

Basal Carbon Sources Supporting Fish Food Webs in Terminal Basin Rivers

by

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Abstract

Terminal basin rivers—those with no outlets to the sea—are unique systems that have been traditionally under-studied despite their widespread occurrence in drier regions of the world. The goal of this study was to elucidate the contributions of terminal basin rivers to broader concepts in lotic ecology using the contrasting frameworks of the River Continuum Concept (RCC) and the Riverine Ecosystem Synthesis (RES). Study sites were chosen for two rivers of the Great Basin, USA, according to coarse-scale hydrogeomorphic variables and included constricted-valley uplands, constricted-valley lowlands, wide-valley uplands, and wide-valley lowlands. Using amino acid, compound specific stable isotope analysis of amino acids (AA-CSIA) of carbon (C), we determined isotopic signatures for fish consumers and their potential food sources. AA-CSIA values for essential and conditionally essential amino acids were used as dietary tracers to estimate the proportional contribution of four different food groups: autochthonous resources (cyanobacteria and green algae), fungi, C₃ plants, and C₄/CAM plants to consumer basal diets using a Bayesian mixing model. Results suggest that consumer tissue of fish from all sites, regardless of site position along the river network, valley hydrogeomorphology, riparian vegetation, or fish species, was primarily derived from autochthonous C, with an average proportional contribution of 79.9±3.1%. This finding lends some support to the RES, in that over the entire river network, >50% of metazoan production was supported by autochthonous resources; however, there was no significant effect of hydrogeomorphology on the types of food sources assimilated. Additionally, we found no effect of site position to support the RCC. Future studies might gather additional data in different river systems.

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Chapter 1: Models and methods in conceptual lotic ecology: A review

Recent developments in the field of ecology suggest that the understanding of ecological processes would benefit from an expanded focus at the macrosystem scale, especially in the context of global climate change and species invasions (Giller et al. 2004, Williams et al. 2013, Clare 2014, Connolly and Waltham 2015, Abelho 2016, Datry et al. 2016, Grabowski and Gurnell 2016). Past studies in lotic ecology have focused primarily on microhabitats and relatively small stream reaches. In more recent attempts to scale up spatially, researchers have employed meta-analyses and extrapolation techniques; however, these types of studies may not be adequate in themselves for understanding natural systems (Hilderbrand and Kershner 2004). The following chapters describe some research activities conducted as part of an international effort to understand the effects of large-scale river hydrogeomorphology on ecosystem function within a macrosystem framework. This novel research project tested hypotheses of riverine theory at the macrosystem scale and has the potential to provide crucial lessons for conservation and management of rivers. In this general introduction, I provide a history of theoretical river ecology, introduce the concept of river macrosystem ecology, and discuss how advancements in analytical techniques can offer new information that may be valuable for understanding the patterns and processes of food webs in the context of the river macrosystem.

Over the last several decades, ecologists have developed a suite of theories to understand the structure and ecological function of rivers. An early attempt by Hawkes (1975) defined rivers as being composed of discrete zones, characterized by the fish inhabiting each segment. This early approach contrasted significantly with later theories, which included the River Continuum Concept (Vannote et al. 1980), the Flood Pulse Concept (Junk et al. 1989), the Riverine

Productivity Model (Thorp and DeLong 1994), the Riverine Ecosystem Synthesis (Thorp et al. 2006, 2008), the River Wave Concept (Humphries et al. 2014), and recent perspectives on river macrosystem ecology (McCluney et al. 2014, Thorp 2014).

The River Continuum Concept

Vannote et al. (1980) introduced the River Continuum Concept (RCC), which described rivers not as composed of discrete zones, but rather as a continuous and predictable network of physical variables from headwaters to river mouth. RCC authors categorized rivers into three major groups, based on their size. These included small headwater streams (1st to 3rd order), mid-sized rivers (4th to 6th order), and large rivers (>6th order). This work used invertebrate feeding group classifications and metabolic ratios to describe available energy along different parts of the river continuum. They proposed that forested headwaters had primary production-to-system respiration ratios less than 1 ($P:R < 1$) and were dominated by shredding invertebrates feeding on terrestrial (allochthonous) leaf material. Well-lit mid-sized streams were thought to have $P:R > 1$ and would be characterized by algal (autochthonous) grazers. Finally, large, deep, turbid rivers were thought to have $P:R < 1$; and because they lack enough light penetration for abundant algal growth in the main channel, they were considered to be dominated by suspension-feeding invertebrates consuming degraded (size and nutritive content) organic material “leaking” from upstream reaches.

The publication of the RCC attracted immediate attention. On one hand, it was celebrated as a novel framework for river theory and for its generation of testable hypotheses (Barmuta and Lake 1982, Culp and Davies 1982). However, some ambiguities regarding its theoretical basis (Statzner and Higler 1985) and its claims that the theory was generalizable for all rivers also

drew some criticism (Winterbourn et al. 1981, Barmuta and Lake 1982, Statzner and Higler 1985, Sedell et al. 1989, Townsend 1989, Junk and Wantzen 2004). Even authors who had been involved in the original manuscript proposed comments and addendums to the 1980 paper (Minshall et al. 1982, Sedell et al. 1989). Despite this fact, the RCC is still regularly taught in the modern ecology classroom (Thorp et al. 2006). This is likely due to its relative simplicity; however, this also means that some of the most important and complex properties of rivers are ignored (Statzner and Higler 1985). Many of the conclusions of the RCC are now understood to be incorrect, for several reasons.

Most notably, there is a large and growing body of evidence countering the RCC's portrayal of river continuity and predictability. In fact, Leopold et al. (1964), a book that was actually cited by the RCC authors, alluded to the discontinuous geomorphic properties of rivers quite early on. Later, Statzner and Higler (1985) used data from the RCC to calculate physical parameters of the river channel and found no uniform downstream pattern. They also argued that, especially at a large scale, rivers had inherent discontinuity (Statzner and Higler 1985). Balon and Stewart (1983) also argued for the discontinuity of river networks, based on their observation that fish assemblages in an African river could not be predicted along a gradient. Many more recent studies, (e.g., Brito et al. 2006, McNeely et al. 2007, Lau et al. 2009, Dalu et al. 2015, Smits et al. 2015, Becerra-Muñoz et al. 2016, Hayden et al. 2016) have also been unable to fit their empirical data to this aspect of the RCC model.

In addition, their treatment of large rivers was inappropriately built from many unqualified assumptions (Thorp and DeLong 1994). For example, the authors of the RCC incorrectly described mid-sized and large rivers as "semi-lentic." This portrayal may have resulted from confusion about stream velocity (higher downstream in general) versus turbulence

(i.e., rivers look slow because of the greatly reduced turbulence in comparison to higher elevation streams). The RCC also failed to appreciate the ecological roles and carbon (C) sources of lateral side channels vs the river's prominent main channel. Sedell et al. (1989) suggested that the RCC was not a good predictor of large river function and that it might be better to consider large rivers as being completely separate systems from their upstream headwaters. This idea, while ignoring the connected nature of these systems, does take the important step of thinking about rivers as being discontinuous along their courses. In fact, Sedell et al. (1989), a coauthor on the original RCC paper, concluded with a surprising statement about large river systems not being continua, but rather complex combinations of patches of different geomorphic properties.

While the RCC had certain flaws, it is important to note that it provided inspiration for decades of research in river ecology and shifted perspectives in lotic science to the ecosystem scale. Subsequent studies have both refuted and agreed with parts of the model, hypothesized new theories, and proposed new scientific methods for testing these ideas.

The Flood Pulse Concept

The Flood Pulse Concept (FPC), proposed by Junk et al. (1989) and based primarily on observations from the Amazon River, suggested that rivers seasonally form connection with their floodplains, areas of very high primary production. This highlighted the importance of allochthonous floodplain C to river food webs as opposed to C "leakage" from further upstream. This concept of lateral C inputs may have been previously ignored because of the transient nature of the organic source (Junk et al. 1989) and the focus of the RCC proponents on the river's main channel. The authors of the FPC argued that flood predictability and duration were better predictors of riverine biota than the longitudinal continuum of the RCC. In response to the

FPC and in the same symposium issue of its original publication, Sedell et al. (1989) commented that perhaps the RCC can only successfully predict the functioning of geologically constricted rivers, with the FPC being a better model for large rivers that are highly interactive with their floodplains. Subsequent FPC publications extended the paradigm for its application to temperate river systems (Tockner et al. 2000). In a 2004 update to the FPC, Junk and Wantzen reviewed the findings of studies relevant to the 1989 hypothesis, concluding that the FPC had been generally accepted but that some aspects (e.g., its interaction with other abiotic variables and its long-term effects on ecological processes) still required further study.

The Riverine Productivity Model

Thorp and Delong (1994) argued that large rivers had been misrepresented in previous hypotheses (RCC; FPC) by undervaluing the role of autochthonous production within river systems. As an alternative hypothesis, they proposed the Riverine Productivity Model (RPM), which claimed that large river consumers were actually assimilating more autochthonous resources and local, lateral inputs of terrestrial matter than refractory particulate matter from upstream reaches as proposed by the RCC. The authors of the RPM agreed that allochthonous C from upstream reaches was likely to be very abundant in large rivers, but suggested that it was unlikely to be assimilated in significant amounts by consumers due to its highly refractile nature and very low nutritional value (high C:N). Instead, Thorp and Delong (1994) argued that large rivers were areas of high complexity, containing areas of autochthonous production harboring invertebrate grazers, as well as areas of direct allochthonous inputs, such as river banks, side channels, and woody debris snags, which, contrary to the predictions of the RCC, attracted invertebrate shredders to large rivers. The RPM argued that these C resources provided the

principal support to the large river food chain at all times of year, independent from the flood pulses considered by the FPC, and particularly for constricted channels. In a study from the Ohio River, Thorp (1992) found empirical evidence for the RPM, a finding that was supported by several others (Naiman 1983, Thorp et al. 1998, Bunn et al. 1999, Lewis et al. 2001, Hoeninghaus et al. 2007). A revision to the RPM made the additional claim that autochthonous C was much more important than even direct, lateral allochthonous inputs and that it may have broader applications than just constricted channel rivers (Thorp and Delong 2002). Thorp and Delong (2002) raised a potential criticism of the RPM based on what they termed the “heterotrophy paradox,” the idea that consumer biomass within river food webs cannot be fueled mostly by autochthonous C because rivers tend to be heterotrophic ($P:R < 1$). Their counter arguments to this heterotrophy paradox were based on three main points: (1) the abundant form of C may not be what is actually assimilated by consumers; (2) the retention of productive algal communities can occur in areas of lower flow velocity (slackwaters) in large rivers, such as along banks and within side channels; and (3) different food web pathways process different types of C, with allochthonous C being principally processed by the microbial-viral and decomposer pathways and higher trophic levels seeking most of their energy from the algal-grazer pathway.

The Riverine Ecosystem Synthesis

The Riverine Ecosystem Synthesis (RES), as proposed by Thorp et al. (2006, 2008), offered a new framework for understanding river ecosystems by “portray[ing] rivers as downstream arrays of large hydrogeomorphic patches (e.g., constricted, braided and floodplain channel areas) formed by catchment geomorphology and climate.” This model integrated concepts from the models before it, but took a strong stance against the RCC by emphasizing the

discontinuous nature of river networks in contrast to the RCC's portrayal of the clinal nature of rivers. The theoretical foundation of RES was based on concepts from hierarchical patch dynamics (Townsend 1989, Wu and Loucks 1995, Poole 2002), ecogeomorphology (Thoms and Parsons 2002), the multiple dimensionality of rivers (Ward 1989), and the riverscape view that "rivers are more than a single thread passing through a terrestrial landscape" (Ward and Tockner 2001, Wiens 2002).

The authors of the RES argued that rivers could not be described as continuous from headwaters to river mouth because the sometimes unpredictable (among rivers and ecoregions), patchy alternation of hydrogeomorphic characteristics along the course of a river presented frequent disruptions of the RCC's idealized clinal concept (Thorp et al. 2006). According to the RES, rivers can be divided at the valley scale into functional process zones (FPZs), which are semi-predictable, repeatable patches with unique hydrogeomorphological characteristics (Thorp et al. 2006). Based on the model of hierarchical patch dynamics, rivers are composed of multiple FPZs, and the specific type and arrangement of FPZs differ increasingly as the spatial scale of the macrosystem landscape increases from basins, to ecoregions, to biomes, and finally to the continental scale. Thorp et al. (2006) hypothesized that each FPZ type would be characterized by an array of unique structural and environmental characteristics, which would then influence the relative availability and abundance of autochthonous and allochthonous C and other nutrients, as well as the function and distribution of associated biota and ecological processes (Figure 1; Figure 2). Researchers can designate FPZs using a GIS-based tool (RESonate; Williams et al. 2013, Kotlinski et al. 2017), which has been tested using data from the Kanawha River (USA; Collins et al. 2015). Although a model with an emphasis on broad spatiotemporal scales can be challenging and expensive to test, several studies have offered support for RES (e.g., Hoeninghaus

et al. 2007, Hoeninghaus et al. 2008, Cross et al. 2013, Smits et al. 2015, and Godoy et al. 2016, Thorp and Bowes 2017). The concepts of RES have also been adapted for use in environmental conservation and management (Flotemersch et al. 2010, Thorp et al. 2013, Čivas et al. 2016).

Recently, the RES concepts of hydrogeomorphological patches (FPZs; Figure 1) and the hierarchical nature of a landscape () have been directly tied to ecological hypotheses and studies of the river macrosystem (McCluney et al. 2014, Thorp 2014). The ecological macrosystem, a relatively new concept in ecology, can be defined as “a hierarchically organized, integrated terrestrial, inland aquatic and/or marine ecological unit of large spatial extent (*c.* 10^2 - 10^6 km² or more depending on the types and sizes of ecosystems present) whose temporal interactions within the unit and with regional through global processes are especially significant over periods of decades to millennia” (Thorp 2014). This concept can be applied to many different systems, but in river ecology, the river macrosystem can be defined as a network of interacting riverscape and floodscape patches. Riverscapes include all currently active main channels, side channels, and backwaters of rivers (Thorp et al. 2006), while floodscapes consist of the normally dry floodplains, floodplain lakes, wetlands, and oxbow lakes (Thorp et al. 2008).

At this macroscale, we can think of rivers as being composed of four unique dimensions: longitudinal, lateral, vertical, and temporal (Ward 1989, Thorp et al. 2006). The longitudinal dimension describes the length of a river and its upstream-to-downstream flow. The lateral dimension includes the entire riverscape, adjacent riparian zone, surrounding floodscape, and the lateral hyporheic and phreatic zones. The vertical dimension describes the depth of the river channel, the river bed, and the deeper hyporheic zone beneath the wetted channel. Finally, the temporal dimension is important for assessing changes in the river macrosystem over time (e.g., the formation of an oxbow lake in a meandering river channel), including short-term changes in

flow, annual variations in discharge, and longer periods of flow history recurring over many decades.

Despite decades of developing new riverine ecosystem hypotheses, gathering the empirical evidence to support them, and the aforementioned inherent flaws in the RCC, the 1980 RCC model is still routinely taught in classrooms (Thorp et al. 2006) and used as a framework for research in river systems today (Dalu et al. 2015, Becerra-Muñoz et al. 2016, Godoy et al. 2016). An overarching goal of the present study is to gather the empirical evidence necessary to understand the functioning of rivers at macrosystem scales, with the added benefit of obtaining data enabling us to test previous ecosystem models. To do this, we take advantages of recent developments in hydrogeomorphic river models and biochemical analytical techniques to determine food web relationships. Placing a particular study system into the context of the hierarchical macrosystem () allows us to ask broader questions about whole riverine landscapes. This makes the complexity of river networks a prominent part of their theory, which is vital for being able to form a generalizable hypothesis, but which also adds to the challenge of identifying and predicting longitudinal patterns and processes in lotic systems (Thorp et al. 2006). The present study will be one of the first to directly test several tenets of the RES.

Progress in Food Web Ecology

Food webs have been well-studied in many areas of ecology because they are useful for elucidating ecosystem-level processes such as resource availability, nutrient cycling, and energy flow (Peterson and Fry 1987, Hairston and Hairston 1993, Hershey et al. 2006). These properties of food webs make them important metrics for studies of ecological macrosystems. However, having accurate and reliable analytical methods is extremely important for correctly interpreting

system food webs (Cole et al. 2011, Thorp and Bowes 2017). Methods in food web ecology have become more advanced and reliable over time, starting with early dietary studies that relied on visual observation of consumer feeding behavior and stomach contents (e.g., Cummins 1974, Cummins and Klug 1979). This method has been largely replaced by dietary analyses based on biochemical stable isotope techniques, including analyses of bulk-tissue (e.g., Peterson and Fry 1987) and, more recently, compound specific stable isotope analysis of amino acids (Chikarishi et al. 2009, Larsen et al. 2013, Bowes and Thorp 2015).

Early food web ecologists focused on the classification of invertebrate taxa into functional feeding groups (FFGs; Cummins 1974, Cummins and Klug 1979). FFGs classified invertebrate consumers by feeding modes (e.g., grazers of benthic algae, shredders of terrestrial leaves, collector-gatherers of particulate from upstream, etc.). While these categorizations were helpful in our understanding of how different feeding behaviors might affect the consumer diet, recent studies suggest that feeding preferences are too complex for this simple classification scheme, which did not take into account food assimilation (Merritt and Cummins 1996). The hypotheses of the RCC were based largely on FFG categorizations and observations of stomach contents, the subjective nature of which may have led to some misleading conclusions.

A turning point in food web research occurred with the application of stable isotope analyses to ecological studies (Peterson and Fry 1987). In aquatic systems, isotopic analyses are especially useful for revealing long-term assimilated dietary preferences of omnivorous consumers (stable isotopes of C; Peterson and Fry 1987, Finlay 2001) and for determining consumer trophic position (stable isotopes of nitrogen; Vander Zanden et al. 1999, Post 2002, Bowes et al. 2014). A commonly used method in aquatic food web studies, bulk-tissue stable isotope analysis (BT-SIA), determines ratios of heavy to light isotopes that have been integrated

as signatures of dietary sources within bulk consumer tissue (Fry 2006). Because the ratio of the heavy to light C isotopes ($^{13}\text{C}:^{12}\text{C}$) undergoes little change during transfer from primary producer to higher consumer, we can use BT-SIA to infer sources of dietary C (Fry 2006). We can use BT-SIA of nitrogen to estimate trophic position and food chain length, an important element of food web structure, because consumers preferentially assimilate the heavier isotope of nitrogen (^{15}N) rather than the lighter ^{14}N (DeNiro and Epstein 1981). This accumulation of ^{15}N through the food chain is an indicator of trophic position. Because of its wide accessibility and low cost, BT-SIA has been used to analyze many food web relationships (e.g., Kling et al. 1992, Finlay 2001, Jepsen and Winemiller 2002, France 2005, Xu et al. 2005, Overman and Parrish 2011). However, BT-SIA signatures of primary producers can vary quite widely depending on when and where they are collected, making it challenging to accurately infer dietary contributions (Post 2002, Xu et al. 2005, Hayden et al. 2006, Ishikawa et al. 2012, Geeraert et al. 2016).

A more refined stable isotope analysis technique, compound specific stable isotope analysis of amino acids (AA-CSIA), provides more precise estimates of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than traditional bulk-tissue analyses by providing an isotopic signature for each amino acid in a tissue samples (Hannides et al. 2009, Walsh et al. 2014, Bowes and Thorp 2015). For this reason, AA-CSIA has proven to be an especially effective method for determining consumer diets and food web relationships within and across complex systems (Walsh et al. 2014, Bowes and Thorp 2015). Because it provides data for both isotopic basal signatures and trophic enrichments, AA-CSIA does not require the characterization of baseline ecosystem isotope signatures (Popp et al. 2007, Hannides et al. 2009, Bowes and Thorp 2015, Thorp and Bowes 2017). Additionally, AA-CSIA food source fingerprints are unaffected by changing environmental conditions or the consumer digestive process (Larsen et al. 2012, Larsen et al. 2013), as are bulk-tissue signatures

(Bowes and Thorp 2015, Geeraert et al. 2016). This analytical approach relies on the fact that essential amino acids (e.g., phenylalanine) are produced only by primary producers and remain physically and chemically conserved after consumer digestion and assimilation, allowing them to act as tracers back to basal C sources (Larsen et al. 2013). The combination of $\delta^{13}\text{C}$ signatures of tissue amino acids produces an identifiable “fingerprint” that can be identified in consumers (Larsen et al. 2013, Bowes and Thorp 2015). Conversely, non-essential amino acids (e.g., glutamic acid) change considerably as they are transferred up the food chain, which provides information about trophic position (Popp et al. 2007, Chikaraishi et al. 2009, Bowes and Thorp 2015). These new applications of AA-CSIA will allow us to test hypotheses about food webs that have been proposed by the RES model in the context of macrosystem ecology. The following chapter uses a macrosystem framework to test hypotheses of the RES according to the basal food sources that provide support to consumer food webs and how those change along the course of a river network.

Chapter 2: Autochthony dominates in endorheic rivers of the Great Basin, USA

Introduction

Carbon (C) is a critical source of energy fueling freshwater food webs. However, determining generalizable patterns of the relative contributions of in-stream algal primary producers (autochthonous C from algae, cyanobacteria, mosses, and aquatic vascular plants) and terrestrial organic matter from the surrounding watershed (allochthonous C) for freshwater systems continues to pose a challenge for ecologists. Over the past half-century, ecologists have studied organic C input to freshwater food webs as a central component to the development of conceptual models regarding river structure and function (e.g., River Continuum Concept, Vannote et al. 1980; Flood Pulse Concept, Junk et al. 1989; River Productivity Model, Thorp and Delong 1994, 2002; Riverine Ecosystem Synthesis, Thorp et al. 2006, 2008).

The Riverine Ecosystem Synthesis (RES; Thorp et al. 2006, 2008) and associated concepts on river macroecology (McCluney et al. 2014, Thorp 2014) may offer new perspectives on rivers and the basal C sources of their consumers, based on valley-to-reach scale hydrogeomorphic metrics of entire river networks, as represented in the RES by repeatable, semi-predictable habitat patches called functional process zones (FPZs). The hydrogeomorphic characteristics of a river may influence the types of food sources available to consumers by affecting physical habitat features such as soil composition, aquatic substrate, or canopy openness. The RES predicts that, while allochthonous C may provide support for some portion of the food web base, autochthonous autotrophy should account for over half of a river's metazoan production, averaged along the entire river network and all times of the year (Thorp et al. 2006, 2008). Autochthonous C may be preferentially incorporated into freshwater food webs because

of its high nutritional content and relatively easy assimilation of this labile nutrient source (low C:N; Thorp and DeLong 1994, 2002). In fact, past studies representing multiple different geographic areas have suggested that aquatic consumers preferentially consume high-quality autochthonous C (e.g., East et al. 2017, Finlay 2001, Brito et al. 2006, Torres-Ruiz et al. 2007, Lau et al. 2009, Becerra-Muñoz et al. 2016, Cashman et al. 2016), even in headwater streams or other systems that tend to have high quantities of terrestrial inputs (McNeely et al. 2007, Macarelli et al. 2011) or in light-limited systems (Bunn et al. 2003, Guo et al. 2016), against the expectations of the River Continuum Concept (Vannote et al. 1980). While other studies have found evidence for an allochthonous trophic base, these studies have taken place mostly in lakes, rather than in rivers (e.g., Cole et al. 2011), or have focused on allochthonous input from terrestrial dietary subsidies, such as terrestrial insects (e.g., Wipfli and Baxter 2010, Bartels et al. 2012).

Almost all theoretical studies of food webs and other ecological research in lotic systems have focused on rivers with waters that eventually reach the ocean, leaving the unique characteristics of terminal basin rivers, or endorheic systems, largely ignored (Bunn et al. 2006; but see Walker et al. 1995, East et al. 2017). Some terminal basin rivers flow to freshwater or saline lakes, while others evaporate in dry basins, a process that is often accelerated by anthropogenic water extraction. These rivers are especially interesting from an ecological perspective because existing conceptual models have been mostly based on rivers exhibiting progressive increases in discharge and decreases in canopy cover as they flow downstream (e.g., River Continuum Concept; Vannote et al. 1980). Despite the dearth of ecological theories and field studies based on terminal basin rivers, they are actually quite common worldwide, occurring principally in Australia, Africa, and central Asia (Bunn et al. 2006). Studying terminal

basin rivers may inform our conceptual river models by elucidating patterns of food web contributions of autochthonous and allochthonous C that may be generalizable for all rivers.

The objective of the present study was to determine the relative contributions of autochthonous and allochthonous C to fish food webs in terminal basin rivers using the macrosystem-scale, hydrogeomorphological framework of the RES as a contrast to the predictable and clinal framework of the RCC. We predicted that our results would support the RES model, rather than the RCC. In this case, we would expect the ratio of autochthonous to allochthonous C to vary predictably among FPZs, with autochthonous C providing the most support to river food webs (>50%) overall for the entire river network. Specifically, we predicted that fish consumers in wide-valley FPZs would rely more heavily on autochthonous resources, while consumers in constricted-valleys would have a heavier reliance on terrestrial allochthonous C. If results support the RCC, food source ratios will vary predictably from upland to lowland FPZ sites and will be influenced by riparian vegetation (food source availability). We tested these predictions for 18 hydrogeomorphic sites of two terminal basin rivers located in the semi-arid steppes of the United States Great Basin. We used amino acid compound specific stable isotope analysis (AA-CSIA) to infer the proportional contributions of autochthonous and allochthonous basal food sources supporting fish consumers.

Methods

Study Area

This study was conducted during July and August 2016 in the Great Basin, USA; Study sites were located in the upper reaches of the Bear River, as well as the entire Carson River, from headwaters to terminus (Figure 3). The Bear River terminates in the Great Salt Lake, while the Carson River evaporates in an arid basin of Nevada. Study rivers were sourced by snowmelt runoff from regional mountain ranges, including the Sierra Nevada (Carson River), or the Uinta (Bear River) mountains. The Great Basin is part of the semi-arid shrubland ecoregion within the temperate steppe biome, where typical riparian vegetation includes coniferous, mixed, and alluvial forest in upper reaches, or alluvial forest, sagebrush scrub, and grasslands in lowland areas (Table 1). Riparian vegetation is often quite different from that of the surrounding watershed, in locations further from the river channel. Major anthropogenic impacts in the area are associated with agriculture, livestock grazing, mining, and species invasion of fish and riparian plants.

Site Selection and Characterization

Rivers were analyzed separately by basin to locate FPZs (interacting patches of unique hydrogeomorphic characteristics) using an updated version of the ArcGIS-based RESonate mapping software (Williams et al. 2013, Kotlinski and Thorp 2017). Cluster analyses performed in R (R Development Core; version 3.2.2) were used to distinguish FPZ sites based on 10 different hydrogeomorphic variables (mean annual precipitation, geology, elevation, valley width, valley floor width, ratio of valley width to floor width, left valley slope, right valley slope, down valley slope, and sinuosity; see Appendix 1). To minimize the complicating effects of

human impact, we chose study sites that were located mostly within government protected lands. In the field, specific replicates of FPZ sites were selected according to water flow and accessibility. Three replicate reaches of each of two different FPZs were sampled in the Bear River, and three replicates of each of four different FPZs were sampled in the Carson River, for a total of 18 sites (6 FPZs x 3 replicates each) among the two endorheic systems. In the Bear River, we sampled both upland constricted-valley and upland wide-valley FPZ types, and in the Carson River, FPZs sampled included constricted-valley uplands, constricted-valley lowlands, wide-valley uplands, and wide-valley lowlands (Table 1; Figure 4). We conducted a riparian survey at each site to classify the riparian zone into four major types based on percent cover estimates of dominant vegetative classes (Table 1). Categories included: coniferous forest (coniferous trees with shrubs close to river banks); mixed forest (both coniferous and deciduous trees); alluvial forest (dominated by small riparian trees and shrubs); and shrub grassland (mostly grasses with areas of bare ground and shrubs throughout; Table 1).

Food Web Sampling

At each FPZ site, dominant species of riparian plants were collected and stored in a plant press for later isotopic analysis for basal food sources. These included: willow (*Salix lucida* and *S. exigua*), maple (*Acer* sp.), pine (*Pinus* sp.), cottonwood (*Populus fremontii*), and sagebrush (*Artemisia tridentata*). Other potential dietary components that were not collected on site were purchased from a laboratory supply (PureBulk.com) or collected locally (Lawrence, KS). These included: green algae (*Chlorella* sp.), cyanobacteria (*Spirulina* sp.), fungi (baker's yeast; *Saccharomyces cerevisiae*), a CAM aquatic macrophyte (*Vallisneria americana*), a C₃ grass (tall fescue; *Festuca arundinacea*), and a C₄ plant (corn; *Zea mays*). Three replicates were analyzed

for each species. Isotopic signatures within broad primary producer categories have been shown to be relatively consistent among major phylogenetic groups and geographic area (Larsen et al. 2012, Larsen et al. 2013, Thorp and Bowes 2017). As demonstrated by Larsen et al. (2013), different phyla of fungi and algae have similar isotopic signatures.

A representative fish sample was collected by a team of researchers at each of 18 sites using a backpack electrofisher, supplemented by seining and gill netting in accordance with the American Fisheries Society standard sampling protocol (Bonar et al. 2009). The length of each sample reach was set at 10x the stream wetted width. After fish were collected and euthanized, samples of caudal peduncle muscle were collected from several individuals of each species caught and were then preserved in 75% EtOH for later isotopic analysis. When possible, three individuals of each fish species were sampled from each replicate site; however, sometimes low abundances of particular species limited our ability to replicate samples, resulting in a total sample size of 1-9 individuals of each species collected at each of six FPZ sites.

Compound Specific Stable Isotope Analysis of Amino Acids

Amino acid compound specific stable isotope analysis (AA-CSIA), a relatively new biochemical method in ecology, is capable of providing more precise (low standard error) results than the more traditionally used stable isotope analyses of bulk-tissue (Bowes and Thorp 2015; Thorp and Bowes 2017, Walsh et al. 2014). In preparation for AA-CSIA, preserved fish muscle was rinsed gently and then soaked in distilled water for 48 h to remove ethanol (as in Arrington and Winemiller 2002). Samples of rinsed fish tissue and plant/fungal tissue were then dried in an oven at 60°C for 48 h or until completely dry. The dried materials of potential food sources and fish were stored in a desiccator and later ground into a homogenized powder using a Wig-L-

Bug® amalgamator. Homogenized tissue samples were weighed into precombusted glass vials in amounts of 10-15 mg of fish muscle or 20-30 mg of plant tissue. In total, 151 samples were sent to Aquatech Enviroscience Laboratories, Inc. (Victoria, BC, Canada) for AA-CSIA of C ($\delta^{13}\text{C}_{\text{AA}}$), where they were acid hydrolyzed, then separated and combusted through a fixed temperature cycle using GC-IRMS (see Walsh et al. 2014 for details). Sample $\delta^{13}\text{C}_{\text{AA}}$ was calculated by relating its isotopic values to those of an international standard (Vienna Pee Dee Belemnite; VPDB). Results are expressed in delta (δ) per mil (‰) notation using the formula, calculated for each amino acid in the sample tissue:

$$\delta^{13}\text{C} = \left(\frac{\left(\frac{^{13}\text{C}}{^{12}\text{C}} \right)_{\text{sample}}}{\left(\frac{^{13}\text{C}}{^{12}\text{C}} \right)_{\text{standard}}} - 1 \right) \times 1000\text{‰}$$

Data Analysis

For all tissues of primary producers and fish, only EAAs, including isoleucine (Ile), leucine (Leu), methionine (Met), phenylalanine (Phe), and valine (Val), as well as, CEAAAs including glycine (Gly) and proline (Pro), were used in analysis to ensure that isotopic signals were representative tracers of basal food sources. Additional EAAs, including threonine (Thr) and lysine (Lys), and CEAAAs, including tyrosine (Tyr) were excluded because their concentrations were undetectable in many samples, which led to missing data values. AA-CSIA isotopic signatures for multiple replicates representative of 12 primary producer species were normalized to their respective means and then tested for statistical separation using principal components analysis (PCA) with the function *prcomp* in the package *FactoMineR* (R Development Core).

Proportional contributions of each food group to fish basal diets were estimated using the Bayesian mixing model “Food Reconstruction Using Isotopically Transferred Signals” (FRUITS; version 2.0; Fernandes et al. 2014). FRUITS executes BUGS (Bayesian inference Using Gibbs Sampling) software and Markov chain Monte Carlo (MCMC) simulation to reconstruct biochemical dietary routes based on isotopic values to provide posterior estimates of food group proportional contributions to the basal diet of a consumer. Individuals collected from site replicates were grouped by species and pooled according to FPZ site prior to analysis (N=1-9). In samples of N=1, GC-IRMS analytical error (± 1.75) was used as a measure of uncertainty. FRUITS was set up to estimate the relative contribution of separable food groups based on one food fraction ($\delta^{13}\text{C}$) and seven dietary proxies (Gly, Ile, Leu, Met, Phe, Pro, and Val). We employed, *a priori*, the model assumptions that all food sources were equally likely to contribute to the consumer diet and that a single food category could make up 100% of the diet. We ran this model in 10,000 iterations for each species, separated by site, to generate Bayesian estimates of the proportion of each basal food source. Proportional dietary results estimated by the Bayesian mixing model, FRUITS, were reported in mean ± 1 SE.

Nested analysis of variance (ANOVA) was used to determine if the proportion of autochthonous C in fish basal diets varied significantly by FPZ (constricted-valley uplands of the Bear and Carson Rivers, constricted-valley lowlands of the Carson River, wide-valley uplands of the Bear and Carson Rivers, or wide-valley lowlands of the Carson River) or among site replicates. Multiple one-way ANOVAs and post-hoc Tukey-Kramer analyses were used to test for statistical significance of the proportions of dietary basal C among different food groups for each site. We tested effects riparian vegetation as potential drivers of autochthonous and allochthonous dietary contributions using a one-way ANOVA. We also used a two-sample t-test

to compare the proportion of autochthonous C in the basal diets of native and nonnative fish species. All proportion data were square-root arcsine-transformed prior to analysis to account for extreme values.

Results

Field Sampling

For all FPZ site replicates (N=18), four sites had riparian zones classified as coniferous forest, two were categorized as mixed forest, seven were represented by alluvial forest, and five were observed to be shrub grasslands (Table 1). Fish consumers were represented by 17 species (n=151). Seven species (n=58) were collected from the two FPZs of the Bear River, with four being native to the area and three being introduced. Thirteen species (n=137) were obtained from the four types of FPZs of the Carson River. Of these, two were native and 11 were introduced. In the upper reaches of the Carson River, five fish species were collected, with two native and three introduced. Overall, from the 17 species collected for the Great Basin ecoregion, six were native, while 11 were introduced to the region (Table 3). Species richness was highest at the lowland wide-valley FPZs of the Carson River (10 species) and lowest at the upland wide-valley FPZs of the Carson River (4 species; Table 3).

Food Source Differentiation

In a principal component analysis (PCA) based on isotopic values of EAAs (Ile, Leu, Met, Phe, and Val) and CEAAAs (Gly and Pro), six potential food sources representing 12 species clustered into four groups along PCA1 and PCA2. The first and second principal components explained 86.81% of the total variance. The resulting four food source groupings included: autochthonous resources (green algae and cyanobacteria), C₃ plants (including trees, shrubs, and grass), C₄/CAM plants (*Zea mays*, and an aquatic macrophyte, respectively), and fungi (yeast; Table 2, Figure 6). Resource groups considered to be allochthonous included: C₃ plants, C₄/CAM plants, and fungi.

Fish Basal Diets

We found statistically significant differences in the proportions of basal food sources within FPZ sites (Figure 8a-f). At the upland constricted-valley sites of the Bear River, autochthonous resources were assimilated in significantly higher proportion than were all other food sources (One-way ANOVA, $F_3=37.55$, $p<0.001$; Figure 8a). In upland wide-valley sites of the Bear River, algae provided the highest dietary component for fish consumers (One-way ANOVA, $F_3=152.91$, $p<0.001$; Figure 8b). At the upland constricted-valley sites of the Carson River, autochthonous resources were assimilated into consumer diets in the highest proportions (One-way ANOVA, $F_3=122.68$, $p<0.001$; Figure 8c). Carbon derived from autochthonous resources had the most significant contribution to the basal diet at the wide-valley upland sites of the Carson River (One-way ANOVA, $F_3=19.27$, $p<0.001$; Figure 8d). At the lowland constricted-valley sites of the Carson River, autochthonous C showed the greatest contribution to the fish basal diet, with C3 plants also being a secondarily important food source (One-way ANOVA, $F_3=73.98$, $p<0.001$; Figure 8e). Finally, in the lowland wide-valley sites of the Carson, autochthonous resources were the most important food sources, statistically, followed by C3 plants (One-way ANOVA, $F_3=97.54$, $p<0.001$; Figure 8f).

On average, resources derived from autochthonous primary producers (algae and cyanobacteria) made up the majority of the fish basal diet for all Great Basin sites ($79.9 \pm 3.1\%$), as estimated by the Bayesian mixing model, FRUITS. Among different FPZ sites, the proportion of basal autochthony ranged from $71.3 \pm 8.1\%$ (upland constricted sites of the Bear River) to $90.1 \pm 3.7\%$ (upland wide-valley sites of the Bear River). There was no significant difference in the proportion of dietary basal autochthony among six FPZ sites, regardless of their position along the river (upland versus lowland) or their valley width (constricted versus wide; Nested

ANOVA, $F_{5,12}=1.74$, $p=0.174$), or site replicates (Nested ANOVA, $F_{5,12}=0.42$, $p=0.950$; Figure 7). There was no effect of riparian vegetation type on the proportion of autochthonous resources in the consumer basal diet (One-way ANOVA, $F_3=0.34$, $p=0.797$). There was no effect of fish invasion status on the proportion autochthony in the basal diet (t-test, $t_{42}=-0.81$, $p=0.421$).

Discussion

Resources derived from autochthonous C were especially important basal food sources for fish consumers at all FPZ sites of the Bear and Carson Rivers. We found that autochthonous C was incorporated into fish food webs in statistically similar proportions between upper and lower river reaches. This finding provides no evidence to support for the River Continuum Concept (RCC), which hypothesizes a clinal change in basal food sources from river headwaters to mouth (Vannote et al. 1980). In fact, the two FPZ sites that showed the highest proportional contribution of allochthonous C₃ material in the fish basal diet were the two lowland FPZs. This finding is exactly the opposite of what we might expect from the RCC, which is that autochthonous material is not important in headwaters but is most important in the mid-order river reaches that these lowland sites represent. The dominance of autochthony lends support to one tenet of the Riverine Ecosystem Synthesis (RES), which posits that, while the proportion of autochthonous resources may be variable at different stream sites, food webs should be supported by >50% autochthonous C, on average, along the entire river network (Thorp et al. 2006, 2008). For this study, green algae (*Chlorella* sp.) and cyanobacteria (*Spirulina* sp.) were treated as one (autochthonous) food source for statistical reasons; however, it is likely that consumers would assimilate nutritious green algae in higher proportion than cyanobacteria, which can be harmful (O'Neil et al. 2012). The low C:N ratio of green algae makes it an important source of energy for metazoans, as it is highly nutritious and easy for consumers to digest and assimilate (Finlay 2001, Brett et al. 2017).

The present study validates suggestions that autochthonous resources provide important support for freshwater food webs in many different types of river sites. Previous studies have also supported the dominance of autochthonous resources to the food web base for dryland rivers

similar to our Bear and Carson study sites (Dodds et al. 2004, Turner and Edwards 2012). There is evidence of this trend occurring in other river systems as well, including even those with high levels of turbidity (Bunn et al. 2003) or forested channels (McNeely et al. 2007). While our study sites along the Bear and Carson Rivers were not particularly turbid, some upland, constricted-valley sites had dense riparian vegetation, which showed statistically similar proportions of autochthonous basal C as other sites with wider valleys and sparser riparian vegetation. This finding reflects previous studies that have shown that riverine consumers are driven by food quality versus quantity (Balcombe et al. 2005, Torres-Ruiz et al. 2007), an idea that goes against the original RCC. Here, it is also important to note that high algal primary production can occur not only in autotrophic systems, but in net heterotrophic systems as well, where stream respiration may balance production via nocturnal algal respiration and the processing of terrestrial C through the microbial-viral loop (Thorp and Delong 2002).

While there were no significant results in the proportions of autochthonous or allochthonous C among different FPZ sites, our results did show some notable trends within sites of different hydrogeomorphic types. Significant differences among the proportions of different food sources within each FPZ site suggest that autochthonous resources were the most important sources of C at all sites, with lowland sites showing a secondary importance of C₃ plants. However, even at these lowland sites, consumers still relied mostly on algae. This finding goes against the assumptions of the RCC, which expects the consumer basal diet to be dominated by allochthonous C in forested upland areas. Consumers in upland constricted-valley areas may have preferentially consumed autochthonous material because coniferous forests made up most of the riparian vegetation at these sites. Areas where waxy and tannic conifer needles dominates the C₃ detritus base would be likely to have less terrestrial C contribution to the basal diet than

sites with more palatable plants representative of mixed or alluvial forests (Webster and Benfield 1986). This trend was especially evident in the coniferous forests of our Bear River upland constricted-channel sites in the Uinta and Wasatch Mountains, which had one of the lowest proportions of assimilated C from C₃ plants at just 5.7%.

Overall, C₃ plants were the most important allochthonous food source, making up $16.0 \pm 2.9\%$ of the basal diets for all Great Basin terminal river sites. While some species had more C derived from C₃ plants than from autochthonous sources in their diets, overall and along the course of the river network, autochthonous C dominated. It is likely that C₃ plants are extremely important to terminal basin systems, but mostly as habitat and substrates and only secondarily as a food source (Sabo et al. 2006). The absence of shredders in dryland systems may have also inhibited the availability of terrestrial C available for higher consumers (Bunn et al. 2006). A higher proportion of C₃ plants in the fish basal diet may arise from the consumption of terrestrial invertebrates, especially when salmonids dominate at a site, such as in the upper constricted valleys of the Bear River (Wipfli and Baxter 2010).

Different FPZ sites were characterized by different fish communities; however, basal resources still tended to be similar among sites. Overall, species diversity was quite low, with some sites being represented by just one species. The majority of species representative of the terminal basin rivers of the Great Basin ecoregion were non-native species that were introduced to the area either accidentally or as game species (salmonids). A higher number of introduced species were found within the warm-water lowlands than the cooler upland sites, which is a well-established trend for invasion (Olden et al. 2006). However, introduced brook, rainbow, and brown trout did have high occurrences in the upper reaches, particularly in the Carson River. Fish species from both the Bear and Carson Rivers were mostly invertivores, with some

omnivores, including the native Tahoe sucker, as well as several introduced warm-water species. Piscivory was also likely for the larger individuals of categorized invertivores. A high availability of larval fish prey may have helped to increase the proportion of autochthonous resources that were integrated into the food web, as observed in Pease et al. (2006). Whether consuming autochthonous resources directly as an omnivore, or indirectly as an invertivore, fish species of different feeding groups displayed similarly high proportions of algae in the basal diet. There was no statistically significant difference between the proportion of basal autochthony in native versus non-native fishes, likely because the introduced species were largely generalist omnivores that were able to fit into the niches originally occupied by species native to these dryland rivers.

As one of the first of its kind, this large-scale food web study contributes to our knowledge of terminal basin river networks, thereby helping to inform general patterns and processes for all lotic systems. We found no evidence to support the RCC, since neither site position along the river network, nor riparian vegetation type was an important driver of assimilated basal resources. Our findings lend support to some, but not all, aspects of the Riverine Ecosystem Synthesis (RES). Autochthonous C dominated the food web base on average, along the entire stream network of two different rivers; however, valley hydrogeomorphology did not drive the consumer basal diet. Future studies in rivers of other ecoregions should improve our understanding of the importance food sources in diverse river types. Our results also offer additional support for AA-CSIA as a relatively new, more precise biochemical method for studying food webs in freshwater systems (see also Thorp and Bowes 2017). We echo several others (e.g., Čivas et al. 2016, Grabowski and Gurnell 2016) with a recommendation for more studies based on large-scale frameworks for more effective system

management, especially in the face of global environmental challenges, such as climate change and species invasion.

Management Implications

Lotic freshwaters are some of the most vulnerable ecological systems (Junk and Wantzen 2004). Terminal basin rivers, although rarely studied, are widespread worldwide, occurring in North America, Africa, Asia, and Australia. Terminal basin rivers, which do flow all of the way to the sea, tend to have intermittent sections, a trend that will likely continue to evaporate with global climate change, making the conclusions drawn from this study and others about dryland rivers especially important for informing the future of other rivers in more mesic ecoregions (Jaeger et al. 2014, Datry et al. 2016). The Great Basin and other arid regions are particularly sensitive to climate change (Sada 2008, Seager et al. 2007), which means that we will need to act quickly and drastically to conserve and manage our freshwater resources in these natural areas.

Non-native fish present a huge challenge to river systems worldwide, but the dryland rivers of the Great Basin are particularly susceptible, due to a history of riparian disturbance and impoundments (Pease et al. 2006). Most species (11 of 17) that were collected in our six FPZ sites in the Great Basin were introduced species. These species were either introduced accidentally, or intentionally as game species (e.g., salmonids and centrarchids). Common carp (*Cyprinus carpio*), which were present in great numbers in the lowland FPZ sites of the Carson River, are known to affect habitat structure by disturbing the benthic habitat, which may limit the growth potential of autochthonous resources (Bajer et al. 2016). For these reasons, it is possible that influences of non-native species may be obscuring natural patterns and processes, which would then obscure the conceptual lessons we could draw from the results of the present study.

Further studies of large-scale patterns in resource consumption are important for the conservation of native fishes. According to Connolly and Waltham (2015), we cannot conserve a fish species without conserving its natural food sources. The broad view of river systems

presented by the framework of the RES and its associated macroecological views may be a way to mediate management challenges, such as the one mentioned by Meffe et al. (2002): that typical management plans, including those designed for the conservation of fish and food webs (Wipfli and Baxter 2010) do not have a broad enough scope to take on our modern-day global-scale challenges.

Tables

Table 1. Description of each FPZ study site in the Bear and Carson Rivers. Riparian vegetation was categorized as follows: Coniferous forest (coniferous trees with willows near banks); Mixed forest (both coniferous and deciduous trees); Alluvial forest (dominated by small riparian trees and shrubs); Shrub grassland (mostly grasses with areas of bare ground and shrubs throughout).

Site	Latitude	Longitude	Geology	Riparian vegetation
Bear River				
Upland Constricted				
Cub River	N 42.13	W 111.64	Alluvium	Mixed forest
Bear River	N 40.89	W 110.84	Alluvium	Coniferous forest
East Fork Bear	N 40.89	W 110.80	Alluvium	Coniferous forest
Upland Wide				
Eight Mile Creek	N 42.53	W 111.58	Alluvium	Alluvial forest
Blacksmith Fork	N 41.60	W 111.59	Bedrock	Shrub grassland
Mill Creek	N 40.93	W 110.74	Alluvium	Alluvial forest
Carson River				
Upland Constricted				
West Fork Carson	N 38.72	W 119.92	Bedrock	Coniferous forest
West Fork Carson	N 38.78	W 119.90	Bedrock	Coniferous forest
Wolf Creek	N 38.58	W 119.70	Bedrock	Mixed forest
Upland Wide				
West Fork Carson	N 38.70	W 119.93	Bedrock	Shrub grassland
West Fork Carson	N 38.75	W 119.94	Bedrock	Shrub grassland
Wolf Creek	N 38.59	W 119.69	Bedrock	Shrub grassland
Lowland Constricted				
East Fork Carson	N 39.12	W 119.70	Alluvium	Alluvial forest
East Fork Carson	N 39.14	W 119.70	Alluvium	Alluvial forest
East Fork Carson	N 39.18	W 119.68	Bedrock	Alluvial forest
Lowland Wide				
East Fork Carson	N 39.25	W 119.58	Alluvium	Alluvial forest
East Fork Carson	N 39.29	W 119.42	Alluvium	Alluvial forest
East Fork Carson	N 39.29	W 119.29	Bedrock	Shrub grassland

Table 2. Isotopic values (‰) from compound specific stable isotope analysis of essential amino acids of carbon for potential basal food sources (mean \pm 1 SE). Essential amino acids include: isoleucine (Ile), leucine (Leu), methionine (Met), phenylalanine (Phe), and valine (Val), and conditionally essential amino acids include: glycine (Gly) and proline (Pro).

Taxa	Gly	Ile	Leu	Met	Phe	Pro	Val
Cyanobacteria							
<i>Spirulina</i> sp.	-37.80 \pm 0.70	-22.39 \pm 0.41	-34.63 \pm 1.00	-23.08 \pm 2.44	-28.46 \pm 0.61	-17.14 \pm 0.86	-31.68 \pm 0.40
Green Algae							
<i>Chlorella</i> sp.	-40.70 \pm 0.39	-23.11 \pm 1.03	-37.29 \pm 0.10	-30.78 \pm 0.51	-31.60 \pm 1.18	-21.28 \pm 0.09	-34.91 \pm 0.52
Fungi							
<i>Saccharomyces cerevisiae</i>	-34.59 \pm 0.36	-10.83 \pm 0.13	-23.28 \pm 0.22	-19.41 \pm 0.52	-19.92 \pm 0.64	-12.36 \pm 0.31	-20.81 \pm 0.08
C ₃ Plants							
<i>Acer</i> sp.	-31.60 \pm 0.46	-20.56 \pm 1.63	-34.29 \pm 0.28	-27.05 \pm 1.35	-26.77 \pm 0.17	-19.29 \pm 0.12	-33.81 \pm 0.22
<i>Artemisia tridentata</i>	-30.66 \pm 1.99	-17.68 \pm 0.48	-33.62 \pm 0.13	-26.89 \pm 0.43	-27.23 \pm 0.39	-16.63 \pm 0.40	-31.58 \pm 0.38
<i>Festuca arundinacea</i>	-32.42 \pm 0.19	-22.72 \pm 0.14	-36.54 \pm 0.22	-34.70 \pm 0.47	-31.27 \pm 0.28	-20.15 \pm 0.12	-34.29 \pm 0.22
<i>Pinus</i> sp.	-31.24 \pm 1.62	-19.89 \pm 1.47	-33.98 \pm 0.53	-30.34 \pm 1.61	-25.52 \pm 0.33	-20.25 \pm 0.29	-34.31 \pm 0.73
<i>Populus fremontii</i>	-34.45 \pm 1.17	-22.07 \pm 1.03	-36.41 \pm 1.67	-28.59 \pm 0.35	-28.50 \pm 0.10	-17.78 \pm 0.06	-32.42 \pm 0.22
<i>Salix exigua</i>	-32.37 \pm 0.16	-16.48 \pm 1.31	-37.89 \pm 0.10	-30.46 \pm 1.19	-27.43 \pm 0.51	-16.67 \pm 0.43	-31.22 \pm 0.09
<i>Salix lucida</i>	-29.98 \pm 0.53	-21.46 \pm 1.26	-31.78 \pm 0.43	-27.12 \pm 0.93	-25.45 \pm 0.16	-19.46 \pm 0.79	-31.77 \pm 0.21
CAM Plant							
<i>Vallisneria americana</i>	-29.89 \pm 0.86	-16.71 \pm 1.04	-28.61 \pm 0.55	-26.43 \pm 0.66	-23.64 \pm 0.13	-13.83 \pm 0.67	-27.09 \pm 0.53
C ₄ Plant							
<i>Zea mays</i>	-25.40 \pm 0.19	-11.86 \pm 0.31	-25.76 \pm 0.66	-18.75 \pm 0.83	-20.82 \pm 0.47	-11.58 \pm 0.15	-23.69 \pm 0.91

Table 3. Presence-absence diversity for fish obtained at each river FPZ site (B=Bear River, C=Carson River; U=Upland, L=Lowland; C=Constricted Valley, W=Wide Valley). Asterisks (*) indicate non-native taxa.

Species	Group	BEAUC	BEAUW	CARUC	CARUW	CARLC	CARLW
<i>Ameirus melas</i> *	OM					x	x
<i>Catostomus tahoensis</i>	OM			x	x	x	x
<i>Cottus beldingii</i>	IN	x	x				
<i>Cyprinus carpio</i> *	OM					x	x
<i>Gambusia affinis</i> *	IN					x	x
<i>Lepomis cyanellus</i> *	IN					x	x
<i>Lepomis macrochirus</i> *	IN						x
<i>Micropterus dolomieu</i> *	IN					x	x
<i>Micropterus salmoides</i> *	IN						x
<i>Oncorhynchus clarki</i>	IN	x	x				
<i>Oncorhynchus mykiss</i> *	IN	x		x			
<i>Pimephales promelas</i> *	OM					x	x
<i>Prosopium williamsoni</i>	IN	x	x				
<i>Rhinichthys cataractae</i>	IN	x					
<i>Rhinichthys osculus</i>	IN			x	x	x	x
<i>Salmo trutta</i> *	IN	x	x	x	x		
<i>Salvelinus fontinalis</i> *	IN		x	x	x		

Figures

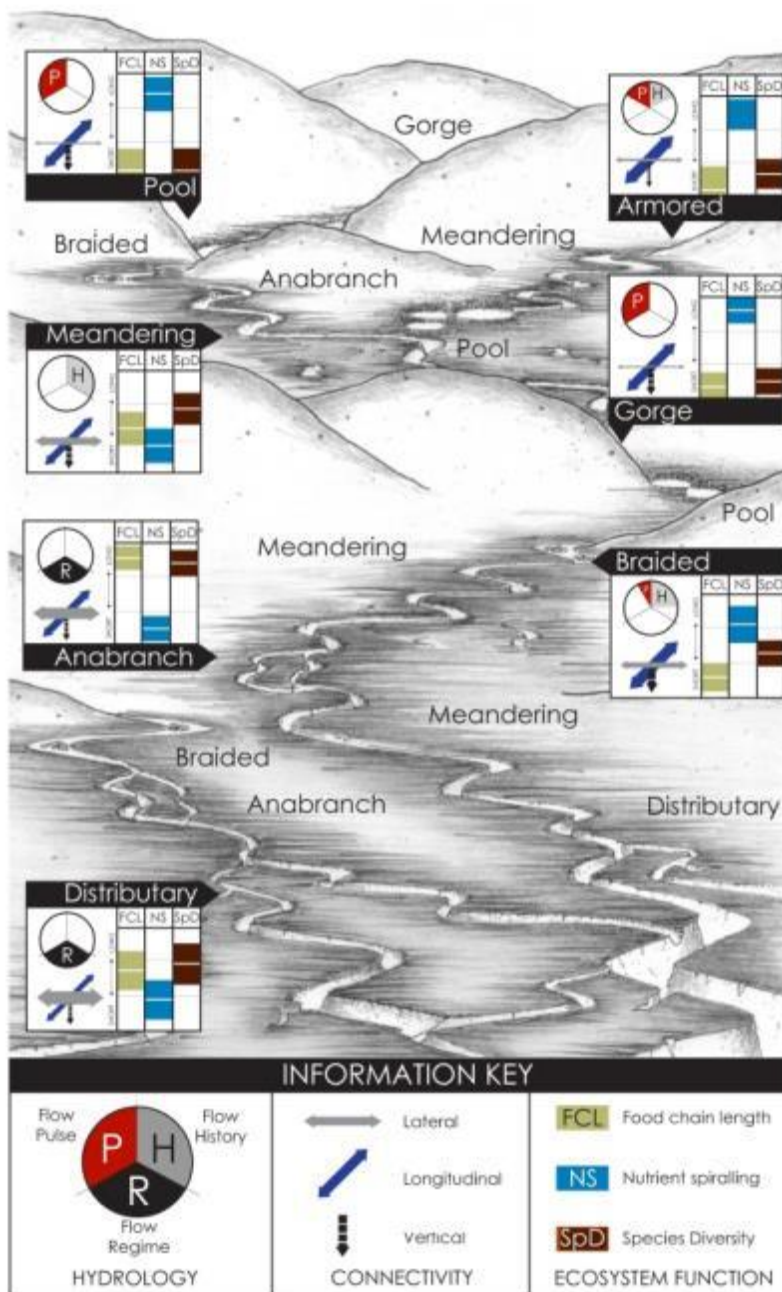


Figure 1. Alternating FPZ types along a river network with corresponding hypothesized differences in ecological function (reprinted from Thorp et al. 2008).

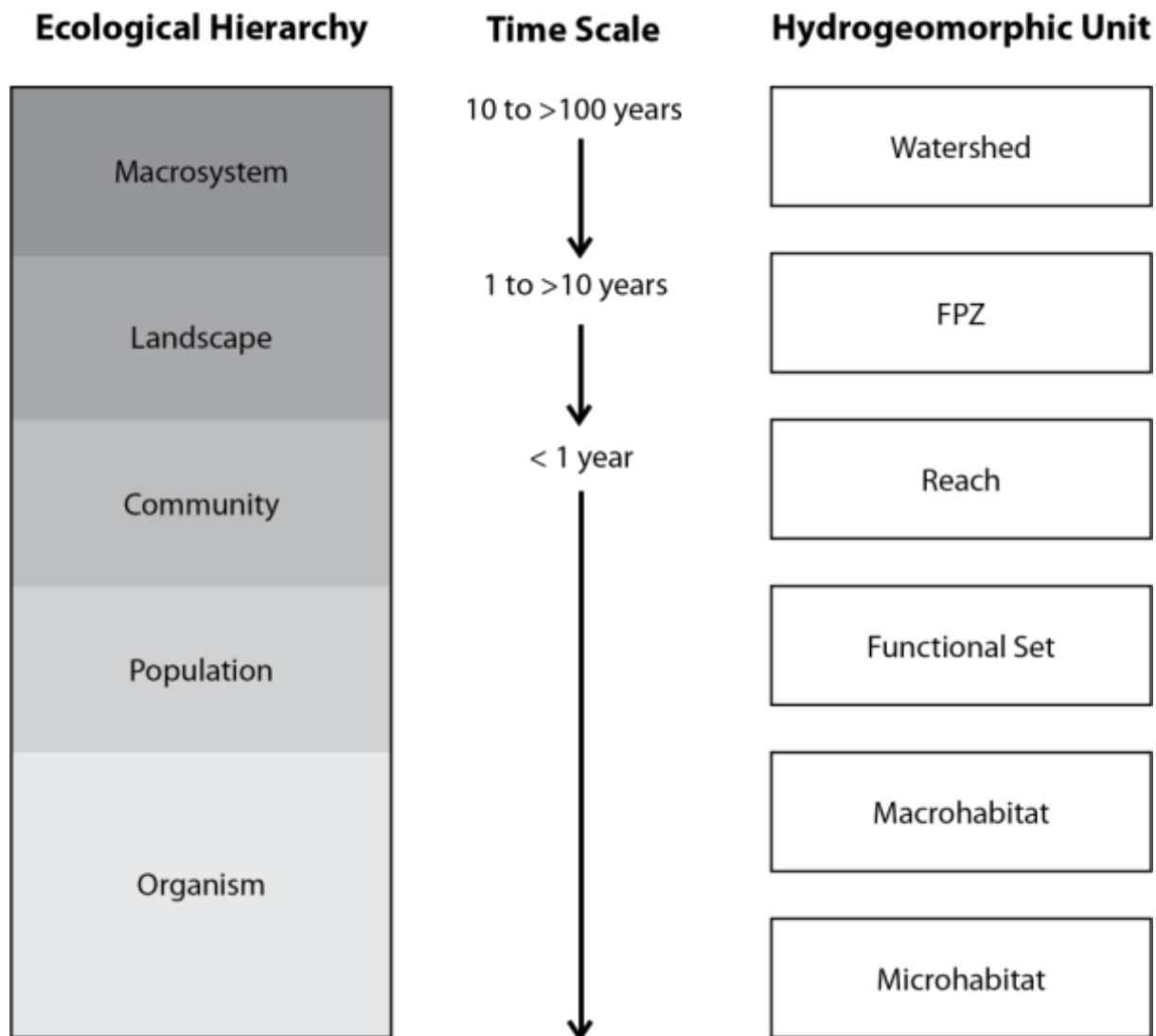


Figure 2. The hierarchical nature of the river macrosystem, which includes landscapes, communities, populations, and organisms and spans short to long time scales.

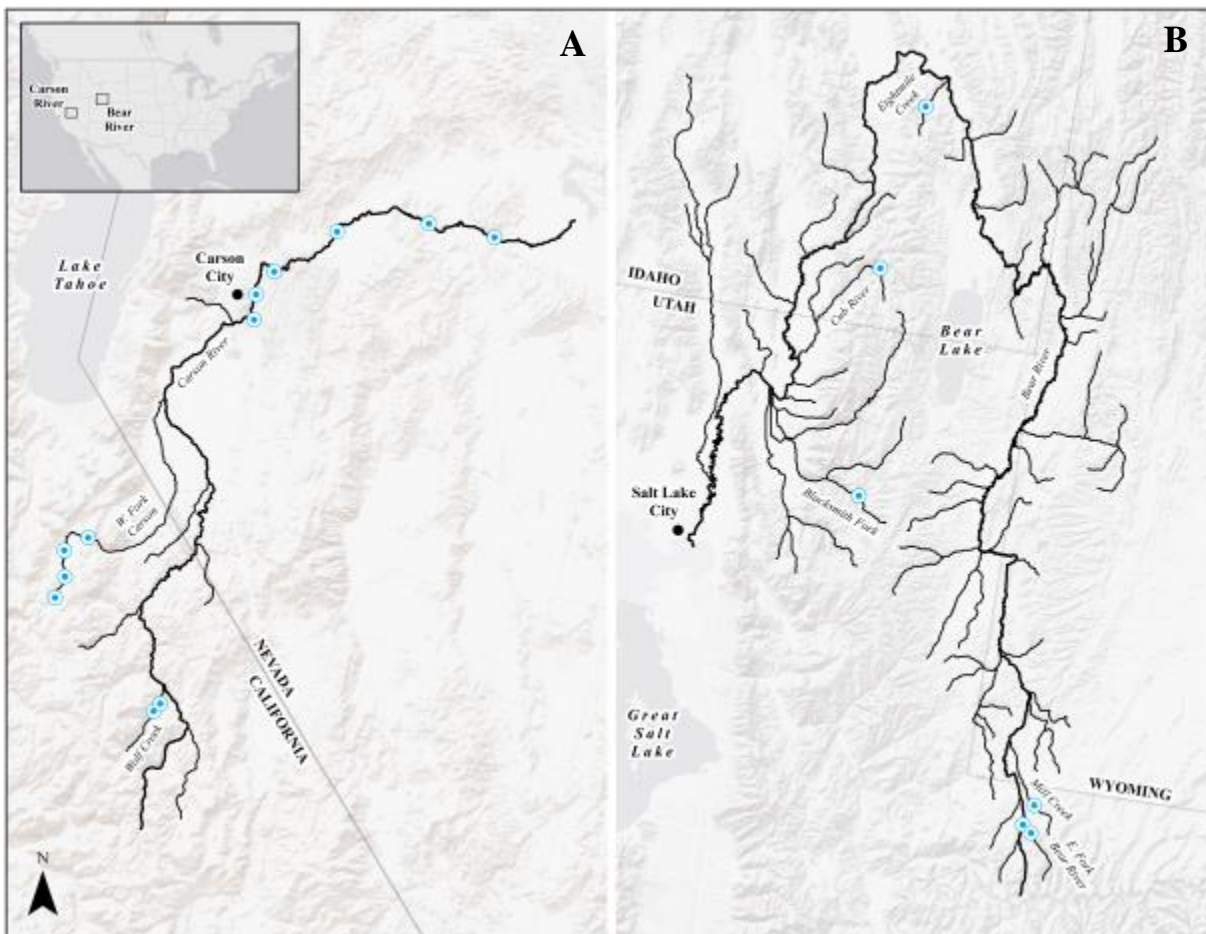


Figure 3. Map showing the locations of study sites by river: (A) Carson River and (B) Bear River. Associated FPZ replicates are represented by the blue target symbols (N=18).



Figure 4a-d. Representative photos of each FPZ site for the Great Basin ecoregion: (A) constricted-valley upland, (B) constricted-valley lowland, (C) wide-valley upland, and (D) wide-valley lowland. Photo credit: Alain Maasri

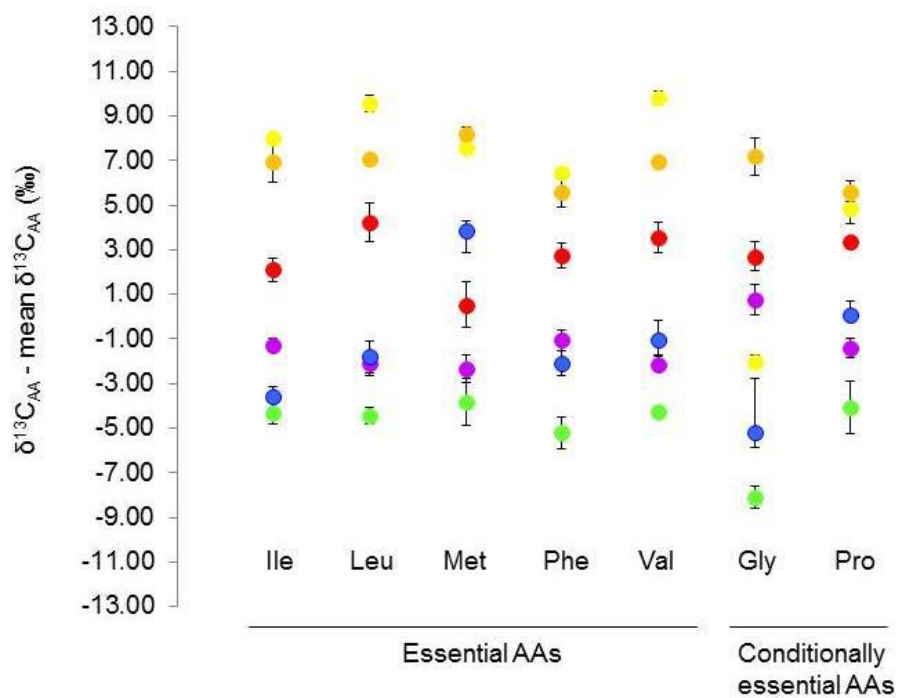


Figure 5. Amino acid carbon “fingerprints” of seven different food sources based on unique combinations of isotopic signatures of essential (Ile, Leu, Met, Phe, Val) and conditionally essential (Gly, Pro) amino acids. Red points represent CAM plants, orange points represent C₄ plants, yellow points represent fungi, green points represent green algae, blue points represent cyanobacteria, and purple points represent C₃ plants.

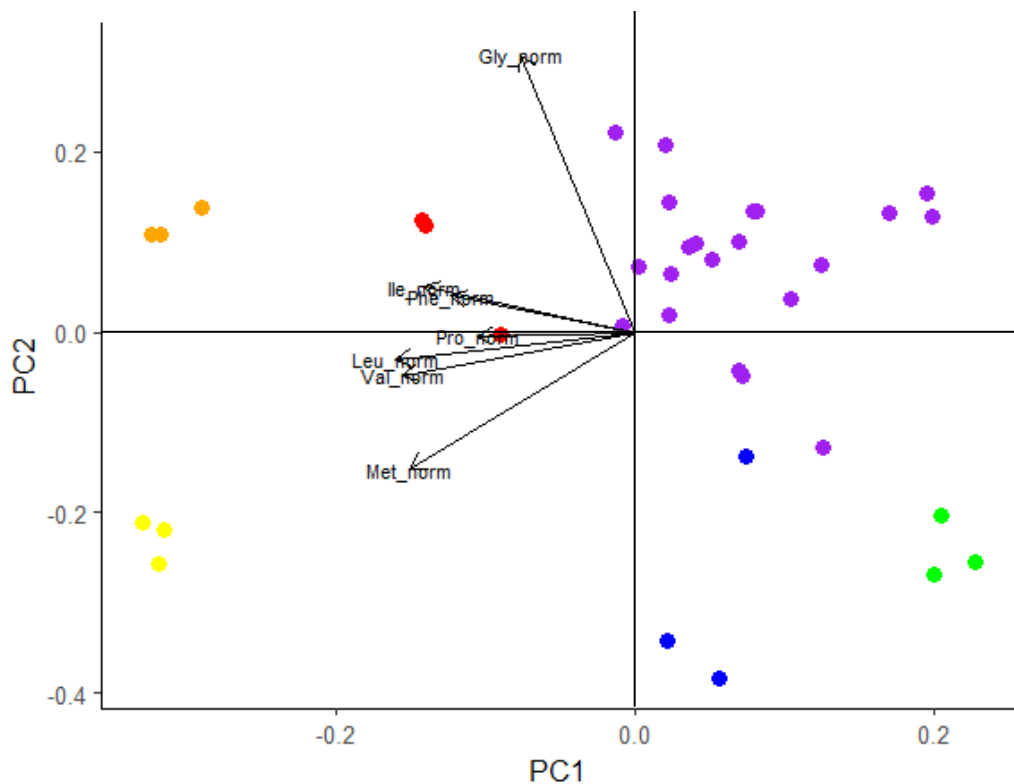


Figure 6. PCA for determining major food categories based on AA-CSIA isotopic fingerprints. Four major groups clustered along PCA1 and PCA 2 with 86.8% of variation explained. Red points represent CAM plants, orange points represent C₄ plants, yellow points represent fungi, green points represent green algae, blue points represent cyanobacteria, and purple points represent C₃ plants.

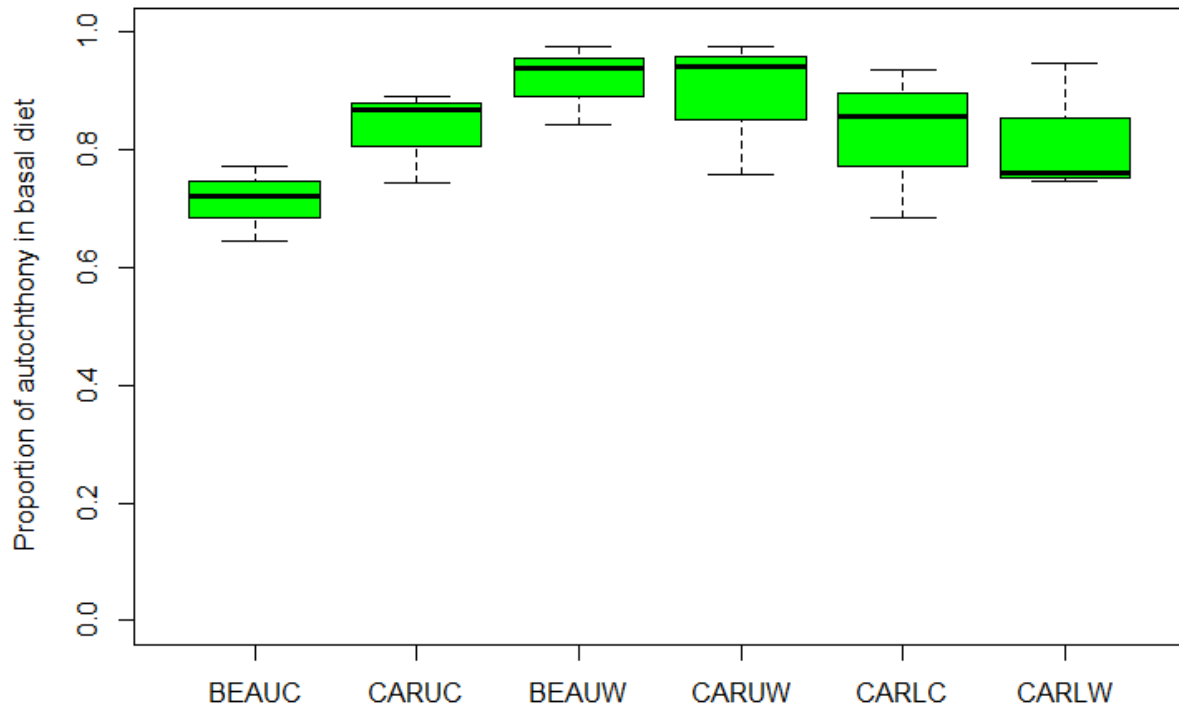


Figure 7. Mean (± 1 SE) proportion of algae in the fish basal diet at six functional process zones in the Bear and Carson Rivers of the Great Basin, USA. Sites include: Bear River upland constricted-valley (BEAUC), Bear River upland wide-valley (BEAUW), Carson River upland constricted-valley (CARUC), Carson River upland wide-valley (CARUW), Carson River lowland constricted-valley (CARLC), and Carson River lowland wide-valley (CARLW).

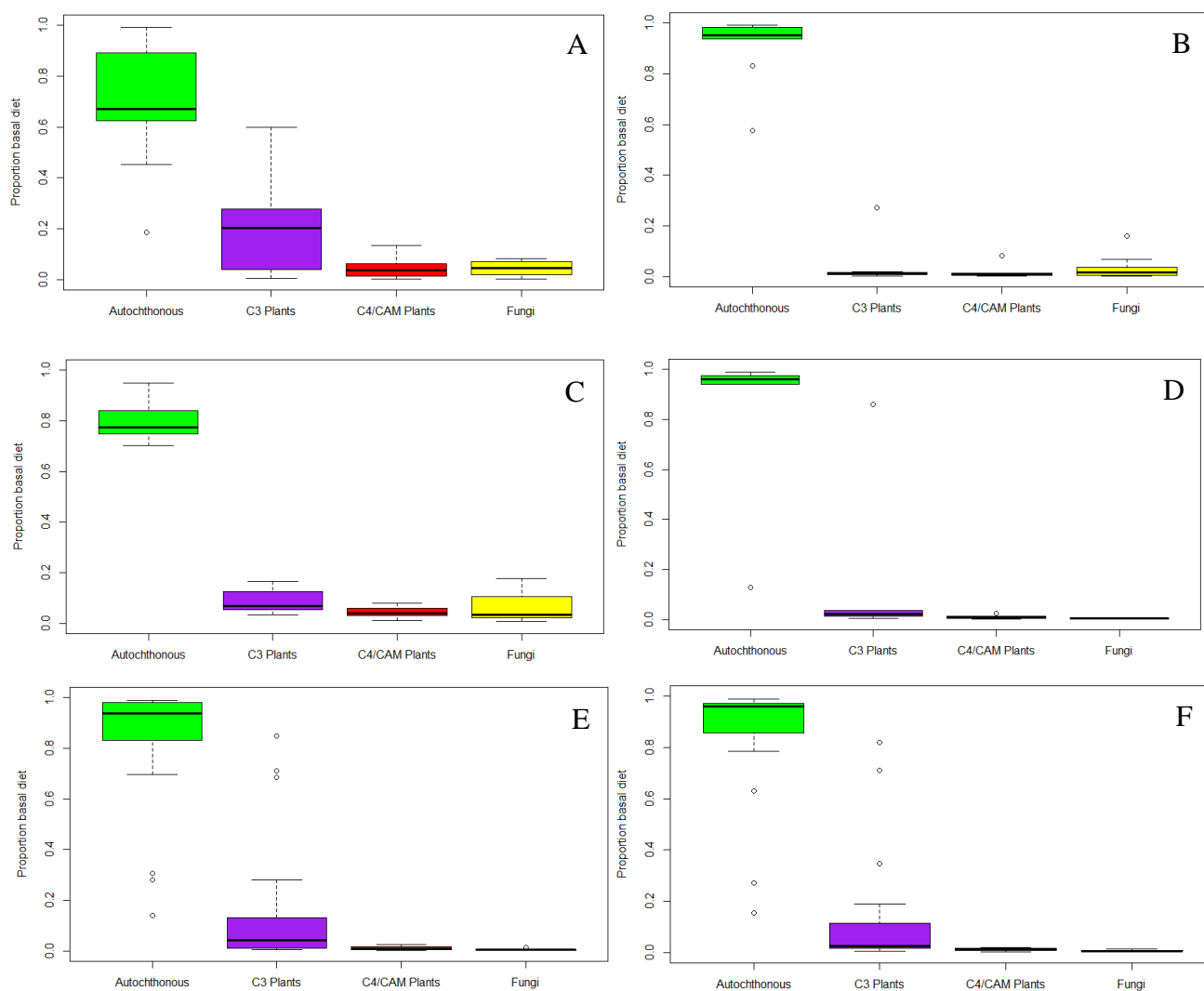


Figure 8a-f. Boxplots showing proportional dietary contributions of each of four food groups to the food web base at six different hydrogeomorphic sites (A) BEAUC = upland constricted-valley sites of the Bear River, (B) BEAUW = upland wide-valley sites of the Bear River, (C) CARUC = upland constricted-valley sites of the Carson River, (D) CARUW = upland wide-valley sites of the Carson River, (E) CARLC = lowland constricted-valley sites of the Carson River, and (F) CARLW = lowland wide-valley sites of the Carson River).

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