Consequences of landscape change on riverine food webs and aquatic-terrestrial linkages

Dissertation

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Abstract

River ecosystems are composed of a spatially and temporally heterogeneous matrix of aquatic, semi-aquatic, and terrestrial elements that are highly coupled via physical, chemical, and biotic linkages. Food webs in river ecosystems reflect this complexity as they can be highly variable over space and time and are characterized by longitudinal (upstream-downstream) and lateral (aquatic-terrestrial) connectivity, which provides energetic resources (e.g., nutrients, organic matter) to consumers in adjacent habitats. Food webs relate information about diversity, community composition, and ecosystem function. However, spatially-explicit food-web data remain scarce for river ecosystems and, thus, environmental determinants of food-web structure remain largely unresolved. In particular, anthropogenic gradients relating to river regulation and land-cover change disrupt hydrogeomorphic regimes, influence water quality, and alter fundamental properties of river ecosystems with potential consequences for cross-boundary linkages and food-web dynamics. At 12 riverine landscape study sites distributed along an urban-rural gradient of the Scioto River system, Ohio, I investigated the influence of anthropogenic and natural environmental factors on (1) reciprocal aquatic-terrestrial invertebrate flux dynamics, (2) trophic structure and food-chain length (FCL) of fish food webs, and (3) the contribution of aquatically-derived energy to terrestrial food webs.
Anthropogenic impacts relating to modified riparian landscape composition, water quality, and dams, as well as natural gradients in river size exerted strong influences on river food webs. A landscape composition gradient from urbanization to grassland-dominated riparian land cover explained patterns in aquatic insect emergence and terrestrial invertebrate inputs to the river. In particular, urban landscapes were positively associated with reduced emergence flux density and biomass and reduced biomass of terrestrial inputs, whereas riparian grasslands were negatively associated with these factors. Fish food webs were characterized by fewer predator species and smaller-bodied prey above dams than below while FCL was shorter above dammed reaches (3.88) than below (4.19). Fish FCL also responded positively to natural gradients in river size (e.g., channel width) ranging from 3.66 – 4.13 at narrower reaches to 4.24 – 4.35 at the widest reaches. Aquatic energy represented a considerable contribution to terrestrial consumers that forage across different spatial scales ranging from sedentary shoreline tetragnathid spiders (76% from aquatic) to riparian swallows (67% from aquatic) and raccoons (59%) that forage over 100s to 1000s of meters. Moreover, terrestrial consumers relied on both benthic algae (33% reliance across all consumers) and phytoplankton (32% reliance), highlighting the importance of separate aquatic energy pathways to terrestrial food webs in mid-size river systems.

Collectively, my results indicate that anthropogenic changes to rivers can have appreciable impacts on riverine food webs. Additionally, I have shown that aquatic energy, in addition to terrestrially-derived energy, can fuel terrestrial food webs in mid-sized rivers and that the aquatic energetic signature can extend further from the river than
previously considered. Finally, because of the inherent relationship between food webs and ecosystem function and stability, I anticipate results from this research will contribute to the ongoing development of a more holistic and functional approach to management and conservation of river-riparian ecosystems in the face of increasing anthropogenic influences.
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Chapter 1: Background and Literature Review

The presence (or absence) of individual species, or groups of species, in a community are influenced by a spatial hierarchy of multiple abiotic factors (Poff 1997). Superimposed onto these abiotic factors are trophic interactions among community members, which further constrain and shape community structure and food webs at the local scale. These biotic components are critical agents within ecosystems, and the complex networks of interactions they form drive the rate and magnitude of important ecological processes, such as transfers and cycling of energy and nutrients, community stability (i.e., resilience to change), and overall ecosystem function (Baxter et al. 2005, Sabo et al. 2009). For example, the number of trophic levels in a food web (i.e., food chain length; FCL) can influence critical ecosystem functions such as, nutrient cycling and primary productivity (Sabo et al. 2009). Human activities on the landscape can have profound effects on fundamental ecosystem properties and processes in river ecosystems with broad consequences for river food webs that we are still just beginning to fully understand.

Overall, human landscape modification (England and Rosemond 2004, Sweeney et al. 2004, Marczak et al. 2010) and river regulation (Csiki and Rhoads 2010) have pronounced effects on fluvial ecosystems, with potential consequences for aquatic-
terrestrial energetic linkages. Although aquatic-terrestrial linkages are becoming increasingly well-understood, the relative importance, temporal dynamics, and spatial heterogeneity of reciprocal energy exchanges remain unresolved, particularly in larger river systems (Woodward and Hildrew 2002, DeLong 2010). In light of widespread anthropogenic disturbance in riverine landscapes, further research is necessary for understanding how food webs and aquatic-terrestrial linkages are embedded in larger landscapes; this will be critical to both conservation and management. By investigating the influence of landscape characteristics on food webs and aquatic-terrestrial linkages in a river system embedded within a complex matrix of urban, agricultural, and natural landscapes, my research will address critical knowledge gaps relating to regulation of energy sources, food web dynamics, and cross-boundary connectivity.

1. River ecosystems and riverine landscapes

Fluvial ecosystems are composed of a suite of multi-dimensional ecological processes playing out on a mosaic of spatially-linked landscape elements (Ward 1989, Church 2002). The complex relationships among these various dimensions have, in part, led to the application of the principles and approaches of landscape ecology to river ecosystems and to “riverscape” (sensu Wiens 2002) and "riverine landscape” (sensu Ward et al. 2002, Thorp et al. 2006) perspectives that recognize rivers as both internally heterogeneous and linked with their surrounding landscapes via boundary dynamics (Sullivan et al. 2007, Ward 1997, Malard et al. 2000, Fausch et al. 2002, Hansen and di Castri 1992). This
emerging conceptual understanding of riverine landscapes represents a fundamental shift, from a coarse-resolution view of streams as homogenous landscape units, to a fine-grain approach that considers their internal structure and dynamics as part of the larger landscape. For example, concepts related to patch dynamics (Wu and Loucks 1995, Pringle et al. 1988, Townsend 1989, Poole 2002) incorporate characteristics of lotic ecosystems including spatial and temporal heterogeneity, hierarchical constructs, directionality, and cross-boundary linkages in characterizing these systems as dynamic mosaics of interconnected patches.

2. Food webs

Food webs depict consumer-resource relationships (i.e., trophic interactions) in ecological communities (Cohen 1978, Pimm 1982). In food webs, consumers and their resources are connected via direct trophic relationships, such as predation, as well as indirect, non-trophic relationships (e.g., competition and facilitation) (Levin 1999, Bruno et al. 2003, Berlow et al. 2004, Polis 1991). Food webs have long been seen as a key to understanding community organization and population dynamics; fundamental to ecosystem processes such as rates of primary production, decomposition, and nutrient cycling; and have potential applications for understanding biodiversity patterns, community stability, and ecosystem resilience (Pimm 1982, DeAngelis 1992, Warren 1994, de Ruiter et al. 2005). As such, food webs provide a powerful way to link structure (e.g., diversity, composition) and function (e.g., fluxes of energy) in ecosystems.
2.1. Food-web descriptors

Food webs can be described in multiple ways (Warren 1994, Pimm 2002, Bersier et al. 2002, Schmidt et al. 2007). At a broad level, food webs can be depicted as connectance webs, energy flow webs, or interaction webs (Paine 1980, Post 2002). Connectance food webs illustrate trophic links among species without any consideration of the magnitude of energy flow across each link. Energy flow food webs also show trophic links among species, however the magnitude of energy transferred through these links is included. Similar to energy flow webs, interaction webs include some measure of the strength of trophic links. Interaction webs differ in that they take in to account the functional effects of organisms in the food web and how trophic interactions affect other food web members, community structure, or ecosystem functions.

Alternatively, food webs can be characterized by quantifiable properties of food web structure and composition. Link-based properties, for example, are formulated from predator-prey matrices (either qualitative and quantitative) and include metrics such as link density and connectance (section 2.1.1). Food-chain length (FCL) is a similar metric in that it describes trophic linkages and energy transfers between basal resources and top predators, but is one-way (i.e., basal to top) and linear (section 2.1.2). Additional descriptors include proportional/compositional-based properties such as predator:prey ratios and omnivory (section 2.1.3), which are typically determined from trophic classification of the comprising taxa. For example, taxa can be classified as top (i.e., only consumers), intermediate (i.e., both prey and consumers), or basal (i.e., only prey). These
species properties are useful for understanding the trophic structure of the food web and for generating additional descriptors such as predator:prey ratios.

2.1.1. Link properties

The linkage structure of trophic networks is an important descriptor of food-web complexity and provides insight into the dynamic processes that structure ecological communities and influence community stability (May 1974, Pimm 1984, Martinez 1992, Warren 1994). A binary, predator-prey, food-web matrix is the basis for deriving many meaningful descriptions of food-web structure. Matrices can be either qualitative, as in connectance webs, or quantitative as in energy flow and interaction webs. Quantitative food webs are useful for understanding the flow of energy or biomass through a food web and thus organisms in the web must be assigned a unit (e.g., biomass or abundance). In this way, food web matrices can also be displayed graphically to illustrate overall food web structure and energy flow. Link density and connectance are both based on the number of trophic links in a food web as well as the number of taxa in the web. Link density is the number of links per taxa, whereas connectance is defined as the number of realized trophic linkages taken as a proportion of all possible linkages.

Connectance is considered a measure of network complexity and can also be thought of as the probability that any two species interact with one another (Warren 1994). Traditional ecological models held that complexity promoted stability in communities and food webs. The belief was that more links among more species would provide enough routes for energy to flow through food webs that any potential
fluctuations in resource abundance or consumer populations would be buffered. However, this viewpoint has been challenged based on information from real food webs (reviewed in Cohen and Newman 1988). When expanding these models to real food webs, complexity, or connectance, is expected to decline with increasing richness in order for the community to remain stable. For example, connectance may decrease with increasing richness because consumers are only able to exploit a limited number of resources, or habitat heterogeneity and body-size relationships can limit trophic interactions by grouping highly-connected taxa into separate food-web compartments (Cohen and Newman 1988). Furthermore, compartmentalization is common in real food webs and imparts benefits to ecological communities by buffering the negative effects of environmental perturbations (Stouffer and Bascompte 2011).

2.1.2. Chain properties

Food webs are comprised of numerous food chains, or one-way linear pathways describing the trophic relationships or transfer of energy from basal resources to top predator taxa. Food-chain length (FCL) and measures of trophic position of food web members reveal substantial information relating to community stability and complexity, and ecosystem function (section 2.1.2). Food-chain length is an important property of food-web structure (e.g., food-web height, number of trophic levels) and has long been considered a measure of food-web complexity as well as a driver of ecosystem function and community structure (DeAngelis 1992, Pimm 2002, Post 2002). Food chains are linear trophic pathways linking a top taxon/consumer with a basal taxon. FCL provides
information on the number of trophic transfers, or energy flow, from the basal resource, through primary and intermediate consumers, and eventually to top predators.

Trophic position is the vertical position of an organism (or group of organisms) and is often inferred from patterns of energy flow through natural food webs using stable isotope techniques (see Section 2.2 for additional information on the use of stable isotopes in food-web research). FCL is measured as the trophic position of the top predator in the web (e.g., “realized FCL”). Realized FCL can also be assessed using simple connectance food webs by counting the number of trophic transfers leading from basal to top trophic positions. Stable isotope techniques offer several advantages. Firstly, the complexity of natural food webs are rarely fully captured in a way that allows construction of completely realized connectance food webs. Thus, trophic interactions are missing or inferred from limited information. In addition, energy-flow food webs are difficult to construct so are generally not available for most systems. Stable isotope techniques also provide a time-integrated measure of energy flow to the organism of interest across all trophic pathways in the web.

2.1.3. Omnivory properties

Properties of omnivory provide useful insight into the degree of connectivity and stability, and the nature of energy transfer and trophic structure of food webs. Taxa are considered to be omnivorous if they consume prey from more than one trophic level. Omnivory is of particular importance when placed within the context of link and chain properties. Trophic omnivory can lead to changes in the trophic position of top and
intermediate predators, thus altering FCL (Post and Takimoto 2007). The degree of
omnivory also may be associated with link properties such that greater omnivory leads to
more trophic linkages and potentially higher connectance (Hall and Raffaelli 1993).
Taken together, food-web descriptors relate ecologically meaningful information about
diversity, community composition, and ecosystem function.

2.2. Stable isotopes in food web research

Stable isotope analysis, in particular using the naturally abundant isotopes of
carbon (C) and nitrogen (N), has become one of the primary methods for analyzing food
web structure (Peterson and Fry 1987, France 1995, Vander Zanden et al. 1999, Post et
al. 2000, Layman et al. 2011). Stable isotopes provide a temporally (and spatially)
integrated picture of trophic interactions and energy flow within food webs and have
application for understanding food web structure and energy exchange (reviewed in
Layman et al. 2011).

Carbon and N are the most common elements used in stable isotope food-web
analysis as they occur in all organic matter (living or dead). Ratios of heavy ($^{15}$N or $^{13}$C)
to light ($^{14}$N or $^{12}$C) isotopes can be used to estimate trophic position (N) and to track the
flow of energy through food webs (C). Stable isotope signatures in plants and animals
represent an integration of the resources that individual has consumed and assimilated
into its tissue. Isotopic compositions, or signatures, of plant and animal tissue are
expressed in terms of parts per thousand (‰) deviation from an established standard (e.g., Pee Dee belemnite limestone for δ^{13}C; atmospheric nitrogen for δ^{15}N):

\[
\delta^{13}C \text{ or } \delta^{15}N = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}}\right) - 1\right] \times 1,000
\]

where \( R = ^{13}\text{C}/^{12}\text{C}\) or \(^{15}\text{N}/^{14}\text{N}\).

2.2.1. Stable isotope applications

One of the most common applications of stable isotopes is for estimating the trophic position of organisms in a food web. The fractionation of nitrogen isotopes, which occurs as a result of the differential uptake and assimilation of isotopically-heavy versus -light N into consumer body tissue, allows for δ^{15}N to be used as a continuous measure of trophic position (DeNiro and Epstein 1981, Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 1999).

\[
\text{TP} = \lambda + \left(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{base}}\right)/\Delta_n
\]

where \( \lambda \) is the trophic position of the selected isotopic baseline; \( \delta^{15}N_{\text{consumer}} \) and \( \delta^{15}N_{\text{base}} \) are the δ^{15}N signatures for the consumer and baseline, respectively; and \( \Delta_n \) is the fractionation rate of nitrogen, which is generally assumed to be 3.4‰ across each trophic level (Post 2002), although others have debated this value (see Vanderklift and Ponsard 2003).
Because the $\delta^{15}$N of primary producers can vary spatially and across ecosystems, an appropriate isotopic baseline must be used in order to compare trophic positions of taxa and FCL across food webs. If appropriate estimates of isotopic baselines are not used then there is no way of determining whether trophic position is based on actual shifts in food web structure and energy flow or if TP is simply based on shifts in isotope signatures at the base of the food web (Post 2002). Appropriate isotopic baselines capture temporal and spatial variation in $\delta^{15}$N. Thus typical baselines include long-lived bivalve mussels or snails (Post et al. 2000, Post 2002) that represent an integration of suspended (e.g., phytoplankton or seston) and benthic (e.g., periphyton) basal resources, respectively. Alternatively, common primary consumers such as aquatic insects (e.g., chironomids; Eitzmann and Paukert 2009) and fish (Hoeinghaus et al. 2008) can be used. In some instances, a careful time-series collection of actual basal resources can be used as a baseline; however, spatial and temporal variability in primary producers is often high (Cabana and Rasmussen 1996, Post 2002).

In food webs where consumers acquire energy from separate sources with distinct sets of basal resources (e.g., fish that consume both aquatic and terrestrial insects) the TP model must be adjusted to incorporate this spatial heterogeneity (Post 2002):

$$TP = \lambda + \left( \delta^{15}N_{\text{consumer}} - \left[ \delta^{15}N_{\text{base1}} \times \alpha + \delta^{15}N_{\text{base2}} \times (1 - \alpha) \right] / \Delta n \right)$$

where $\alpha$ is the proportion of N acquired from baseline one (base1).
If it is assumed that the movements of C and N through the food web are similar, a simple 2-end-member linear mixing model is sufficient to estimate $\alpha$ (see also section 2.2.2):

$$\alpha = (\delta^{13}C_{\text{consumer}} - \delta^{13}C_{\text{base2}})/(\delta^{13}C_{\text{base1}} - \delta^{13}C_{\text{base2}}).$$

2.2.2. Stable isotope applications: Identifying and quantifying energy sources

Another important application for stable isotopes, particularly in coupled river-riparian ecosystems, is identifying the source(s) of energy supporting different consumers (e.g., aquatic versus terrestrial C sources). Stable isotope mixing models have been developed to partition the relative contribution of different resource pools based on the isotope signatures of resources and the isotope composition present in the tissue of consumers. Both linear (Phillips 2001, Phillips and Gregg 2001, Phillips and Gregg 2003) and Bayesian (Jackson et al. 2009, Moore and Semmens 2008, Parnell et al. 2010) mixing models are currently used in this procedure.

*Linear mixing models:* This type of mixing model uses a linear mass-balance equation could to identify the contribution of different source pools of energy acquired by consumers. One limitation of linear models is that the number of resource pools cannot exceed the number of stable isotope tracers by more than one. Thus, given two isotope tracers (e.g., $\delta^{13}C$ and $\delta^{15}N$), the relative contributions of up to three source pools can be identified. To account for the
potential contribution of more sources, more complex mathematical models have been developed (e.g., IsoSource; Phillips and Gregg 2003).

Bayesian mixing models: This family of mixing models uses Bayesian statistics to identify relative contributions of different source pools. Most linear mixing models do not incorporate uncertainty in model parameters, such as source pool variation or variation in trophic fractionation. Bayesian models (e.g., MixSIAR; Stock and Semmens 2013) can account for the variability present in natural systems. Output from Bayesian mixing models are true probability distributions (in contrast to linear models whose output is simply a summary of possible contributions) and thus their results can be used in subsequent analyses (Parnell et al. 2010, Layman et al. 2011).

3. Food webs in riverine landscapes

Because fluvial systems are embedded within, and also exert influences on the surrounding landscape, the structure and dynamics of riverine communities, and thus riverine food webs as well, can be extremely complex. Food webs in riverine landscapes incorporate a multitude of taxa from both aquatic and terrestrial environments that often cross the land-water interface as part of their foraging and life-cycle activities and can rely heavily on energy subsidies (aquatic-to-terrestrial energy fluxes and vice-versa) from adjacent habitats. In addition, food webs in larger river systems are expected to
fundamentally differ from food webs in small streams largely based on shifts in the type and amount of basal resources and the energetic pathways leading to higher consumers.

3.1. River food web models

Paradigms such as the River Continuum Concept (RCC; Vannote et al. 1980) highlighted the unidirectional pathways of energy between terrestrial and aquatic ecosystems in which terrestrially-derived organic matter (e.g., leaves) and nutrients provide energy to the base of aquatic food webs, either directly as litterfall in small forested streams, or indirectly as transported particulate matter from upstream sources to downstream consumers and decomposers. In the RCC, longitudinal gradients represent a fundamental aspect of riverine ecosystems as shifts in the availability and form of basal resources create subsequent shifts in food web structure through bottom-up processes. However, the RCC has not been explicitly tested in larger river systems (>5th order) and other concepts such as the Flood Pulse Concept (FPC; Junk et al. 1989) and the Riverine Productivity Model (RPM; Thorp and Delong 1994) offer additional insight into the nature and sources of organic matter that drive secondary production in larger river food webs. The FPC explicitly considered the importance of floodplains in which rivers and their adjacent floodplains are components of an integrated system, linked by hydrological and ecological interactions. Most importantly, flood pulses that inundate and then drain from floodplains are thought to recruit allochthonous material into the river that can subsequently be used by aquatic consumers. In the RPM, Thorp and Delong (1994)
proposed that aquatic consumers rely mainly on energy derived principally through local autochthonous production of phytoplankton, benthic algae, and other aquatic plants, whereas direct inputs of leaves and other terrestrial material provides some secondary support to aquatic consumers. Other components that can be added into an overall model of riverine food webs include the Nutrient Spiraling Concept (Newbold et al. 1981) where nutrients that are assimilated into living tissue (e.g., plants, animals) are stored, transformed, recycled, and transported along the channel in a downstream “spiral”.

Although findings by Grubaugh and Anderson (1989) highlighted the importance of floodplain-derived organic matter in large rivers in support of the FPC, the relative importance of autochthonous C sources (e.g., algae) to aquatic consumers in larger streams and rivers is becoming increasingly recognized (i.e., RPM). Thorp and Delong (2002), for example, demonstrated that autochthonous C sources were driving production in large river food webs. In large floodplain rivers, organic matter in the form of phytoplankton (from both main channel and floodplain water bodies) and drifting benthic microalgae are often the major contributors fueling secondary production in river food webs (Lewis et al. 2001, Delong and Thorp 2006). Terrestrially-derived detritus has been found to be almost exclusively confined to the microbial loop and therefore contributes very little to production of higher consumers in larger systems (Lewis et al. 2001, Thorp and Delong 2002).

Collectively, the concepts discussed above, along with others (see Poole 2010 for a comprehensive review on biophysical theoretical developments in stream science) have led to more recent advances in landscape perspectives in aquatic ecology. Whereas,
Fausch et al. (2002) promoted an holistic view of the entire, spatially heterogeneous fluvial environment as a means to understanding interactive processes across spatial and temporal scales influencing riverine fish communities, Wiens (2002) sought to establish linkages between terrestrial and aquatic ecology and proposed a marriage between the principles of traditional landscape ecology and river science. More recently, Thorp et al. (2006) proposed the Riverine Ecosystem Synthesis (RES), which incorporated many of the predominant ecological concepts in river ecology into an integrated, holistic model of river ecosystem biocomplexity across spatiotemporal scales. The RES views rivers as suites of riverine landscape patches, which consist of the riverscape (sensu Wiens 2002), the sub-bankfull inundation areas, and the supra-bankfull inundation areas including permanently wetted floodplain waterbodies, all of which interact to form the exceedingly complex, linked character of riverine food webs.

3.2. *Aquatic-terrestrial linkages*

Rivers are intimately connected to the adjacent terrestrial landscape through exchanges of energy and materials (Vannote et al. 1980, Junk et al. 1989, Polis et al. 1997). River food webs are also spatially heterogeneous and considered to be ‘open’ (Polis et al. 1996); thus food webs can be influenced by ecological processes that occur in adjacent systems, particularly processes that provide inputs of allochthonous energy (Polis and Strong 1996, Jeffries 2000, Huxel and McCann 1998) or that facilitate dispersal of organisms into or out of the local community (Post et al. 2002). Recent
research, particularly in small stream systems, has greatly improved our understanding of aquatic-terrestrial linkages and a growing body of literature provides evidence that reciprocal transfers of energy between streams and their adjacent riparian zones are important elements that drive food-web structure and community dynamics in both aquatic and terrestrial habitats (Nakano and Murakami 2001, Baxter et al. 2005, Murakami and Nakano 2002, Iwata et al. 2003, Marczak et al. 2007, Burdon and Harding 2008, Marcarelli et al. 2011). In particular, reciprocal exchange of invertebrates — comprised of aquatic insects dispersing from the river in their adult stage (hereafter “emergent insects”), as well as terrestrial invertebrates accidentally entering the river — represent critical energetic pathways linking river and riparian habitats (Figure 1.1).

Figure 1.1. Reciprocal food-web linkages (e.g., energy flows represented by arrows) in a stream-riparian ecosystem (from Sullivan and Rodewald 2012).
Because invertebrates can substantially contribute to the energy budgets of both aquatic and terrestrial consumers, shifts in the magnitude and composition of invertebrate subsidies can influence community structure and food-web dynamics in recipient habitats (reviewed in Baxter et al. 2005). Thus, bidirectional flows of invertebrates are becoming increasingly recognized as critical to the maintenance and diversity of linked river-riparian food webs.

**Terrestrial-to-aquatic invertebrate flux:** Terrestrial arthropods entering streams (via gravity, wind, surface runoff, and other vectors) provide high-quality food resources for aquatic consumers including fish (Mason and Macdonald 1982) and predatory insects (e.g., larval odanates; Kraus 2010). For example, Kawaguchi and Nakano (2001) found that terrestrial invertebrates represented ~50% of the annual diet of salmonids in headwater streams of northern Japan, with seasonal summer contributions reaching 68%–77%. Furthermore, Cloe and Garman (1996) showed that terrestrial invertebrate prey consumption by centrarchids (e.g., *Lepomis spp.*) was relatively constant across a gradient of stream size, suggesting that the importance of terrestrial arthropods to aquatic consumers is not constrained to small headwater systems.

**Aquatic-to-terrestrial invertebrate flux:** In the opposite direction, the flux of emergent insects into the riparian zone represents an important food resource for a suite of terrestrial consumers, including terrestrial invertebrates (Henschel et al. 2005).
Patterns of emergent insect flux can influence dietary composition as well as the distribution of riparian consumers. For instance, Sanzone et al. (2003) observed that streamside orb-weaving and ground-dwelling spiders derived nearly 100% and 68% of their energy budgets from emergent insects, respectively. Insectivorous birds, such as common nighthawks (*Chordeiles minor*), are known to actively select for larger and more abundant flying prey and thus have been found to spatially track aquatic insect emergence (Todd et al. 1998).

Cross-boundary invertebrate subsidies can elicit numerical responses in recipient consumer populations as well. Kawaguchi et al. (2003) experimentally reduced the abundance of terrestrial invertebrates entering the stream and observed a decrease in local fish abundance. Likewise, Burdon and Harding (2008) found that abundances of both ground-dwelling and web-building spiders at the aquatic-riparian interface were closely related to the availability of their emergent insect prey. Furthermore, Sabo and Power (2002) showed that reductions in abundance (by 49%) and biomass (by 38%) of emergent insect subsidies resulted in a nearly 3-fold reduction in the abundance of riparian lizards.

Reciprocal energy subsidies have also been implicated as a mechanism driving shifts in food-web dynamics. By subsidizing secondary consumers such as fish, terrestrial invertebrate inputs can have indirect effects on benthic aquatic insect communities resulting in trophic cascades (Nystrom et al. 2003). An experimental reduction of
terrestrial invertebrate inputs resulted in increased consumption of benthic prey by stream fishes and a subsequent increase in the growth of benthic periphyton (Nakano et al. 1999). Emergent insect fluxes have also led to elevated densities of riparian spiders (Henschel et al. 2001) and birds (Murakami and Nakano 2002), which in turn can increase local predation pressure and depress terrestrial insect populations. Bidirectional fluxes of invertebrates can thus be a critical component of linked aquatic-terrestrial ecosystem function (Richardson et al. 2010).

3.3. **Relative importance of aquatic versus terrestrial carbon supporting terrestrial riparian food webs**

Rather than sources of energy, streams and rivers have traditionally been viewed largely as recipients of terrestrially-derived materials (Vannote et al. 1980, Nakano et al. 1999, Power et al. 2001). However, the existence and importance of reciprocal energy fluxes (i.e., aquatic-to-terrestrial) are increasingly recognized as subsidizing terrestrial consumers including spiders, ground beetles, lizards, bats, and birds (Sabo and Power 2002, Sanzone et al. 2003, Paetzold et al. 2005, Fukui et al. 2006, Alberts et al. 2013), as well as larger predators, such as kingfishers, herons, osprey, otters, and raccoons, which are integral members of broader riverine food webs (Kelly 1996, Leberg and Kennedy 1998, Clavero et al. 2003, Gehrt 2003, Sullivan and Rodewald 2012). Although the importance of aquatic subsidies to terrestrial food webs has been clearly evaluated (reviewed in Baxter et al. 2005, Sullivan and Rodewald 2012), the quantitative
contribution of aquatically-derived C has not been well resolved. Given that aquatic algae, in particular diatoms, can be both highly productive and superior in nutritional quality, relative to terrestrially-derived detritus, aquatic-to-terrestrial energy subsidies (e.g., emerging aquatic insects) are likely to assimilate and transport a greater proportion of aquatically-derived C to terrestrial consumers (Power 1984, Hanson et al. 1985, Jackson and Fisher 1986). Furthermore, aquatic algae production resides in two distinct compartments — benthic algae and suspended phytoplankton — yet the potential contribution of aquatically-derived C from phytoplankton to terrestrial food webs has also not been explicitly considered. Phytoplankton might be expected to be important in larger streams and rivers where planktonic primary production is often greater and is viewed as being a key component in fueling aquatic secondary production (Thorp et al. 1998, Thorp and DeLong 2002, DeLong 2010). Many aquatic insects (e.g., grazers) largely feed on benthic algae however; some also rely heavily on suspended algae (i.e., phytoplankton) or terrestrially-derived detritus (e.g., collectors) (Rounick et al. 1982, Cummins et al. 1989). Thus, terrestrial food webs can be subsidized with a mixture of both “recycled” terrestrially-derived carbon C as well as aquatically-derived C as terrestrial predators consume emerging insects from the river (Iwata 2007, Gratton et al. 2008, Kraus and Vonesh 2012). Quantitatively addressing the cross-habitat contribution of aquatic production is a critical step in holistic food web ecology and might be expected to be particularly important in mid-size rivers, where a mixture of both benthic and planktonic primary production are expected to contribute to aquatic food webs.
4. Environmental factors and river food webs

The hierarchical structure of river ecosystems suggests strong influences of spatially-explicit environmental factors on the structure of biological communities and river-riparian food webs (Poff 1997, Power and Dietrich 2002, Burcher et al. 2007). Because food webs are set within the context of riverine landscapes, an integration of landscape and food-web ecology is critical but remains unresolved (Polis et al. 1997, Power and Dietrich 2002, Baxter et al. 2005). The composition of biotic communities is largely constrained by a suite of interacting environmental factors, which has important consequences for food-web structure by supplying the available species pool and constraining trophic interactions (Poff 1997). Environmental variation has been found to influence food-web dynamics, among them FCL, in lotic ecosystems (Winemiller 1990, Thompson and Townsend 1999, Power et al. 2008).

4.1. Natural environmental influences on river food webs

Three major avenues of environmental influence have been examined: energy availability, disturbance, and ecosystem size. Although much of this work has been conducted to investigate environmental determinants of FCL, the underlying mechanisms might also be expected to drive patterns of diversity and community composition, as well as other structural elements of food webs, including network complexity (e.g.,
connectance) and the degree of trophic omnivory, which subsequently feed back into FCL.

Energy, or resource, availability has long been considered an important “bottom-up” constraint on communities and food webs, in particular FCL (Lindeman 1942, Pimm 1982, Lawton 1999). Some have proposed that there is an inherent relationship between food-web structure and energy availability (e.g., Polis and Strong 1996) with an overall lengthening of food chains as resource availability increases (Pimm 1982). The inefficiency of energy transfer from resource to consumer (typically about 10%) presumes that FCL should correspond positively to increased energy availability or energy efficiency (Yodzis 1984). For example, Post and Takimoto (2007) outlined proximate mechanisms that cause shifts in FCL: addition, insertion, and omnivory. The additive mechanism can alter FCL through addition or removal or top predators, such as might be expected if energy availability were the primary driver of FCL and were high enough to support additional trophic levels. However, there has not always been a strong case for this relationship in stream ecosystems (but see Thompson and Townsend 2005). There is evidence that longer food chains are found at intermediate levels of resource availability (Diehl and Feissel 2001). Energetic constraints may set the limit on the number of trophic levels at low resource availability (Pimm and Kitching 1987); whereas omnivory can potentially limit FCL as the availability of resources becomes greater (Post and Takimoto 2007). Very high resource availability, especially as allochthonous subsidies, can lead to elevated consumer densities that, in turn, reduce intermediate and primary consumers, creating an “apparent trophic cascade” and forcing top predators to
feed on increasingly lower trophic levels (Polis et al. 2000). In contrast, allochthonous subsidies may instead encourage food web stability and weaken the effects of trophic cascades via increased omnivory (McCann and Hastings 1997, Huxel and McCann 1998), although extremely high amounts of inputs can have a destabilizing effect (e.g., "the paradox of enrichment"; Rosenzweig 1971). In addition to the quantity of inputs, the quality, or type, of allochthonous inputs are important for determining the overall effect of subsidies on receiving food webs (Marcarelli et al. 2011).

Environmental disturbance is considered to be a strong influence on aquatic food webs. Pimm and Lawton (1977) suggested that food webs were controlled by disturbance regimes, with shorter food chains and lower trophic connectivity characterizing food webs that experience frequent or extreme disturbances. Environmental disturbances reduce taxonomic and functional diversity leading to shifts in food-web structure including reduced linkage density (Townsend et al. 1998) and potentially shorter food chains as top and intermediate predators are lost from the community (Power et al. 2006). In fluvial systems, environmental disturbance is often in the form of hydrological variability and changes to sediment inputs or movement (Power et al. 1996). Although flow regimes have important consequences for community composition in streams (Fisher et al. 1982, Poff and Allan 1995), results pertaining to the effect of discharge variability on food webs have been equivocal (Post 2002, Sabo et al. 2009). Power et al. (1996) found that frequent flooding favored disturbance-resistant benthic macroinvertebrate taxa that were less resistant to predation, thereby effectively lengthening food chains via more efficient energy transfer to predators. Others have
observed shorter food chains, and lower connectance, with increasing levels of disturbance (Townsend et al. 1998).

Ecosystem size is also an important influence on FCL (Vander Zanden et al. 1999, Post et al. 2000). Addition of top predators, insertion of intermediate predators, and changes in the degree of trophic omnivory are all potential mechanisms for ecosystem size-related shifts in food webs (Post 2002, Post and Takimoto 2007, Vander Zanden and Fetzer 2007, Sabo et al. 2010). Larger ecosystems are generally expected to support longer food chains because they can harbor not only more species but also incorporate larger-bodied top predators, which subsequently occupy higher trophic positions within the web (Cohen and Newman 1991). In contrast, increasing ecosystem size could also potentially shorten food chains if greater species richness leads to omnivory or if greater habitat heterogeneity (or spatial separation of habitats) minimizes predator efficiency or the ability of predators to exploit certain prey. In addition to the effects of ecosystem size on FCL, increased omnivory and greater species richness should lead to higher connectance in larger systems; whereas the effects of increased habitat heterogeneity or spatial segregation could be expected to decrease connectance via prey refugia and compartmentalization (Warren 1994).

4.2. Anthropogenic influences on river food webs

Because of the hierarchical structure of river ecosystems, and the close coupling of terrestrial and aquatic environments in riverine landscapes, activities that disrupt or
alter ecosystem processes also can disrupt the structure and dynamics of riverine food webs (DeAngelis et al. 1989, Polis et al. 1997, Woodward and Hildrew 2002, Finlay 2004). The majority of research to date has focused on discrete communities, often only in distinct habitats, and at small spatial scales while spatially-explicit food-web data are lacking, particularly in larger streams and rivers (Levin 1992, Woodward and Hildrew 2002). Furthermore, anthropogenic landscape disturbances and river regulation (e.g., dams) are prevalent worldwide thus making it imperative to understand the role of these human-mediated environmental disturbances on river food webs.

_Agriculture:_ The effects of row-crop agriculture on fluvial systems are characterized by elevated inputs of pesticides, nutrients (from fertilizers), and sediment, increased bank erosion, and altered hydrology (Lenat 1984, Johnson et al. 1997, Allan 2004). Nutrient inputs (e.g., nitrogen and phosphorous) from fertilizer runoff can promote aquatic primary production and eutrophication of aquatic systems (Carpenter et al. 1998). Sedimentation considered a key factor impacting aquatic biota, mainly through benthic habitat alteration and increased turbidity (Sullivan et al. 2006, Sullivan and Watzin 2010). Sedimentation is often linked directly with runoff from exposed soil in agricultural landscapes but can also stem from agricultural-induced changes to stream hydrology (e.g., via tile drainage systems, increased surface runoff, and modified evapotranspiration of cultivated plants v. riparian forest), geomorphology (e.g., channelization), and loss of riparian vegetation leading to bank erosion. Intact riparian areas can
mitigate sediment and nutrient influx from surrounding landscapes (Naiman and Decamps 1997). Jones et al. (1999) found that deforestation of riparian areas increased embeddedness (i.e., the degree to which benthic sediments are surrounded and encased by finer sediment particles such as silt) and decreased benthic habitat heterogeneity. However, agricultural landscapes are often devoid of natural, intact riparian areas.

Stream channelization, one of the most widespread physical disturbances associated with agriculture, can have direct effects on discharge regimes, channel morphology, and in-stream habitat in agricultural landscapes (Lau et al. 2006). Channel geometry and habitat heterogeneity are particularly important influences on community composition and the dynamics of reciprocal energy exchanges (see Polis et al. 1997). For example, Iwata et al. (2003) found that insect emergence and flux of aquatic insects into the riparian forest increased concurrently with channel sinuosity. Furthermore, the authors showed that the abundance of insectivorous birds was positively influenced by the elevated abundance of insects but also the increased availability or foraging areas (i.e., stream edge) provided by more sinuous channels.

Urbanization: Although agriculture can have strong influences on fluvial ecosystems, the acute effects of urbanization are of particular importance as greater than 80% of the Earth’s human population is projected to live in cities within 50 years (United Nations 2007). Conversion to urban land cover has
numerous physico-chemical effects on fluvial systems, although much of what is currently known pertains more specifically to smaller streams instead of large rivers. Walsh et al. (2005) synthesized the suite of physico-chemical and biological impairments in urban streams and coined the term “urban stream syndrome”. Modified hydrological regimes and changes to sediment dynamics in urban systems can have significant impacts on fluvial geomorphology and benthic habitats (Paul and Meyer 2001, Leopold 1968, Lane 1955). Impervious surfaces (e.g., paved roads and parking lots, and intensively manicured lawns) typical of urban and suburban landscapes limit the infiltration of precipitation and lead to greater surface runoff that is then efficiently routed through storm drains and directly into river channels. The resulting higher magnitude floods, shorter lag time (between precipitation and flood events), and limited infiltration act in concert to disrupt hydrologic regimes with concurrent impacts to channel morphology and negative effects on stream biota (Paul and Meyer 2001).

Characteristic effects of urban-driven shifts in hydrology include bank and bed erosion leading to incision, channel widening, and reduced habitat heterogeneity (Hollis 1975, Booth 1990, Pizzuto et al. 2000, Hession 2001).

*River regulation:* Physical disturbances within the river channel and adjacent floodplain severely disrupt longitudinal and lateral connectivity in fluvial systems and influence the composition of biotic communities and food web dynamics. These disturbances include channelization, as well as dams, levees, and other flow
regulation structures (hereafter referred to as ‘river regulation’). River regulation has become ubiquitous in many areas of the world including the United States where there are over 75,000 dams >2 meters (m) in height (Poff et al., 2006). River regulation structures constrain longitudinal and lateral connectivity in rivers and create unique conditions that are atypical of those expected along unregulated rivers, including modified – usually reduced – hydrologic variability and floodplain access, and greater retention of sediment, nutrients, and organic matter from upstream sources (Ward and Stanford 1983, Ward and Stanford 1995, Kondolf 1997). Dams disrupt longitudinal gradients predicted by the RCC (Serial Discontinuity Concept; Ward and Stanford 1995) not only by reducing hydrological variability and trapping transported material, but also through the creation of impoundments that artificially increase ecosystem size. In this way river regulation also increases channel stability (e.g., reduced channel migration and braiding in alluvial systems and reduced floodplain heterogeneity). The effects of river regulation have wide-ranging consequences for organisms inhabiting the river and its riparian area both upstream and downstream of the physical structure. In some large modified river systems, severed river-floodplain connections can have drastic, and negative, consequences for aquatic community biodiversity and food web structure (Power et al. 1996).
5. Study system

My study system is located in central Ohio, USA and consists of the middle and lower section (~150 km) of the Scioto River and a short section of the lower reaches of its largest tributary, the Olentangy River (Figure 1.2). Human landscape modification is prevalent throughout much of the Scioto River Watershed and in many areas, encroachment into the riparian zone and extensive modifications to the riverine landscape are severe.

Figure 1.2. Map of Ohio showing the Scioto River system with major tributaries. Study reaches are indicated in the blow-out.
The Scioto begins in Auglaize County in unglaciated west-central Ohio and flows for approximately 372 km to its confluence with the Ohio River at Portsmouth, Ohio where the Scioto is a 6th order river. The Olentangy River joins the Scioto near The Ohio State University campus in Columbus. A number of lowhead dams obstruct flow and alter riverine habitats in the upper Scioto and many of its tributaries, including the Olentangy. There are two large dams (< 10 m) on the Scioto, which form O’Shaughnessy and Griggs Reservoirs near the city of Columbus. Greenlawn dam, in south Columbus, is the final existing dam on the Scioto River mainstem. Tributaries of note include (from upstream to downstream) Big Walnut Creek, Big Darby Creek (State and National Scenic River), Deer Creek, Paint Creek, Salt Creek, and Sunfish Creek (Figure 1.2).

The Scioto River Watershed encompasses nearly 17,000 km² and much of the basin consists of agricultural land cover (~65%) especially in the northern 2/3 of the drainage. Urban development is also prominent in certain areas as the river flows near, or directly through, several small to medium cities (Circleville, Chillicothe, Waverly, Piketon, and Portsmouth) and a major metropolitan area of nearly 2 million inhabitants (Columbus). Natural land cover, forest, grassland, and wetland is distributed in patches of various sizes throughout the basin with some areas of extensive second-growth forest cover found mainly in the southern, glaciated, portions of the watershed downstream of Chillicothe.

Numerous problems are associated with human land use in the basin. Most notably are issues with (1) excessive sedimentation from surface and bank erosion stemming from agricultural practices and construction and development projects; (2) poor
water quality from non-point agricultural runoff and various point sources stemming from combined sewer outflows and effluent from wastewater treatment facilities, and discharges from industry; and (3) hydrogeomorphic shifts from expanding impervious surface cover, channel straightening (especially of tributaries), and in-stream flood control structures. Despite these issues, throughout much of its length, the Scioto River has been designated as meeting or exceeding the Ohio EPA Warmwater Habitat designation. Only a relatively short section of the mainstem through the city of Columbus does not meet this designation because of the extensively altered river channel and the presence of two large dams and several smaller flow regulation structures.

I selected twelve 1200-m study reaches in the Scioto (10) and Olentangy (2) Rivers in central Ohio, USA that followed a gradient of adjacent land-use and land-cover characteristics largely representative of the human and natural environmental landscape gradients present in the system — this gradient ranged from reaches whose riparian landscapes were heavily-modified by humans (e.g., urban, agricultural), to reaches that consisted of a heterogeneous mixture of human and natural elements, and finally reaches that were largely composed of natural land cover. I used land-cover data from the USGS national land cover dataset (NLCD; Jin et al. 2013) in a GIS to assist in site selection and I chose the study reaches based on their adjacent land-cover characteristics. My final selection of study reaches was based largely on information from my GIS mapping, but I performed numerous site visits to ground-truth GIS results and assess the feasibility of access and/or gain landowner permission.
6. Summary of objectives

Although streams and rivers are considered biodiversity hotspots and provide critical ecosystem services to cultures worldwide, they are among the most highly modified ecosystems on Earth (Vorosmarty et al. 2000). Understanding the influence of human activities on river food webs is critical for addressing the potential impacts of future development and sustainability of streams and rivers. However, to date much of the research examining food web dynamics and aquatic-terrestrial linkages in lotic systems has been conducted in relatively unmodified headwater systems (e.g., Nakano and Murakami 2001, Kawaguchi et al. 2003), and to a lesser extent in large river systems, such as the upper Mississippi and Ohio Rivers (Thorp and DeLong 1994). Comparatively little work has been conducted in mid-size river systems such as the Scioto. My overarching goal of this research was to investigate landscape influences — stemming from human landscape modification and river regulation — on fundamental properties of river food webs and cross-boundary energetic linkages across the aquatic-terrestrial interface. Within this framework I have developed three main research objectives, each of which corresponds to a dissertation chapter that will be submitted for publication to a scientific journal.

**Objective 1:** Investigate the influence of riparian landscape composition and nearshore vegetation structure on the magnitude and composition of reciprocal invertebrate fluxes (e.g., aquatic emergent insects exiting the river and terrestrial
invertebrates falling into the river) along an urban-rural riparian landscape gradient.

**Objective 2:** Explore the relationship between modified riverine landscapes (e.g., altered riparian landscape composition and river regulation) and fish-centered food webs, specifically by assessing the roles that natural and human gradients play in structuring the trophic structure and food-chain length of fish food webs in river ecosystems.

**Objective 3:** Quantify the contribution of aquatic carbon (including both benthic algae and suspended phytoplankton compartments) in supporting terrestrial riparian consumers in linked aquatic-terrestrial food webs.

I anticipate that this work will contribute to general ecological and food-web theory and, more specifically, to food-web theory in river systems in human modified landscapes. I also anticipate my work will contribute to the continued advancement of functional, integrative riverine landscape approach to management and conservation of river-riparian ecosystems.

All research activities involving live animals were conducted under state (Ohio Department of Natural Resources Wild Animal Collection Permit 15-49) and federal permits (USGS Federal Bird Banding Permit 23515) and approved by The Ohio State
Chapter 2: Broken bonds: landscape change alters reciprocal river-riparian invertebrate fluxes

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Summary

1. Reciprocal fluxes of invertebrates in stream-riparian ecosystems represent an important energetic linkage between aquatic and terrestrial habitats with broad ranging effects on recipient consumers and food webs. However, the consequences of riparian landscape change on invertebrate fluxes have not been widely investigated, particularly in larger streams and rivers.

2. We measured bidirectional invertebrate fluxes at twelve river reaches distributed across an urban-rural riparian land use and land cover gradient in the Scioto River system (Ohio, USA).

3. Model-selection results indicated that high-intensity urban development exerted contrasting effects on terrestrial-to-aquatic invertebrate flux density (+ relationship) and biomass (- relationship), partially accounted for by shifts in community composition and body size. Riparian grassland cover, associated with rural landscapes, also influenced variation in both the density (range: 2.8 – 18.9 individuals m$^{-2}$ day$^{-1}$) and biomass (range: 7.1 – 58.7 mg m$^{-2}$ day$^{-1}$) of the terrestrial-to-aquatic invertebrate flux.

4. Riparian grassland cover was the most important factor in the best models for predicting both density ($R^2 = 0.61$; range: 12.8 – 116.8 individuals m$^{-2}$ day$^{-1}$) and biomass ($R^2 = 0.65$; range: 1.4 – 27.9 mg m$^{-2}$ day$^{-1}$) of the aquatic-to-terrestrial invertebrate flux, where relatively larger-bodied taxa dominated the flux at rural reaches.

5. On the whole, invertebrate flux was increasingly net emergent (i.e., greater aquatic emergent insect export from the river than terrestrial invertebrate input into the river)
density and increasingly net terrestrial in biomass along the urban-rural gradient. A single factor model that included grassland land cover explained much of the variation in net density flux \( \omega_i = 0.44; + \) relationship. Grassland cover received support as an environmental determinant of net biomass flux as well, however, the relationship was negative.

6. Overall, we present evidence that riparian landscape composition can have pronounced effects on reciprocal invertebrate fluxes in river-riparian systems. In particular, urbanization strongly reduced the aquatic emergent flux. Human-induced shifts in bidirectional aquatic-terrestrial invertebrate exchanges might be expected to have consequences for linked river-riparian biodiversity and food webs, although further investigation will be needed to explicitly address these effects.
Introduction

Rivers are intimately connected to the adjacent terrestrial landscape through exchanges of energy and materials (Vannote et al., 1980; Junk, Bayley & Sparks, 1989; Polis, Anderson & Holt, 1997). Reciprocal exchange of invertebrates – comprised of aquatic insects dispersing from the river in their adult stage (hereafter “emergent insects”) as well as terrestrial invertebrates accidentally entering the river – represent critical energetic pathways linking river and riparian habitats. Because invertebrates can substantially contribute to the energy budgets of both aquatic and terrestrial consumers, shifts in the magnitude and composition of invertebrate subsidies can influence community structure and food-web dynamics in recipient habitats (reviewed in Baxter, Fausch & Saunders, 2005). Thus, bidirectional flows of invertebrates are becoming increasingly recognized as critical to the maintenance and diversity of linked river-riparian food webs.

Terrestrial arthropods entering streams (via gravity, wind, surface runoff, and other vectors) provide high-quality food resources for aquatic consumers including fish (Mason & Macdonald, 1982) and predatory insects (e.g., larval odanates; Kraus, 2010). For example, Kawaguchi and Nakano (2001) found that terrestrial invertebrates represented ~50% of the annual diet of salmonids in headwater streams of northern Japan, with seasonal summer contributions reaching 68-77%. Furthermore, Cloe and Garman (1996) showed that terrestrial invertebrate prey consumption by centrarchids (e.g., Lepomis spp.) was relatively constant across a gradient of stream size, suggesting
that the importance of terrestrial arthropods to aquatic consumers is not constrained to small headwater systems.

In the opposite direction, the flux of emergent insects into the riparian zone represents an important food resource for a suite of terrestrial consumers, including terrestrial invertebrates (Henschel, Mahsberg & Stumpf, 2001; Paetzold, Bernet & Tockner, 2006; Burdon & Harding, 2008), lizards (Sabo & Power, 2002), insectivorous birds (Iwata, Nakano & Murakami, 2003; Alberts, Sullivan & Kautza, 2013), and bats (Fukui et al., 2006). Patterns of emergent insect flux can influence dietary composition as well as the distribution of riparian consumers. For instance, Sanzone et al. (2003) observed that streamside orb-weaving and ground-dwelling spiders derived nearly 100% and 68% of their energy budgets from emergent insects, respectively. Insectivorous birds, such as common nighthawks (*Chordeiles minor*), are known to actively select for larger and more abundant flying prey and thus have been found to spatially track aquatic insect emergence (Todd, Poulin & Brigham, 1998).

Cross-boundary invertebrate subsidies can also elicit numerical responses in recipient consumer populations. Kawaguchi et al. (2003) experimentally reduced the abundance of terrestrial invertebrates entering the stream and observed a decrease in local fish abundance. Likewise, Burdon and Harding (2008) found that abundances of both ground-dwelling and web-building spiders at the aquatic-riparian interface were closely related to the availability of their emergent insect prey. Furthermore, Sabo and Power (2002) showed that reductions in abundance (by 49%) and biomass (by 38%) of emergent insect subsidies resulted in a nearly 3-fold reduction in the abundance of riparian lizards.
Reciprocal energy subsidies have also been implicated as a mechanism driving shifts in food-web dynamics. By subsidizing secondary consumers such as fish, terrestrial invertebrate inputs can have indirect effects on benthic aquatic insect communities resulting in trophic cascades (Nystrom, McIntosh & Winterbourn, 2003). An experimental reduction of terrestrial invertebrate inputs resulted in increased consumption of benthic prey by stream fishes and a subsequent increase in the growth of benthic periphyton (Nakano et al., 1999). Emergent insect fluxes have also led to elevated densities of riparian spiders (Henschel, Mahsberg & Stumpf, 2001) and birds (Murakami & Nakano, 2002), which in turn can increase local predation pressure and depress terrestrial insect populations.

Bidirectional fluxes of invertebrates can thus be a critical component of linked aquatic-terrestrial ecosystem function (Richardson, Zhang & Marczak, 2010). However, human modification of riparian areas has pronounced effects on stream ecosystems (England & Rosemond, 2004; Sweeney et al., 2004; Marczak et al., 2010), with potentially profound, yet relatively unexplored, consequences for coupled aquatic-terrestrial invertebrate fluxes (although note that many studies have independently considered relationships between riparian land cover/vegetation and either terrestrial or aquatic insects; e.g., Sponseller, Benfield & Valett, 2001; Roy et al., 2005; Francis & Schindler, 2009). This is particularly the case for river (vs. small stream) systems, where there has traditionally been less of a focus on the importance of terrestrial invertebrates to stream consumers (Vannote et al., 1980).
Within this context, we investigated the influence of riparian landscape composition (i.e., riparian land use and land cover, nearshore vegetation structure) on reciprocal aquatic-terrestrial fluxes of invertebrates at twelve river reaches distributed along an urban-rural landscape gradient in Ohio, USA. This effort enabled us to empirically assess shifts in the patterns of reciprocal invertebrate flux from highly urbanized Columbus, OH (15th largest US city by population; USCB, 2010) along a continuum of land-cover change extending into rural agricultural, grassland, and forested areas.

We had two major objectives in this research. First, we sought to estimate the relative magnitude of reciprocal invertebrate fluxes along a gradient of urban-rural riparian landscape composition. Because changes to riparian vegetation can have direct impacts on terrestrial invertebrate abundance and diversity by modifying habitat structure or reducing its availability (Mason & Macdonald, 1982; Laeser, Baxter & Fausch, 2005), we predicted that the terrestrial-to-aquatic flux would be greater at rural reaches with more intact riparian vegetation. In addition, because human land use and land cover (LULC) can have strong effects on aquatic insect communities through modified hydrologic and sediment regimes and elevated nutrient inputs (reviewed by Allan, 2004) we predicted that the overall magnitude of aquatic-to-terrestrial emergent insect flux would be reduced as urbanization increased. Our second objective was to describe the community composition of invertebrate fluxes. Because both river and riparian habitats in urban areas are known to be less spatially complex and characterized by modified hydrology and relatively poor water quality, we expected that, for both aquatic and
terrestrial invertebrate communities, urbanization would result in shifts in community composition including changes in functional diversity such as mean body. Longitudinal position along the river continuum (i.e., ecosystem size) is generally associated with factors that likely play important roles in aquatic-terrestrial flux magnitude and composition (e.g., river size, flow variability, and sediment distribution); however, we expected that the urban-rural riparian landscape composition gradient would override these effects. Additional details relative to our hypotheses can be found in Table 2.1.

We used a model selection approach (Burnham & Anderson, 1998) to evaluate the relative strength of evidence supporting our hypotheses. We complemented model-selection with constrained ordination to further describe the relationship between riparian landscape composition and invertebrate community composition. Collectively, understanding how human landscape alterations drive shifts in aquatic-terrestrial invertebrate fluxes may shed light on potential effects on recipient consumers and spatially-explicit riverine food webs.

Methods

Study system and experimental design

Our study system included the Scioto River and its major tributary the Olentangy River (hereafter ‘Scioto River’) in central and southern Ohio (OH), USA (Figure 2.1). The Olentangy River is the largest tributary of the Scioto, joining the mainstem near
downtown Columbus, OH (~1.2 million people; USCB, 2010). The Scioto River flows for 372 km, draining a 16,882-km² catchment comprised of agriculture (~69%), forest (~21%), and urban LULC (~9%) (White, Johnston & Miller, 2005). There are multiple lowhead dams and three larger water storage reservoirs within and upstream of Columbus (Figure 2.1). However, the river is unregulated from the southern extent of the city until it reaches its terminus at the Ohio River. The varied land uses are reflected in an urban-rural gradient, making it an appropriate model system to study the ecological consequences of alterations in riparian landscape composition.

We selected 12 study reaches whose adjacent riparian areas represented a range of urban to rural (e.g., forested, agricultural, and grassland) landscapes. Each study reach represented a unique river segment based on similar valley features and channel morphology. Reaches were ~1,200 m, which adequately represented variability in flow habitats and is consistent with established protocols for sampling aquatic macroinvertebrates in rivers (Herlihy & Lazorchak, 2000; Flotemersch et al., 2006). Given the spatial arrangement of LULC types within the basin, some clustering among the study sites was unavoidable. On average, reaches were located ~18 river km apart, although there was some variability (SD = 16.8 km).

We used a GIS (ArcGIS 10.1, Esri, Redlands, CA) to delineate 100-m buffers within the riparian zone on both sides of each reach. We considered this spatial extent sufficient for capturing the influences of riparian landscape composition on both aquatic and terrestrial insect communities (reviewed by Lee, Smyth & Boutin, 2004). Within the 100-m buffer, we calculated the relative proportions of 14 different LULC classes from
the 2006 National Land Cover Database (NLCD; Fry et al., 2011). These 14 classes were distributed into 6 broader categories that represented the major LULC types found within our study system (Table 2.1, Figure 2.1). To estimate ecosystem size, as a measure of longitudinal position along the river, we used the hydrology extension in ArcGIS 10.1 to generate drainage area above the downstream terminus of each of the study reaches.

Field and laboratory methods

From 2010-2013, we measured reciprocal invertebrate fluxes over two 10-day sampling periods: once in early summer and once in late summer. Sampling was staggered so that ‘early’ and ‘late’ sampling efforts were conducted in different years at each of the study reaches to capture both seasonal as well as potential annual variation in invertebrate flux. Although there were distinct differences in flux magnitude across sampling periods (see Results) we decided to combine “early” and “late” for our analyses because we were interested in understanding a time-integrated flux across the leaf-out period. Sampling effort was consistent with other studies that have measured invertebrate fluxes into and from streams and rivers (Alberts, Sullivan & Kautza, 2013; Johnson, Fritz & Price, 2013; Meyer & Sullivan, 2013).

To measure emergent insects, we deployed 6 pyramid-style floating emergence traps (1-m² surface area) following Alberts et al. (2013). Traps were deployed in the predominant flow habitats (e.g., pool, riffle, and run) represented in each study reach and were likewise distributed along the entire longitudinal extent of the reach. To measure
terrestrial arthropod flux into the river, we distributed 8 floating pan traps (0.4-m$^2$ surface area) roughly equidistantly along each bank (i.e., 4 traps on each side) along the entire longitudinal extent of the reach. Pan traps were partially filled with water and a small amount of soap, which acted as a surfactant to more effectively trap invertebrates (Greenwood, O'Dowd & Lake, 2004; Meyer & Sullivan, 2013).

All invertebrates we collected were identified to family and enumerated. We dried invertebrates for 48-hours in a drying oven ($60^\circ$ C) and weighed (by family for each reach) to the nearest 0.1 mg (Sanzone et al., 2003; Akamatsu, Toda & Okino, 2007). From these data, we calculated total emergent and terrestrial biomass flux (i.e., the biomass of invertebrates emerging from the river or entering the river measured as a flux; mg m$^{-2}$ day$^{-1}$), total emergent and terrestrial density flux (i.e., the number of invertebrates emerging from the river or entering the river measured as a flux; number m$^{-2}$ day$^{-1}$), mean body size of individuals by family, and net flux density and net flux biomass [calculated by subtracting terrestrial from emergent estimates following Meyer & Sullivan (2013)].

At each reach we surveyed nearshore vegetation structure and composition within 6, 3 X 3-m quadrats at the rivers edge. Quadrats were representative of the dominant bankside vegetation types and approximately evenly spaced along the river’s edge from upstream to downstream along the length of the reach. Within the quadrats, we visually surveyed the proportion of tree canopy and shrub canopy cover (%) and the number of woody stems >10 centimeters (cm) diameter at breast height (dbh), either alive or dead (woody stems >10 cm m$^{-2}$). We included tree density in addition to tree canopy cover to
account for the potential influences of woody stems to serve as habitat for terrestrial arthropods while not necessarily contributing to canopy cover.

To account for potential influences of nutrient concentrations on emergent insect productivity, we collected 6, 250-milliliter (ml) water samples for total nitrogen (N) and phosphorous (P) measurements from each reach: 3 samples collected laterally across the channel at evenly-spaced intervals both near the upstream and downstream ends of each reach (6 samples total). Samples were composited by upstream and downstream locations separately and analyzed at the Ohio State University Service Testing and Research Lab (STAR Lab, Wooster, OH) for concentrations in milligrams liter\(^{-1}\) (mg L\(^{-1}\)) of N and P. Given limited variability in P among the study reaches, we excluded it from further analysis (see details in Statistical Methods, below).

Statistical methods

Our primary analytical method was based on an information theoretic approach using ordinary least squares regression and Akaike Information Criterion adjusted for small sample sizes (AICc). We developed 6 sets of models representing alternative hypotheses regarding the influence of riparian landscape composition and aquatic nutrient concentrations on reciprocal invertebrate fluxes (Table 2.2). We constructed all potential models for each dependent variable, including the null (i.e., intercept only) model, and used \(\Delta\text{AIC}c (\text{AIC}c_i - \text{AIC}c_{\text{min}})\) to evaluate the relative support of each individual model in its set of candidate models. We retained all potential models with \(\Delta\text{AIC}c \leq 4\), as this
included both highly supported models (ΔAICc ≤ 2) as well as those that garnered substantial secondary support (Burnham & Anderson, 2002; Burnham & Anderson, 2004). Subsequently, we calculated Akaike weights (ω_i) to indicate the probability that a model was the best supported among all of the candidate models in the set. Prior to modeling, we checked for correlations (|r| ≥ 0.80) among our chosen set of predictors and if significant correlations were detected we did not include the correlated variables in the same model (Burnham & Anderson, 2002). We checked that the assumptions of multivariate parametric analyses were met, and if not, appropriate transformations were performed (e.g., log_{10} of terrestrial flux biomass and emergent flux density). Regression and correlations analyses were performed using JMP 10.0 (SAS Institute Inc., Cary, NC).

We used constrained ordination (canonical correspondence analysis; CCA) to further explore relationships between community composition of invertebrate fluxes and riparian land cover (within 100-m buffers), nearshore vegetation structure (from shoreline vegetation surveys), and aquatic N. We used the same predictor variables from our candidate regression models in the environmental data matrix for CCA. The species matrix consisted of the flux density and flux biomass estimates for all individual invertebrate taxa. We performed 4 separate ordinations (terrestrial flux density, terrestrial flux biomass, emergent flux density, and emergent flux biomass) and constructed biplots for each. Ordination analyses were performed with Canoco for Windows 4.5 (ter Braak & Šmilauer, 2002).
Results

Riparian landscape composition and aquatic nutrients

Riparian landscapes varied in the relative proportions of LULC across the urban-rural gradient in our study system, as expected based on our study design (Figure 2.1). Nearshore vegetation structure also varied widely along the urban-rural gradient (Table 2.3). Mean total N concentrations in river waters ranged from 0.25 mg L\(^{-1}\) to >6 mg L\(^{-1}\) across study reaches. In general, reaches surrounded by, or directly downstream of, agricultural landscapes had greater concentrations of total N. Mean river water total P concentrations were generally between 0.06 mg L\(^{-1}\) and 0.54 mg L\(^{-1}\), except at one reach (Reach 5) where P was found at a much higher concentration (1.04 mg L\(^{-1}\)) than the other reaches. Both P (\(\bar{x} = +0.02\) mg L\(^{-1}\)) and N (\(\bar{x} = -0.27\) mg L\(^{-1}\)) exhibited limited within-reach (e.g., upstream to downstream) variability, at least in part pointing to invariant internal material cycling within our study reaches (e.g., Newbold et al., 1982) (but note Reaches 8 and 12, where N concentrations were substantially lower downstream than upstream; Table 2.3).

Reciprocal invertebrate fluxes

Overall, we collected and identified 7,655 individuals from 16 orders and 148 families of terrestrial invertebrates from our pan traps and 64,341 individuals from 6
orders and 27 families of aquatic insects from our emergence traps. Terrestrial flux density ranged from ~3 to ~19 individuals m\(^{-2}\) day\(^{-1}\); whereas emergent insect flux density was greater overall and ranged from ~13 to ~116 individuals m\(^{-2}\) day\(^{-1}\) (Table 2.4). Total terrestrial biomass was 16,054.9 mg (dry) and emergent insect biomass was 14,643.5 mg (dry) across all study reaches resulting in flux estimates between 7.1 – 58.7 mg m\(^{-2}\) day\(^{-1}\) for terrestrial invertebrates and between 1.4 – 27.9 mg m\(^{-2}\) day\(^{-1}\) for emergent insects (Table 4). Although we combined ‘early’ and ‘late’ samplings in our analyses, there were some differences in flux magnitude between the two sampling periods (see Appendix A).

All but one reach (Reach 3) exhibited a net positive flux density of emergent insects. Net flux density ranged from -5.8 to +97.8 individuals m\(^{-2}\) day\(^{-1}\). Although fewer in number, terrestrial invertebrates were generally larger bodied than emergent insects and thus constituted a positive net flux of terrestrial biomass across nearly all reaches (Table 2.4). Only reaches 5 and 10 were net emergent in biomass and both were characterized by very low densities of moderately-sized terrestrial invertebrate inputs coupled with either high densities of small-bodied (Reach 5) or moderate densities of large-bodied emergent insects (Reach 10). A suite of Diptera (e.g., Muscidae, Chloropidae, Cecidomyiidae, and Sciaridae), Hymenoptera (e.g., Formicidae, Mymaridae, and Diapriidae), Coleoptera (e.g., Staphylinidae, Curculionidae, and Chrysomelidae), and non-insect taxa (e.g., Tetrignathidae, Linyphiidae, and collembolans) numerically dominated the terrestrial-to-aquatic flux. Large, heavy-bodied non-insect taxa (e.g., Julidae and several families of spiders) dominated terrestrial flux
biomass at most reaches. Chironomidae comprised >85% of the relative abundance of the emergent insect flux across all reaches and dominated emergent biomass (>70% of total emergent biomass) at most reaches. Trichoptera taxa, especially Hydropsychidae and Leptoceridae, were important components of the emergent insect flux for both density and biomass.

*Influence of riparian landscape composition on invertebrate fluxes*

Terrestrial-to-Aquatic Flux

Our most strongly supported models related to flux density and flux biomass (Table 2.5). High-intensity urban development was an important variable in models for terrestrial invertebrate flux magnitude, accounting for nearly 30% of the variation observed in density (+ relationship) and 13% in biomass (- relationship) in the top models. Terrestrial invertebrate flux was also positively associated with riparian grassland in the best model for density and alternative models for biomass. Nearshore tree density was a positive predictor in the best model for flux biomass.

The first two axes of our ordinations explained 31% and 37% of the variation in flux density and flux biomass, respectively. Biplots for both density and biomass showed a clear separation between urban (e.g., development and shrub cover) and rural along the first axis (Figure 2.2). Along the second axis for flux density, a distinct forest-to-open (e.g., grassland and crops) gradient emerged. The second axis for flux biomass illustrated a gradient from nearshore areas dominated by trees to those dominated by shrub cover.
Our ordination results indicated that rural riparian landscapes, those characterized by open land cover (e.g., grasslands and crops) and nearshore trees, supported fluxes of larger-bodied Coleoptera, Lepidoptera, and non-insect (e.g., arachnids and Julidae) taxa; whereas more highly developed, urban riparian areas were largely dominated by higher densities of small-bodied Aphididae, Mymaridae, Sciaridae, and Cecidomyiidae. Our terrestrial flux biomass biplot (Figure 2.2 b) also illustrated a positive relationship between larger-bodied invertebrates and indicators of rural riparian landscapes (e.g., forest, crops, and nearshore tree canopy cover).

Aquatic-to-Terrestrial Flux

Riparian grassland cover was the most influential variable in our models predicting emergent insect flux magnitude and constituted the only variable in top models for both density and biomass (Table 2.5). The first two axes of our emergent insect flux ordinations explained 51% of the variation in flux density and 45% of the variation in flux biomass. The first axis for density and biomass was primarily associated with a gradient from agricultural crops and nearshore tree canopy cover to urban riparian development and nearshore shrub cover (Figure 2.3). The second axis for both density and biomass illustrated a gradient from open (e.g., grasslands and crops) riparian areas with higher aquatic N concentrations to more developed riparian areas with a high proportion of nearshore shrub and/or canopy cover.

Our ordination results indicated that Chironomidae density was positively associated with riparian development, although this relationship was weak (Figure 2.3 a).
In contrast, Hydropsychidae, the third most abundant emergent taxon, was more closely aligned with total N, nearshore tree density, and crops, all characteristic of rural riparian landscapes (Figure 2.3 a). Emergent flux biomass closely tracked density across our study reaches as evidenced by similar predictors for both in our model sets. Our flux biomass biplot showed that less abundant, but larger-bodied taxa (e.g., Heptageniidae, Leptoceridae, Coenigrionidae, Crambidae, and Perlidae) were positively associated with riparian forest and nearshore tree canopy cover (Figure 2.3 b). In addition the flux biomass biplot also showed that abundant, smaller-bodied taxa (e.g., Chironomidae) were closely associated with urban riparian landscapes.

Net Flux

As the proportion of riparian grassland increased, the invertebrate flux became increasingly net emergent in density, and conversely, net terrestrial in biomass (Table 2.5). Grassland accounted for a substantial proportion \( R^2 = 0.77 \) of the variation in net flux density but only a relatively minor proportion \( R^2 = 0.14 \) for net flux biomass. Total N was positively related to net flux biomass in the best model as well as alternative models in the set. Low-intensity urban development was positively associated with net flux biomass in an alternative model indicating that either low levels of riparian urbanization were positively related to emergent insect flux, negatively related to terrestrial flux, or both.
Discussion

In stream and river ecosystems, both aquatic and terrestrial invertebrate communities may vary along natural longitudinal gradients (e.g., stream size, hydrology and sediment distribution, riparian vegetation composition), as well as with landscape disturbance, yet neither association has been well resolved with respect to the influence on bidirectional invertebrate fluxes (reviewed in Baxter, Fausch & Saunders, 2005). We found strong evidence that invertebrate fluxes aligned with an urban-rural riparian landscape gradient (Figure 2.4). Flux density and biomass of emergent insects and flux biomass of terrestrial invertebrates all increased from urban to rural reaches. These changes were largely associated with increased riparian grassland cover, higher aquatic nutrient concentrations, and greater nearshore tree cover in rural landscapes. In contrast, we observed the highest terrestrial invertebrate densities at both extremes of the urban-rural gradient, driven separately by riparian development and nearshore shrub cover in urban landscapes, and riparian grassland and nearshore tree cover in rural landscapes. Despite expectations suggesting longitudinal shifts in aquatic insect community composition and relative inputs of terrestrial invertebrates (see Vannote et al., 1980), we did not find a strong influence of longitudinal position (i.e., ecosystem size/drainage area) on invertebrate flux magnitude. However, the presence of dams in our study system may have diminished the overall influence of longitudinal position by disrupting natural gradients in discharge, stream size, and sediment distribution (see Ward & Stanford, 1983; Ward & Stanford, 1995). The density of emergent insects dispersing from the river was almost always
greater than that of terrestrial invertebrates entering the river. Conversely, the biomass of
the emergent insect export was consistently less than that of the terrestrial invertebrate
input. Thus, in general, the relative difference in flux magnitudes became increasingly net
emergent in density (i.e., emergent > terrestrial) and net terrestrial in biomass (i.e.,
terrestrial > emergent) moving from urban to rural riparian landscapes.

Reciprocal Invertebrate Fluxes

For emergent insects, grassland land cover, characteristic of rural riparian
landscapes in our study area, garnered the strongest support as a predictor for both flux
density and biomass (Table 2.5). Grasslands were mostly located adjacent to the
riverbank and physically separated the river from other land-cover patches farther inland
(typically cultivated crops). The relative effectiveness of grassland buffers in capturing
sediments and minimizing bank erosion is of particular importance as the distribution of
aquatic macroinvertebrates is strongly related to benthic substrate characteristics
(Richards & Host, 1993; Minshall & Robinson, 1998).

Our alternative model including total N received substantially less support ($\omega_i = 0.08$ vs. $\omega_i = 0.43$ for the top “grassland” model) for emergent flux density and was not
included in any of the models for emergent flux biomass (Table 2.3). Although elevated
nutrient concentrations are commonly correlated with secondary production of aquatic
invertebrates (Lenat & Crawford, 1994; Johnson et al., 2013), most studies of this kind
survey benthic communities that include non-emergent taxa (e.g., Oligochaeta and
Nematoda). Because we measured only emergent insect flux, we may be missing this proportion of benthic secondary production supported by aquatic N.

Community composition of the emergent insect flux was also associated with the urban-rural gradient. High densities of relatively small-bodied, collector-gatherer taxa (e.g., Chironomidae) were associated with characteristics of urban river reaches in our system (Figure 2.3 a and b). Urbanization has been linked with aquatic invertebrate communities dominated by dipterans and non-insect taxa (Roy et al., 2003). Through replacement of emergent with non-emergent taxa (e.g., Oligochaeta and Nematoda), urbanization may also limit emergent flux magnitude. In addition, many of our urban reaches were characterized by dams (Figure 2.1), which tend to reduce flow variability, increase retention and deposition of sediment and organic matter, and artificially increase depth and width of the channel in upstream impoundments (Santucci, Gephard & Pescitelli, 2005; Graf, 2006; Poff et al., 2007). Thus, aquatic insects which rely on benthic periphyton (e.g., grazers; mostly Heptageniidae in our system), interstitial habitat, or those that collect drifting organic matter (e.g., collector-filterers; e.g., Hydropsychidae) were limited in our urban study reaches that were also modified by dams (Figure 2.3 a).

In contrast, free-flowing rural river reaches supported greater densities of larger-bodied, collector-filterers (e.g., Hydropsychidae), shredders (e.g., Leptoceridae), predators (e.g., Coenigrionidae), and less tolerant collector-gatherers (e.g., Baetidae) (Figure 2.3 a).

We found substantial weight of evidence for characteristics of both urban (high-intensity development) and rural (grassland, and nearshore canopy cover and tree density) riparian zones as landscape determinants of terrestrial invertebrate flux magnitude.
Although we did not expect to find a positive relationship between flux density and urban development, both top-down (e.g., fewer predators) and bottom-up (e.g., increased plant productivity) processes have been implicated as key factors driving terrestrial invertebrate abundances in urban landscapes (Faeth et al., 2005; Raupp, Shrewsbury & Herms, 2010). We found a negative relationship between terrestrial flux density and tree canopy cover, in part because of the close associations between several of the most abundant terrestrial taxa (e.g., Aphididae, Cecidomyiidae, and Sciaridae) and shrub-dominated nearshore areas in urban riparian zones (Figure 2.2 a and b). Hoover, Shannon, and Ackerman (2007) suspected that the relative contribution of terrestrial invertebrates was greater in reaches with less tree canopy cover because the expansion of the shrub layer provided better habitat. River regulation that inhibits lateral flood pulses (as in our study system, where 4 of the 5 urban reaches were near dams) can contribute to the proliferation of upland-adapted shrub species in riparian areas. In particular, the invasive Amur honeysuckle (*Lonicera maackii*) has become widely distributed in urbanized riparian zones of the Scioto River system and has recently been linked with elevated abundance of terrestrial insects (Loomis & Cameron, 2014).

As with measures of emergent flux magnitude, terrestrial flux biomass increased along an urban-rural gradient and was associated with urban-related shifts in community composition. High-intensity development was the predominant urban variable in our models and was characterized by open (i.e., less woody vegetation) riparian areas, shrub-dominated nearshore areas, and abundant but small-bodied terrestrial invertebrates (e.g., Collembola, Thripidae, Aphididae, and Cecidomyiidae; Figure 2.2 a). Similarly, Roy et
al. (2005) observed that terrestrial invertebrate flux density entering streams was greater in open urban riparian zones, and also largely comprised of smaller-bodied taxa (e.g., Collembola and Diptera). We found that larger-bodied taxa such as predatory invertebrates (e.g., arachnids, Carabidae, and Staphylinidae) were associated with rural riparian landscapes (Figure 2.2 a and b) and contributed to greater terrestrial flux biomass in these reaches.

Although we anticipated that riparian forest cover would be positively associated with increased terrestrial invertebrate flux magnitude, we instead observed that grassland cover received widespread model support and had a significant positive influence on both flux density and biomass of terrestrial invertebrates (Table 2.5). Edwards and Huryn (1996) found similar results; terrestrial invertebrate input from native, less-intensively grazed grassland riparian areas essentially matched the magnitude of inputs from forested riparian areas. Romaniszyn, Hutchens, and Wallace (2007) also observed greater abundances of terrestrial invertebrates into streams flowing through pasture-grassland. Because inputs of terrestrial invertebrates to streams are considered “accidental” and can be mediated by physical forces such as wind or precipitation events (Bridcut, 2000), it is likely that invertebrates in open grasslands (relative to forest) are more exposed to wind, rain, and other elements that may increase their proclivity to enter the river channel.

Nearshore tree density was an important variable in our models for terrestrial invertebrate flux biomass. Wood-boring coleopterans, leaf-chewing lepidopterans, Formicidae, and arachnids were closely associated with nearshore tree density in our study (Figure 2.2 a and b). These taxa were generally larger-bodied and included the
greatest contributors to overall flux biomass, and, as they were relatively poor flyers (e.g., coleopterans) or wingless (e.g., lepidopteran larvae, most Formicidae we collected, and non-insect taxa), were likely entering the river directly from trees along the bank. A greater relative abundance of non-flying terrestrial invertebrates has been generally associated with forested stream reaches in other studies as well (Edwards & Huryn, 1996; Kawaguchi & Nakano, 2001). In addition, trees located along the channel margin can serve as important habitat and refugia for flying terrestrial invertebrates, particularly in modified riparian areas relatively devoid of trees elsewhere. For example, Whitaker, Carroll, and Montevecchi (2000) found elevated concentrations of insects in forested buffers following clear cutting and concluded that the remnant trees served as a windbreak that collected insects blown in from the adjacent open landscapes.

Net Flux and Implications for Riverine Food Webs

We found a net positive flux density of emergent insects and a net positive flux biomass of terrestrial invertebrates across nearly all study reaches (Table 2.4). Factors regulating density and biomass for unidirectional fluxes were also important predictors in our models for net flux. For example, rural landscapes characterized by patches of grassland cover were positively associated with flux density and biomass for both terrestrial invertebrates and emergent insects in our models. However, the relative strength of these relationships differed, leading to flux density becoming increasingly net emergent from urban-to-rural as the relative density of emergent insects increased more than terrestrial inputs. In addition, the positive relationship between urban land cover and
terrestrial flux density contributed to a more balanced exchange of invertebrates in urban landscapes.

Net flux biomass exhibited a different trend. Although the biomass of both terrestrial invertebrate inputs and emergent insect flux increased from urban-to-rural, the increase in terrestrial biomass was greater, leading to increasingly greater net terrestrial biomass inputs along the urban-rural gradient. Terrestrial biomass increased mostly through shifts in community composition toward larger-bodied taxa. Emergent flux biomass increased mostly because of higher densities of emergent insects but also partly through shifts in flux composition toward larger-bodied taxa. Total N received some moderate support in our models for net flux biomass suggesting that aquatic nutrient concentrations can also prompt elevated emergence of larger-bodied aquatic insects and contribute to shifts in net flux.

Changes in cross-system invertebrate subsidies could lead to broad-ranging effects to both aquatic and riparian food webs. Appreciable research has focused on the contributions of terrestrial invertebrates to drift-feeding fishes (e.g., trout and other salmonids) in small streams (Wipfli, 1997; Nakano et al., 1999; Kawaguchi & Nakano, 2001). Although larger stream and river systems like the Scioto can support trophically-diverse fish food webs, only a few fish foraging guilds likely consume terrestrial invertebrates as a significant proportion of their diets (e.g., some cyprinids and centrarchid species). Thus, it is less certain how terrestrial invertebrate subsidies might influence food webs in larger warmwater rivers. However, shifts in the magnitude and composition of terrestrial invertebrate inputs might preferentially subsidize select groups
of secondary aquatic consumers potentially leading to trophic cascades or shifts in food-chain length (Marczak, Thompson & Richardson 2007). Body size of terrestrial invertebrates also likely plays a critical role in the relative importance of the subsidy to fish and other aquatic consumers, whereby larger-bodied invertebrate inputs may support greater abundance or biomass of generalist insectivores or prompt shifts in foraging locations (e.g., greater foraging efforts spent in nearshore areas) for both insectivorous fish and their predators.

In the opposite direction, shifts in the emergent insect flux may be highly consequential for terrestrial food webs (Jackson & Fisher, 1986; Baxter, Fausch & Saunders, 2005). In our study system, predatory invertebrates – especially those taxa that heavily depredate emergent insects such as ground beetles (Carabidae; Paetzold, Schubert & Tockner, 2005) and orb-weaving spiders (e.g., Tetrignathidae; Sanzone et al., 2003) – were closely associated with rural riparian landscapes characterized by a greater magnitude of the emergent insect flux. Shifts in emergent flux magnitude and composition may also have important consequences for riparian birds. Tree swallows (*Tachycineta bicolor*), for example, have been found to actively select larger-bodied (McCarty & Winkler, 1999) and aquatic (McCarty, 1997; Alberts, Sullivan & Kautza, 2013) prey items, implicating emergent flux composition in foraging and energetic dynamics. Alterations in reciprocal invertebrate subsidies extend to conservation concerns. For instance, landscape changes that results in reductions in aquatic insect food sources are of particular concern relative to North American aerial insectivorous birds, which are experiencing widespread population declines (reviewed in Nebel *et al.*, 2010).
Changes in the composition of the emergent flux may also alter dispersal patterns of adult aquatic insects with implications for the spatial influence of aquatic prey subsidies into terrestrial systems (i.e., "biological stream width", sensu Muehlbauer et al., 2014). In our study, for instance, we found a clear relationship between rural riparian landscapes and larger-bodied emergent insects (Figure 2.3 a and b), many of which are relatively strong flyers (e.g., most trichopterans, Coenigrionidae, and Sciomyzidae; Marden 2008) and can likely disperse further from the river.

Understanding the environmental influences that structure bidirectional invertebrate fluxes in rivers is a critical step to anticipating the potential effects on aquatic and terrestrial consumer populations and linked river-riparian food webs. Our results show how modification of riparian landscape composition can severely alter the magnitude and composition of bidirectional invertebrate fluxes and potentially overwhelm natural longitudinal patterns that may exist. In particular, our results suggest that urbanization strongly alters reciprocal invertebrate subsidies, largely decoupling the aquatic-to-terrestrial flux. Shifts in flux biomass and flux density were also accompanied by changes in community composition along the urban-rural gradient. Additional research is needed to empirically assess how changes in reciprocal invertebrate flux might influence broader food-web dynamics of river ecosystems in human-dominated landscapes. We anticipate that the results from this study will contribute to a growing understanding of cross-boundary energy exchanges in large stream and river systems and their importance to functional, diverse food webs.
Acknowledgements

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References


Practical Information-Theoretic Approach. 2nd edition. Springer-Verlag, New York, NY, USA.


Table 2.1. Alternative hypotheses and the independent variables (LULC and nearshore vegetation representing an urban-rural riparian landscape gradient) tested in multivariate linear regression modeling. Density is the flux of individuals m\(^{-2}\) day\(^{-1}\) and biomass is mg m\(^{-2}\) day\(^{-1}\). Net flux refers to the difference of aquatic emergent flux magnitude (i.e., density and biomass) minus terrestrial invertebrate flux magnitude. Positive values indicate a net flux of aquatic emergent insects from the river; negative values represent a net flux of terrestrial invertebrates into the river. FOREST represents riparian woodlands of deciduous tree and shrub species. CROPS indicate cultivated croplands (predominantly corn and soybean). D_HIGH represents medium- to high-intensity urban development (e.g., industrial or commercial) and D_LOW is low-intensity urban development (e.g., residential, parkland, and abandoned parcels). GRASS indicates native grassland, fallow fields, and managed hay. SHRUB is the proportion of nearshore (e.g., riverbank) shrub cover and CANOPY is the proportion of nearshore tree canopy cover. TREES is the density of nearshore woody stems >10cm diameter at breast height (dbh). TOTAL_N is the concentration of aquatic nitrogen (mg L\(^{-1}\)) at each reach. CATCHMENT is the total area (km\(^{2}\)) of land upstream from the outlet of each reach (i.e., drainage area).
<table>
<thead>
<tr>
<th>Hypotheses</th>
<th>Independent variables</th>
<th>Hypotheses</th>
<th>Independent variables</th>
<th>Hypotheses</th>
<th>Independent variables</th>
</tr>
</thead>
<tbody>
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<td>1. Biomass will decrease from rural-to-urban</td>
<td>FOREST, GRASS, CROPS, CANOPY, TREES</td>
<td>1. Biomass will decrease from rural-to-urban</td>
<td>FOREST, GRASS, CROPS, CANOPY, TOTAL_N, D_HIGH, D_LOW</td>
<td>1. Biomass will be increasingly net emergent from rural-to-urban</td>
<td>FOREST, GRASS, CANOPY, TREES, TOTAL_N, D_HIGH, D_LOW</td>
</tr>
<tr>
<td>2. Density will decrease from rural-to-urban</td>
<td>D_HIGH, D_LOW, SHRUB, CATCHMENT</td>
<td>2. Density will decrease from rural-to-urban</td>
<td>D_HIGH, D_LOW, SHRUB, CATCHMENT</td>
<td>2. Density will be increasingly net terrestrial from rural-to-urban</td>
<td>D_HIGH, D_LOW, SHRUB, CATCHMENT</td>
</tr>
</tbody>
</table>

Table 2.1.
Table 2.2. The 2006 National Land Cover Database (NLCD) land-cover classes used to populate the 5 LULC categories used in our analyses. The 6th category (WATER/WETLAND) was omitted from analyses because of its limited representation across our study reaches (see Methods).

<table>
<thead>
<tr>
<th>Original LULC variables (NLCD 2006)</th>
<th>Selected LULC categories used in analyses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Developed open space</td>
<td>Low-intensity development (D_LOW)</td>
</tr>
<tr>
<td>Developed low intensity</td>
<td></td>
</tr>
<tr>
<td>Barren land</td>
<td></td>
</tr>
<tr>
<td>Developed medium intensity</td>
<td>High-intensity development (D_HIGH)</td>
</tr>
<tr>
<td>Developed high intensity</td>
<td></td>
</tr>
<tr>
<td>Deciduous forest</td>
<td>Forest (FOREST)</td>
</tr>
<tr>
<td>Evergreen forest</td>
<td></td>
</tr>
<tr>
<td>Mixed forest</td>
<td></td>
</tr>
<tr>
<td>Grassland</td>
<td>Grassland/pasture/hay (GRASS)</td>
</tr>
<tr>
<td>Pasture/hay</td>
<td></td>
</tr>
<tr>
<td>Cultivated crops</td>
<td>Cultivated crops (CROPS)</td>
</tr>
<tr>
<td>Open water</td>
<td>Open water/wetlands (WATER/WETLAND)</td>
</tr>
<tr>
<td>Herbaceous wetlands</td>
<td></td>
</tr>
<tr>
<td>Woody wetlands</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.3. Vegetation characteristics from nearshore vegetation surveys and aquatic nutrient concentrations from water samples at the 12 Scioto River study reaches. SHRUB is the proportion of shrub cover and CANOPY is the proportion of tree canopy cover. TREES is the density of woody stems >10cm dbh. TOTAL_N and TOTAL_P are the concentrations of nitrogen and phosphorous (mg L\(^{-1}\)), respectively. Difference is the change in nutrient concentration between upstream and downstream sampling points of each study reach.

<table>
<thead>
<tr>
<th>REACH</th>
<th>SHRUB</th>
<th>CANOPY</th>
<th>TREES</th>
<th>TOTAL_N</th>
<th>Difference</th>
<th>TOTAL_P</th>
<th>Difference</th>
</tr>
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<td>R1</td>
<td>0.33</td>
<td>0.51</td>
<td>0.15</td>
<td>1.10</td>
<td>-0.52</td>
<td>0.07</td>
<td>-0.02</td>
</tr>
<tr>
<td>R2</td>
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<td>0.82</td>
<td>0.17</td>
<td>0.95</td>
<td>+0.14</td>
<td>0.08</td>
<td>+0.01</td>
</tr>
<tr>
<td>R3</td>
<td>0.51</td>
<td>0.35</td>
<td>0.20</td>
<td>1.12</td>
<td>+0.31</td>
<td>0.06</td>
<td>0.00</td>
</tr>
<tr>
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<td>0.13</td>
<td>0.69</td>
<td>+0.26</td>
<td>0.05</td>
<td>-0.02</td>
</tr>
<tr>
<td>R5</td>
<td>0.06</td>
<td>0.74</td>
<td>0.22</td>
<td>6.02</td>
<td>+0.30</td>
<td>1.04</td>
<td>+0.04</td>
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<tr>
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<td>0.30</td>
<td>0.06</td>
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<td>+0.28</td>
<td>0.54</td>
<td>+0.01</td>
</tr>
<tr>
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<td>0.15</td>
<td>4.10</td>
<td>+1.14</td>
<td>0.28</td>
<td>+0.03</td>
</tr>
<tr>
<td>R8</td>
<td>0.07</td>
<td>0.66</td>
<td>0.30</td>
<td>1.02</td>
<td>-2.01</td>
<td>0.34</td>
<td>+0.09</td>
</tr>
<tr>
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<td>0.00</td>
<td>0.63</td>
<td>0.33</td>
<td>4.27</td>
<td>+0.02</td>
<td>0.39</td>
<td>+0.02</td>
</tr>
<tr>
<td>R10</td>
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<td>0.73</td>
<td>0.26</td>
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<td>+0.19</td>
<td>0.14</td>
<td>+0.05</td>
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<tr>
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<td>0.83</td>
<td>0.28</td>
<td>0.25</td>
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<td>+0.02</td>
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<tr>
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<tr>
<td>SD</td>
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<td>0.22</td>
<td>0.08</td>
<td>2.06</td>
<td>1.14</td>
<td>0.29</td>
<td>0.04</td>
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</table>
Table 2.4. Flux density (individuals m\(^{-2}\) day\(^{-1}\)), flux biomass (mg m\(^{-2}\) day\(^{-1}\)), and mean body size (mg) of invertebrates observed at 12 Scioto-Olentangy study reaches. Net flux refers to the difference of aquatic emergent flux magnitude minus terrestrial invertebrate flux magnitude. Positive values indicate a net flux of aquatic emergent insects from the river; negative values represent a net flux of terrestrial invertebrates into the river.

<table>
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<tr>
<th>REACH</th>
<th>Density</th>
<th>Biomass</th>
<th>Mean size</th>
<th>Density</th>
<th>Biomass</th>
<th>Mean size</th>
<th>Density</th>
<th>Biomass</th>
<th>Mean size</th>
<th>Net flux</th>
<th>Density</th>
<th>Biomass</th>
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<td>11.5</td>
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<td>-5.7</td>
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<td>1.8</td>
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<td>0.2</td>
<td>+16.1</td>
<td>-12.1</td>
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<tr>
<td>R12</td>
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<td>2.2</td>
<td>15.6</td>
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<td>0.4</td>
<td>-8.2</td>
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<td>9.4</td>
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Table 2.5. Retained regression models (ΔAICc ≤ 4) with corresponding AICc scores, Akaike weights (ω_i), and variation explained (R^2). Null models (i.e., intercept only) are also included. See Table 1 caption for independent variable descriptions.

<table>
<thead>
<tr>
<th>Density flux</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>ω_i</th>
<th>P</th>
<th>R^2</th>
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<tr>
<td><strong>Terrestrial</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GRASS(+), D_HIGH(+)</td>
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<td>0.00</td>
<td>0.21</td>
<td>&lt;0.05</td>
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<tr>
<td>CANOPY(-)</td>
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<td><strong>Net</strong></td>
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<td></td>
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<tr>
<td>GRASS(+), TOTAL N(+)</td>
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<table>
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<tr>
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<th>ΔAICc</th>
<th>ω_i</th>
<th>P</th>
<th>R^2</th>
</tr>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
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Figure 2.1. Location and relative proportions of land use and land cover within 100-m riparian buffers at 12 study reaches of the Scioto (R1 and R4-R12) and Olentangy (R2 and R3) Rivers, Ohio, USA. FOREST represents riparian woodlands of deciduous tree and shrub species. CROPS indicate cultivated agricultural croplands of predominantly corn and soybeans. D_HIGH represents medium- to high-intensity urban development (e.g., industrial or commercial) and D_LOW is low-intensity urban development (e.g., residential, parkland, and abandoned parcels). GRASS indicates native grassland, fallow fields, and managed hay. Locations of mainstem dams are also shown.
Figure 2.2. (a) Ordination biplots based on canonical correspondence analysis (CCA) of the data for riparian land cover, nearshore vegetation, and terrestrial invertebrate flux density (a) and flux biomass (b) at the 12 study reaches of the Scioto River system. Biplots are constrained to the most common (sampled at ≥ 6 of 12 reaches) and abundant (≥ 5 individuals where present) taxa (24 of 148 families) for density and the most common and heaviest (≥ 5 mg where present) taxa (23 of 148 families) for biomass.
Figure 2.2. (b) Ordination biplots based on canonical correspondence analysis (CCA) of the data for riparian land cover, nearshore vegetation, and terrestrial invertebrate flux density (a) and flux biomass (b) at the 12 study reaches of the Scioto River system. Biplots are constrained to the most common (sampled at ≥ 6 of 12 reaches) and abundant (≥ 5 individuals where present) taxa (24 of 148 families) for density and the most common and heaviest (≥ 5 mg where present) taxa (23 of 148 families) for biomass.
Figure 2.3. (a) Ordination biplots based on canonical correspondence analysis (CCA) of the data for riparian land cover, nearshore vegetation, aquatic nitrogen concentration, and aquatic emergent insect flux (a) density and (b) biomass at the 12 study reaches of the Scioto River system. Biplots are constrained to the most common (sampled at $\geq 6$ of 12 reaches) and abundant ($\geq 5$ individuals where present) taxa (14 of 27 families) for flux density and the most common and heaviest ($\geq 5$ mg where present) taxa (12 of 27 families) for flux biomass.
Figure 2.3. (b) Ordination biplots based on canonical correspondence analysis (CCA) of the data for riparian land cover, nearshore vegetation, aquatic nitrogen concentration, and aquatic emergent insect flux density (a) and flux biomass (b) at the 12 study reaches of the Scioto River system. Biplots are constrained to the most common (sampled at ≥ 6 of 12 reaches) and abundant (≥ 5 individuals where present) taxa (14 of 27 families) for flux density and the most common and heaviest (≥ 5 mg where present) taxa (12 of 27 families) for flux biomass.
Figure 2.4. A synthesis of the key relationships between reciprocal river-riparian invertebrate fluxes and riparian landscape composition along an urban-rural gradient of the Scioto River system. The thickness of bars represents flux magnitude; narrow sections indicate relatively low magnitudes and wider sections indicate higher magnitudes. “D” is flux density and “B” is flux biomass. Density is the flux of individuals m$^{-2}$ day$^{-1}$ and biomass is mg m$^{-2}$ day$^{-1}$. Net flux refers to the difference of aquatic emergent flux magnitude (i.e., density or biomass) minus terrestrial invertebrate flux magnitude. Positive values indicate a net flux of aquatic emergent insects from the river; negative values represent a net flux of terrestrial invertebrates into the river. Land-cover and nearshore vegetation variables that represent key characteristics of urban and rural riparian landscapes are displayed at the top of the figure. See Table 1 for explanation of land-cover and nearshore vegetation variables.
Chapter 3: Anthropogenic and natural determinants of fish food-chain length in a mid-size river system

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(Formatted for Ecological Applications)
Abstract

Food-chain length (FCL) is a key factor underlying patterns of energy flow and trophic structure in food webs. Natural gradients in resource availability, ecosystem size, and disturbance are thought to govern FCL in rivers. However, anthropogenic influences including landscape modification (e.g., land-cover change) and river regulation (e.g., dams) on FCL remain largely unresolved. We characterized fish-food webs at twelve river reaches distributed across an urban-rural gradient of the Scioto River system (Ohio, USA) to assess the effects of both natural (e.g., ecosystem size, longitudinal position along river) and anthropogenic (e.g., dams, urbanization) factors, as well as the potential influence of food-web structure (e.g., diversity, predator mean body size, intermediate predator richness). Stable isotope-derived estimates of maximum trophic position ranged from 3.66 to 4.35, which is comparable to global values of FCL in rivers. Path analysis models explained 76%-84% of the variation in FCL. Dams negatively influenced FCL largely via elimination of top predator taxa, reduced fish diversity, and shifts in assemblage composition. Agricultural landscapes were negatively related to FCL mainly via indirect positive effects on aquatic nutrients (which negatively influence on FCL) and negative effects on channel width (which positively influence on FCL). FCL was also negatively related to drainage area yet this effect was mediated by the positive influence of drainage area on channel width. Overall, we interpret these results to suggest that human alteration can be the primary determinant of FCL in regulated rivers such as the Scioto. In particular, disruption of hydrogeomorphic gradients integrate changes in both...
energy flow and food-web architecture, thereby shortening FCL and destabilizing food webs.
Introduction

Food-chain length (FCL) is an important measure of food-web complexity as well as a critical driver of ecosystem function and community structure (Pimm 2002, Post 2002a, Post and Takimoto 2007). Multiple environmental factors interact to explain patterns of FCL in aquatic food webs, including resource availability, environmental stability or disturbance, and ecosystem size (Post et al. 2000, Thompson and Townsend 2005, Vander Zanden and Fetzer 2007, Sabo et al. 2009). Collectively, these factors can contribute to an overall lengthening of food chains through addition of top predators or insertion of intermediate taxa (Cohen et al. 1993, Post and Takimoto 2007), and shifts in omnivory (Post et al. 2000). The efficiency of energy transfer through food chains is typically low with approximately 10% on average transferred from prey to consumer (Pimm 2002). Thus, resource availability is thought to influence FCL based on energetic constraints such that more basal energy resources should promote greater FCL (Yodzis 1984). Theoretically, shorter food chains are expected in unstable, frequently disturbed systems (Pimm and Lawton 1977, Sabo et al. 2010), yet empirical evidence has been equivocal (Walters and Post 2008, Warfe et al. 2013). Disturbance can influence FCL through loss of species, especially top predators, or changes in species composition via physical displacement and/or shifts in resource availability (Pimm and Kitching 1988, Marks et al. 2000, Parker and Huryn 2006). Ecosystem size has been shown to be positively associated with FCL in part because habitat availability and heterogeneity, as
well as species richness, tend to increase with ecosystem size (Cohen and Newman 1991, Vander Zanden et al. 1999, Post et al. 2000).

In spite of increased understanding of environmental determinants of FCL in fluvial ecosystems, spatially-explicit riverine food webs remain poorly described (Woodward and Hildrew 2002), which hinders evaluation of the mechanisms driving aquatic food web dynamics, particularly in large stream and river systems that tend to be understudied relative to their smaller counterparts. This is of particular relevance given the physical, ecological, and energetic gradients along which rivers are thought to operate (Vannote et al. 1980, Poole 2002, Thorp et al. 2006). For example, the River Continuum Concept suggests that rivers follow predictable longitudinal gradients in resource availability upon which biotic communities are structured (Vannote et al. 1980). However, there are exceptions to this general framework, particularly in larger systems where access to resources in adjacent floodplains may be critical to riverine biotic communities as sources of energy (Junk et al. 1989, Sedell et al. 1989, Thorp et al. 1998, Tockner et al. 2000) or as critical habitat and refugia for fish and other organisms during specific life-history phases or periods of overbank flow (Bayley 1995, Amoros and Bornette 2002, Sullivan and Watzin 2009).

In addition to natural environmental gradients, rivers worldwide are subject to human landscape modification and river regulation (Paul and Meyer 2001, Allan 2004, Walsh et al. 2005). Both river regulation and alterations in land use and land cover (LULC) have been shown to strongly influence river structure and function (Ward and Stanford 1995, Allan and Johnson 1997, Nilsson and Berggren 2000, Roy et al. 2005,
Roy et al. 2007). River regulation has become ubiquitous in many areas of the world, including the United States where there are over 75,000 dams >2 m in height (Poff et al. 2007). Dams constrain longitudinal and lateral connectivity in rivers and lead to reduced hydrologic variability and floodplain access, and increased retention of sediment, nutrients, and organic matter (Ward and Stanford 1983, Ward and Stanford 1995, Stanley and Doyle 2003, Csiki and Rhoads 2010). Dams and their associated impoundments can shift the relative availability of basal energy resources with subsequent changes to FCL. For instance, Hoeinghaus et al. (2008) concluded that reservoir food webs (versus food webs from non-impounded river reaches) were more complex largely because the presence of phytoplankton created additional trophic links between basal and top consumers. In addition to reduced flow variability, dams also can artificially increase ecosystem size, both of which are purported mechanisms lengthening food chains (Sabo et al. 2010).

Urbanization and conversion to agricultural land cover represent globally-common landscape alterations (Sanderson et al. 2002). The acute effects of urbanization are of particular importance as greater than 80% of the Earth’s human population is projected to live in cities within 50 years (United Nations 2007). Urban landscapes are characterized by impervious surfaces, stormwater conveyance systems, and modified riparian vegetation, all of which facilitate the rapid transport of water, sediment, and chemical pollutants into rivers (Walsh et al. 2005). As a consequence, hydrological regimes tend to be more variable and extreme, water quality can be severely impaired, and habitat heterogeneity tends to be reduced (Paul and Meyer 2001, Konrad and Booth
These disturbances have been shown to influence aquatic food webs in multiple ways. In hydrologically-stable environments, organisms less vulnerable to predation (e.g., sessile, armored grazer macroinvertebrates) might be expected to dominate lower trophic levels, leading to reduced FCL (Power 2006). In contrast, dynamic, stochastic environments might also produce shorter food chains because of the elimination of taxa (Pimm and Kitching 1988, Sabo et al. 2010). For example, McHugh et al. (2010) suggested that disturbance played a role in reducing FCL in streams by limiting the availability of intermediate predators as prey for top predators. The influence of reduced habitat heterogeneity on FCL may also be important in urban systems. Eitzmann and Paukert (2010) found urban river reaches that were characterized by low habitat heterogeneity and reduced fish diversity supported top predators that occupied a relatively lower trophic position than top predators in more heterogeneous, non-urban river reaches.

Likewise, FCL in agricultural rivers should reflect the elevated inputs of pesticides, nutrients, and sediment; loss of riparian forest; increased bank erosion; and modified channel morphology typical of rivers flowing through agricultural landscapes (Lenat 1984, Lenat and Crawford 1994, Johnson et al. 1997). Nutrient inputs [e.g., nitrogen (N) and phosphorous (P)] increase aquatic primary productivity that can subsequently lead to greater productivity at higher trophic levels and support longer food chains (Carpenter et al. 1998). Sedimentation can contribute to both homogenization of benthic habitat and increased water-column turbidity with negative consequences for benthic invertebrate community diversity, aquatic primary productivity, and sight-feeding
fishes (Wood and Armitage 1997, Henley et al. 2000, Sutherland et al. 2002, Sullivan et al. 2006, Sullivan and Watzin 2010). Sediment inputs from agricultural landscapes are particularly important for supporting benthic detrivores, such as gizzard shad, which are common in many impounded larger river systems in the Midwest, USA (Vanni et al. 2005).

Thus, in modified landscapes, which represent approximately 75% of Earth’s habitable land surface (Sanderson et al. 2002), pluralistic explanations related to both natural environmental gradients and anthropogenic change might be expected to exert strong influences on riverine FCL. Our primary objective was to explore the relative influence of LULC, river regulation, and ecosystem size and position (i.e., longitudinal river position) on fish food-web dynamics in a multiuse river system typical of the American Midwest. To do this, we used naturally abundant stable isotopes of carbon (C) and N to derive FCL of fish food-webs at 12 river reaches distributed along approximately 150 km of urban, agricultural, and undeveloped (e.g., forest, grassland, and wetland) landscapes of the Scioto River system, a major tributary of the Ohio River. We used path analysis to investigate the direct and indirect effects of riparian land cover, lateral (i.e., floodplain access) and longitudinal (i.e., dams) connectivity, ecosystem size as a measure of longitudinal position (i.e., drainage area), local habitat size (i.e., channel width), and water quality on FCL. We also described fish assemblage diversity and size structure as additional potential mechanisms related to FCL (see Post and Takimoto 2007).
Although trophic shifts are expected to follow natural longitudinal gradients in rivers (Power and Dietrich 2002), we expected that the combined effects of urbanization, agriculture, and river regulation would represent the dominant environmental determinants of fish FCL, as depicted in our hypothesized path model (Figure 3.1). Whereas recent research has highlighted varied environmental determinants of FCL, empirical evidence has largely been derived from less disturbed systems (e.g., McHugh et al. 2010, Sullivan et al. Submitted). We present novel evidence from a highly modified system that illustrates the strong influences of human landscape modification and river regulation on fish FCL in rivers.

Methods

Study system

The Scioto River flows for 372 km through central and southern Ohio (OH), USA (Figure 3.2), draining a 16,882-km² catchment comprised of agriculture (~69%), forest (~21%), and urban LULC (~9%) landscapes (White et al. 2005). The Olentangy River is the largest tributary of the Scioto, joining the mainstem near downtown Columbus, OH (~1.2 million people; USCB 2010). River regulation (e.g., dams, levees) and extensive urbanization are concentrated within the greater Columbus Metropolitan Area (Figure 3.2), although smaller urban centers are distributed throughout the catchment. South of Columbus, agriculture is the predominant land use, although there are scattered remnants
of remnant riparian forest and grassland patches throughout the Scioto River corridor. This combination of land use in the catchment makes the Scioto an appropriate model system to study the relative effects of natural and anthropogenic gradients on fish food webs.

We used a combination of remotely-sensed data using ArcGIS 10.1 (Esri, Redlands, CA, USA) and ground-truthing to preliminarily assess LULC of the adjacent riparian landscape of 12 study reaches, which represented a range of highly-modified (e.g., urban LULC and dams) to less modified (e.g., rural LULC, no dams) riverine landscapes. Each study reach represented a distinct river segment based on similar valley features and channel morphology. Reaches were ~1,200 m in length (upstream to downstream), which adequately represented variability in flow habitats and surpassed reach lengths commonly suggested for surveying river fish assemblages (Emery et al. 2003).

*Environmental variables*

We used ArcGIS 10.1 to delineate 500-m buffers on both sides of each study reach. Within the extent of the buffer, we calculated the relative proportion of urban (i.e., developed open space, developed low-intensity, developed medium-intensity, and developed high-intensity), agriculture, and natural land cover (i.e., forest and grassland) using the 2011 National Land Cover Database (NLCD; Jin et al. 2013). We considered 500 m to represent a spatial extent sufficient for capturing the influences of human
landscape modification on river ecosystem function and riverine fish assemblages. Our 500 m buffer was chosen because this extent fully incorporated floodplains, the influence of human land cover encroaching into the riparian area, and was broad enough to include some portion of adjacent uplands that likely had effects on the river, especially in reaches where slopes were steeper.

We assessed longitudinal connectivity by counting the total number of dams downstream of each study reach as we considered the cumulative effects of downstream dams as barriers to fish movement from downstream reaches to be a critical factor influencing upstream fish assemblages (Santucci et al. 2005). To assess the degree of lateral, river-floodplain hydrologic connectivity, we measured the areal extent of active floodplains (i.e., floodplain area) at each reach using a combination of GIS and field surveys (Tagwireyi 2014).

To estimate ecosystem size as a measure of longitudinal position, we used the Hydrology Extension in ArcGIS 10.1 to generate drainage area of the catchment from the downstream terminus of each study reach. However, because of the potential influences of adjacent land cover and dams on channel morphology, we also assessed local ecosystem size using a laser rangefinder to estimate bankfull channel width (m) at 3 cross-sections (top, middle, bottom) distributed along each reach using the lower extent of persistent woody vegetation, the flat top of depositional features, and the transition from steep to gentle slopes as indicators of bankfull height (Rosgen 1996, VTDEC 2003).

To assess water quality and aquatic nutrient concentrations we collected 6, 250-mL water samples once at each reach during a stable, low-flow period in late summer or
early autumn during the same year (2010, 2011, 2012, or 2013) in which we surveyed fish assemblages (3 samples collected laterally across 2 channel-spanning transects near the upstream and downstream ends of the reach). We composited samples by upstream and downstream locations separately. Samples were subsequently analyzed for total N (mg L\(^{-1}\)), total P (mg L\(^{-1}\)), and total dissolved solids (TDS; mg L\(^{-1}\)) at the Ohio State University Service Testing and Research Lab (STAR Lab, Wooster, OH, USA).

Food-web variables

From 2010–2013, we surveyed fish assemblages using a generator-powered pulsator boat-mounted electrofisher (5.0 GPP; Smith-Root, Vancouver, WA, USA). To standardize sampling effort, we stratified reaches by bottom, middle, and top portions of the reach and by right bank, mid-channel, and left bank, and subsequently sampled each of these 9 sections for 600 s, for a total of 5,400 s of total electrofishing per reach. We electrofished each reaches once at night, during stable, low-flow periods from late summer to early autumn (Sanders 1992). We held captured fish in an onboard, aerated livewell where all individuals were identified to species, enumerated, measured (mm), and weighed (g). We dispatched 3 to 6 adult individuals from the most common species representing each of the major trophic guilds (Table 3.1) for use in stable isotope analysis. Only adults were retained for isotope analysis in order to minimize ontogenetic diet shifts exhibited in some species (e.g., gizzard shad; *Dorosoma cepedianum*). We transported specimens used for stable isotope analysis on ice to the laboratory where they
were kept frozen until processing. In the laboratory, we removed a small piece of dorsal white muscle tissue from each individual fish specimen, and freeze-dried the tissue for 24 h (Lyophilizer, Labconco Corporation, Kansas City, MO, USA). White muscle was deemed the most appropriate tissue type because it exhibits less variability in isotopic signatures than other tissues and the stable isotope turnover rate is weeks to months, which is sufficiently long to integrate the assimilated resources consumed by fish over the course of our sampling (Hobson 1999). Tissue samples were ground into a fine powder using a mortar-and-pestle and packed into tin capsules.

From our fish assemblage surveys, we calculated species richness and Shannon-Weiner Diversity Index ($H'$) (Shannon and Weaver 1963):

$$H' = - \sum_{i=1}^{R} p_i \ln p_i$$  \hspace{1cm} \text{(equation 1)}

where $p_i$ is the proportional abundance of species $i$.

We also counted the number of species from basal (i.e., only prey), intermediate (i.e., can be prey and predators), and top trophic positions (i.e., only predators) (see Table 3.1). In addition, we calculated mean body size (mm) for all individuals belonging to basal, intermediate, or top trophic positions. Fish predators generally consume other fish as prey when they are <50% of their total length (Lawrence 1958), although body depth of prey is also a key measure of vulnerability to predation (Hambright et al. 1991, Nilsson and Bronmark 2000). Thus, we separated individuals from basal taxa into 2 groups: individuals that were small enough to be available to top and intermediate
predators as prey (hereafter “prey”) and individuals of basal species that were likely sufficiently large to be invulnerable to predation. Select individuals from prey taxa were only considered as vulnerable to top (and intermediate) predators when less than a specified length (e.g., less than 150 mm for deep-bodied or well-defended taxa such as the sunfishes and juvenile catfishes; less than 200 mm for soft-rayed and less deep-bodied fishes such as redhorse sucker species). From the mean body size calculations we derived mean prey:top predator body size ratios.

We collected benthic periphyton 3 times (mid-June, mid-July, and mid-August) from each study reach in staggered across consecutive years during the course of the study (2010-2013). Periphyton was collected by selecting removable benthic substrate particles (e.g., large gravel, cobble, and rocks), brushing algae from the surface onto a tray, and rinsing into an opaque plastic sample jar. Samples from at least 10 different substrate particles were collected from the bottom, middle, and top of each reach. Benthic algae samples were stored on ice and transported to the laboratory. Subsequently, animal material, non-algal detrital material, and filamentous macroalgae were removed from the samples (i.e., leaving predominantly diatoms and other microalgae). Samples were then filtered through a GF/F filter, which were subsequently exposed to HCl fumes for 4 h to remove inorganic carbonates, and dried for 48 h at 60°C (Lorrain et al. 2003).

We collected terrestrial detritus (e.g., leaves from dominant riverbank trees and shrubs) from 8 floating pan traps near the banks on both sides of the channel distributed equidistantly along the entire length of each reach. Pan traps were set for 2 10-d periods (mid-June and mid-August in alternate years) to collect a representative sample of the
terrestrial vegetation entering the river during the study period. In the laboratory, vegetation was sorted into woody and non-woody (e.g., leaves) components and cleaned of any non-plant material. Detrital samples were dried for 48 h at 60°C. Leaves from dominant riparian vegetation types were composited by reach and sampling period and ground to a fine powder using a ball mill grinder. Only non-woody vegetation was used in stable isotope analyses.

*Food chain length and trophic position*

All samples were analyzed for C and N by continuous flow isotope ratio mass spectrometry (Delta PlusXP, Thermofinnigan, Bremen, Germany) at the Washington State University Stable Isotope Core (Pullman, WA, USA). Stable isotope ratios are reported in δ notation as parts per thousand (‰) deviation from an established standard (e.g., Pee Dee belemnite limestone for δ\(^{13}\)C; atmospheric N for δ\(^{15}\)N):

\[
\delta^{13}\text{C or }\delta^{15}\text{N} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right)\right] \times 1000
\]

where \(R = \frac{^{13}\text{C}}{^{12}\text{C}}\) or \(\frac{^{15}\text{N}}{^{14}\text{N}}\).

We used δ\(^{13}\)C and δ\(^{15}\)N values to estimate trophic position (TP) of fishes and FCL of fish food webs (estimated as the maximum TP of the top predator species at each reach) (Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 1999):
\[ TP = \lambda + (\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{base1}} \times \alpha + \delta^{15}N_{\text{base2}} \times (1 - \alpha))/\Delta_n \]  
(equation 2)

where \( \lambda = TP \) of the baseline (i.e., TP = 1 for the primary producers we used as the baselines); \( \alpha = \) the proportion of N acquired from baseline one (i.e., terrestrial detritus); and \( \Delta_n = \) fractionation rate of N [which has been assumed to be 3.4‰ increase across each trophic level (Post 2002b); however, we used the more recently derived estimate of 2.54‰ as our mean N fractionation in TP calculations (see Vanderklift and Ponsard 2003)].

If it is assumed that the movements of C and N through the food web are similar, a simple 2-end-member linear mixing model is sufficient to estimate \( \alpha \):

\[ \alpha = (\delta^{13}C_{\text{consumer}} - \delta^{13}C_{\text{base2}})/(\delta^{13}C_{\text{base1}} - \delta^{13}C_{\text{base2}}). \]  
(equation 3)

Although long-lived bivalve molluscs or snails have been suggested as appropriate baselines (Post et al., 2000) because they represent a time-integrated signature of primary producer \( \delta^{13}C \), the direct use of primary producers is acceptable if they are collected across the range of time that other food-web organisms are being sampled (Post 2002b), as in this study. We used terrestrial detritus (e.g., leaves entering the river from deciduous riparian tree species; \( \delta^{13}C_{\text{base1}} \)) and benthic periphyton (\( \delta^{13}C_{\text{base2}} \)) as our reach-specific baselines.
Statistical methods

We used path analysis (Wright 1921, 1934) to test an *a priori* model regarding the influence of human landscape modification and river regulation on fish food webs (Figure 1). Path analysis is a powerful tool for testing hypotheses, assessing the relative importance of variables within the model, and illustrating causal relationships among variables in ecological applications (Shipley 1997, Shipley 2002). Path analysis was especially appropriate in our study because of its ability to represent direct and indirect relationships among intercorrelated and hierarchically-structured environmental variables. We used the path-model approach to predict FCL of fish food webs from direct and indirect influences of longitudinal position along the river continuum, riparian land-cover composition, and river regulation via physical and water-quality characteristics at the reach scale (i.e., mean channel width, floodplain area, TDS, and total N and P concentrations). We constructed a series of candidate path models, including the overidentified (saturated) model with all variables and all possible pathways based on our hypothesized environment-FCL relationships. We then used an information theoretic approach (Akaike Information Criterion adjusted for small sample size; AICc) to evaluate the relative support for each of our candidate models. We retained all models with ΔAICc ≤ 2, which included the most highly supported models (Burnham and Anderson 2002). Subsequently, we calculated Akaike weights (ωi) to indicate the probability that a model was the best supported among all of the candidate models in the set. We used SPSS AMOS 21 (IBM, Armonk, NY, USA) to construct and analyze path models. Maximum
likelihood was used to estimate path coefficients and evaluate model fit. We used $\chi^2$ test to determine overall model significance (e.g., when $\chi^2$ $p$-value is $> 0.05$ the model is significantly different from the full, saturated model). We also used several indices to judge individual model fit, including the comparative fit index (CFI), goodness-of-fit index (GFI), and root mean square error of approximation (RMSEA) (Hoyle 1995, Schumaker and Lomax 2004).

We complemented our path analysis with simple linear regression to explore the influences of composition and size structure of fish assemblages (e.g., species richness, identity of top predator taxa, mean prey and predator body size, and mean prey:predator body size ratio) on FCL as potential ecological mechanisms underlying the observed environment-FCL relationships. The assumptions of univariate parametric analyses were met. We used JMP 10.0 (SAS Institute Inc., Cary, NC, USA) for regression analyses. Furthermore, we also performed a test for potential spatial autocorrelation (Moran’s $I$) of FCL in R (R Core Team 2014) because of the potential influence on fish food webs of underlying, unmeasured environmental variables linked with the spatial distribution of our study reaches.

**Results**

A wide range of LULC within a 500-m buffer characterized our study reaches, from heavily urban (R1–R4, R7, and R10), to largely agricultural (R5, R6, R9, and R12), to relatively undeveloped (R8 and R11) landscapes (Table 3.2). In addition, downstream
dams impounded R1, R2, and R3. Mean channel width and floodplain area both varied considerably and did not fully align with drainage area. Because of the strong influence of river regulation, channel width did not conform to an upstream-downstream gradient of increasing size. For example, R1 and R3 were as wide, or wider than R9–R11; R4 was the third widest reach; and R7 was the widest. Floodplain area was constrained in highly-modified upstream reaches ($\bar{x} = 0.22 \text{ km}^2$; SD = 0.05) where berms, flow regulation, and urban development and transportation infrastructure were common; greater in broader agricultural valleys of the middle reaches ($\bar{x} = 0.77 \text{ km}^2$; SD = 0.15); and then constrained again as the river entered the unglaciated lower reaches and became more entrenched ($\bar{x} = 0.43 \text{ km}^2$; SD = 0.07) (Table 3.2 and Figure 3.3). Overall, aquatic nutrient concentrations (total N + total P) were higher within agricultural reaches ($\bar{x} = 4.74 \text{ mg L}^{-1}$; SD = 2.00) than at both urban and undeveloped reaches combined ($\bar{x} = 1.46 \text{ mg L}^{-1}$; SD = 1.33). Average total dissolved solids were lowest at reaches in urban landscapes ($\bar{x} = 230.9 \text{ mg L}^{-1}$; SD =36.2) and highest at agricultural reaches ($\bar{x} = 341.5 \text{ mg L}^{-1}$; SD = 58.1), although the highest TDS measurement was from R8, which was heavily forested (likely because of the influence of a tributary entering upstream of the reach that receives effluent from a nearby paper mill).

Fish food webs

We surveyed 3,741 individual fish from 50 species and 3 hybrids across the 12 study reaches. Fish assemblage richness ranged from 20 (R9) to 28 (R3 and R6), although
across all reaches diversity was lowest at R3 ($H' \approx 2.10$) and highest at R6 ($H' \approx 2.79$).

Abundance ranged from 134 (R9) to 815 (R3) individuals per reach. The most abundant species across all reaches was gizzard shad, which accounted for nearly 27% of all fish collected. Golden redhorse (*Moxostoma erythrurum*), bluegill (*Lepomis macrochirus*), freshwater drum (*Aplodinotus grunniens*), smallmouth bass (*Micropterus dolomieu*), smallmouth buffalo (*Ictiobus bubalus*), river carpsucker (*Carpoides carpio*), silver shiner (*Notropis photogenis*), and bluntnose minnow (*Pimephales notatus*) were also common and abundant across most of the study reaches. The sunfishes (e.g., bluegill and smallmouth bass) were relatively more abundant in impounded ($\bar{x} = 216$ individuals per reach) than free-flowing reaches ($\bar{x} = 13$ individuals per reach); whereas other common species were notably absent above dams [e.g., freshwater drum, longnose gar (*Lepisosteus osseus*), smallmouth buffalo].

Trophic position of fishes ranged from 2.21 to 4.35 across the study reaches, with the greatest within-site range of 2.14 at R4. Detritivorous (e.g., gizzard shad) and omnivorous [bluntnose minnow and common carp (*Cyprinus carpio*)] species typically occupied the lowest trophic position (Table 3.3). *Micropterus* species [i.e., largemouth (*M. salmoides*), smallmouth, and spotted bass (*M. punctulatus*)], channel catfish (*Ictalurus punctatus*), and flathead catfish (*Pylodictus olivaris*) were common intermediate predators, although largemouth bass, smallmouth bass, and flathead catfish were top predators at some reaches (R1–R3). Fish FCL ranged from 3.66 (R2) to 4.35 (R4) (see Appendix B); the most common top predators included smallmouth bass, largemouth bass (*Micropterus salmoides*), and flathead catfish (*Pylodictus olivaris*) in
reaches influenced by dams and piscivorous saugeye (*Sizostedion vitreum x S. canadense*) and longnose gar elsewhere.

Most reaches were characterized by a relatively large proportion of the fish assemblage made up of large-bodied basal taxa (e.g., common carp, smallmouth buffalo, and river carpsucker) and thus much of the assemblage was largely invulnerable to predation by other fishes (R12, 37% basal species to R9, 76% basal species). However, at impounded reaches (R1–R3), smaller-bodied taxa represented 63%–81% of the fish assemblage, comprising a large available prey base. Mean body size of top predators ranged according to taxon: largemouth bass at R3 ($\bar{x} = 256.9$ mm; SD = 82.2), smallmouth bass at R2 ($\bar{x} = 262.2$ mm; SD = 65.8), longnose gar at R4 ($\bar{x} = 612.3$ mm; SD = 106.8), and longnose gar at R9 ($\bar{x} = 631.0$ mm; SD = 89.0). Mean body size of prey taxa ranged from less than 95 mm (R6, R9, R10, and R11), where smaller-bodied individuals of common sunfishes [e.g., bluegill and longear sunfish (*Lepomis megalotis*)], minnows (e.g., bluntnose minnow and silver shiner), and juveniles of other common species (e.g., golden redhorse) predominated, to greater than 115 mm (R4, R5, R8, and R12), where larger-bodied sunfishes and gizzard shad were the dominant prey species. The ratio of mean prey size to mean predator size varied from reaches with mean prey size < about 20% of mean predator size (R6, R9, and R10) to reaches with prey and predator closer in relative size (R2, R3, R5, and R7). Mean body size of intermediate predators ranged from < 250 mm (R2, R4, and R5) where relatively smaller-bodied black and white crappie, largemouth, smallmouth, and spotted bass, and white bass comprised the intermediate predator assemblage to > 300 mm at several reaches where larger
channel and flathead catfish occupied intermediate predator trophic positions. Intermediate predators were approximately 60%–80% as large as top predators in general. However, intermediate predators were at least as large or larger than top predators at R3 and R7.

Models and mechanisms

We retained 8 of 19 path models (ΔAICc ≤ 2) (Table 3.4). All retained models were significant (χ²; p-value > 0.05) and most met acceptable levels of model fit (e.g., CFI and GFI > 0.95; RMSEA < 0.05). Models ranked 6–8 failed to reach the 0.05 cutoff for RMSEA and were not considered further. Our 5 retained models accounted for a substantial amount of variation (whole model R² ranged from 0.70 to 0.84) and illustrated complex direct and indirect relationships among environmental predictor variables and FCL (Table 3.4). To capture and highlight the influences of the suite of LULC types in the study system, we focus most of our attention on the strongest models that included each of the predominant LULC types present in the system (e.g., model 1 agriculture, model 3 urban, and model 4 natural; Table 3.4 and Figure 3.4 a–c). In addition, fish FCL was only weakly spatially autocorrelated (Moran’s I; p = 0.103), which we interpret to indicate that, if not for the clustering of dams in and around Columbus, FCL was not controlled by underlying spatial influences.

Overall, dams consistently exerted strong, negative, direct effects on FCL in our models. The indirect effect of dams was negligible as dams in our system had
insignificant influences on channel width, water quality, and aquatic nutrients. Dams did have significant negative effects on floodplain area, however the influence of floodplain area on FCL was largely insignificant. Urban LULC showed positive, albeit insignificant, direct effects on FCL. More importantly, urban LULC had a positive influence on FCL through indirect negative effects on aquatic nutrients and floodplain area both of which (aquatic nutrients in particular) had negative effects on FCL in our system. Although agriculture itself positively influenced FCL, the overall effect of agricultural LULC on FCL was negative via strong indirect pathways leading to elevated aquatic nutrient concentrations and reduced channel width. Channel width was strongly and positively related to FCL throughout our model set. Natural LULC had no significant direct or indirect effects on FCL according to our models. Drainage area was negatively related to FCL through a direct pathway and positively related to FCL through indirect pathways involving channel width (+ relationship) and aquatic nutrients (- relationship). In general, TDS had a negligible positive influence on FCL as evidenced by the overall lack of significant pathways, either directly from TDS to FCL, or via indirect effects of LULC, drainage area, or dams on TDS.

Linear regression results indicated that fish assemblage diversity and trophic structure were potential biotic mechanisms related to FCL. FCL increased with assemblage diversity ($R^2 = 0.37, F = 5.97, p = 0.04$; Figure 3.5 a), intermediate predator richness ($R^2 = 0.38, F = 6.16, p = 0.03$; Figure 3.5 b), and mean top predator body size ($R^2 = 0.35, F = 5.49, p = 0.04$; Figure 3.5 c). Conversely, FCL was negatively related to the proportion of fish assemblage as prey ($R^2 = 0.40, F = 6.55, p = 0.03$; Figure 3.5 d) and
to mean prey:top predator body size ratio ($R^2 = 0.25$, $F = 3.18$, $p = 0.10$; not shown), although only weakly. Mean prey size, mean intermediate predator size, proportion of fish assemblage as top predators, and proportion of fish assemblage as intermediate predators were not associated with FCL ($p < 0.05$).

**Discussion**

Our results from a mid-sized river along an urban-rural landscape gradient showed a complex suite of direct and indirect influences of both anthropogenic and natural environmental factors on food-chain length of fish assemblages. The negative effect of dams, and to a somewhat lesser extent drainage area and nutrient concentrations, and the positive effects of channel width and agricultural LULC emerged as the most important environmental drivers of fish FCL. Fewer intermediate and top predator taxa, relatively small-bodied top predators, and abundant populations of small prey species characterized fish food webs in impounded river reaches. In contrast, those in free-flowing reaches consisted of larger-bodied top predators, greater richness of intermediate and top taxa, and less abundant but more diverse prey assemblages. These patterns are likely in part a function of the impacts of human-mediated environmental disturbances that lead to shifts in riparian landscape composition (from natural to urban or agriculture), physical river characteristics, and water quality, all of which shape the productivity and structure of aquatic communities. Our research illustrates that river regulation is a key factor governing FCL in modified river systems, potentially via shifts in natural
hydrogeomorphic gradients and limiting longitudinal connectivity in river systems. Further, physical river characteristics, specifically drainage area and channel width, and water chemistry both exerted significant direct effects on FCL in our models. In addition, these local physico-chemical factors were also influenced by human landscape modifications in our study system, thus leading to additional indirect effects of human-altered landscapes on fish FCL. Modifications to river ecosystem structure, to the extent which it alters FCL, may have profound consequences for community diversity, stability, and resilience (Pimm 2002).

FCL ranged from 3.66 to 4.35, and falls within ranges reported elsewhere in systems where fish are the top consumers (Post et al. 2000, Pimm 2002, Hoeinghaus et al. 2008). For example, Vander Zanden and Fetzer (2007) reported a mean difference of 0.5 trophic levels between stream and lake food chains from around the world. However, Post et al. (2000) observed a broader range of FCL across systems (~1.5 trophic levels) where increases in ecosystem size were sufficient to allow the addition of a top predator. Changes to fish FCL in our study system were likely via a combination of mechanisms including addition or deletion of top predators, insertion of intermediate predators, and shifts in the degree of omnivory (Post and Takimoto 2007). The addition of top predators such as longnose gar and saugeye to fish assemblages below dams, for instance, led to increased FCL (addition mechanism) and the appearance of additional intermediate predator taxa at R4, R7, and R8 corresponded to the 3 longest food chains in the system (i.e., insertion mechanism). Increased trophic omnivory may also be a plausible mechanism constraining FCL at reaches where top predators are forced to consume
small, lower trophic level prey because of limited availability of more appropriate size prey (e.g., R1–R3, R5, R6, and R9–R11).

River size and longitudinal position

Drainage area has often been reported as a strong positive driver of FCL in fluvial systems with the effects stemming from increased habitat size, greater habitat availability and heterogeneity, and reduced upstream-to-downstream flow variability (Post et al. 2000, Thompson and Townsend 2005, Sabo et al. 2010). Ecosystem size is also positively linked with species richness (in particular addition of top predators), diversity, and productivity, thereby providing a mechanistic understanding of the FCL-ecosystem size relationship (Schoener 1989, Cohen and Newman 1991, Post et al. 2000, Post and Takimoto 2007).

However, we found that drainage area negatively influenced fish FCL. The upstream location of dams within our study system likely confounded the use of drainage area as a measure of ecosystem size relating to longitudinal position. By disrupting the downstream transport of sediment and organic matter, dams can partially reset longitudinal gradients (e.g., Ward and Stanford 1995, Power et al. 1996, Cross et al. 2013) and, thus, reaches downstream of dams do not fully incorporate the upstream drainage area but rather the drainage area at a point beginning below the closest upstream dam. Channel width on the other hand, a local measure of ecosystem sized used in ours and other FCL studies (e.g., McHugh et al. 2010), was positively related to FCL likely for
similar reasons that drainage area is linked with FCL (e.g., greater habitat size leading to greater species richness and diversity, addition of top predators, and enhanced productivity). Ultimately, the application of ecosystem-size as a predictor of FCL is hobbled by the ability to objectively quantify ecosystem size (Hoeinghaus et al. 2008), which can be particularly problematic in highly regulated systems characterized by discontinuous habitat units (Ward and Stanford 1983, Ward and Stanford 1995).

Energy availability in natural systems is thought to operate along a gradient of river size and channel openness (Vannote et al. 1980, Thorp et al. 1998). However, energy availability was unlikely to limit FCL in our study system. Firstly, the Scioto and lower Olentangy are sufficiently wide along their mainstem lengths such that nearly the entire width remains unshaded except for a relatively narrow portion along the banks and thus aquatic primary productivity is not limited by lack of sunlight. Furthermore, almost 70% of the Scioto River Basin consists of agricultural land cover and rivers in agricultural landscapes are often markedly enriched in nutrients via soil erosion and runoff from adjacent croplands (reviewed by Allan 2004). Consistent with this pattern, our path models showed that agriculture had a strong positive effect on N and P concentrations.

Although productivity was unlikely to limit FCL in our system, we expected that elevated nutrient inputs might be expected to enhance local aquatic productivity and lead to longer food chains based on the productivity hypothesis (Townsend et al. 1998, Pimm 2002), yet our models suggested otherwise. Jepsen and Winemiller (2002) found similar results in nutrient-poor versus nutrient-rich tropical systems and suggested increased
trophic omnivory as a likely explanation. In our system, increased omnivory might also be possible. For example, elevated nutrient concentrations could drive aquatic primary productivity, although this production is likely sequestered in the biomass of large-bodied taxa that are invulnerable to predation (e.g., river carpsucker, silver redhorse, smallmouth buffalo), representing a trophic dead-end. These invulnerable taxa were more abundant at agricultural reaches, comprising more than half of the total population, and may intercept and assimilate much of the available resource base, thus limiting the production of prey available to predators and forcing intermediate and top predators to share similar prey (e.g., small-bodied and from lower trophic levels). Most agricultural, high-nutrient reaches where FCL was relatively shorter supported only one top predator (except at R12), providing further evidence of the inefficiency of transport from basal resources to top predators in these high-nutrient systems.

Because we used N and P as indicators of nutrient enrichment, and thus as surrogates for aquatic productivity, this may have limited our ability to draw conclusions for several reasons (although note that Post et al. 2000 used total P as a measure of productivity in lakes). Firstly, our system is unlikely to be nutrient limited based on background measures of nutrient concentrations in streams across the US (Dubrovsky et al. 2010), and thus N and P in the water column may simply be in excess of what is needed to support aquatic primary production. Secondly, aquatic primary productivity also may not be the main pathway of energy transfer from primary consumers through top predators. For example, gizzard shad, a common prey species in our system, are detritivores and consume large quantities of benthic organic sediments (some of which is
aquatic and some of which is terrestrially-derived) (Vanni et al. 2005). Finally, nutrient-rich agricultural runoff may also be laden with fine sediments, herbicides, and pesticides, thus potentially negating the effects of elevated nutrient availability on aquatic primary (and secondary) productivity. Fine sediments, whether embedding larger benthic substrates or suspended in the water column, limit aquatic primary productivity via shading or smothering (Henley et al. 2000). Pesticides, herbicides, and other harmful pollutants linked with agricultural effluents can also have severe consequences for river food webs, including changes in primary productivity (Delong and Brusven 1992) and negative effects of bioaccumulation of toxins in higher trophic level organisms (Kidd et al. 1999, Jardine et al. 2012).

Hydrogeomorphology

Hydrogeomorphic characteristics of rivers have been shown to influence fish assemblages and fish food webs in multiple ways (Power et al. 1996, Townsend et al. 1998, Bunn and Arthington 2002, Hoeinghaus et al. 2007). However, over half of the large rivers in the world are influenced by dams (Nilsson et al. 2005) and as of 1999, 75,000 dams existed in the continental United States, (Graf 1999), with ~28,000 dams in the Midwest and 4,796 in Ohio alone. Dams fragment and disrupt the movement of water, sediment, nutrients, and organisms through a riverine system, with significant effects on geomorphic, chemical, and biological processes that often extend beyond the channel to floodplain and riverine wetland environments (Ligon et al. 1995, Nilsson et al.
The vast majority of all dams are small or lowhead dams (< 4 m in height), which, despite their size, can have pronounced influences on river ecosystems (Santucci et al. 2005, Csiki and Rhoads 2010).

In our study, dams exerted the single greatest effect on FCL across all our models (Figure 3.4 a–c). Moreover, FCL was 7% lower in reaches upstream of dams ($\bar{x} = 3.88$) than in free-flowing reaches ($\bar{x} = 4.19$). This result is in contrast to Hoeinghaus et al. (2008), who showed that FCL in reservoirs tended to be longer than in free-flowing reaches because of additional trophic links via intermediate planktivore pathways, which were largely absent in the non-impounded reaches of their study system. However, in contrast to the large dams (>10 m in height) characterizing Hoeninghaus et al.’s (2008) study, lowhead dams typical of our system were < 4 m in height, and thus differences in planktonic productivity between free-flowing and impounded reaches in our study system may not have been as profoundly different, nor its effect on fish FCL.

We found a distinct difference in fish-assemblage composition and food-web structure between reaches above dams and those downstream of dams. Diversity at impounded reaches was typically lower than undammed reaches and assemblages tended to be numerically-dominated by a few, smaller-bodied, basal species (e.g., bluntnose minnow, juvenile sunfishes, and small gizzard shad). Dams prohibit the passage and upstream establishment of some of the more common top predators found in reaches immediately downstream of dams, such as longnose gar, saugeye, and muskellunge. The apex trophic position at dammed reaches was occupied by species that held intermediate trophic positions elsewhere (e.g., flathead catfish, largemouth bass, smallmouth bass).
FCL was likely constrained at dammed reaches because the taxa that occupied the top predator trophic position were not strict piscivores and therefore consume other non-fish prey (e.g., crayfish), at least to some degree. Based on assemblage composition and isotope information, coupled with limited prey options (e.g., from prey:predator body size constraints and high relative abundances of only a few prey taxa), we infer that top predators at dammed reaches were limited to consuming low trophic level basal prey (e.g., omnivorous bluntnose minnow or detritivorous gizzard shad). Elsewhere, larger-bodied top predators had a greater diversity of prey available to them, including access to prey at higher trophic positions (e.g., benthic invertivores and intermediate predators). Intermediate predators in particular represented an additional trophic linkage between smaller basal taxa and top predators where top predators were sufficiently large to consume intermediate taxa. Note that at R4, which had the highest overall FCL, top predators were sufficiently large enough to consume nearly all of the intermediate predators present at the reach.

Conclusions

Fish food webs in rivers are shaped by myriad environmental influences that dictate assemblage diversity, composition, and productivity (Power et al. 2008, Eitzmann and Paukert 2009, Hoeinghaus et al. 1998, Cross et al. 2013). FCL is an important descriptor of the trophic structure of fish food webs and shifts in FCL can modify assemblage structure via altered trophic interactions, and rates of nutrient cycling and
primary productivity (Deangelis et al. 1989, Pace et al. 1999). Given the importance of FCL, developing a clearer understanding of how human-mediated environmental effects influence assemblage structure and FCL is critical. Here we have shown that dams have an overwhelming negative effect on FCL in a large river system, likely through exclusion of one (or more) top predators, limited intermediate predator richness, and the proliferation of small, basal prey species. We also observed that ecosystem size was an important control on FCL, largely via local measures of channel width rather than measures of drainage area, although channel width was positively influenced by drainage area in our models leading to a positive indirect effect on FCL. Finally, we found effects of riparian landscape composition on FCL, most notably as indirect effects of human-modified land cover on physical and chemical characteristics of the reach.

Several prominent hypotheses have been developed regarding controls on FCL in aquatic food webs, including ecosystem size, resource availability, and disturbance (most commonly connected with measures of flow variability) (Post 2002, Sabo et al. 2009). Although we considered our measures of ecosystem size (drainage area, channel width) and physical environmental disturbances (dams, human modified land cover) to be adequate, our measures of aquatic nutrients may not have captured the full extent of reach-scale productivity (Sabo et al. 2009), thus we were not able to fully assess the role of resource availability on FCL. A more explicit measure of resource availability, such as quantifying the rate of aquatic primary productivity, may refine our conclusions regarding the effects of nutrients on FCL. In addition, the influence of other chemical
parameters could potentially constrain FCL, such as pesticides, heavy metals, and pharmaceutical chemicals.

Our conclusions contribute to an increased understanding of the mechanisms that regulate food-webs by providing insight into the complex, interactive influences of anthropogenic river modification and natural environmental gradients on fish FCL. Most notably we illustrate that the negative effects on FCL, resulting from shifts in fish assemblage composition and trophic structure associated with the disruption of hydrogeomorphic gradients, caused by dams can overwhelm the influences of natural environmental determinants. Given the increasing trend of dam removals across the United States (Graf 2005), our results lend important insights into the potential restoration of functional food-webs following dam removal. Lastly, evidence from the Scioto River, which is representative of mid-sized rivers across the American Midwest, indicates that shifts in food-web architecture, and decreased community stability, both occur along a gradient of human-mediated environmental change, suggesting that dam removal alone may be insufficient for fully restoring fish food webs in similar systems.
Acknowledgements

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Table 3.1. Fish species collected and feeding guilds represented from the 12 Scioto River system study reaches (2010–2013). Species selected for stable isotope analyses indicated with an asterisk (*). Relative TP is relative trophic position; basal taxa do not prey on any other fish species and top taxa are not depredated by any other fish species. Intermediate taxa can be both prey and/or predators.
<table>
<thead>
<tr>
<th>Relative Feeding Guild</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Detritivore</td>
<td>Gizzard shad (<em>Dorosoma cepedianum</em>)</td>
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<tr>
<td></td>
<td>White sucker (<em>Catostomus commersoni</em>)</td>
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<tr>
<td>Herbivore</td>
<td>Bigmouth buffalo (<em>Ictiobus cyprinellus</em>)</td>
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<td></td>
<td>Central stoneroller (<em>Campostoma anomalaum</em>)</td>
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<td></td>
<td>Northern hog sucker (<em>Hypentelium nigricans</em>)</td>
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<tr>
<td>Omnivore</td>
<td>Bluntnose minnow (<em>Pimephales notatus</em>)</td>
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<tr>
<td></td>
<td>Common carp (<em>Cyprinus carpio</em>)</td>
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<tr>
<td></td>
<td>Golden shiner (<em>Notemigonus crysoleucas</em>)</td>
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<td></td>
<td>Highfin carpsucker (<em>Carpodoides velifer</em>)</td>
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<td></td>
<td>Quillback carpsucker (<em>Carpoides cyprinus</em>)</td>
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<td></td>
<td>River carpsucker (<em>Carpoides carpio</em>)</td>
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<td></td>
<td>Sand shiner (<em>Notropis stramineus</em>)</td>
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<td></td>
<td>Smallmouth buffalo (<em>Ictiobus bubalus</em>)</td>
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<tr>
<td>Invertivore (benthic)</td>
<td>Black buffalo (<em>Ictiobus niger</em>)</td>
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<td></td>
<td>Blue sucker (<em>Cycleptus elongatus</em>)</td>
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<td></td>
<td>Dusky darter (<em>Percina sciens</em>)</td>
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<td></td>
<td>Golden redhorse (<em>Moxostoma erythrurum</em>)</td>
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<td></td>
<td>Logperch (<em>Percina caprodes</em>)</td>
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<td></td>
<td>River redhorse (<em>Moxostoma carinatum</em>)</td>
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<td>Shorthead redhorse (<em>Moxostoma macrolepidotum</em>)</td>
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<td></td>
<td>Silver redhorse (<em>Moxostoma anisurum</em>)</td>
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<tr>
<td>Invertivore</td>
<td>Bluegill (<em>Lepomis macrochirus</em>)</td>
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<td></td>
<td>Brook silverside (<em>Labides thalassinus</em>)</td>
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<td>Emerald shiner (<em>Notropis atherinoides</em>)</td>
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<td></td>
<td>Green sunfish (<em>Lepomis cyanellus</em>)</td>
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<td></td>
<td>Hybrid sunfish (<em>Lepomis spp.</em>)</td>
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<td>Longear sunfish (<em>Lepomis megalotis</em>)</td>
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<td>Orange-spotted sunfish (<em>Lepomis humilis</em>)</td>
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<td>Pumpkinseed (<em>Lepomis gibbosus</em>)</td>
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<td>Redear sunfish (<em>Lepomis microlophus</em>)</td>
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<td>Silverjaw minnow (<em>Notropis buccatus</em>)</td>
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<td></td>
<td>Silver shiner (<em>Notropis photogenis</em>)</td>
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<td>Skipjack herring (<em>Alosa chrysocloris</em>)</td>
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<td></td>
<td>Spotfin shiner (<em>Cyprinella spiloptera</em>)</td>
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<td>Yellow bullhead (<em>Ameiurus natalis</em>)</td>
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<td>Invertivore/carnivore</td>
<td>Black crappie (<em>Pomoxis nigromaculatus</em>)</td>
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<td></td>
<td>Channel catfish (<em>Ictalurus punctatus</em>)</td>
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<td></td>
<td>Flathead catfish (<em>Pylodictis olivaris</em>)</td>
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<td></td>
<td>Freshwater drum (<em>Aplodinotus grunniens</em>)</td>
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<td></td>
<td>Hybrid striped bass (<em>Morone saxatilis X M. chrysops</em>)</td>
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<td></td>
<td>Largemouth bass (<em>Micropterus salmoides</em>)</td>
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<td></td>
<td>Rock bass (<em>Ambloplites rupestris</em>)</td>
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<td>Smallmouth bass (<em>Micropterus dolomieu</em>)</td>
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<td>Spotted bass (<em>Micropterus punctulatus</em>)</td>
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<td>White bass (<em>Morone chrysops</em>)</td>
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<td></td>
<td>White crappie (<em>Pomoxias annularis</em>)</td>
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<td>Macro-parasite</td>
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<td>Carnivore (piscivore)</td>
<td>Longnose gar (<em>Lepisosteus osseus</em>)</td>
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<td></td>
<td>Muskellunge (<em>Essox masquinongy</em>)</td>
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<td></td>
<td>Sauger (<em>Stizostedion canadense</em>)</td>
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<tr>
<td></td>
<td>Saugeye (<em>Stizostedion vitreum X S. canadense</em>)</td>
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<td>Shortnose gar (<em>Lepisosteus platostomus</em>)</td>
</tr>
<tr>
<td></td>
<td>Walleye (<em>Stizostedion vitreum</em>)</td>
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</tbody>
</table>

Table 3.1
Table 3.2. Environmental variables used as predictors in path models. The proportion of land use and land cover (LULC) is from the 2011 National Land Cover Dataset within a 500-meter riparian buffer at each of the 12 Scioto River system study reaches (R1–R12). “Urban” is a composite measure of developed open-space, developed low-intensity, developed medium-intensity, and developed high-intensity; “Agricultural” is rowcrop agriculture; and “Natural” is a composite of forest and grasslands.

<table>
<thead>
<tr>
<th>Riparian landscape composition</th>
<th>R1</th>
<th>R2</th>
<th>R3</th>
<th>R4</th>
<th>R5</th>
<th>R6</th>
<th>R7</th>
<th>R8</th>
<th>R9</th>
<th>R10</th>
<th>R11</th>
<th>R12</th>
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</thead>
<tbody>
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<td>Urban LULC</td>
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<th>Water quality-nutrients</th>
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<td>Total dissolved solids (TDS) (mg L⁻¹)</td>
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<td>Mean channel width (m)</td>
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<td>Floodplain area (km²)</td>
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Table 3.3. Trophic position (TP) for common fish species representing trophic guilds and fish food-chain length (FCL) as measured by TP of top predator taxa across all 12 study reaches of the Scioto River system, Ohio (means followed by standard deviations in parentheses).

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<th>Detritivore</th>
<th>R1</th>
<th>R2</th>
<th>R3</th>
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<th>R5</th>
<th>R6</th>
<th>R7</th>
<th>R8</th>
<th>R9</th>
<th>R10</th>
<th>R11</th>
<th>R12</th>
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<td>Gizzard shad (Dorosoma cepedianum)</td>
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<td>2.67 (0.40)</td>
<td>3.11 (0.17)</td>
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<td>-</td>
<td>2.64 (0.12)</td>
<td>2.97 (0.11)</td>
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<tr>
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<td>2.84 (0.09)</td>
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<td>2.49 (0.09)</td>
<td>2.21 (0.07)</td>
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<td>2.40 (0.08)</td>
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<tr>
<td>Golden redhorse (Moxostoma erythrurum)</td>
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<td>3.04 (0.10)</td>
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<td>2.83 (0.21)</td>
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<td>Saugeye (Esox lucius x E. macrourus)</td>
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Table 3.4. Eight (of 19) retained path models for the direct and indirect effects of drainage area, dams, LULC, physical channel characteristics, and water quality on fish FCL in the Scioto system, OH. The full model is reported for comparison. We used a model-selection approach (AICc) to select the most highly-supported models based on ΔAICc (< 2) and Akaike weight (ωᵢ). All models were significant (p-value from χ² test > 0.05) and accounted for a substantial proportion of variation in FCL. We also used several indices to judge individual model fit, including the comparative fit index (CFI), goodness-of-fit index (GFI), and root mean square error of approximation (RMSEA).

Models 6–8 did not meet the goodness-of-fit criteria.

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<th>R²</th>
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<th>δAICc</th>
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Figure 3.1. Hypothesized path model of direct and indirect effects of riparian land use/land cover (LULC), ecosystem size (drainage area and channel width), longitudinal (dams) and lateral connectivity (floodplain area), and water quality [total dissolved solids (TDS) and total nitrogen (N) and phosphorous (P) concentrations] on food-chain length (FCL) of riverine fish food webs. One-headed arrows indicate a causal link and two-headed arrows indicate a correlation with no causality implied.
Figure 3.2. Locations of the 12 Scioto River system study reaches (Ohio, USA) and the relative proportions of land use and land cover (LULC) in adjacent 500-m buffers. Urban land cover is split into high-intensity development (dark red) and low-intensity development (pink) and natural land cover is split into forest (green) and grassland (yellow). LULC derived from the 2011 USGS National Land Cover Dataset.
Figure 3.3. Relationship between drainage area (km$^2$) and mean channel width (m) (left axis) and floodplain area (km$^2$) (right axis). The relationships were not significant ($p > 0.05$). Points to the left of the vertical bar are study reaches located upstream of dams.
Figure 3.4. Path diagrams for the top 3 (figures a, b, and c) candidate path models (of 19) from an information theoretic model-selection approach (AICc). Natural land use/land cover (LULC) showed no significant effect on FCL, either directly or indirectly, however, we included it in path model c as a reference point when comparing with the other models (a and b). Each pathway is labeled with a standardized partial regression coefficient indicating the strength of the relationship. One-headed arrows indicate an assumed causal link and two-headed arrows indicate a correlation with no causality implied. \( R^2 \) values above the model indicate the total variance explained by the model.
Figure 3.4 (a-c).
Figure 3.5. Relationships between (a) fish assemblage diversity and fish FCL ($R^2 = 0.37$, $F = 5.97, p = 0.04$), (b) intermediate predator species richness and fish FCL ($R^2 = 0.38, F = 6.16, p = 0.03$), (c) mean size of top predator and fish FCL ($R^2 = 0.35, F = 5.49, p = 0.04$), and (d) the proportion of fish assemblage as prey and fish FCL ($R^2 = 0.40, F = 6.55, p = 0.03$). Dashed lines indicate 95% confidence curves.
Figure 3.5 a.

Figure 3.5 b.
Chapter 4: Aquatically-derived energy fuels terrestrial food webs in a mid-size regulated river system

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Abstract

Rivers are increasingly recognized as subsidizing adjacent terrestrial food webs, largely via depredation of aquatic organisms (e.g., emergent insects, crayfish) by terrestrial consumers. However, because these prey organisms assimilate both aquatic (e.g., benthic algae, phytoplankton) and terrestrial (e.g., leaves from riparian vegetation) primary production, river subsidies to terrestrial consumers may represent a combination of aquatic and terrestrially-derived energy. To date, the explicit contribution of aquatic energy to terrestrial consumers has not been fully explored, particularly in the context of larger streams and rivers, where both benthic algae and phytoplankton might be expected to be of quantitative importance to aquatic invertebrates, and in turn, to terrestrial food webs of which they are a component. Empirically estimating the contribution of aquatically-derived energy to terrestrial food webs is a critical step in further understanding subsidy dynamics in river systems. At 12 reaches along a 150-km segment of the Scioto River (Ohio, USA), a 6th order tributary of the Ohio River, we quantified the relative contribution of aquatic energy from both benthic algae and phytoplankton to a suite of terrestrial riparian consumers that spatially integrate the landscape across distinct spatial extents through their foraging activities (tetragnathid spiders, rove beetles, adult damselflies, riparian swallows, and raccoons). In order to explicitly quantify the relative contribution of aquatically-derived energy to terrestrial consumers we used naturally abundant stable isotope measurements ($\delta^{13}$C and $\delta^{15}$N) from benthic algae, phytoplankton, and terrestrial vegetation, which enabled us to evaluate both the
contribution of aquatic energy to terrestrial food webs, as well as the extent to which this energy extends into terrestrial landscapes. Overall, we found that terrestrial consumers obtained a greater proportion of their energy from aquatic (65%) than from terrestrial (35%) sources. In particular, shoreline tetragnathid spiders obtained more energy from aquatic sources (76%) than did wider-ranging swallows (67%) and raccoons (59%). Collectively, benthic algae contributed 33% and phytoplankton 32% to terrestrial consumers. Swallows and rove beetles obtained less energy from phytoplankton (18% and 22%, respectively) than did tetragnathid spiders (47%) and damselflies (45%). Taken together our findings show that aquatic-derived energy is a critical resource for terrestrial food webs and that both benthic algae and phytoplankton are important pathways in mid-size rivers. We also show that river-derived aquatic energy contributes to terrestrial consumers across broad spatial scales and may be an important landscape-scale energetic linkage between rivers and upland habitats.

*Key words:* Scioto River, aquatically-derived carbon, food web, riparian, spatial, phytoplankton, mid-size river
Introduction

Streams and rivers have traditionally been viewed as recipients rather than sources of energy, whereby inputs of terrestrial plant material and invertebrates fuel aquatic food webs (Vannote et al. 1980, Nakano et al. 1999, Power et al. 2004). Reciprocal energy fluxes (i.e., aquatic to terrestrial), however, are increasingly recognized as subsidizing terrestrial consumers including spiders, beetles, lizards, bats, and birds largely via larval insects that emerge from the stream as winged adults (hereafter “emergent insects”) (Sabo and Power 2002, Sanzone et al. 2003, Paetzold et al. 2005, Fukui et al. 2006, Alberts et al. 2013). For example, emergent insects have been reported to comprise 50%–100% of the diets of riparian spiders in small streams (Henschel et al. 2001, Kato et al. 2003, Sanzone et al. 2003), and 50%–80% of the diets of predatory riparian beetles in both small streams (Paetzold et al. 2005) and larger systems (Hering and Plachter 1997). Emergent insects are also widely recognized as important constituents in the diets of riparian aerial insectivorous birds such as tree swallows (*Tachycineta bicolor*), where they can make up 50%–85% of swallow diet (Blancher & McNicol 1991, Wayland et al. 1998, Alberts et al. 2013). Aquatic-to-terrestrial subsidies of crayfish can also be important energetic resources for larger predators, such as kingfishers, herons, otters, and raccoons, which are integral members of broader river-riparian food webs (Greenwood 1982, Manning 1990, Kelly 1996, Leberg and Kennedy 1998, Clavero et al. 2003, Gehrt 2003, Sullivan and Rodewald 2012).
Although many aquatic insect taxa feed primarily on benthic algae (e.g., grazers), including diatoms, others rely heavily on suspended algae (i.e., phytoplankton), terrestrially-derived detritus, or a combination of both aquatic and terrestrially-derived food sources (e.g., collector-gatherers) (Rounick et al. 1982, Cummins et al. 1989). Likewise, crayfish are highly omnivorous and often consume substantial quantities of terrestrial detritus and aquatic macrophytes (France 1996, Thorp et al. 1998, Correia and Anastacio 2008). Thus, both emergent insects and crayfish can subsidize terrestrial food webs with a mixture of both “recycled” terrestrially-derived energy as well as aquatically-derived energy (Iwata 2007, Gratton et al. 2008, Kraus and Vonesh 2012).

Despite our current understanding of stream subsidies to terrestrial food webs (reviewed in Baxter et al. 2005, Sullivan and Rodewald 2012), the quantitative importance of aquatically-derived C from benthic algae is not well resolved — although might be expected to be appreciable given that benthic algae (and diatoms in particular) are highly productive and thought to be higher in nutritional quality relative to most terrestrially-derived detritus (Power 1984, Hanson et al. 1985, Jackson and Fisher 1986). Furthermore, the potential contribution of aquatically-derived energy from phytoplankton to terrestrial food webs has also not been explicitly considered in larger streams and rivers but could be important in cases where the role of planktonic primary production supports a significant amount of aquatic secondary production (Thorp et al. 1998, Thorp and DeLong 2002, DeLong 2010). DeLong and Thorp (2006), for example, indicated that suspended algae represented the predominant contribution to diets of primary consumers (e.g., common collector-gatherers including Chironomidae and net-spinning
hydropsychid caddisflies) in the upper Mississippi River. Although generally considered more important in large rivers, phytoplankton can also be locally important for aquatic consumers in smaller systems where backwaters, eddies, and impounded sections can serve as nurseries for phytoplankton and as potential sources to downstream areas (Schiemer et al. 2001, Thorp and DeLong 2002).

Collectively, therefore, both benthic algal and planktonic compartments of river food webs may be important sources of energy for recipient terrestrial food webs. Quantitatively addressing the cross-habitat contribution of aquatic production is therefore a critical step in holistic food-web ecology and might be particularly important in large streams to mid-size rivers, where both benthic and planktonic primary production are expected to contribute to aquatic food webs. Aquatic emergent macrophytes may also be a source of aquatically-derived energy to terrestrial consumers via crayfish depredation by terrestrial predators. Additionally, whereas most studies in fluvial systems have highlighted the consequences of cross-boundary energy exchange for habitats and organisms at, or within a short distance of, the aquatic-terrestrial interface (reviewed by Baxter et al. 2005, Richardson et al. 2010), assessing how far the influence of aquatic energy extends beyond the water’s edge (i.e., through movement of consumers at different spatial scales) is a highly-relevant question to food-web ecology at the landscape scale. In a recent synthesis, Muehlbauer et al. (2014) concluded that although most aquatic food resources were used by terrestrial consumers within a couple meters of the channel, the availability and use of these aquatic resources by terrestrial consumers can extend over 0.5 km inland from the channel. However, the explicit contribution of
aquatically-derived energy via aquatic primary production to terrestrial consumers was not estimated.

Natural longitudinal gradients in stream size, shading, flow variability, sediment distribution, and floodplain access structure aquatic primary consumer communities as well as the productivity and nutritional quality of aquatic (benthic algae, phytoplankton, and macrophytes) versus terrestrial energetic sources (Pingram et al. 2012). These natural gradients ultimately shape the relative importance of different basal food sources transported from aquatic to terrestrial food webs. For example, channel canopy cover both regulates aquatic primary productivity and provides inputs of terrestrial detritus, which together can shift the relative proportion of aquatically- versus terrestrially-derived energy to terrestrial consumers via differential consumption and assimilation of these basal food resources by emergent insects and crayfish. The relative importance of benthic algae versus phytoplankton is also likely to shift based on longitudinal position and river size, with phytoplankton of greater importance to food webs in larger rivers (DeLong and Thorp 2006). However, anthropogenic disturbances can disrupt natural environmental gradients and shift the ratio of terrestrial consumer reliance on aquatic versus terrestrial prey. For example, urban-induced shifts in hydrogeomorphology and water quality can lead to reduced aquatic invertebrate diversity with communities dominated by tolerant and non-insect taxa (Roy et al. 2003, Johnson et al. 2013), many of which do not emerge from water as part of their life cycles (e.g., amphipods, oligocheates, snails) and thus are not available to most terrestrial consumers. In addition, river regulation (i.e., dams) constrains flow variability, promoting phytoplankton production (Grobelaar and Toerien...
1985, Kendall et al. 2001, Sullivan et al. 2001), and potentially reducing aquatic consumer reliance on terrestrial energy inputs.

In the present study, we evaluated the contribution of aquatically-derived energy to a suite of terrestrial consumers common to riparian areas (e.g., adult damselflies, rove beetles, tetragnathid spiders, riparian swallows, and raccoons) at 12 river reaches distributed along 150 km of the Scioto River system, Ohio, USA. Our primary objective was to quantify, using natural abundance stable isotope analyses ($\delta^{13}$C and $\delta^{15}$N), the contributions of aquatic-derived energy from both benthic algae and phytoplankton to riparian consumers that spatially integrate the landscape at different spatial scales. Riparian tetragnathid spiders, for instance, assimilate aquatic energy largely at the aquatic-terrestrial interface (Henschel et al. 2001, Kato et al. 2003, Sanzone et al. 2003). In contrast, riparian swallows tend to forage within 250 m to 400 m from their nest sites during the breeding season (Quinney and Ankney 1985, Dunn and Hannon 1992, Robertson et al. 1992, McCarty and Winkler 1999), potentially consuming both aquatic and terrestrial prey. Raccoons are also known to travel relatively long distances, sometimes several kilometers, between various habitats during nightly feeding forays (Greenwood 1982). Sampling these spatially-integrating riparian consumers allowed us to produce empirical estimates of the contribution of aquatic energy at increasing spatial extents (i.e., from spiders to raccoons) from the river channel.

In addition, we sought to align our findings with both natural environmental gradients in river systems (e.g., stream size, relative longitudinal position, canopy cover) and human modifications (e.g., dams, floodplain access, water quality). Our study
system, which extended along an urban-rural landscape gradient, allowed us to explore the influence of human modifications on the contribution of aquatically-derived energy to terrestrial food webs, including the relative contribution of phytoplankton versus benthic algae.

Because riparian consumers are often highly reliant on aquatic subsidies, and aquatic food webs in intermediate to large river systems are thought to be predominantly fueled by autochthonous production in many cases (DeLong et al. 2001, Thorp and DeLong 2002; but see Zeug and Winemiller 2008 for alternative results), we predicted that terrestrial consumers would be highly connected to aquatic resources and obtain a relatively greater proportion of their energy from aquatic than terrestrial primary producer pathways. We anticipated that aquatically-derived energy would vary across reaches in response to physical, chemical, and land-cover characteristics. In particular, we hypothesized that terrestrial consumers would assimilate more aquatic energy at wider reaches and along reaches with higher nutrient concentrations (N and P) – conditions that likely enhance aquatic primary productivity. Because of reduced flow variability and increased pool habitat in impounded reaches, we predicted that phytoplankton would contribute a greater proportion of aquatic energy to terrestrial consumer diets at dammed reaches. Finally, we hypothesized that terrestrial consumers with sedentary feeding strategies (tetragnathid spiders) or limited dispersal ability (rove beetles) would obtain a greater proportion of their energy from aquatic sources because of their being confined to nearshore foraging locations. In contrast, we predicted that aquatically-derived energy
would contribute less to wider-ranging consumers that more broadly integrate both aquatic and terrestrial food sources into their diets (riparian swallows and raccoons).

Methods

Study system

The Scioto River flows for 372 km through central and southern Ohio, USA (Figure 4.1), draining a 16,882-km² catchment comprised of agricultural (~69%), forested (~21%), and urban (~9%) land use and land cover (LULC; White et al. 2005). The Olentangy River is the largest tributary of the Scioto, joining the mainstem near downtown Columbus, OH, USA (~1.2 million people; USCB 2010).

From 2010–2013 we conducted food-web research at 12 study reaches along a 150-km length of the Scioto River system extending from just north of Columbus, OH to shortly before the confluence with the Ohio River (Figure 4.1). Each reach was ~1,200 m in length and varied considerably in riparian landscape composition, water chemistry, and physical river characteristics (Table 4.1; see Appendix C for detailed methods regarding the measurement and calculation of environmental variables). Drainage area ranged from 1,348 km² to 14,679 km². Reaches 1–3 (i.e., R1–R3) were impounded by downstream dams; R4 was located at the southern extent of the city of Columbus ~1,000 m downstream of the farthest downstream dam in the system (Figure 4.1). Mean bankfull channel width ranged from approximately 50 m (R2, R5, and R6) to over 150 m (R7).
Because of the strong influence of river regulation, channel width did not conform to an upstream-downstream gradient of increasing size. For example, R1 and R3 were as wide, or wider than R9–R11; R4 was the third widest reach; and R7 was the widest. Floodplain area was constrained in highly-modified upstream reaches ($\bar{x} = 0.22$ km$^2$; SD = 0.05) where berms, flow regulation, and urban development and transportation infrastructure were common; greater in broader agricultural valleys of the middle reaches ($\bar{x} = 0.77$ km$^2$; SD = 0.15); and then constrained again as the river entered the unglaciated lower reaches and became more entrenched ($\bar{x} = 0.43$ km$^2$; SD = 0.07).

Riparian landscape composition of the reaches ranged from urban development (R1–R4, R7, and R10) to extensive agriculture within the adjacent riparian zone (e.g., 100-m buffer: R5, R9, and R12) and/or at broader scales (e.g., 500-m buffer: R6, R8, and R10). Although riparian forest was present to some degree at all reaches, field surveys revealed that forest cover was largely confined to a relatively narrow band (<50 m) in urban and agricultural landscapes. In addition, riparian forests in urban reaches consisted of a dense understory of invasive Amur honeysuckle (*Lonicera maackii*). Open grassland was absent from R1–R4 but comprised a substantial proportion of the undeveloped land cover at several reaches (R5, R7–R9, and R11).

Total dissolved solids (TDS) and dissolved oxygen (DO) tended to be lower in impounded and/or urban-influenced reaches (R1–R4, R7, and R10: TDS, $\bar{x} = 240.4$ mg L$^{-1}$, SD = 39.9; DO, $\bar{x} = 11.19$ mg L$^{-1}$, SD = 2.37) than elsewhere (“non-urban/non-impounded” reaches: TDS, $\bar{x} = 368.8$, SD = 75.3; DO, $\bar{x} = 12.56$, SD = 1.49). In contrast, pH was similar across the 12 study reaches. Reaches within largely agricultural
landscapes (R5–R7, R9, R10, and R12) exhibited higher nutrient concentrations (total N, \( \bar{x} = 4.260 \text{ mg L}^{-1}, \text{SD} = 1.494 \); total P, \( \bar{x} = 0.418 \text{ mg L}^{-1}, \text{SD} = 0.345 \)) than elsewhere (total N, \( \bar{x} = 0.852 \text{ mg L}^{-1}, \text{SD} = 0.335 \); total P, \( \bar{x} = 0.115 \text{ mg L}^{-1}, \text{SD} = 0.109 \)).

*Primary producers*

We performed coordinated collections of aquatic primary producers three times (mid-June, mid-July, and mid-August) at each study reach. We staggered our collections across three successive years (2010–2013) to capture interannual variability and aligned our primary producer collection activities with those of emergent insects, crayfish, and terrestrial riparian consumers. We collected benthic algae by brushing attached algal growth from the surfaces of large gravel, cobble, and rocks onto a tray and rinsing into an opaque plastic sample jar following Reavie et al. (2010). We obtained algal samples from at least 10 different substrate particles collected at the bottom, middle, and top of each reach (30 samples total). Benthic algal samples were stored on ice and transported to the laboratory, where they were rinsed with distilled water and picked clean of any animal material, non-algal detrital material, and filamentous algae. For phytoplankton, we collected a 250-mL bulk sample of water just below the surface from the top, middle, and bottom of each reach. We scheduled collections to coincide with low-flow periods to minimize the presence of suspended detrital material in the samples. Water samples were stored on ice in opaque plastic containers for transport to the laboratory, where samples were combined by reach (750 mL total) and filtered through a sieve (200-μm mesh) to
remove any larger particles consisting of terrestrial plant or animal material. Likewise, we collected emergent macrophytes during the same timeframe by selecting 10–15 leaves from several different individual plants from emergent macrophyte beds at each reach. In the lab we thoroughly rinsed macrophyte samples with distilled water to remove any sediment or non-plant material.

We collected terrestrial vegetation from 8 floating pan traps (0.4-m²) deployed for two 10-d periods (mid-June and mid-August) and staggered by year over the course of the study. Pan traps were deployed near the bank on both sides of the river and were evenly distributed along the length of the reach. In the laboratory, we sorted vegetation into woody and non-woody (e.g., leaves) components and removed any non-plant material. The predominant nearshore riparian vegetation collected in our pan traps included American sycamore (*Platanus occidentalis*), boxelder (*Acer negundo*), Eastern cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanica*), silver maple (*Acer saccharinum*), and Amur honeysuckle (at urban reaches).

*Primary aquatic consumers — emergent insects and crayfish*

We collected adult aquatic insects over two 10-d sampling periods (once in early summer and once in late summer) over the course of three years. Sampling was staggered so that “early” and “late” sampling efforts were conducted in different years at each of the study reaches to capture both seasonal as well as potential annual variation in invertebrate communities. At each reach, we deployed 6 pyramid-style floating
emergence traps (1-m²) following Alberts et al. (2013). Traps were deployed in the predominant flow habitats (e.g., pool, riffle, and run) represented in each study reach and distributed along the entire longitudinal extent of the reach. We stored and transported emergent trap samples in ethanol (70%). We identified and enumerated all invertebrates to family. Insects were then dried for 48 h in a drying oven (60° C) and weighed (by family for each reach) to the nearest 0.1 mg (Sanzone et al. 2003, Akamatsu et al. 2007). From these data, we calculated emergent insect abundance (number) and biomass (mg) for each reach. We also processed the most common and abundant emergent insect taxon across all reaches — Chironomidae (midges) — for subsequent stable isotope analysis (see following section on stable isotope analysis for details). We estimated the potential availability of aquatically-derived C via emergent insect transport to terrestrial consumers by multiplying the biomass of adult chironomids, which composed 52%–93% (\(\bar{x} = 68.7\%\)) of emergent insect biomass across the study reaches, by their mean relative proportion of aquatic C as inferred from stable isotope analysis.

We collected rusty crayfish (Orconectes rusticus), the most common crayfish in the study system, with commercially available conical crayfish traps (400-mm x 200-mm, 25-mm openings; Plano Molding Co., Plano, IL, USA). At each reach we set 5 unbaited traps in common crayfish habitat (e.g., rocky substrates, large wood, adjacent to macrophytes beds). We checked traps daily until a minimum of 4–6 individual crayfish from each reach were collected. Specimens were transported to the laboratory on ice where they were subsequently frozen until stable isotope analysis.
Secondary terrestrial consumers

We collected a suite of secondary terrestrial consumers over the same temporal period as our collections of primary producers. Terrestrial consumer taxa were selected to be representative of common riparian taxa in the study system as well as to reflect taxa that integrated the riparian landscape across spatial scales (Figure 4.2).

We used floating pan traps (see terrestrial vegetation collection methods) to collect terrestrial invertebrate secondary consumers along the river’s edge. Pan traps were partially filled with water and a small amount of soap, which acted as a surfactant to effectively trap invertebrates (Greenwood et al. 2004, Meyer and Sullivan 2013). We selected rove beetles (Staphylinidae), tetragnathid spiders (Tetragnathidae), and narrow-winged damselflies (Coenagrionidae) because these taxa represented the most common and abundant predatory invertebrates surveyed in our study system and are known to depredate emergent insects. Although larval damselflies are aquatic, we classified adults as terrestrial consumers because following emergence they live the remainder of their adult stage in the terrestrial environment. All invertebrates were preserved in 70% ethanol in the field, transported to the laboratory, and identified to family.

We captured aerial insectivorous birds (riparian swallow species; Hirudinidae) from each reach using mist nets or nest boxes (see Alberts et al. 2013 for details relative to nest-box methodology). Based on observations of local swallow behavior and flight patterns, we positioned mist nets (2.7 m x 12 m, 30 mm mesh) in the most likely locations (i.e., near shore, across sections of the river) to intercept birds at each reach. We
set and monitored mist nets during periods of greatest bird activity (e.g., morning and afternoon) and immediately removed any bird intercepted by the net. All bird collections were conducted during the breeding season (approximately June–July in the study area; 2010–2013) as daily movement patterns of swallows are constrained to areas around the nest during this time. The swallow species [bank (*Riparia riparia*), cliff (*Petrochelidon pyrrhonota*), northern rough-winged (*Stelgidopteryx serripennis*), and tree (*Tachycineta bicolor*) swallows] of our study are obligate aerial insectivores that breed in river-riparian ecosystems offering appropriate nesting sites (e.g., tree cavities, vertical river banks, and bridges; Robertson et al. 1992, Brown and Brown 1995, DeJong 1996, Garrison 1999). We banded all captured birds with aluminum USFWS size 0 bands (bank and northern rough-winged swallows) or size 1 bands (cliff and tree swallows). We drew blood from the jugular vein of adult swallows for use in stable isotope analysis following Sullivan and Vierling (2012) and Alberts et al. (2013). We revisited each reach and continued to capture birds until we collected blood from at least 3–6 individuals (except at R5 where we were only able to capture 2 birds). We stored blood in centrifuge tubes in 70% ethanol for transport to the laboratory.

We trapped raccoons in Tomahawk box traps (Tomahawk Live Trap Co., Tomahawk, WI, USA), baited with marshmallows and anise extract, during July and August 2012–2014. Bait was only used as an attractant and was unavailable for raccoon consumption. We deployed 4 traps at night in the riparian area along the length of each reach and within 50 m of the river and checked traps at dawn the following morning. We used an intramuscular injection of Telazol to immobilize captured raccoons following
Gehrt et al. (2001). During the period of immobilization, we drew blood from the jugular vein. All trapping and handling of raccoons followed the guidelines of the American Society of Mammology (Sikes et al. 2011). All research activities involving live animals were conducted under state (Ohio Department of Natural Resources Wild Animal Collection Permit 15-49) and federal permits (USGS Federal Bird Banding Permit 23515) and approved by The Ohio State University Institutional Animal Care and Use Committee (Protocols: 2009A0215, 2009A0215-R1, 2011A00000049, 2011A00000049-R1).

**Stable isotope analysis**

For benthic algae and phytoplankton, we filtered samples through filter paper (GF/F) and subsequently exposed filters to concentrated HCl fumes for 4 h in a glass desiccator to remove carbonates (CO$_2^-$) from the samples, which can potentially have a confounding effect on $\delta^{13}$C signatures (Lorrain et al. 2003). Following acid fumigation, we dried the filters containing the benthic algae and phytoplankton samples in a drying oven for 48 h at 60° C, then scraped the concentrated samples from the surface of the filters into pre-weighed tin capsules for isotope analysis. We composited macrophyte leaves by reach and sampling period and then dried the composite samples at 60° C for 48 h. For terrestrial vegetation, leaves were composited from dominant riparian vegetation (collected from floating pan traps) for each reach and dried at 60° C for 48 h. We used a ball-mill grinder or a mortar and pestle to homogenize terrestrial vegetation.
and macrophyte samples into a fine powder. We transferred all dried and homogenized vegetation samples into pre-weighed tin capsules for isotope analysis.

We separated the desiccated Chironomidae by reach and by sampling period into 2 bulk samples per reach. We then homogenized each sample separately and processed 3 per reach. We removed abdominal muscle tissue from 3–4 crayfish per reach and subsequently freeze-dried (Lyophilizer, Labconco Corporation, Kansas City, MO, USA) the tissue for 24 h. We dried all swallow and raccoon blood samples from each reach for 48 h at 60° C. We used a mortar and pestle to homogenize Chironomidae, crayfish, swallow, and raccoon sample materials into a fine powder. We then transferred all dried, homogenized, and powdered tissue and blood samples into pre-weighed tin capsules for isotope analysis.

All samples were analyzed for C and N content and isotopic signatures by continuous flow elemental analysis isotope ratio mass spectrometry (Delta PlusXP, ThermoFinnigan, Bremen, Germany) at the Washington State University Stable Isotope Core (Pullman, WA, USA). Stable isotope ratios are reported in δ notation as parts per thousand (‰) deviation from an established standard (e.g., Pee Dee belemnite limestone for δ¹³C; atmospheric nitrogen for δ¹⁵N):

\[
\delta^{13}C \text{ or } \delta^{15}N = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000
\]

where \( R = ^{13}C/^{12}C \) or \(^{15}N/^{14}N\).
Food-web analysis

We used a Bayesian mixing model approach to estimate the relative contribution of aquatic energy sources to terrestrial consumers. Bayesian mixing models are considered an improvement over linear models in that they are able to account for uncertainty and variation in stable isotope source values and trophic discrimination factors (Parnell et al. 2013). In addition, unlike linear models, Bayesian mixing models provide true probability distributions of the relative contribution of different sources to consumers (Layman et al. 2011). The limited δ¹³C separation between American water willow (*Justicia americana*), the only species of aquatic macrophyte present in our study system, and terrestrial vegetation (see Results section for details), prompted us to use a 3-source (rather than 4-source) model including benthic algae (aquatic), phytoplankton (aquatic), and terrestrial vegetation. We employed widely-used values for trophic discrimination factors in our modeling as outlined by Post et al. (2002). However, because of the capability of Bayesian mixing models to incorporate variation in discrimination factors, we were able to include a range of potential discrimination values, in particular for N, for which the trophic discrimination has been reported to be substantially less than the oft-cited 3.4‰ (see Vanderklift and Ponsard 2003).

We generated estimates of the relative contribution of different potential energy sources to consumers using the MixSIAR graphical user interface (Stock and Semmens 2013) in R (R Core Team 2014). MixSIAR incorporates advances in mixing-model theory from two earlier models MixSIR and SIAR (Moore and Semmens 2008, Parnell et
al. 2008, Parnell et al. 2012), and similar to SIAR, uses Markov Chain Monte Carlo (MCMC) methods to estimate posterior distributions of variables of interest that are specified in the model (e.g., proportion of aquatic C from benthic algae in riparian spiders). In order to interpret results of the MixSIAR output the model must converge. We used visual interpretations of trace plots, as well as several standard MCMC diagnostics, including Gelman-Rubin, Heidelberger-Welch, and Geweke tests to assess model convergence (Stock and Semmens 2013). For the Gelman-Rubin test, values < ~1.1 are acceptable and indicate convergence of the model (Gelman et al. 2003). For the Heidelberger-Welch test, MixSIAR reports “passed” or “failed” for each variable. The Geweke test uses a 2-sided z-test to compare the mean of the first part of each chain with the mean of the second part of the chain. The means should be approximately the same to ensure convergence of the model; a large z-score indicates model rejection (Stock and Semmens 2013).

**Environmental-food web relationships**

We used a combination of linear regression, principal component analysis (PCA), and analysis of variance (ANOVA) to test for the relative influence of anthropogenic and natural environmental gradients and river regulation on the contribution of aquatically-derived C to terrestrial consumers. We performed PCA on a suite of variables (riparian landscape composition, physical reach characteristics, water chemistry, and aquatic nutrients; see table 4.4) that we had selected *a priori* as potential environmental drivers.
on the contribution of aquatically-derived energy to terrestrial consumers. We retained PCA axes with eigenvalues $>1$ for use in subsequent linear regression models (Rencher 1995, Sullivan and Watzin 2008). We used key independent variables (i.e., variables with the strongest loadings in our PCA) in simple linear regression to highlight relationships between human and natural environmental variables and the relative contribution of aquatically-derived energy to terrestrial consumers. Finally, we used ANOVA to test for differences in the relative contribution of benthic algae versus phytoplankton to terrestrial consumers in dammed versus undammed reaches. The data we used in linear regression analysis and ANOVA met univariate assumptions. We used JMP 10.0 (SAS Institute Inc., Cary, NC, USA) for all statistical analyses.

**Results**

Signatures of $\delta^{13}C$ were the least depleted for benthic algae ($\bar{x} = -21.68\%o$) and most depleted for phytoplankton ($\bar{x} = -31.83\%o$); aquatic macrophytes ($\bar{x} = -29.07\%o$) and terrestrial vegetation ($\bar{x} = -28.08\%o$) were distributed between these values. Across all study reaches, $\delta^{15}N$ was considerably more enriched for aquatic primary producers ($\bar{x} = 9.57\%o$) than terrestrial vegetation ($\bar{x} = 5.69\%o$). We were aware of the difficulty in obtaining pure algal samples, whether benthic or suspended, for use in our mixing models (DeLong and Thorp 2006, Zeug and Winemiller 2008). However, we made a concerted effort to remove as much non-algal materials from our samples. The fact that the range of $\delta^{13}C$ and $\delta^{15}N$ signatures for our benthic algae and phytoplankton were very similar to
those reported in DeLong and Thorp (2006) gave us additional confidence that our aquatic end members were accurately represented by our benthic algae and phytoplankton samples. On average, $\delta^{13}$C and $\delta^{15}$N signatures of terrestrial primary producers were separated by 4‰ ($\delta^{13}$C and $\delta^{15}$N) from phytoplankton, and 6‰ ($\delta^{13}$C) and 4‰ ($\delta^{15}$N) from benthic algae (Table 4.2), thus allowing confidence in our mixing models. We chose not to include aquatic macrophytes in our mixing models because of the limited separation in $\delta^{13}$C between macrophytes and terrestrial vegetation. Our mixing models for estimating the relative contribution of different energy sources to terrestrial riparian consumers met the minimum requirements of convergence based on examination of the trace plots and diagnostic tests.

**Aquatic- versus terrestrially-derived energy**

MixSIAR results indicated that the proportion of aquatic energy (derived from benthic algae and phytoplankton combined) contributing to all terrestrial consumers varied from 0.55 (R9) to 0.72 (R1 and R8) ($\bar{x} = 0.65; \text{SD} = 0.05$) (Figure 4.3). On average, tetragnathid spiders obtained 76%, damselflies obtained 72%, and riparian swallows obtained 67% of their energy from aquatic sources. Tetragnathids obtained <40% of their energy from aquatic primary producers at one reach (R7); damselflies only obtained <60% of their energy from aquatic sources at two heavily agricultural reaches (R5 and R9); and riparian swallows only obtained <50% of their energy from aquatic sources at R5, R9 and R10. Raccoons also obtained an appreciable amount of their
energy from aquatic sources ($\bar{x} = 0.59; SD = 0.13$). Unlike the other terrestrial consumers in the study, rove beetles obtained the majority of their energy from terrestrial sources (aquatic: $\bar{x} = 0.40; SD = 0.21$).

**Contributions of benthic algae versus phytoplankton**

The relative contribution of phytoplankton versus benthic algae to terrestrial consumers varied across reaches and by taxon (Figure 4.3). However, some general patterns emerged. Considered collectively, terrestrial consumers across all reaches obtained approximately equal proportions of energy from benthic algae ($\bar{x} = 0.33; SD = 0.05$) and phytoplankton ($\bar{x} = 0.32; SD = 0.06$). At R1–R4, terrestrial consumers obtained a greater proportion of energy from phytoplankton ($\bar{x} = 0.37$) than elsewhere ($\bar{x} = 0.28$). In general, benthic algal energy sources contributed more to terrestrial riparian consumers at reaches with wider, open channels (R7, R8, R11, R12) ($\bar{x} = 0.38; SD = 0.03$) than at other reaches ($\bar{x} = 0.30; SD = 0.02$). Tetragnathid spiders and damselflies both obtained a relatively large proportion of their energy from phytoplankton-based trophic pathways ($\bar{x} = 0.46$, SD = 0.19 and $\bar{x} = 0.42$, SD = 0.16, respectively). In contrast, rove beetles ($\bar{x} = 0.20; SD = 0.12$), riparian swallows ($\bar{x} = 0.18; SD = 0.13$), and raccoons ($\bar{x} = 0.15; SD = 0.07$) obtained considerably less of their energy through phytoplankton pathways.
Vectors of C transport from aquatic to terrestrial consumers

The abundance of emerging adult chironomids ranged from 1,357 (R3) to 11,068 (R9) (\(\bar{x} = 4,622;\) SD = 3,263) (Table 4.3). Chironomidae was the most common and abundant taxon across all reaches, comprising 62%–99% of total emergent insect abundance and >50% of total emergent insect biomass. MixSIAR results illustrated that chironomids provisioned both aquatically-derived and “recycled” terrestrial energy to terrestrial consumers (Table 4.3). Chironomids transported a large proportion of aquatic energy (\(\bar{x} = 0.72;\) SD = 0.19) into riparian zones, except at reaches 4, 7, and 9 where they were more reliant on detrital pathways, and thus transported a greater proportion of terrestrially-derived energy to riparian consumers. Crayfish were heavily reliant on aquatically-derived energy (\(\bar{x} = 0.72;\) SD = 0.07) from both benthic algae (\(\bar{x} = 0.32;\) SD = 0.05) and phytoplankton (\(\bar{x} = 0.40;\) SD = 0.08) pathways and thus likely serve as a potentially key vector of aquatically-derived energy sources to larger terrestrial predators (e.g., raccoons, kingfishers, herons).

The total estimated availability (as measured by biomass) of aquatic energy (i.e., benthic algae and phytoplankton) to terrestrial consumers via emerging chironomids was 3 to 10 times greater than terrestrially-derived energy at 7 of 12 reaches (R1–R3, R5, R6, R8, and R10), 2 times greater at R11 and R12, and approximately equal at R4 (Table 4.3). At R7 and R9, recycled terrestrial energy in chironomid biomass was greater than that of aquatically-derived energy. The relative availability of aquatic energy in adult
chironomids was closely tracked by the proportion of aquatically-derived energy in
tetragnathid spiders (Figure 4.4), but not in the other terrestrial consumers (not shown).

*Environmental drivers*

We retained 4 principal component axes that collectively accounted for 82% of
the variance in our environmental dataset (Table 4.4). The first principal component
(PC1) accounted for 48% of the variance and captured an urban-to-agricultural gradient
across our study system with urban LULC variables ($r^2 = 0.06–0.08$; negative
relationships) and agricultural LULC and aquatic nutrient variables ($r^2 = 0.05–0.09$;
positive relationships) all loading on this axis. The second principal component (PC2)
explained 15% of the variance and represented a gradient from forested riparian
landscapes (which tended to have low aquatic nutrient concentrations) to reaches with
higher aquatic nutrient concentrations. Total P and phosphate (both $r^2 = 0.07$; positive
relationship), total N ($r^2 = 0.11$; positive relationship) and forest LULC at 100 m ($r^2 =
0.21$; negative relationship) and 500 m ($r^2 = 0.23$; negative relationship) were the most
influential loadings for PC2. The third PC axis (PC3) accounted for 11% of the remaining
variance. Grassland at 500 m ($r^2 = 0.20$; negative relationship) and shoreline shrub
canopy ($r^2 = 0.23$; positive relationship) showed strong positive loadings on PC3. The
fourth PC axis (PC4) explained the remaining 8% of variance among the axes retained
from the PCA. Mean channel width ($r^2 = 0.53$) showed a strong positive loading on this
axis. Principal component axes that were not retained were largely representative of weak
gradients between low- and high-intensity development, and between low nutrient, grassland-dominated riparian landscapes and high nutrient reaches.

Regression analysis of the principal component axes illustrated relationships between natural and human environmental variables and the reliance on aquatically-derived energy by terrestrial consumers. Overall, terrestrial consumers obtained less C from aquatic sources as grassland land cover increased ($R^2 = 0.41, p = 0.026$; Figure 4.5). This relationship was particularly evident in the damselflies and riparian swallows ($R^2 = 0.54, p = 0.006$ and $R^2 = 0.32, p = 0.051$, respectively; Figure 4.5). For riparian swallows, the proportion of aquatically-derived C was positively linked to channel width ($R^2 = 0.32, p = 0.054$; Figure 4.6). In contrast, tetragnathid spiders were increasingly more reliant on aquatic C at narrower reaches ($R^2 = 0.42, p = 0.023$; Figure 4.6).

Anthropogenic impact on aquatic-to-terrestrial C fluxes was further explored by comparing the phytoplankton versus benthic algae contribution between impounded and non-impounded reaches. Terrestrial consumers from reaches located at impoundments above dams, or in reaches located directly below dams, obtained a significantly greater proportion of aquatic C from phytoplankton (reaches influenced by dams: $\bar{x} = 37\%$; reaches not influenced by dams: $\bar{x} = 28\%$) than from benthic algae sources (ANOVA, $p = 0.005$; Figure 4.7).
Discussion

Although autochthonous aquatic organic matter appears to be of quantitative importance in higher-order streams and rivers, its importance to river food webs has not been frequently studied (but see Cummins 1974, Minshall 1978, Thorp and DeLong 2002, DeLong and Thorp 2006). Likewise, despite increased conceptual and empirical understanding of the importance of aquatic energy subsidies to terrestrial food webs (Polis et al. 1997, Baxter et al. 2005, Sullivan and Rodewald 2012), the reliance of terrestrial consumers on aquatic autochthonous energy is not well quantified. In the Scioto River, a 6th order tributary of the Ohio River, we found that terrestrial consumers representing a range of riparian taxa (including invertebrates, birds, and mammals) obtained about two-thirds of their energy from aquatic primary producers. Across all taxa, terrestrial consumers obtained approximately equal contributions of energy from benthic algae and phytoplankton pathways, although tetragnathid spiders and damselflies obtained a substantially greater proportion of energy from phytoplankton. Most reliant on aquatic energy pathways were the tetragnathid spiders, which construct horizontal webs along the shoreline. However, more mobile consumers such as riparian swallows and raccoons, which move 100s to 1000s of meters during their nightly foraging activities, were also highly reliant on aquatic energy, thus transporting autochthonous river-derived energy well beyond the aquatic-terrestrial interface. Forest and grassland land cover as well as hydrogeomorphic features (e.g., impoundments, channel width) were related to the reliance of terrestrial consumers on aquatiously-derived energy, suggesting that the
contribution of aquatic sources to terrestrial food webs is a function of both natural and human-mediated environmental gradients. We interpret our collective results as evidence that aquatic primary production can appreciably fuel terrestrial food webs in temperate mid-order rivers and that phytoplankton can be a key source (in addition to benthic algae) of aquatically-derived energy to terrestrial consumers. Our results reinforce and extend the notion of the “stream signature” (*sensu* Muehlbauer et al. 2014) by empirically estimating the contribution of aquatically-derived energy to a host of terrestrial consumers that integrate the landscape across different spatial extents.

Although food subsidies from streams and rivers represent important energetic sources for myriad terrestrial consumers, to our knowledge the explicit contribution of aquatic autotrophy to terrestrial consumers has not been widely explored. Long-held conceptual understandings of small headwater streams suggest that the bulk of emergent insect energy is derived from terrestrial detritus (especially in forested landscapes), and to a lesser extent benthic algal pathways (Vannote et al. 1980, Wallace et al. 1997, Rosi-Marshall and Wallace 2002). In larger systems, however, because of the generally refractory nature of much terrestrial detritus and the importance of phytoplankton to aquatic invertebrate consumers (Thorp and DeLong 1994, DeLong and Thorp 2006), emergent insects may export large quantities of aquatically-derived energy. Intermediate-sized rivers (i.e., mid-order), such as the Scioto River system, might be expected to contribute a mixture of basal energy sources to terrestrial food webs due to conditions that promote benthic algae (e.g., open channels, relatively shallow water depth), phytoplankton (e.g., open channels, backwaters and areas of high water retention time),
and inputs and retention of macrophytes and terrestrial vegetation (e.g., shoreline vegetation, floodplains).

On average, terrestrial riparian consumers in our study system obtained nearly two-thirds of their energy from aquatic primary producer pathways (Figure 4.3). We found that the relative contribution of aquatically-derived energy was greatest in tetragnathid spiders (76%), followed by damselflies (72%), riparian swallows (67%), raccoons (59%) and rove beetles (27%). Differences in the contribution of aquatic energy to terrestrial consumers may stem from a suite of physico-chemical environmental drivers that determine aquatic-to-terrestrial transport of autochthonous aquatic energy (via emergent insects and crayfish) by controlling aquatic primary productivity and retention and nutritional quality of terrestrial detrital resources (Woodward and Hildrew 2002, Walters et al. 2007, Sullivan 2013). Behavioral traits of both aquatic prey and terrestrial consumers, such as dispersal and foraging strategies, respectively, also likely played an important role in the variability of aquatic energy contribution to terrestrial consumers across taxonomic groups. For example, swallows forage over broader spatial scales than tetragnathid spiders and thus have the capacity to integrate a greater diversity of terrestrial insect taxa. Here, we briefly discuss the role of Chironomidae as a vector of aquatically-derived energy to terrestrial consumers. Subsequently, we discuss the relative contribution of aquatic energy for each of our focal taxonomic groups, focusing on potential mechanisms driving the observed results.
Chironomidae, which represented the dominant emergent insect family in both abundance and biomass across our system, are generally collector-gatherers as larvae that consume a mixture of aquatic (e.g., benthic algae and phytoplankton) and terrestrially-derived particulate organic matter (Merritt et al. 2008). Consistent with the notion that consumers select resources based on nutritional quality rather than availability (Marcarelli et al. 2011) and that terrestrial detritus is generally considered to be of lower energetic quality than aquatic primary production (Thorp and DeLong 1994), we found that, on the whole, chironomids transported more aquatic (72%) than terrestrial (28%) energy to riparian consumers. However, at some reaches, in particular at R7, R9, and R12, chironomids transported considerably more terrestrially-derived energy to terrestrial consumers than at the other reaches. This may have been because the terrestrial vegetation was of greater nutritional quality (e.g., greater N content) to aquatic primary consumers at these reaches (as well as reaches R5, R6 and R10; Appendix D): in our system, C:N ratios of terrestrial vegetation were lower at reaches with elevated aquatic nutrient concentrations (i.e., R5–R7, R9, R10, R12; $\bar{x} = 18.77$) than elsewhere ($\bar{x} = 23.73$). The availability and retention of terrestrial vegetation inputs, together with shifts in nutritional quality of detritus, may have also contributed to the assimilation and transport of terrestrial energy by emerging aquatic insects. Hydrogeomorphic and riparian characteristics such as slackwaters, eddies, and overhanging shoreline vegetation would be expected to facilitate input and retention of terrestrial organic matter; however,
emerging chironomids from study reaches with a predominance of these characteristics (e.g., R1–R3, R6, R10) did not always reflect this.

**Contribution of aquatic energy to terrestrial consumers**

Except for tetragnathid spiders (Figure 4.4), the proportion of aquatic energy in terrestrial consumers did not closely track the proportional availability of aquatic energy in chironomids. This may indicate that tetragnathid spiders were largely limited to feeding on the most abundant emergent insects available (i.e., chironomids), whereas insectivorous damselflies and swallows, while still obtaining most of their energy from aquatic sources, were likely consuming a broader variety of prey. The intimate reliance on aquatic energy pathways for tetragnathid spiders was not surprising given that they are highly-specialized predators that build their webs over, or very near, the water and have been found to rely almost exclusively on emergent insects (Henschel et al. 2001, Kato et al. 2003, Sanzone et al. 2003). Tetragnathid spiders were almost wholly supported by aquatically-derived C at most reaches and closely tracked the availability of aquatic energy transported via emergent insects. For example, emerging adult chironomids transported substantially less aquatic energy to terrestrial consumers at R4, R7, R9, and R11 (~50% aquatic C), which was subsequently reflected in elevated terrestrial signatures of tetragnathid spiders at these reaches. Channel width had a negative influence on the contribution of aquatic energy to tetragnathid spiders (Figure 4.6). We measured channel width as bankfull width and in many of the widest reaches in our study system there were...
extensive bars present that dissociated bankside vegetation (where spider webs were located) from the wetted channel where aquatic insects emerged.

Damselflies, in contrast to spiders, are more mobile predators that are less constrained by microscale landscape features, although they rarely range far from water (Jonsen and Taylor 2000). Most damselflies are considered generalists, whose diet reflects the relative abundance of available insect prey (Baird and May 1997, May and Baird 2002), including emergent insects. We found that overall damselflies obtained 72% of their energy from aquatic sources. Damselfly reliance on aquatic energy sources was fairly consistent across reaches (52–87%), even where emerging insect prey were transporting a greater proportion of terrestrially-derived energy. Damselfly mobility likely enables use of a broader suite of prey resources than shoreline tetragnathid spiders, including aquatic insects that emerge directly from the open mid-channel sections of the river and bypass spiders situated in bankside vegetation. Mid-channel emerging insects may consume and transport more aquatic energy than shoreline insects at some reaches and the ability of damselflies to use mid-channel emerging insects may contribute to the large proportion (and narrow range) of aquatic C found in damselflies. Open riparian landscapes also may facilitate damselflies foraging away from the river channel where flying terrestrial insects (e.g., various dipterans, small hymenopterans and lepidopterans) are expected to comprise a greater proportion of their diet, as evidenced by the negative relationship between grassland land cover and the contribution of aquatic energy to damselflies (Figure 4.5).
Riparian swallows were also heavily reliant on aquatically-derived energy as they obtained only 10% and 5% less from aquatic sources, on average, than did either tetragnathid spiders or damselflies, respectively. Swallows obtained a larger proportion of their C from aquatic sources in reaches with wider channels (Figure 4.6), likely because river channels offer preferred foraging habitat for swallows in forested landscapes and because larger channels ultimately export more emergent insects on which swallows prey (Gratton and Vander Zanden 2009). Open riparian landscapes (e.g., non-forested), in contrast, can facilitate foraging into upland areas where greater a proportion of terrestrial insects may be expected to contribute to swallow diets (Thomas et al. 1999, Ockinger and Smith 2007). Our results align somewhat with these previous observations, as swallows captured from some open grassland and agricultural landscapes (R5 and R9) obtained a relatively large proportion (55%–72%) of their energy from terrestrial sources. However, the elevated terrestrial energy contribution found in riparian swallows from these reaches may have come from recycled terrestrial energy transported via emergent insects, in particular at R9 (Table 4.3), rather than directly from consuming terrestrial invertebrates. Tree swallows, in particular, have been found to rely on a mixture of both emergent and terrestrial insects (Blancher and McNicol 1991, Wayland et al. 1998). In the same region as the present study, Alberts et al. (2013) found that emergent insects contributed 46%–84% (by weight) to tree swallow diet, and that tree swallows were less reliant on emergent prey at reaches in smaller systems and with more open landscapes. More broadly, our findings show that channel size and landscape context (i.e., open vs.
forested) may be critical environmental determinants of swallow reliance on aquatic energy.

Raccoons, while broadly omnivorous, can rely heavily on aquatic energy via crayfish (Hamilton 1951, Greenwood 1981, Gehrt 2003). We found crayfish in the Scioto system to be comprised largely of energy from aquatic sources (Table 4.3). Thus crayfish, when consumed by riparian predators represent an important vector of aquatic energy transport to terrestrial food webs. Raccoons also are known to range over several km during nightly foraging, potentially incorporating food resources from a variety of sources, yet we found that raccoons obtained the majority of their energy from aquatic sources (59% on average). The greatest reliance on aquatic energy by raccoons was at R4 (67%) and R7 (81%). Both reaches were located within broader urban settings yet had relatively intact, forested riparian buffers, and had minimal (R7) or nonexistent (R4) agricultural land cover, and were free-flowing. Aquatic energy contributed 51% to raccoons at the other reaches where they were captured (R2, R3, R8, R10). R2 and R3 were highly urbanized and provided limited riparian forest cover, whereas R8 and R10 had ample access to agricultural crops nearby. Raccoons incorporated a greater proportion of non-aquatic food sources in these particular types of landscapes likely because of the availability of nutritious and easily obtained resources, for example human food waste and backyard bird feeders in urban and residential landscapes or cultivated crops, such as corn, in agricultural landscapes.

Rove beetles at R3, R6–R9, and R12 obtained only 24% of their energy from aquatic primary producer pathways. Predatory ground-dwelling beetles that occupy
nearshore areas are known to consume aquatic prey, however the predominant emergent taxa in our system (e.g., chironomids and hydropsychid caddisflies) emerge directly from the water surface rather than crawl out onto the bank or bankside vegetation to emerge and thus might be expected to be less accessible to rove beetles (e.g., Herring and Plachter 1997, Paetzold et al. 2005). Additionally, rove beetles collected at the majority of reaches were small-bodied (generally 0.2 mg to 0.3 mg), which may have limited their ability to depredate the larger-bodied hydropsychid caddisflies (mean body size ~1 mg) that we observed crawling and resting on the bank following emergence at some reaches. Conversely, rove beetles were considerably larger (most were in the range of 1mg to 2 mg) at R1, R2, R4, R5, R10 and R11 where they obtained 44%–74% of their energy from aquatic sources. In addition, some of these reaches also supported stoneflies, which crawl onto land to emerge (Malison et al. 2010), providing more accessible prey for larger-bodied rove beetles. Other investigators have suggested that deposition of drifting invertebrates, whether aquatic or terrestrial, onto gravel bars and other nearshore areas can be a substantial subsidy for riparian beetles (Paetzold et al. 2006), which might represent an important mechanism for understanding the contribution of aquatic energy to riparian rove beetles and other ground-dwelling riparian insectivores. Furthermore, algae can become available to terrestrial herbivores (e.g., grasshoppers; Bastow et al. 2002) during periods of low water, representing an additional pathway of aquatic energy to terrestrial consumers.
Phytoplankton can be a critical source of energetic support for aquatic primary consumers, particularly in larger rivers with open canopies and where depth and turbidity may constrain benthic algal production (DeLong 2010, Pingram et al. 2012). Phytoplankton also has relatively high nutritive value to aquatic primary consumers, thus its importance to secondary production may be disproportionate to its abundance or biomass in the system (Thorp and DeLong 1994). However, to our knowledge, the contribution of aquatic C from phytoplankton to terrestrial food webs has not been explicitly considered in river food web studies of this kind. The relative importance of phytoplankton to both aquatic and terrestrial food webs may vary based on both natural environmental gradients (e.g., river size, channel morphology) and anthropogenic drivers (e.g., nutrient and sediment inputs, impoundments). Phytoplankton can be plentiful in mid-size rivers; in particular in areas where flow, and thus downstream transport of suspended algae, is inhibited allowing for in situ suspended algal production (Reynolds and Pescy 1996). Phytoplankton may be even more prevalent in intermediate size rivers than large systems because depth and turbidity are often reduced in middle reaches of river systems (Vannote et al. 1980). More specifically, although we did not measure concentration or biomass of phytoplankton, historically phytoplankton has been found at high densities at several locations throughout the Scioto River (Kehr et al. 1941, Herdendorf et al. 1979). In our system, terrestrial consumers on the whole obtained 31% of their energy through phytoplankton-based pathways, suggesting that aquatic energy
from phytoplankton is a significant contributor to terrestrial food webs in mid-size rivers — a pathway not previously considered.

In our study, the contribution of phytoplankton to terrestrial consumers varied by taxonomic group. Tetragnathids and damselflies obtained 46% and 42%, respectively; whereas, rove beetles and riparian swallows obtained <20% of their energy from phytoplankton. It is likely that spiders, and to a lesser extent damselflies, largely consumed Chironomidae, the dominant emergent taxon, which transported a larger proportion of energy from phytoplankton sources than from terrestrial (and benthic algal) sources across most reaches. Collector-gatherer (e.g., Chironomidae) and collector-filterer aquatic invertebrate taxa that inhabit hotspots of phytoplankton recruitment and production (e.g., eddies and shoreline habitats, lateral slackwater and floodplain waterbodies; Reynolds and Descy 1996) are likely to be highly dependent on phytoplankton food sources. In contrast, swallows obtained substantially more energy from benthic algal sources and therefore were probably targeting less abundant but larger-bodied emergent taxa such as grazing mayflies (e.g., Heptageniidae) that were common at most reaches across our study system. Whereas spiders and damselflies may target the most abundant emergent insect taxa available, swallows likely select from among the most energetically-profitable prey types irrespective of abundance (Rooney et al. 2008). Swallows also can forage more broadly over open channel segments where swifter flow may limit phytoplankton production, except in impounded areas.

Contributions of aquatic energy from phytoplankton were significantly greater at reaches influenced by dams (Figure 4.7), as might be expected given the longer residence
time of water (Reynolds et al. 1994, Reynolds and Descy 1996, Sellers and Bukaveckas 2003). Dams also regulate flow variability, which together with longer water residence time, facilitates fine sediment deposition and improved water clarity, leading to greater *in situ* phytoplankton production. Even 30 km to 40 km downstream of dams (R5 and R6) a considerable proportion of the total energy transported via chironomids (69%) and crayfish (41%) originated from phytoplankton. At the remainder of the study reaches (starting 93 km downstream from nearest dam) only 34% of the energy transported by emergent insects and 36% of energy transported by crayfish was derived from phytoplankton on average. It seems unlikely, however, that the high proportion of planktonic source material at R5 and R6 was a residual effect from phytoplankton being transported downstream from upstream impoundments. A more plausible explanation results from a combination of channel morphology and the influence of nutrient concentrations. R5 and R6 had numerous areas with long water residence times (e.g., slow-moving pools, backwaters, eddies, and floodplain waterbodies connected to main channel; Tagwireyi 2014), and contained the highest nutrient concentrations (Table 4.1) — factors that likely contributed to phytoplankton productivity and the importance of phytoplankton to both aquatic and terrestrial consumers.

*Spatial extent of aquatic energy transport into adjacent terrestrial landscapes*

Aquatically-derived energy contributed substantially to terrestrial food webs in both nearshore riparian consumers (e.g., tetragnathid spiders) as well as broader-ranging
organisms (e.g., riparian swallows, raccoons). We interpret these results to indicate that river-derived primary production is of quantitative importance in fueling adjacent terrestrial food webs. Furthermore, through wide-ranging terrestrial consumers that spatially link riverine and upland habitats, aquatically-derived energy is transported far from the river. This has important implications for understanding the functional biological width of a river (Muehlbauer et al. 2014) as well as the fundamental role of rivers as key energy contributors to landscape-level food webs. This latter point is of particular merit given that cross-boundary energy subsidies can have important consequences for consumers and recipient food webs, including elevated predator abundance and concurrent top-down effects (Polis et al. 1997).

We did not see an appreciable decline in the relative contribution of aquatic sources in consumer taxa foraging at greater spatial extents. Tetragnathid spiders, damselflies, riparian swallows, and raccoons all obtained >50% of their energy from aquatic sources. Although riparian swallows have the capacity to integrate both aquatic and terrestrial energy sources over a wider spatial scale than the other insectivorous secondary consumers we considered (Quinney and Ankney 1985, Dunn and Hannon 1992, Robertson et al. 1992) they still obtained 67% of their energy from aquatic sources suggesting a preference for aquatic prey. Only rove beetles – which are more mobile than web-building spiders, but not as mobile as damselflies, swallows. or raccoons – obtained less than half of their energy from aquatically-derived sources.

Based on a meta-analysis of Muehlbauer et al. (2014), the stream-derived component of terrestrial food webs declined to 50% by 1 m to 2 m away from the stream
and to 10% by 1000 m to 2000 m in intermediate size systems (e.g., stream order 3–6). In our system, we observed that, riparian swallows, which forage over considerable distances (250 m to 400 m from nest), and raccoons, which can travel several kilometers during nightly foraging forays (Greenwood 1982), obtained 67% and 59% of their energy from aquatic sources, respectively, thus potentially extending and refining the stream signature beyond what has been previously considered. In addition, aquatic energy from local source pools can potentially be transported across extremely long distances as riparian swallow species migrate from summer nesting areas to wintering habitat as far south as the Caribbean and Central and South America following the nesting season.

Conclusions

Despite significant advances in understanding the importance of aquatic subsides to terrestrial food webs (Baxter et al. 2005, Richardson et al. 2010, Sullivan and Rodewald 2012), there have not been concerted efforts to quantify the contribution of aquatically- (e.g., benthic algae and phytoplankton) versus terrestrially-derived (e.g., terrestrial detritus recycled in aquatic organism biomass and terrestrial vegetation) energy to terrestrial secondary consumers. In this study, we illustrate the integral role of aquatically-derived energy in supporting terrestrial consumers in both nearshore and upland environments in a mid-sized river system. In particular, we highlight the contribution of phytoplankton-based energy pathways to terrestrial consumers, which we found to be of quantitative significance.
Our results have important implications for understanding the prominent role that river-derived energy plays in terrestrial riparian food webs and how that role shifts across anthropogenic and natural environmental gradients. In particular, LULC gradients from open grassland to forest led to elevated contributions of aquatic energy to terrestrial consumers, likely through shifts in landscape composition that facilitated broader foraging opportunities for mobile consumers (e.g., swallows). In addition, the availability and nutritional quality of terrestrially-derived energy to aquatic primary consumers likely played an important role in the magnitude of aquatic energy transferred to terrestrial riparian consumers.

Local contributions of terrestrial detritus from floodplains and nearshore areas can represent the dominant energy source to aquatic food webs in some larger river systems (Junk et al. 1989, Tockner et al. 2000, Zeug and Winemiller 2008). However, some investigators have debated the importance of detrital material to aquatic food webs, particularly in large temperate river systems, contending that relatively minimal amounts of detritus are actually assimilated into primary consumer biomass and thus providing minor contributions to the aquatic food web as a whole (Thorp and DeLong 2002). Likewise, our results showed that terrestrially-derived energy was a secondary contributor to aquatic primary consumers. We saw no indication that floodplain area was related to the proportion of terrestrially-derived energy in either emergent insects or terrestrial consumers. Given that our measurements of floodplain access were limited to a simple measure of area, we propose that a more nuanced investigation into the role of
floodplains in mid-order rivers could provide additional insight into local-scale patterns of aquatic energy transported to terrestrial food webs.

Our study also illustrates the inherent complexity of aquatic-terrestrial energetic linkages in modified landscapes. We found that terrestrial riparian consumers obtained aquatic energy approximately equally from both benthic algae and phytoplankton pathways across the entire study system. The strong contribution of phytoplankton to terrestrial consumers was of particular importance, as this pathway has not been previously considered to our knowledge. Anthropogenic gradients relating to land cover, water quality, and river regulation influenced the relative importance of phytoplankton-derived aquatic energy in terrestrial riparian food webs. In particular, in our study system there was a clear relationship between relative contribution of phytoplankton and the influence of dams.

Our findings contribute to the maturing understanding of the energy sources that drive food webs in riverine landscapes. In particular, the relative contribution of terrestrial versus autochthonous aquatic energy in fueling intermediate to large river food webs (≥4th order) is a controversial issue that has not been fully resolved (reviewed in Thorp et al. 2006; Aufdenkampe et al. 2011), but appears to be quantitatively significant in our study system. In small streams, Nakano and Murakami (2001) demonstrated that the “forest feeds the stream” during the summer. Here we present evidence that in larger systems, aquatic primary productivity can be a major player in fueling terrestrial food webs, and that the contribution of aquatically-derived energy is appreciable both near shore as well as deeper into terrestrial ecosystems. We also illustrate that different
compartments of aquatic production (benthic algae versus phytoplankton) differentially support terrestrial consumers in intermediate-sized systems, but that the contribution of phytoplankton can be significant. Finally, our findings have broad application for understanding the role of rivers in driving food-web connectivity across landscapes and the influence of anthropogenic and natural gradients on these patterns. We provide clear empirical evidence that aquatically-derived energy from rivers subsidizes terrestrial consumers across a range of spatial scales from the aquatic-terrestrial interface well into riparian and upland habitats. Hence, river system integrity is critical not only for aquatic food webs but also for the terrestrial food webs that rely on aquatic primary production. In this way, our results can be applied to conservation, restoration, and management activities that target aquatic-terrestrial connectivity.
Acknowledgements

Research support was provided by state and federal funds appropriated to The Ohio State University, Ohio Agricultural Research and Development Center and by the Ohio Division of Wildlife, USFWS State Wildlife Grants through the Ohio Biodiversity Conservation Partnership (SMPS). We would like to thank Jeremy Alberts, Paradzayi Tagwireyi, Mikelis Berzins, Lyndsay Boaz, Dannielle Vent, Alayna Dorobek, and Kristin Shearer for their help in the field and laboratory, and Katie Hossler for her help reviewing early drafts of the manuscript. We would also like to acknowledge Dr. Barb Wolfe, Amanda Steinagel, and Isabel Plourde for their assistance with the raccoon portion of this project.
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Table 4.1. Environmental variables describing riparian landscape composition (from GIS and vegetation surveys), water chemistry and aquatic nutrient concentrations, and physical river characteristics at the 12 Scioto River study reaches.

<table>
<thead>
<tr>
<th>Riparian landscape composition</th>
<th>R1</th>
<th>R2</th>
<th>R3</th>
<th>R4</th>
<th>R5</th>
<th>R6</th>
<th>R7</th>
<th>R8</th>
<th>R9</th>
<th>R10</th>
<th>R11</th>
<th>R12</th>
<th>MEAN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Developed low-intensity (100m)</td>
<td>0.60</td>
<td>0.42</td>
<td>0.32</td>
<td>0.32</td>
<td>0.14</td>
<td>0.00</td>
<td>0.37</td>
<td>0.00</td>
<td>0.20</td>
<td>0.17</td>
<td>0.00</td>
<td>0.21</td>
<td></td>
</tr>
<tr>
<td>Developed low-intensity (500m)</td>
<td>0.68</td>
<td>0.35</td>
<td>0.16</td>
<td>0.39</td>
<td>0.07</td>
<td>0.00</td>
<td>0.35</td>
<td>0.00</td>
<td>0.23</td>
<td>0.05</td>
<td>0.00</td>
<td>0.19</td>
<td></td>
</tr>
<tr>
<td>Developed high-intensity (100m)</td>
<td>0.14</td>
<td>0.28</td>
<td>0.68</td>
<td>0.22</td>
<td>0.00</td>
<td>0.00</td>
<td>0.14</td>
<td>0.00</td>
<td>0.20</td>
<td>0.00</td>
<td>0.00</td>
<td>0.14</td>
<td></td>
</tr>
<tr>
<td>Developed high-intensity (500m)</td>
<td>0.24</td>
<td>0.52</td>
<td>0.84</td>
<td>0.49</td>
<td>0.00</td>
<td>0.00</td>
<td>0.37</td>
<td>0.01</td>
<td>0.16</td>
<td>0.00</td>
<td>0.00</td>
<td>0.22</td>
<td></td>
</tr>
<tr>
<td>Forest (100m)</td>
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<td>0.30</td>
<td>0.00</td>
<td>0.39</td>
<td>0.29</td>
<td>0.33</td>
<td>0.38</td>
<td>0.34</td>
<td>0.29</td>
<td>0.29</td>
<td>0.30</td>
<td>0.29</td>
<td></td>
</tr>
<tr>
<td>Forest (500m)</td>
<td>0.09</td>
<td>0.11</td>
<td>0.00</td>
<td>0.07</td>
<td>0.03</td>
<td>0.35</td>
<td>0.05</td>
<td>0.33</td>
<td>0.05</td>
<td>0.16</td>
<td>0.55</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td>Grassland (100m)</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.16</td>
<td>0.00</td>
<td>0.12</td>
<td>0.17</td>
<td>0.24</td>
<td>0.01</td>
<td>0.11</td>
<td>0.04</td>
<td></td>
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<tr>
<td>Grassland (500m)</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.20</td>
<td>0.00</td>
<td>0.06</td>
<td>0.13</td>
<td>0.35</td>
<td>0.03</td>
<td>0.08</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Cultivated crops (100m)</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.62</td>
<td>0.37</td>
<td>0.07</td>
<td>0.23</td>
<td>0.60</td>
<td>0.20</td>
<td>0.20</td>
<td>0.71</td>
<td></td>
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<tr>
<td>Cultivated crops (500m)</td>
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<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.70</td>
<td>0.64</td>
<td>0.15</td>
<td>0.50</td>
<td>0.61</td>
<td>0.42</td>
<td>0.33</td>
<td>0.80</td>
<td></td>
</tr>
<tr>
<td>Shrub canopy (Shoreline)</td>
<td>0.33</td>
<td>0.64</td>
<td>0.51</td>
<td>0.19</td>
<td>0.06</td>
<td>0.09</td>
<td>0.06</td>
<td>0.07</td>
<td>0.00</td>
<td>0.03</td>
<td>0.03</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td>Tree canopy (Shoreline)</td>
<td>0.51</td>
<td>0.82</td>
<td>0.35</td>
<td>0.79</td>
<td>0.74</td>
<td>0.30</td>
<td>0.16</td>
<td>0.66</td>
<td>0.63</td>
<td>0.73</td>
<td>0.83</td>
<td>0.55</td>
<td></td>
</tr>
<tr>
<td>Shrub canopy (50m)</td>
<td>0.17</td>
<td>0.24</td>
<td>0.10</td>
<td>0.51</td>
<td>0.19</td>
<td>0.05</td>
<td>0.09</td>
<td>0.03</td>
<td>0.08</td>
<td>0.06</td>
<td>0.11</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Tree canopy (50m)</td>
<td>0.59</td>
<td>0.78</td>
<td>0.05</td>
<td>0.93</td>
<td>0.25</td>
<td>0.75</td>
<td>0.19</td>
<td>0.67</td>
<td>0.10</td>
<td>0.70</td>
<td>0.46</td>
<td>0.27</td>
<td></td>
</tr>
</tbody>
</table>

| Water chemistry               |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Total dissolved solids (TDS)   | 265  | 178.1| 218  | 229  | 413.7| 394.8| 264.7| 485.9| 307.8| 288.1| 307.3| 303.2| 304.6|
| Nitrate (mg L⁻¹)              | 0.423| 0.928| 0.679| 0.229| 6.435| 6.260| 4.785| 4.170| 4.880| 4.540| 4.320| 4.050| 4.000|
| Phosphate (mg L⁻¹)            | 0.049| 0.050| 0.027| 0.031| 1.024| 0.594| 0.302| 0.333| 0.402| 0.392| 0.392| 0.392| 0.392|
| Total phosphorous (mg L⁻¹)    | 0.074| 0.075| 0.059| 0.052| 1.040| 0.544| 0.279| 0.335| 0.392| 0.144| 0.097| 0.106| 0.266|
| Total nitrogen (mg L⁻¹)       | 1.099| 0.953| 1.116| 0.685| 6.020| 5.690| 4.100| 1.015| 4.270| 3.565| 0.246| 1.912| 2.556|

| Physical characteristics     |      |      |      |      |      |      |      |      |      |      |      |      |      |
| Drainage area (km²)           | 2,605| 1,348| 1,368| 4,145| 5,966| 6,757| 9,351| 2,981| 2,571| 43,351| 44,714| 679 |
| Downstream dams (number)      | 3    | 4    | 3    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | -    |
| Distance from upstream dam (km)| 6.1  | 0.0  | 1.7  | 1.0  | 30.6 | 38.1 | 93.2 | 104.8| 121.7| 151.9| 156.1| 161.0| -    |
| Mean channel width (m)        | 78   | 50   | 83   | 119  | 50   | 50   | 154  | 100  | 79   | 71   | 86   | 84.4 | -    |
| Floodplain area (km²)         | 0.20 | 0.25 | 0.18 | 0.27 | 0.72 | 0.99 | 0.71 | 0.66 | 0.40 | 0.32 | 0.44 | 0.51 | 0.47 |

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Table 4.2. Mean and SD (in parentheses) for $\delta^{13}$C and $\delta^{15}$N of aquatic and terrestrial primary producers and terrestrial secondary consumers at the 12 Scioto River study reaches.

<table>
<thead>
<tr>
<th></th>
<th>Primary producers</th>
<th>Terrestrial consumers</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Benthic algae</td>
<td>Phytoplankton</td>
<td>Terrestrial vegetation</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(Tetragnathidae)</td>
</tr>
<tr>
<td>R1</td>
<td>$\delta^{13}$C</td>
<td>-21.12 (1.34)</td>
<td>-26.38 (0.35)</td>
</tr>
<tr>
<td></td>
<td>$\delta^{15}$N</td>
<td>11.07 (2.03)</td>
<td>-25.85 (0.64)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>9.21 (2.06)</td>
<td>-25.82 (0.62)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.46 (0.14)</td>
<td>-24.73 (0.40)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-27.97 (0.42)</td>
<td>-29.19 (0.95)</td>
</tr>
<tr>
<td>R2</td>
<td>$\delta^{13}$C</td>
<td>-22.57 (3.61)</td>
<td>-27.87 (1.60)</td>
</tr>
<tr>
<td></td>
<td>$\delta^{15}$N</td>
<td>10.95 (0.92)</td>
<td>-29.19 (0.95)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8.22 (2.09)</td>
<td>-26.97 (0.21)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.13 (0.21)</td>
<td>-24.55 (0.66)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.00 (1.21)</td>
<td>-21.52 (0.75)</td>
</tr>
<tr>
<td>R3</td>
<td>$\delta^{13}$C</td>
<td>-17.22 (0.84)</td>
<td>-30.54 (0.59)</td>
</tr>
<tr>
<td></td>
<td>$\delta^{15}$N</td>
<td>8.42 (1.31)</td>
<td>-24.08 (2.87)</td>
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<tr>
<td></td>
<td></td>
<td>9.42 (1.22)</td>
<td>-28.50 (1.01)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.19 (0.36)</td>
<td>-24.38 (0.52)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>13.46 (0.34)</td>
<td>-20.39 (-)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>7.60 (0.39)</td>
<td>-29.99 (1.42)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.32 (0.98)</td>
<td>-31.35 (3.39)</td>
</tr>
<tr>
<td>R4</td>
<td>$\delta^{13}$C</td>
<td>-24.00 (2.43)</td>
<td>-28.05 (0.41)</td>
</tr>
<tr>
<td></td>
<td>$\delta^{15}$N</td>
<td>9.75 (2.62)</td>
<td>-26.52 (0.20)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10.12 (2.52)</td>
<td>-27.19 (0.28)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.91 (0.21)</td>
<td>-25.88 (0.51)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.30 (1.91)</td>
<td>-22.70 (0.25)</td>
</tr>
<tr>
<td>R5</td>
<td>$\delta^{13}$C</td>
<td>-23.58 (0.20)</td>
<td>-27.55 (1.05)</td>
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<tr>
<td></td>
<td>$\delta^{15}$N</td>
<td>9.86 (1.43)</td>
<td>-26.28 (2.23)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8.64 (1.42)</td>
<td>-25.61 (1.54)</td>
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<td></td>
<td>6.86 (0.01)</td>
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<tr>
<td></td>
<td></td>
<td>12.09 (0.58)</td>
<td>-</td>
</tr>
<tr>
<td>R6</td>
<td>$\delta^{13}$C</td>
<td>-20.64 (1.61)</td>
<td>-24.92 (2.16)</td>
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<tr>
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<td>$\delta^{15}$N</td>
<td>8.90 (1.78)</td>
<td>-26.71 (0.95)</td>
</tr>
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<td></td>
<td></td>
<td>9.80 (1.03)</td>
<td>-24.26 (0.93)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>6.52 (0.64)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.46 (0.30)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>9.92 (0.91)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.77 (1.16)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.03 (1.05)</td>
<td>-</td>
</tr>
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<td>R7</td>
<td>$\delta^{13}$C</td>
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<td>$\delta^{15}$N</td>
<td>8.51 (1.11)</td>
<td>-28.96 (1.75)</td>
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<td>8.65 (0.69)</td>
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<td>7.19 (0.18)</td>
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<td>11.30 (1.02)</td>
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<td>12.36 (0.57)</td>
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<td>9.72 (0.27)</td>
<td>-</td>
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<td></td>
<td>11.34 (1.24)</td>
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<td>12.78 (0.90)</td>
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<td>12.71 (0.67)</td>
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<td>9.93 (0.60)</td>
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<td>11.77 (0.57)</td>
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<td>10.37 (0.85)</td>
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<td>$\delta^{15}$N</td>
<td>8.84 (1.13)</td>
<td>-24.96 (1.44)</td>
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<td>10.03 (0.23)</td>
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<td>5.40 (0.08)</td>
<td>-23.36 (0.24)</td>
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<tr>
<td></td>
<td></td>
<td>14.00 (2.28)</td>
<td>-20.00 (0.77)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10.68 (1.77)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.28 (1.53)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>7.91 (0.77)</td>
<td>-</td>
</tr>
<tr>
<td>R11</td>
<td>$\delta^{13}$C</td>
<td>-22.25 (5.72)</td>
<td>-27.00 (1.35)</td>
</tr>
<tr>
<td></td>
<td>$\delta^{15}$N</td>
<td>9.00 (1.32)</td>
<td>-26.44 (0.59)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.33 (1.65)</td>
<td>-26.40 (0.98)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.22 (0.04)</td>
<td>-25.15 (0.34)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.90 (0.72)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.72 (1.15)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.04 (1.90)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10.87 (0.47)</td>
<td>-</td>
</tr>
<tr>
<td>R12</td>
<td>$\delta^{13}$C</td>
<td>-21.84 (6.48)</td>
<td>-29.14 (1.11)</td>
</tr>
<tr>
<td></td>
<td>$\delta^{15}$N</td>
<td>9.69 (2.27)</td>
<td>-24.11 (1.99)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>9.50 (0.97)</td>
<td>-25.94 (1.47)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5.09 (0.17)</td>
<td>-26.77 (0.54)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.23 (0.65)</td>
<td>-24.28 (0.75)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8.09 (0.19)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.23 (1.48)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.15 (1.00)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 4.3. Abundance and biomass (mg) of Chironomidae, the most numerically-dominant emergent insect family collected from floating emergent traps across the 12 study reaches. Mixing model (MixSIAR) estimates for the proportions of aquatically-derived energy in emerged adult Chironomidae and crayfish, which are both important prey for a suite of terrestrial riparian consumers. Subsequently we calculated the relative proportion of aquatic energy consisting of either benthic algae or phytoplankton pathways. Also included are estimates of the total available biomass of aquatic and terrestrial energy transported to terrestrial consumers via emerging chironomids.

<table>
<thead>
<tr>
<th>Chironomidae</th>
<th>R1</th>
<th>R2</th>
<th>R3</th>
<th>R4</th>
<th>R5</th>
<th>R6</th>
<th>R7</th>
<th>R8</th>
<th>R9</th>
<th>R10</th>
<th>R11</th>
<th>R12</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance</td>
<td>3402</td>
<td>2737</td>
<td>1357</td>
<td>2606</td>
<td>6145</td>
<td>5316</td>
<td>10333</td>
<td>5821</td>
<td>11068</td>
<td>3278</td>
<td>1608</td>
<td>1789</td>
</tr>
<tr>
<td>Biomass (mg)</td>
<td>197.9</td>
<td>326.4</td>
<td>152.4</td>
<td>505.1</td>
<td>1998.3</td>
<td>636.2</td>
<td>2373.3</td>
<td>762.3</td>
<td>2699.3</td>
<td>1217.0</td>
<td>799.3</td>
<td>574.4</td>
</tr>
<tr>
<td>AQUATIC (SD)</td>
<td>0.92 (0.25)</td>
<td>0.94 (0.26)</td>
<td>0.87 (0.10)</td>
<td>0.53 (0.43)</td>
<td>0.81 (0.13)</td>
<td>0.80 (0.27)</td>
<td>0.45 (0.22)</td>
<td>0.92 (0.25)</td>
<td>0.39 (0.12)</td>
<td>0.81 (0.15)</td>
<td>0.64 (0.31)</td>
<td>0.59 (0.33)</td>
</tr>
<tr>
<td>AQUATIC-Benthic algae</td>
<td>0.06</td>
<td>0.16</td>
<td>0.20</td>
<td>0.13</td>
<td>0.22</td>
<td>0.07</td>
<td>0.17</td>
<td>0.15</td>
<td>0.21</td>
<td>0.37</td>
<td>0.46</td>
<td>0.36</td>
</tr>
<tr>
<td>AQUATIC-Phytoplankton</td>
<td>0.94</td>
<td>0.84</td>
<td>0.80</td>
<td>0.87</td>
<td>0.78</td>
<td>0.93</td>
<td>0.83</td>
<td>0.85</td>
<td>0.79</td>
<td>0.63</td>
<td>0.54</td>
<td>0.64</td>
</tr>
<tr>
<td>Available chironomid biomass (mg)</td>
<td>15.8</td>
<td>19.6</td>
<td>19.8</td>
<td>237.4</td>
<td>265.7</td>
<td>127.2</td>
<td>1305.3</td>
<td>61.0</td>
<td>1646.6</td>
<td>231.2</td>
<td>266.1</td>
<td>235.5</td>
</tr>
<tr>
<td>From &quot;recycled&quot; terrestrial sources</td>
<td>182.1</td>
<td>306.8</td>
<td>132.6</td>
<td>267.7</td>
<td>1132.6</td>
<td>509.0</td>
<td>1068.0</td>
<td>701.3</td>
<td>1052.7</td>
<td>985.8</td>
<td>473.2</td>
<td>338.9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Crayfish (Orconectes rusticus)</th>
<th>R1</th>
<th>R2</th>
<th>R3</th>
<th>R4</th>
<th>R5</th>
<th>R6</th>
<th>R7</th>
<th>R8</th>
<th>R9</th>
<th>R10</th>
<th>R11</th>
<th>R12</th>
</tr>
</thead>
<tbody>
<tr>
<td>AQUATIC (SD)</td>
<td>0.79 (0.18)</td>
<td>0.73 (0.20)</td>
<td>0.86 (0.13)</td>
<td>0.74 (0.24)</td>
<td>0.70 (0.22)</td>
<td>0.70 (0.24)</td>
<td>0.61 (0.25)</td>
<td>0.64 (0.24)</td>
<td>0.74 (0.25)</td>
<td>0.72 (0.27)</td>
<td>0.76 (0.22)</td>
<td>0.70 (0.24)</td>
</tr>
<tr>
<td>AQUATIC-Benthic algae</td>
<td>0.50</td>
<td>0.44</td>
<td>0.29</td>
<td>0.42</td>
<td>0.36</td>
<td>0.47</td>
<td>0.49</td>
<td>0.53</td>
<td>0.54</td>
<td>0.42</td>
<td>0.45</td>
<td>0.51</td>
</tr>
<tr>
<td>AQUATIC-Phytoplankton</td>
<td>0.50</td>
<td>0.56</td>
<td>0.71</td>
<td>0.58</td>
<td>0.64</td>
<td>0.53</td>
<td>0.51</td>
<td>0.47</td>
<td>0.46</td>
<td>0.58</td>
<td>0.55</td>
<td>0.49</td>
</tr>
</tbody>
</table>
Table 4.4. Eigenvalues >1 and the percent variance explained by the principal component axes, as well as each principal component’s loadings and proportion of variance ($r^2 = \text{loading}^2 / \text{eigenvalue}$) shared with the principal component axes.

<table>
<thead>
<tr>
<th></th>
<th>PC1 Loading</th>
<th>PC1 $r^2$</th>
<th>PC2 Loading</th>
<th>PC2 $r^2$</th>
<th>PC3 Loading</th>
<th>PC3 $r^2$</th>
<th>PC4 Loading</th>
<th>PC4 $r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Developed low-intensity (100m)</td>
<td>-0.83</td>
<td>0.07</td>
<td>0.24</td>
<td>0.02</td>
<td>0.04</td>
<td>0.00</td>
<td>0.07</td>
<td>0.00</td>
</tr>
<tr>
<td>Developed low-intensity (500m)</td>
<td>-0.74</td>
<td>0.06</td>
<td>0.17</td>
<td>0.01</td>
<td>0.09</td>
<td>0.00</td>
<td>0.14</td>
<td>0.01</td>
</tr>
<tr>
<td>Developed high-intensity (100m)</td>
<td>-0.77</td>
<td>0.06</td>
<td>0.36</td>
<td>0.04</td>
<td>-0.04</td>
<td>0.00</td>
<td>-0.13</td>
<td>0.01</td>
</tr>
<tr>
<td>Developed high-intensity (500m)</td>
<td>-0.85</td>
<td>0.08</td>
<td>0.35</td>
<td>0.04</td>
<td>-0.01</td>
<td>0.00</td>
<td>0.01</td>
<td>0.00</td>
</tr>
<tr>
<td>Forest (100m)</td>
<td>0.23</td>
<td>0.01</td>
<td>-0.79</td>
<td>0.21</td>
<td>0.40</td>
<td>0.07</td>
<td>-0.04</td>
<td>0.00</td>
</tr>
<tr>
<td>Forest (500m)</td>
<td>0.30</td>
<td>0.01</td>
<td>-0.83</td>
<td>0.23</td>
<td>0.27</td>
<td>0.03</td>
<td>-0.09</td>
<td>0.00</td>
</tr>
<tr>
<td>Grassland (100m)</td>
<td>0.68</td>
<td>0.05</td>
<td>0.04</td>
<td>0.00</td>
<td>-0.50</td>
<td>0.11</td>
<td>0.47</td>
<td>0.14</td>
</tr>
<tr>
<td>Grassland (500m)</td>
<td>0.65</td>
<td>0.04</td>
<td>0.16</td>
<td>0.01</td>
<td>-0.68</td>
<td>0.20</td>
<td>0.27</td>
<td>0.05</td>
</tr>
<tr>
<td>Cultivated crops (100m)</td>
<td>0.83</td>
<td>0.07</td>
<td>0.11</td>
<td>0.00</td>
<td>-0.16</td>
<td>0.01</td>
<td>-0.15</td>
<td>0.01</td>
</tr>
<tr>
<td>Cultivated crops (500m)</td>
<td>0.91</td>
<td>0.09</td>
<td>-0.04</td>
<td>0.00</td>
<td>0.03</td>
<td>0.00</td>
<td>-0.16</td>
<td>0.02</td>
</tr>
<tr>
<td>Shrub canopy (Shoreline)</td>
<td>-0.19</td>
<td>0.00</td>
<td>0.32</td>
<td>0.03</td>
<td>0.72</td>
<td>0.23</td>
<td>-0.04</td>
<td>0.00</td>
</tr>
<tr>
<td>Tree canopy (Shoreline)</td>
<td>-0.77</td>
<td>0.06</td>
<td>0.20</td>
<td>0.01</td>
<td>-0.12</td>
<td>0.01</td>
<td>-0.42</td>
<td>0.11</td>
</tr>
<tr>
<td>Total dissolved solids (mg L$^{-1}$)</td>
<td>0.01</td>
<td>0.00</td>
<td>-0.47</td>
<td>0.08</td>
<td>-0.59</td>
<td>0.15</td>
<td>-0.35</td>
<td>0.08</td>
</tr>
<tr>
<td>Dissolved oxygen (mg L$^{-1}$)</td>
<td>0.84</td>
<td>0.07</td>
<td>-0.16</td>
<td>0.01</td>
<td>0.16</td>
<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Nitrate (mg L$^{-1}$)</td>
<td>0.83</td>
<td>0.07</td>
<td>0.37</td>
<td>0.05</td>
<td>0.18</td>
<td>0.01</td>
<td>0.03</td>
<td>0.00</td>
</tr>
<tr>
<td>Phosphate (mg L$^{-1}$)</td>
<td>0.81</td>
<td>0.07</td>
<td>0.45</td>
<td>0.07</td>
<td>0.04</td>
<td>0.00</td>
<td>-0.15</td>
<td>0.01</td>
</tr>
<tr>
<td>Total phosphorous (mg L$^{-1}$)</td>
<td>0.78</td>
<td>0.06</td>
<td>0.45</td>
<td>0.07</td>
<td>0.00</td>
<td>0.00</td>
<td>-0.17</td>
<td>0.02</td>
</tr>
<tr>
<td>Total nitrogen (mg L$^{-1}$)</td>
<td>0.70</td>
<td>0.05</td>
<td>0.58</td>
<td>0.11</td>
<td>0.19</td>
<td>0.02</td>
<td>-0.08</td>
<td>0.00</td>
</tr>
<tr>
<td>Mean channel width (m)</td>
<td>-0.22</td>
<td>0.01</td>
<td>-0.07</td>
<td>0.00</td>
<td>0.19</td>
<td>0.02</td>
<td>0.92</td>
<td>0.53</td>
</tr>
<tr>
<td>Floodplain area (km$^2$)</td>
<td>0.78</td>
<td>0.06</td>
<td>0.07</td>
<td>0.00</td>
<td>0.53</td>
<td>0.12</td>
<td>0.06</td>
<td>0.00</td>
</tr>
</tbody>
</table>

|                  |           |           |           |           |           |           |           |
| Eigenvalue       | 9.54      | 2.99      | 2.27      | 1.60      |
| % Variance       | 48%       | 15%       | 11%       | 8%        |
Figure 4.1. Location 12 Scioto River system study reaches (Ohio, USA) and the relative proportions of land use/land cover (LULC) in adjacent 100-m and 500-m buffers. LULC from 2011 USGS National Land Cover Dataset.
Figure 4.2. Conceptual model of the spatial relationships between terrestrial riparian consumers and the river channel. The spatial extent at which each consumer forages is indicated by the relative position of each taxon (as a measure of lateral distance into the riparian area away from the channel and over the river, if applicable).
Figure 4.3. Reliance on aquatic (separated into phytoplankton and benthic algae compartments) and terrestrial energy by a suite of terrestrial secondary consumers at 12 reaches across the Scioto River system, Ohio, USA. Estimates are based on Bayesian mixing models performed with the MixSIAR package in R.
Figure 4.4. Relationship between the relative proportion of aquatic energy (benthic algae and phytoplankton combined) transported in the tissue of the dominant emergent aquatic insect taxon (Chironomidae) and the corresponding proportion of aquatic energy in shoreline tetragnathid spiders ($p = 0.016, R^2 = 0.45$). Dashed lines represent 95% confidence curves.
Figure 4.5. Relationship between the proportion of grassland land cover (in 500 m riparian buffer) and the relative proportion of aquatic energy (benthic algae and phytoplankton combined) in all terrestrial consumers (tetragnathid spiders, rove beetles, narrow-winged damselflies, riparian swallows, and raccoons) ($p = 0.026, R^2 = 0.41$; △ symbol and solid – line), in narrow-winged damselflies (Coenagrionidae) only ($p = 0.006, R^2 = 0.54$; □ symbol and – – line), and in riparian swallows only ($p = 0.051, R^2 = 0.32$; ● symbol and – – line).
Figure 4.6. Relationship between mean channel width (m) and the relative proportion of aquatic energy (benthic algae and phytoplankton combined) in tetragnathid spiders ($p = 0.023, R^2 = 0.42$; ◊ symbol and — line) and in riparian swallows ($p = 0.054, R^2 = 0.32$; ● symbol and — line).
Figure 4.7. Difference in the contribution of aquatic energy via phytoplankton to all terrestrial consumers at reaches influenced by dams (R1–R4) and reaches that were not influenced by dams (R5–R12) (ANOVA; $p = 0.005$, $F = 12.66$, $df = 1$).
Chapter 5: Summary and Conclusions

Although fluvial ecosystems are considered biodiversity hotspots and provide critical ecosystem services to human cultures worldwide, they are among the most highly modified systems on Earth (Vorosmarty et al. 2000). Understanding the role of human influences on rivers is therefore critical for addressing the potential impacts of future development and sustainability of flowing water ecosystems and the organisms that reside therein. Food webs relate information about diversity, community composition, and ecosystem function and provide a spatio-temporally integrated view of both the structure and as well as function in ecological communities. However, spatially-explicit food-web data remain scarce for river ecosystems and thus environmental determinants of food-web structure remain largely unresolved. In addition, to date, much of the research examining food-web dynamics and aquatic-terrestrial linkages in lotic systems has been conducted in relatively unmodified headwater systems (e.g., Nakano and Murakami 2001, Kawaguchi et al. 2003), and to a lesser extent in much larger river systems, such as the upper Mississippi and Ohio Rivers (Thorp and DeLong 1994). Comparatively little food-web work has been conducted in mid-size river systems (i.e., 4th-6th order), which exhibit a complex combination of physical, chemical and biological
elements resembling those of both small and large systems. My overarching goal of this research was to investigate landscape influences — mainly stemming from human landscape modification and river regulation — on fundamental properties of river food webs and cross-boundary energetic linkages across the aquatic-terrestrial interface in the 5th-6th order Scioto River system of central and southern Ohio. Within this framework I have developed three main research objectives, each of which corresponded to a chapter within my dissertation.

In my first research chapter, I explored the influence of human-modified riverine landscapes on reciprocal (aquatic-terrestrial) invertebrate flux dynamics and composition. Identifying the environmental influences that structure these reciprocal invertebrate fluxes in rivers is a critical step in understanding their effects on aquatic and terrestrial consumers and linked river-riparian food webs, subjects that were explored in subsequent research chapters. My results from this study showed how modified riparian landscapes can severely alter the magnitude and composition of bidirectional invertebrate fluxes and potentially override the influence of natural longitudinal patterns in river systems. In particular, my results suggested that urbanization led to declines in density and biomass of emergent insects and decreased biomass of terrestrial invertebrate inputs, thus largely decoupling aquatic-terrestrial ecological connections. I anticipate that the results from this study will contribute to a growing understanding of the dynamics of cross-boundary energy exchanges in modified river systems and spur further investigation into the importance of bidirectional invertebrate fluxes within the context of maintaining or restoring functional river food webs in the face of anthropogenic disturbance.
In my second research chapter, I examined the influence of river regulation and riverine landscape characteristics on food chain length (FCL) of spatially-explicit fish food webs. My conclusions contribute to an increasing understanding of the mechanisms that regulate aquatic food webs by providing insight into the complex, interactive influences of anthropogenic river modification and natural environmental gradients on fish FCL. Most notably I illustrated that dams exerted overwhelming negative effects on fish FCL, mostly resulting from shifts in assemblage composition (e.g., lower diversity) and trophic structure (e.g., fewer top and intermediate predator taxa) associated with the disruption of natural hydrogeomorphic gradients and physical barriers to fish dispersal. These conclusions lend support to the potential restoration of stable, functional fish food webs following dam removal. However, further evidence from my study system, which is representative of mid-sized rivers across the American Midwest, indicated that shifts in food-web architecture occurs along a gradient of human-mediated environmental change, suggesting that dam removal alone may be insufficient for fully restoring fish food webs.

In my final research chapter, I investigated the importance of aquatically-derived energetic resources (i.e., derived specifically from aquatic primary production) to terrestrial consumers in river food webs. My findings contribute to the growing understanding of the major energy sources that drive food webs in riverine landscapes, in particular, the relative importance of autochthonous aquatic energy in fueling intermediate to large river food webs (≥4th order). In small streams, Nakano and Murakami (2001) demonstrated that the “forest feeds the stream”, but here I present evidence that in larger systems, aquatic primary production can be a major player in
fueling terrestrial food webs. This aquatic energy contribution was appreciable both nearshore, as well as, deeper into terrestrial ecosystems via wide-ranging, mobile organisms (e.g., swallows and raccoons), thus adding to an emerging conceptual understanding of “biological stream width” (Muehlbauer et al. 2014). I also illustrated that the contribution of phytoplankton, an aquatic-to-terrestrial energetic pathway not previously considered, was shown to be an appreciable pathway of aquatic energy contributions to terrestrial consumers. Omitting the contribution of phytoplankton can thus lead to underestimations of the importance of aquatic energy to terrestrial food webs.

Finally, my overall findings have broad applications for understanding the role of rivers in driving food-web connectivity across landscapes as well as the influence of anthropogenic and natural gradients on these patterns. I have introduced clear empirical evidence that human activities play an important role in driving cross-boundary energy exchanges and lead to considerable shifts in river food-web structure. Furthermore, my results indicate that aquatically-derived energy from rivers subsidizes terrestrial consumers across a range of spatial scales from the aquatic-terrestrial interface well into riparian and upland habitats. Hence, river system integrity is critical not only for aquatic food webs but also for the terrestrial food webs that rely on aquatic primary production. In this way, my results can be applied to conservation, restoration, and management activities that promote longitudinal (e.g., upstream-downstream) and lateral (e.g., aquatic-terrestrial) connectivity, which are critical elements for maintaining or restoring fully-functioning river-riparian ecosystems.
Bibliography


food web structure, as determined by delta C-13 and delta N-15, in a eutrophic and an oligotrophic lake. Canadian Journal of Fisheries and Aquatic Sciences 56:2193-2202.


Size Have No Influence on Food Chain Length in Seasonally Connected Rivers.

Plos One 8:e66240.


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Appendix A. Additional invertebrate flux results for Chapter 2

<table>
<thead>
<tr>
<th>TERRESTRIAL (ALL)</th>
<th>EMERGENT (ALL)</th>
<th>NET FLUX (Emergent - Terrestrial)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S$</td>
<td>$H'$</td>
<td>No. m$^{-2}$ day$^{-1}$ Mg m$^{-2}$ day$^{-1}$ Mean mg</td>
</tr>
<tr>
<td>R1 66 3.222 7.8 11.5 1.5 15 0.755 45.7 3.4 0.1</td>
<td>37.8</td>
<td>-8.2</td>
</tr>
<tr>
<td>R2 74 3.523 7.8 12.7 1.8 15 0.231 23.7 3.7 0.2</td>
<td>15.9</td>
<td>-10.0</td>
</tr>
<tr>
<td>R3 74 3.542 7.1 10.4 1.8 15 0.609 12.8 1.4 0.4</td>
<td>-5.8</td>
<td>-5.7</td>
</tr>
<tr>
<td>R4 62 3.301 9.1 16.8 1.8 7 0.476 25.2 4.8 0.2</td>
<td>16.1</td>
<td>-12.1</td>
</tr>
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</tr>
<tr>
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<th>NET FLUX (Emergent - Terrestrial)</th>
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<td>$H'$</td>
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<tr>
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<tr>
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<td>-7.5</td>
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<tr>
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<tr>
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<td>-12.9</td>
</tr>
<tr>
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<tr>
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<tr>
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<tr>
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</tr>
<tr>
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<td>-15.1</td>
</tr>
<tr>
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<td>-6.9</td>
<td>-3.8</td>
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<tr>
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<td>-6.1</td>
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<tr>
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<td>15.9</td>
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</tr>
<tr>
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</tr>
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<td>-17.7</td>
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Appendix B. Food chain length and relative trophic positions of the most common top and intermediate predators in fish food webs along the Scioto River system
Appendix C. Detailed methods regarding measurement of environmental variables used in description of study system for Chapter 4

We used a GIS (ArcGIS 10.1; Esri, Redlands, CA, USA) to select a set of potential study reaches based on LULC in the adjacent riparian landscape. We then used site visits to narrow our selection to 12 study reaches that represented highly-modified (e.g., urban LULC and dams) to less modified (e.g., rural forested, agricultural, and grassland LULC, and no dams) riverine landscapes. Each study reach represented a unique river segment based on similar valley features and channel morphology and was ~1,200 m in length.

We used a GIS to delineate 100-m and 500-m buffers within the riparian zone on both sides of each reach and subsequently calculated the relative proportion of all non-agricultural human LULC (i.e., ‘urban-suburban-exurban’: developed open space, developed low-intensity, developed medium-intensity, and developed high-intensity), as well as row-crop agriculture, grassland, and forest using the 2011 National Land Cover Database (NLCD; Jin et al. 2013). We surveyed vegetation structure and composition within six 3-m × 3-m quadrats at the rivers edge. Quadrats were located along three transects approximately evenly spaced from upstream to downstream along the length of the reach. Within the quadrats, we visually surveyed the coverage of tree canopy cover (%) and shrub canopy cover (%). To estimate ecosystem size as a measure of longitudinal position, we used a GIS to generate drainage area of the catchment from the downstream terminus of each of the study reaches. However, because of the influences of adjacent
land cover and dams on channel morphology, we also assessed local ecosystem size using a laser rangefinder (Bushnell Scout, Bushnell Outdoor Products, Overland Park, Kansas, USA) to estimate bankfull channel width (m) at three cross-sections (top, middle, bottom) distributed along the reach using the lower extent of persistent woody vegetation, the flat top of depositional features, and the location of transition from steep to gentle slopes as indicators of bankfull height (Rosgen 1996, VTDEC 2003). To assess the degree of lateral connectivity, we measured the areal extent of active floodplains at each reach using a combination of GIS and field surveys. We assessed the influence of river regulation by counting the number of dams downstream of the reach and the distance to the nearest upstream dam.

To account for potential influences of water chemistry and nutrient concentrations to aquatic insect productivity and emergence, and nutritional quality of basal primary producers, we collected six 250-mL water samples for total nitrogen (N), nitrate (NO$_3^-$), total phosphorous (P), and phosphate (PO$_4^{3-}$) measurements from each reach: three samples collected laterally across the channel at evenly-spaced intervals both near the upstream and downstream ends of each reach (six samples total). Samples were composited by upstream and downstream locations separately and analyzed at the Ohio State University Service Testing and Research Lab (STAR Lab, Wooster, OH, USA) for concentrations (mg L$^{-1}$) of NO$_3^-$, PO$_4^{3-}$, total N, and total P. Water samples were also tested for concentration of total dissolved solids (TDS). We used a handheld YSI (YSI Incorporated, Yellow Springs, Ohio, USA) to measure other basic water quality metrics including dissolved oxygen concentration (DO; mg L$^{-1}$), pH, and oxidation-reduction
potential (ORP). We measured water quality at three points (right bank, mid-channel, left bank) across three transects (top, middle, and bottom) at each reach. Water quality surveys were completed three times (mid-June, mid-July, and mid-August).
Appendix D. C:N ratios for aquatic and terrestrial primary producers used in stable isotope analyses for Chapter 4

<table>
<thead>
<tr>
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<th>Benthic algae</th>
<th>Phytoplankton</th>
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<th>Terrestrial vegetation</th>
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