32.3% sd = 12.9%	ε = 31.0% sd = 12.4%
	Largemouth Bass	*Micropterus salmoides*	ε = 27.4% sd = 10.2%	ε = 25.4% sd = 9.5%	ε = 24.5% sd = 9.0%

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APPENDIX E

CHAPTER 5 CASE STUDY CALCULATIONS

INTEGRATED ECOSYSTEM CALCULATIONS FOR LAKE CASE STUDY

Zooplankton (Crustacea and *Chaoborus* spp.) and fish (*Cyprinidae*, *Lepomis* spp., and *Micropterus salmoides*) were considered pelagic consumers with benthic and terrestrial primary production both as external resources. Zoobenthos (*Chironomidae* and Odonata) were considered benthic consumers with pelagic and terrestrial primary production as external resources. Cycling efficiency was calculated for both sources of external resources to the pelagic ecosystem compartment, C_{benthic}, $C_{\text{terrestrial}}$. When calculating integration, contributions of both sources of external resources were summed for each taxon to yield the total fraction of resource use from external primary production.

Abbreviations Used in Equations

Consumers: Crustacea (Cru), *Chaoborus* spp. (Cha), *Chironomidae* (Chi), Odonata (Odo), *Cyprinidae* (Cyp), *Lepomis* spp. (Lep), *Micropterus salmoides* (Mic)
Resources: Pelagic (pel), benthic (ben), terrestrial (ter)

Crampton Lake

$$C = \left(\left(\frac{Cha}{Cru}\right)/\,1 + \left(\frac{Odo}{Chi}\right)/\,1 + \left(\frac{Lep}{Che} + \frac{Lep}{Chi} + \frac{Lep}{Odo}\right)/\,3 + \left(\frac{Mic}{Che} + \frac{Mic}{Chi} + \frac{Mic}{Odo} + \frac{Mic}{Lep}\right)/\,4\right)/\,4$$

$$R = \frac{\text{min(mean(Chi}_{\text{pel}}\text{, Odo}_{\text{pel}}\text{), mean(Cru}_{\text{ben}}\text{, Cha}_{\text{ben}}\text{, Lep}_{\text{ben}}\text{, Mic}_{\text{ben}}\text{))}}{\text{max(mean(Chi}_{\text{pel}}\text{, Odo}_{\text{pel}}\text{), mean(Cru}_{\text{ben}}\text{, Cha}_{\text{ben}}\text{, Lep}_{\text{ben}}\text{, Mic}_{\text{ben}}\text{))}}$$

$$I = 2 * \{ \text{mean}[(\text{Chi}_{\text{pel}} + \text{Chi}_{\text{ter}}), (\text{Odo}_{\text{pel}} + \text{Odo}_{\text{ter}})] * \text{mean}[\text{Chi}_{\text{ben}}, \text{Odo}_{\text{ben}}] + \text{mean}[(\text{Cru}_{\text{ben}} + \text{Cru}_{\text{ter}}), (\text{Cha}_{\text{ben}} + \text{Cha}_{\text{ter}}), (\text{Lep}_{\text{ben}} + \text{Lep}_{\text{ter}}), (\text{Mic}_{\text{ben}} + \text{Mic}_{\text{ter}})] * \text{mean}[\text{Cru}_{\text{pel}}, \text{Cha}_{\text{pel}}, \text{Lep}_{\text{pel}}, \text{Mic}_{\text{pel}},)] \}$$

Peter Lake

$$C = \left(\left(\frac{Cha}{Cru}\right)/\,1 + \left(\frac{Odo}{Chi}\right)/\,1 + \left(\frac{Lep}{Che} + \frac{Lep}{Chi} + \frac{Lep}{Odo}\right)/\,3 + \left(\frac{Cyp}{Che} + \frac{Cyp}{Chi} + \frac{Cyp}{Odo}\right)/\,3\right)/\,4$$

$$R = \frac{\text{min(mean(Chi}_{\text{pel}}\text{, Odo}_{\text{pel}}\text{), mean(Cru}_{\text{ben}}\text{, Cha}_{\text{ben}}\text{, Lep}_{\text{ben}}\text{, Cyp}_{\text{ben}}\text{))}}{\text{max(mean(Chi}_{\text{pel}}\text{, Odo}_{\text{pel}}\text{), mean(Cru}_{\text{ben}}\text{, Cha}_{\text{ben}}\text{, Lep}_{\text{ben}}\text{, Cyp}_{\text{ben}}\text{))}}$$

$$I = 2 * \{ \text{mean}[(\text{Chi}_{\text{pel}} + \text{Chi}_{\text{ter}}), (\text{Odo}_{\text{pel}} + \text{Odo}_{\text{ter}})] * \text{mean}[\text{Chi}_{\text{ben}}, \text{Odo}_{\text{ben}}] + \text{mean}[(\text{Cru}_{\text{ben}} + \text{Cru}_{\text{ter}}), (\text{Cha}_{\text{ben}} + \text{Cha}_{\text{ter}}), (\text{Lep}_{\text{ben}} + \text{Lep}_{\text{ter}}), (\text{Cyp}_{\text{ben}} + \text{Cyp}_{\text{ter}})] * \text{mean}[\text{Cru}_{\text{pel}}, \text{Cha}_{\text{pel}}, \text{Lep}_{\text{pel}}, \text{Cyp}_{\text{pel}},)] \}$$

Paul Lake

$$C = \left(\left(\frac{Cha}{Cru}\right)/\,1 + \left(\frac{Odo}{Chi}\right)/\,1 + \left(\frac{Mic}{Che} + \frac{Mic}{Chi} + \frac{Mic}{Odo} + \frac{Mic}{Lep}\right)/\,4\right)/\,3$$

$$R = \frac{\min(\ \mathrm{mean}(Chi_{pel}, Odo_{pel}), \mathrm{mean}(Cru_{ben}, Cha_{ben}, Mic_{ben})\ )}{\max(\ \mathrm{mean}(Chi_{pel}, Odo_{pel}), \mathrm{mean}(Cru_{ben}, Cha_{ben}, Mic_{ben})\ )}$$

$$I = 2 * \{\ \mathrm{mean}[(Chi_{pel} + Chi_{ter}), (Odo_{pel} + Odo_{ter})] * \mathrm{mean}[Chi_{ben}, Odo_{ben}] + \mathrm{mean}[(Cru_{ben} + Cru_{ter}), (Cha_{ben} + Cha_{ter}), (Mic_{ben} + Mic_{ter})] * \mathrm{mean}[Cru_{pel}, Cha_{pel}, Mic_{pel},)]\ \}$$

Tuesday Lake

$$C = \left(\left(\frac{Cha}{Cru}\right)/\,1 + \left(\frac{Odo}{Chi}\right)/\,1 + \left(\frac{Cyp}{Che} + \frac{Cyp}{Chi} + \frac{Cyp}{Odo}\right)/\,3\right)/\,3$$

$$R = \frac{\min(\ \mathrm{mean}(Chi_{pel}, Odo_{pel}), \mathrm{mean}(Cru_{ben}, Cha_{ben}, Cyp_{ben})\ )}{\max(\ \mathrm{mean}(Chi_{pel}, Odo_{pel}), \mathrm{mean}(Cru_{ben}, Cha_{ben}, Cyp_{ben})\ )}$$

$$I = 2 * \{\ \mathrm{mean}[(Chi_{pel} + Chi_{ter}), (Odo_{pel} + Odo_{ter})] * \mathrm{mean}[Chi_{ben}, Odo_{ben}] + \mathrm{mean}[(Cru_{ben} + Cru_{ter}), (Cha_{ben} + Cha_{ter}), (Cyp_{ben} + Cyp_{ter})] * \mathrm{mean}[Cru_{pel}, Cha_{pel}, Cyp_{pel},)]\ \}$$

APPENDIX F

ASU IACUC PROTOCOL APPROVALS

Institutional Animal Care and Use Committee (IACUC)
Office of Research Integrity and Assurance
Arizona State University
660 South Mill Avenue, Suite 312
Tempe, Arizona 85287-6111
Phone: (480) 965-6788 *FAX:* (480) 965-7772

Animal Protocol Review

ASU Protocol Number: **18-1622R RFC 2**
Protocol Title: **Ecological niche of riparian predators**
Principal Investigator: **John Sabo**
Date of Action: **4/26/2018**

The animal protocol review was considered by the Committee and the following decisions were made:

The request for changes was approved to add additional field sites, 27 lizards and Heather Bateman as additional personnel.

If you have not already done so, documentation of Level III Training (i.e., procedure-specific training) will need to be provided to the IACUC office before participants can perform procedures independently. For more information on Level III requirements see https://researchintegrity.asu.edu/training/animals/levelthree.

Total # of Animals: **695**
Species: **Reptiles** **Unalleviated Pain/Distress: No**

Protocol Approval Period: **1/25/2018 – 1/24/2021**

Sponsor: **N/A**
ASU Proposal/Award #: **N/A**
Title: **N/A**

Signature: for C. Shalley Date: 5/4/2018
IACUC Chair or ***Designee***

Institutional Animal Care and Use Committee (IACUC)
Office of Research Integrity and Assurance
Arizona State University
660 South Mill Avenue, Suite 315
Tempe, Arizona 85287-6111
Phone: (480) 965-4387 *FAX:* (480) 965-7772

Animal Protocol Review

ASU Protocol Number:	**15-1418R**
Protocol Title:	**Collaborative Research: Effects of Flow Regime Shifts, Antecedent Hydrology, Nitrogen Pulses and Resource Quantity and Quality on Food Chain Length in Rivers**
Principal Investigator:	**John Sabo**
Date of Action:	**2/26/2015**

The animal protocol review was considered by the Committee and the following decisions were made:

The protocol was approved as modified.

If you have not already done so, documentation of Level III Training (i.e., procedure-specific training) will need to be provided to the IACUC office before participants can perform procedures independently. For more information on Level III requirements see https://researchintegrity.asu.edu/training/animals/levelthree.

Total # of Animals:	**9,381**	
Species:	**Amphibians**	**Pain Level: C-4,206**
Species:	**Fish**	**Pain Level: C-5,175**

Protocol Approval Period: **2/26/2015 – 2/25/2018**

Sponsor:	**National Science Foundation**
ASU Proposal/Award #:	**14071867**
Title:	**Collaborative Research: Effects of Flow Regime Shifts, Antecedent Hydrology, Nitrogen Pulses and Resource Quantity and Quality on Food Chain Length in Rivers**

Signature: Augustowski for C Johnson
IACUC Chair or Designee

Cc: IACUC OfficeIACUC Chair

APPENDIX G

ARIZONA GAME AND FISH DEPARTMENT SCL

State of Arizona
Game and Fish Department
No refunds/Not transferable

LICENSE YEAR: 2017
HQ - PHOENIX
FREE E-NEWS SIGNUP
www.azgfd.gov/signup

DATE: 03/01/2017
RESIDENT: 11 yr 00 mo

LIC #SP510143 **SCIENTIFIC COLLECTING** **VALID:** 01/01/2017 – 12/31/2017

09/14/1970	6' 01"	190	BRN	BLN	M
BIRTH-DATE	HEIGHT	WEIGHT	EYES	HAIR	SEX

JOHN L SABO
427 E TYLER MALL
TEMPE, AZ 85281

I hereby certify all information on this license is true.

NOT VALID UNTIL SIGNED

SCIENTIFIC COLLECTING LICENSE STIPULATIONS
JOHN L. SABO ▪ ARIZONA STATE UNIVERSITY

1. The following are agents under this license for the activities below: Ethan Baruch Leah Gaines

   The licensee OR the agent(s) MUST be present at all activities conducted under authority of this license and must have a copy of the license and stipulations present at all times while conducting activities.

2. This license allows stipulated activities to be conducted: **in the Verde River near Paulden, Agua Fria River near Mayer, Wet Beaver Creek near Rimrock (Yavapai County); Sycamore Creek near Fort McDowell (Maricopa County); Bonita Creek near Morenci (Graham County); Eagle Creek near Morenci and San Francisco near Clifton (Greenlee County); San Pedro River near Charleston and Ramsey Creek near Sierra Vista (Cochise County); and the Santa Cruz River near Nogales and Babacomari near Sonoita (Santa Cruz County);** Additional licenses/permission from the land owner/manager or resource management agency must be acquired prior to conducting activities.

3. Prior to field collections and sampling you must notify by email to the appropriate Aquatic Wildlife Program Managers and Coordinators (see list that follows). We recognize that you have regularly scheduled monitoring efforts and would like to better coordinate to reduce duplication of effort (by us or other investigators), better respond to public and law enforcement inquiries on activities that might be perceived by them as illegal, and to assist other investigators in acquiring needed specimens for propagation and research. Failure to email the Regional Aquatic Wildlife Program Managers and Program Coordinator could result in revocation and denial of future licenses. Approval of coordinated activities may take the form of email correspondence or hard copy letter. ***Include a Carbon Copy (CC) to scpermits@azgfd.gov in all email notifications.**

   Region II contact: Scott Rogers (srogers@azgfd.gov); 928-214-1245
   Region III contact: Matt Chmiel (mchmiel@azgfd.gov); 928-692-7700
   Region V contact: Don Mitchell (dmitchell@azgfd.gov ; 520-628-4451)
   Region VI contact: Curt Gill (cgill@azgfd.gov); 480-324-3545
   Statewide Native Aquatic Supervisor: Julie Carter (jcarter@azgfd.gov); 623-236-7576
   CAP Conservation Program Manager: Tony Robinson (trobinson@azgfd.gov); 623-236-7376
   Topminnow/Pupfish Coordinator: Ross Timmons (rtimmons@azgfd.gov); 623-236-7509

4. You are authorized to capture and release unlimited numbers of native and non-native fish in coordination with the appropriate species leads and Regional Program Manager listed in stipulation #3; Non-target species must

be released alive; removal of non-native fish is on a case-by-case basis and must be coordinated with the Regional Program Manager.

1. You are authorized to Catch and release (alive and unharmed) with the use of dip nets and electrofishing of nonnative and native fish on a case-by-case basis and must be coordinated with the Regional Program Manager.

2. Use the Department's Electrofishing guidelines (Minimizing Electrofishing Injury) for any/all surveys using that gear type.

3. You are authorized to collect the following species in accordance to your federal regulations and permitting; disperse your collection to 3 individuals per site:

8.

Scientific Name	Common Name	Licensed Take
Agosia chrysogaster	Longfin dace	*108*
Ameiurus melas	Black bullhead	*24*
Ameiurus natalis	Yellow bullhead	*36*
Catostomus clarkii	Desert sucker	*96*
Catostomus insignis	Sonora sucker	*60*
Cyprinella lutrensis	Red shiner	*36*
Cyprinus carpio	Carp	*24*
Gambusia affinis	Western mosquitofish	*36*
Gila robusta	Roundtail chub	*48*
Ictalurus punctatus	Channel catfish	*36*
Lepomis cyanellus	Green sunfish	*24*
Lepomis macrochirus	Bluegill	*96*
Micropterus dolomieu	Smallmouth bass	*48*
Micropterus salmoides	Largemouth bass	*48*
Oncorhynchus mykiss	Rainbow trout	*24*
Pimephales promelas	Fathead minnow	*36*
Pylodictis olivaris	Flathead catfish	*36*
Rhinichthys osculus	Speckled dace	*36*
Salmo trutta	Brown trout	*84*

9. Please report any/all "fish kills" to the appropriate regional AGFD office (c/o Regional Fisheries Program Manager) as soon as possible.

10. You are authorized to capture by hand or hand-held implement and release at the site of capture, collect samples (toe clips), unlimited numbers of amphibians and reptiles (open season species). Survey for or capture of federally listed species requires a permit from the U.S. Fish and Wildlife Service.

11. All aquatic sampling gear, including waders and irrigation boots, should be disinfected with a solution of quaternary ammonium or 10% bleach after sampling each site, to reduce the spread of exotic organisms and pathogens.

12. When sampling for fish within streams known to be occupied by or designated habitat for Mexican gartersnakes, you must coordinate with **AGFD Amphibians and Reptile Program Manager, Tom Jones (tjones@azgfd.gov; 623-236-7735)** ***email preferred*****.**

   a. When using funnel-type traps (e.g., Gee Minnow traps, Promar® minnow traps, hoop nets) to survey in habitat occupied by Mexican gartersnakes, use only 1/8 inch mesh traps. Traps should be set with a portion of the trap above the water so that any captured snakes will be able to breathe.
   b. When surveying for gartersnakes, check traps at least twice a day (am and pm) or more often after deployment until traps are removed from the site.
   c. All unattended nets/traps must be labeled with the Scientific Collecting Licensee's name, SP license number, and contact information.

a. Any snakes that dies, as a result of sampling must be collected and turned over to the Gartersnake Projects Coordinator.
b. Any efforts that specifically target Mexican gartersnakes (*Thamnophis eques*) require a federal license.
c. All new localities (i.e., previously unknown sites or sites that have not been occupied for 5 years or more), and dead or die-offs must be reported to AGFD Amphibians and Reptile Program Manager within 5 business days of discovery.

10. You are authorized to salvage wildlife found dead or die during handling (salvage of federally listed or protected species requires a federal permit).

11. The disposition of all wildlife handled or surveyed during activities must be reported on the *SCL Report Form* provided (captured/released alive, incidentals captured in traps, collected, fatalities, salvaged, and including positive location from surveys).

END

State of Arizona
Game and Fish Department
No refunds/Not transferable

LICENSE YEAR: 2018
HQ - PHOENIX
FREE E-NEWS SIGNUP
www.azgfd.gov/signup

DEPT-ID: **L17251940**
DATE: 02/14/2018
RESIDENT: 00 yr 00 mo

LIC #SP619758 **SCIENTIFIC COLLECTING** **VALID: 01/01/2018 – 12/31/2018**

11/17/1992	5' 10"	145	BRN	BRN	M
BIRTH-DATE	HEIGHT	WEIGHT	EYES	HAIR	SEX

I hereby certify all infor mation on this license is true.

ETHAN BARUCH
427 E TYLER MALL
TEMPE, AZ 85281

NOT VALID UNTIL SIGNED

SCIENTIFIC COLLECTING LICENSE STIPULATIONS
ETHAN BARUCH ▪ ARIZONA STATE UNIVERSITY

1. The following are agents under this license for the activities below:

   Stacey Brockman Leah Gaines

   The licensee OR the agent(s) MUST be present at all activities conducted under authority of this license and must have a copy of the license and stipulations present at all times while conducting activities.

2. This license allows stipulated activities to be conducted: **in San Pedro River near Charleston (Cochise County); Agua Fria River near Mayer (Yavapai County);** Additional licenses/permission from the land owner/manager or management agency must be acquired prior to conducting activities.

3. You are authorized to capture, toe-clip, collect blood samples and release at site of capture up to three hundred (300) ornate tree lizard (*Urosaurus ornatus*)

4. You are authorized to capture, toe-clip, collect blood samples and release at site of capture up to two hundred (200) each of southwestern fence lizard (*Sceloporus cowlesi*) and plateau lizard (*S. tristichus*).

   The licensee OR the agent(s) MUST be present at all activities conducted under authority of this license and must have a copy of the license and stipulations present at all times while conducting activities.

5. You are authorized to salvage (including tissue sampling) unlimited numbers of open and closed season amphibians and reptiles found dead (salvage of federally listed or protected species requires a federal permit).

6. The disposition of all wildlife handled or surveyed during activities must be reported on the *SCL Report Form* provided (captured/released alive, incidentals captured in traps, collected, fatalities, salvaged, and including positive location from surveys).

   END