Ant and spider dynamics in complex riverine landscapes of the Scioto River basin,

Ohio: implications for riparian ecosystem structure and function

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

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2014

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Abstract

In recent years, a holistic ecosystem conceptualization has emerged that structurally and functionally links the river, and its riparian and floodplain zones into an integrated ecological unit – the riverine landscape. The array of riverine landscapes distributed across a river system represents biophysical complexity over broad spatial and temporal scales. Internal riverine landscape patchiness (e.g., gravel bars, mudflats, swamps, etc.), on the other hand, represents heterogeneity at finer spatiotemporal scales. Collectively, an understanding of environmental drivers and consequences of riverine landscape patch dynamics is critical to both basic riverine science as well as to management and conservation efforts. However, despite the well-documented importance of river corridors (e.g., as biological refuges in human-modified landscapes), the role of riverine landscape pattern and composition on ecosystem structure and function is largely unknown.

In this dissertation, I worked at 12 study reaches distributed along an urban-rural gradient of the Scioto River, Ohio, USA. To better understand environmental drivers of riverine landscape distribution and physical heterogeneity, I investigated the influence of internal (river size, lateral flow connectivity) and external (catchment land use and land cover) factors on site-specific riverine landscape patterns. At a finer scale, I used riparian

spiders of the family Tetragnathidae and ants as model organisms to explore the associations between internal riverine landscape patchiness and the distribution, diversity, and trophic dynamics [e.g., trophic position (TP)] of riparian arthropod communities. Because of a growing recognition of the importance of aquatic-to-terrestrial energetic subsidies (largely in the form of aquatic insects that emerge from the water as adults) to riparian and terrestrial food webs, I gave particular consideration to the reliance of aquatic carbon [C (C_A)] of riparian spiders and ants.

Riverine landscape patchiness was measured using a combination of field (vegetation surveys, canopy photography, shoreline habitat measurements) and remotesensing approaches [e.g., using a GIS, aerial photos, and Light Detection and Ranging (LiDAR) data]. Ants and spiders were surveyed on each side of the river at each study reach. A suite of analytical methods were used including Analysis of Variance (ANOVA), linear regression, Principal Component Analysis (PCA), Maximum Entropy (MaxEnt) modeling, a model-selection approach using Akaike Information Criterion (AIC) and Non-Metric Multidimensional Scaling (NMDS).

I found that a mixture of external and internal factors were associated with riverine landscape pattern (patch area and shape and size) including drainage area (a proxy for ecosystem size), proximity to impoundment (a proxy for lateral flow connectivity), and catchment land use and land cover (e.g., % urban, % agriculture). Percent impervious surfaces in the catchment, for instance, was strongly related to more convoluted patch shapes in the riverine landscape. Riparian ant density and diversity were highly variable along the urban-rural gradient. Agricultural riverine landscapes exhibited lower ant density but elevated ant diversity. Patch area, edge, and shape emerged as important predictors of ant diversity whereas patch composition, as well as patch area, edge, and patch density were strongly related to ant density. However, MaxEnt modeling indicated that patch-type influenced ant habitat choice less than gradients in distance from surface water.

Patch composition was strongly associated, with TP and C_A of ants (*Formica subsericea*) greatest at crop patches (TP = 1.79, C_A = 91%). I observed that both terrestrial (habitat) and aquatic (emergent insect food resources) were important environmental determinants of riparian tetragnathid distribution, trophic dynamics, and the capacity of spiders to ecologically link aquatic and terrestrial ecosystems. For example, tetragnathid TP, which averaged 2.45 across all study reaches, was largely driven by emergent insect density. For both ants and spiders, C_A was positively related to TP ($R^2 = 0.14$ for ants, $R^2 = 0.48$ for spiders), suggesting that algal-based energy pathways contribute to more complex riparian food webs.

Collectively, these findings indicate that patchiness in riverine landscapes exerts strong influences on the distribution, diversity, and trophic dynamics of riparian arthropod consumers. Additionally, my results contribute to a growing understanding of the impacts of landscape change in river corridors, and suggest that integrating conservation efforts at both broad (e.g., catchment) and fine scales (e.g., the aquaticterrestrial interface) will be an important step in maintaining diverse, functional riverriparian ecosystems. In particular, I found that urbanization is likely to prompt changes in riverine landscape structure as well as arthropod distribution, diversity, and trophic structure. Because these findings provide evidence that spatial habitat patterns within riverine landscapes can influence the structure and functions of riparian ecosystems, they also lend insight into the utility of landscape ecology to river science. Dedicated to my wife Annah and son Rodney

Acknowledgements

I would like to thank Adam Kautza, Jeremy Alberts, and Lars Meyer for their help in the field, and for providing good company. This dissertation was made possible in part by state and federal funds appropriated to The Ohio State University, Ohio Agricultural Research and Development Center. I want to say thank you to Dr. P. Charles Goebel and Dr. Desheng Liu for serving on my committee.

Many thanks to Dr. Mažeika Sullivan for the much needed guidance, help, and fundamentally, the patience he had with me.

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Chapter 1: Background and Literature Review

A central aim of ecosystem science is to understand fluxes of materials and organisms over space and time (Loreau and Holt 2004, Scheiner and Willig 2008). Interactions among the biotic components (organisms) occur in many forms (e.g., predation, herbivory, competition, and mutualism) and strongly influence the distribution and density of species, as well as food-web architecture (Schmitz et al. 2008, Sargeant et al. 2010, Takimoto and Post 2013). In aquatic systems, abiotic environmental features including water chemistry and quality (e.g., pH, dissolved oxygen, conductivity, redox reactions, nutrients, etc.) (Capderrey et al. 2013, Hadley et al. 2013, Pandey and Pandey 2013) as well as physical characteristics (hydrology and hydraulics, fluvial geomorphology, habitat heterogeneity) (King et al. 2012, Sullivan 2013) are thought to be strong determinants of biotic patterns and processes (Crecco and Savoy 1985, Poff 1997). For example, Sabo et al. (2010) illustrated that ecosystem size and hydrologic variability (i.e., disturbance) of streams and rivers was strongly related to food-chain length, a fundamental measure of food-web structure and stability. In riparian areas, abiotic factors including soil moisture, sunlight penetration, and ground substrate influence vegetation communities, which are major drivers of the distribution and

diversity of riparian fauna (Strong et al. 1984, Gregory et al. 1991, Herrera and Dudley 2003, Lockaby et al. 2005).

In river systems, biotic processes play out on a highly heterogeneous and variable stage partly because of the disturbance effect of flow dynamics. Although river ecologists have long recognized that rivers are uniquely embedded in and highly influenced by their surrounding landscapes (Hynes 1975), rivers have largely been considered as one of many elements that comprise the landscape mosaic (Wiens 2002a). Recently, a more holistic and detailed ecological view that reflects the diverse internal spatiotemporal and ecological dimensions that constitute a river system has emerged. The complex relationships among these dimensions have, in part, led to the application of the principles and approaches of landscape ecology to stream ecosystems and to "riverscape" (*sensu* Wiens 2002b) and "riverine landscape" (*sensu* Ward et al. 2002, Thorp et al. 2006) perspectives that recognize rivers as both internally heterogeneous and intimately linked with their surrounding landscapes via boundary dynamics (Hansen and di Castri 1992, Ward 1997, Malard et al. 2000, Fausch et al. 2002b, Sullivan et al. 2007).

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 recognizes the internal structure and dynamics of rivers as part of the broader landscape. Concepts related to patch dynamics (Pringle et al. 1988, Townsend 1989, Wu and Loucks 1995, Poole 2002) incorporate fundamental characteristics of lotic ecosystems including, disturbance heterogeneity, hierarchy, directionality, and spatiotemporal linkages in characterizing fluvial ecosystems as dynamic mosaics of interconnected patches.

Polis (1997) was among the first to pioneer the integration of landscape and foodweb ecology. Subsequently, multiple investigators undertook studies aimed at characterizing material and nutrient fluxes across aquatic-terrestrial habitats (e.g., Collier et al. 2002, Sanzone et al. 2003, Ballinger and Lake 2006). The influence of nutrient flows on the stability of food webs (Marleau et al. 2010) and the linkages between habitats and trophic levels (e.g., Gibb and Cunningham 2011) have also received recent attention. Additionally, increased attention on the fluxes of contaminants between aquatic and terrestrial systems has contributed to the broader understanding of cross-system trophic dynamics (Walters et al. 2008, Sullivan and Rodewald 2012).

However, although understanding how environmental patterns constrain trophic levels, energy flow, and nutrient dynamics is central to ecosystem science (Schmitz et al. 2008), our understanding of these relationships in riverine ecosystems remains limited (Baxter et al. 2005, Schmitz et al. 2008). Thus, this dissertation will help fill knowledge gaps regarding both the maintenance and function of riverine landscapes by contributing to an improved understanding of the distribution and trophic dynamics of arthropods in riparian areas associated with large streams and rivers.

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A landscape perspective of rivers

The landscape perspective of rivers recognizes a stream, its floodplain (i.e., the flat area adjacent to a river formed from sediment deposition from the river under present climatic conditions and regularly covered with water during moderate to high flow events), and riparian area (i.e., transitional zones between terrestrial and aquatic systems characterized by gradients in biophysical conditions, ecological processes, and biota) as an integrated ecological unit (Wiens 2002b, Sullivan et al. 2007). This perspective developed over a span of multiple decades. Hynes (1975) postulated that stream hydrology, chemistry, and geomorphology were direct byproducts of the unique vegetation, topography, soils, and geology of the stream's catchment. Subsequent theories focused on the longitudinal and lateral river-landscape connections. The River Continuum Concept (RCC) (Vannote et al. 1980) conceptualizes the river system as a continuum of habitats arranged from the headwater to the mouth with productivity and species distribution as a function of stream network position and catchment context. In particular, the RCC predicts a shift from terrestrial carbon (C) sources in headwater streams to increasingly autotrophic C sources in mid-order reaches and a decreasing trend thereafter. The Nutrient Spiraling Concept (Newbold et al. 1981) added the dimension that nutrients are assimilated into living tissue, stored, transformed, recycled, and transported along the channel. The Serial Discontinuity Concept (Ward and Stanford 1995) presents a broad theoretical perspective of regulated lotic systems: stream regulation (e.g., impoundments) modifies the abiotic and biotic components of the system thereby disrupting the longitudinal gradient outlined

in the RCC. The Flood Pulse Concept (FPC) (Junk et al. 1989) was the first to explicitly consider floodplain dynamics. The FPC describes rivers and their adjacent floodplains as integrated components of a larger dynamic river system, linked by hydrological and ecological interactions. Central to this concept are pulses of discharge that determine the magnitude and spatial distribution of connectivity across river-floodplain gradients. Flood pulses are also thought to recruit allochthonous material into the river. Thorp and Delong (1994) proposed the River Productivity Model (RPM), proposing that in some river sections, materials and energy are derived principally through local production of phytoplankton, benthic algae, and other aquatic plants, as well as directly from the riparian zone via leaves (as well as other sources of C).

Collectively, these and many other theories [as the above is not meant to be an exhaustive list; see Poole (2010) for a comprehensive review on biophysical theoretical developments in stream science] have served as an underpinning for recent advances in landscape perspectives to aquatic ecology. In particular, Fausch et al. (2002b) promulgated that a holistic view of the entire, spatially heterogeneous river environment was necessary to understanding interactive processes across spatial and temporal scales. Wiens (2002b) explicitly sought to establish linkages between terrestrial ecology and aquatic ecology, and to "bring landscape ecology into the water", thereby proposing the integration of the principles of landscape ecology with river science. Thorp et al. (2006) proposed the Riverine Ecosystem Synthesis (RES), an integrated, holistic model of river ecosystem biocomplexity across spatiotemporal scales from headwaters to large rivers.

The RES views rivers as suites of riverine landscape patches, which consist of the riverscape (*sensu* Wiens 2002b), the sub-bankfull inundation areas, and the suprabankfull inundation areas including permanently wetted floodplain waterbodies.

Thus, as a landscape perspective of rivers continues to develop, so does an understanding of the varied connectivity within and among riverine landscapes that drives resource patterns and creates heterogeneous resource patch structures (Poff 1997, Ward and Schiemer 1999). Today, riverine landscapes are increasingly understood as comprised of a complexity of diverse patches created by the movement and distribution of water and sediment through the system. The riverine landscape is often comprised of active and relict river channels, point bars, oxbow lakes, meander scrolls, natural levees, and backwater sloughs, swamps, mud flats and terraces, etc., each representing a diversity of successional stages (Ward et al. 2002b). Additionally, fluvial processes (transportation and deposition of sediments) produce and maintain patches, and ecotones (transitional zones between adjacent patches) representing important patch connectivity that drives the spatiotemporal dynamics of riverine ecosystems (Hufkens et al. 2009). At a coarse scale of resolution, riverine landscapes are complex ecotones between adjacent uplands, while at finer scales, riverine landscapes resemble a heterogeneous pattern of patches and stand out as complex landscapes in their own right (Wiens 2002b, Hufkens et al. 2009).

The high levels of spatiotemporal heterogeneity contribute to the rich biodiversity characteristic of riverine landscapes (Ward et al. 1999) as described by the habitat

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heterogeneity hypothesis (MacArthur et al. 1966). In riverine landscapes, heterogeneity may be a crucial driver of structure and function of local communities of organisms (Jarolimek et al. 1999, Tockner and Stanford 2002, Sieben et al. 2009). Heterogeneity may influence genetic diversity and gene flow in riverine species (Huey et al. 2008), habitat types (Robinson et al. 2002), and variation within and between vegetation zones (Sieben et al. 2009). However, riverine landscapes now represent a declining proportion of the world's ecosystems and are increasingly composed of a matrix of fragmented habitats of varying scales principally due to anthropogenic land use (Foley et al. 2005, Winter et al. 2008).

Patch dynamics in riverine landscapes

Patchiness is a ubiquitous feature in both terrestrial and aquatic systems that has been recognized in the ecological literature for many years (e.g., Pickett and Thompson 1978, Harper et al. 1993, Bowers and Dooley 1999, Paudel and Yuan 2012). Indeed, patch dynamics concepts have been central to landscape ecology (Forman and Godron 1981, Wiens 2002a, Turner 2005). Patchiness refers to "the spatial pattern of patches and/or the variability of such spatial pattern in terms of patch content, size, density, diversity, juxtaposition, and structural and boundary characteristics" (Wu 1995). The drivers of patchiness may involve both natural and anthropogenic forces.

The view of ecological systems as mosaics of patches has its origin in the Pattern and Process Hypothesis by Watt (1947) followed by a suite of refining concepts. The patchiness concept was developed further by the theory of Island Biogeography (MacArthur and Wilson 1967). Mathematical descriptions of patch pattern and patch dynamics then followed (e.g., Levin and Paine 1974). Other landmarks in the conceptual development of patchiness in ecosystems include the Shifting Mosaic Steady State (SMSS) developed by Bormann and Liken (1979). The SMSS concept describes a forested landscape where patches of that landscape are at different phases of ecosystem development, but the landscape's total plant composition remains fairly constant through time. Pickett and Thompson (1978) suggest that patches in landscapes exist in three phases (i.e., potential, active, and degraded). The potential state changes to an active state through colonization by dispersing species arriving from other active or degrading patches. Patches transform from the active state to the degraded state when the patch is abandoned, and patches change from degraded to potential through a process of recovery.

Patches represent distinct structural and process units and result in the heterogeneous distribution in space or time of abiotic and biotic resources (Forman 1995). Patches vary in size, shape, type, heterogeneity, and boundary characteristics that in turn influence the flow of materials through the system (Kotliar and Wiens 1990). Patch structure is scale- and context-dependent such that patch mosaics form nested hierarchies (Wu and Loucks 1995), particularly in rivers and catchments (Frissel et al. 1986, Poff 1997, Montgomery 1999). Patch hierarchies are structured or constrained based on how organisms respond to heterogeneity (Kotliar and Wiens 1990). Patch structure varies according to the functional scale of observation, i.e., a patch at one scale

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may provide suitable resources for one species, but may prove to be a barrier to another species (Wiens 2002b). Because ecological systems operate across multiple scales, understanding the geometry of patch structure is central to understanding the ecology of landscapes (Forman 1995). As patch size increases, an increase in the complexity and diversity of habitat is expected (MacArthur and Wilson 1967), but patch variability is scale-dependent with decreasing heterogeneity at coarse-scales (Forman 1995). The interplay of patches across spatial and temporal scales defines abiotic and biotic resource availability. The functional linkages between patches across scales establish resource patterns that in turn affect species distribution, pattern, demographics, competition, dispersal, and colonization rates (Wu and Loucks 1995).

Today, rivers are thought to be patchy and strongly hierarchical systems, thus a hierarchical patch dynamics perspective can be useful for interpreting interactions between structure and function in fluvial landscapes (Poole 2002). This perspective integrates other concepts including heterogeneity, hierarchy, and directionality across spatial scales in river science. Because rivers are thought to be scale-dependent and to operate as a nested hierarchy of spatial scales (Allen and Starr 1982, Vaughan et al. 2009), factors at the broader scale (e.g., catchment or landscape) influence those at the local scale (e.g., reach). This progression of ecological thinking that a river system is, at least in part, an amalgam of patches (Thorp et al. 2006, Carbonneau et al. 2012) provides a useful framework for understanding the complex interactions of ecological and hydrogeomorphic factors across variable spatial and temporal scales.

Land-cover fragmentation resulting from human activities in riparian zones is yet another driver of patchiness in riverine landscapes, and is an increasingly common global phenomenon (Naiman et al. 1993, Wu 1995) leading to alterations in the diversity and densities of species within ecosystems, altered biogeochemical cycles, and hastened extinctions (Kauffman and Krueger 1984, Hill 1996, Miller et al. 2003, Moore et al. 2005). The conceptualization of landscapes as mosaics of patches has also encouraged increased consideration of the flow of energy and organisms across patch (Loreau and Holt 2004) and ecosystem (Polis et al. 1997, Paetzold et al. 2005, Sullivan and Rodewald 2012) boundaries, which might be expected to be appreciably altered by landscape change in the riparian zone.

Food webs and cross-boundary ecological linkages in riverine landscapes

The notion that resource fluxes couple adjacent ecosystems is well established (e.g., Polis et al. 1997, Lamberti et al. 2010). Nutrient transfers (via matter and organisms) to recipient habitats are known as spatial resource subsidies (Power 2001). These subsidies may have strong impacts on the structure and dynamics of populations, communities, and food webs of recipient systems (Polis et al. 1997). The transfer of spatial resource subsidies may be via myriad channels including translocation by wind, migration, and dispersal (Polis et al. 1997, Fausch et al. 2002a).

The flux of subsidies from terrestrial to aquatic environments (e.g., plant litter fall) has long been recognized (Fisher and Likens 1973, Hynes 1975, Vannote et al.

1980). Inputs of arthropods into streams have also been shown to be critical energetic components of stream food webs (Nakano et al. 1999). For example, Nakano and Murakami (2001) reported that terrestrial arthropods accounted for an annual average of 44% of fish diets in the Horonai Stream, Tomakomai Experimental Forest Hokkaido, Japan. Reciprocal transfers in the opposite direction (aquatic to terrestrial and/or riparian environments), particularly in the form of aquatic emergent insects, are increasingly recognized as subsidizing terrestrial consumers (Henschel et al. 2001, Baxter et al. 2005, Sullivan and Rodewald 2012) (Figure 1). Akamatsu et al. (2004) for instance, estimated that aquatic emergent insects comprised 84% of the diet of riparian web-building spiders.



Figure 1. Representation of reciprocal food-web linkages (e.g., energy flows represented by arrows) in a stream-riparian ecosystem (from Sullivan and Rodewald 2012).

A number of complex and dynamic biotic and abiotic factors moderate the importance of aquatic production to terrestrial consumers and communities. These include spatial and temporal shifts in the relative productivities of habitats (Lynch et al. 2002, Chan et al. 2007) coupled by trophic exchange (Nakano and Murakami 2001), predator-prey life history traits (Baxter et al. 2005), and features of the riparian ecotone such as boundary permeability (Polis et al. 1997, Cadenasso et al. 2003). These factors, along with life-history trait compatibility of both the subsidy (e.g., delivery, quality, quantity) and consumer community (e.g., mobility, ability to capture and assimilate prey), can have strong direct and indirect effects on patterns of retention and energetic pathways.

Naturally abundant stable isotopes as a tool in describing trophic dynamics

The chemicals that make up matter, including living tissues, naturally occur in elements, which differ on the number of neutrons they contain (Inger and Bearhop 2008). Variation in stable isotope ratios makes it possible to use stable isotope signatures as tracers in ecological applications including studies focused on trophic position (enrichment studies), population (mark–recapture techniques), migration (isotopically-enriched labeling techniques), and diet assimilation and foraging behavior (Hobson and Wassenaar 1999, Hood-Nowotny and Knols 2007). In living organisms, the difference in isotope signatures is caused by variant rates of reaction at enzymatic levels (Deniro and Epstein 1978, Hood-Nowotny and Knols 2007). For example, photosynthesis utilizes the lighter

isotope of CO_2 (¹²C), but will use heavier isotopes, depending on water availability and on the photosynthetic pathway. Consequently, the concentration of stable isotopes in plant tissue can be used as a major distinguishing characteristic of plants from xeric, mesic, and aquatic environments (Inger and Bearhop 2008). Thus, it is both theoretically and empirically possible to track stable isotopes of interest across the ecological landscape to understand nutrient pathways (McCutchan et al. 2003).

The underlying theoretical basis which makes stable isotope analysis important to ecosystem ecology is that the isotopic composition of an organism, as expressed in various body tissues, reliably reflects assimilated nutrients and is relative to the trophic level within the organism's respective community (Kelly 2000, Post 2002). The ratio of ¹⁵N:¹⁴N (δ^{15} N) can be used to estimate trophic position because the δ^{15} N of a consumer is enriched by 3-5‰ relative to its diet (Post 2002). In contrast δ^{13} C is enriched by only 0.0 - 0.4‰ (Kelly 2000) or 0–1‰ (Inger and Bearhop 2008) by consumers as it passes through the food web. More importantly, ¹³C values of autotrophs tend to vary according to environmental factors and by photosynthetic pathway [e.g., C3, C4, CAM; see O'Leary (1988) and McConnaughey et al. (1997)]. Hence, ¹³C can be used to trace the sources of C to consumers (Lepoint et al. 2004, Inger and Bearhop 2008). However the precise levels of enrichment of both C and N by consumers are still debatable because some studies (e.g., McCutchan et al. 2003) report the mean isotopic shift for C as 0.5 $\pm 0.13\%$ rather than 0.0%, and the mean isotopic shift for N as 2.0 $\pm 0.65\%$. The reported differences, however could be caused by choice of body parts, measuring techniques and

technology, and dietary preferences of target organisms used by the researchers (McCutchan et al. 2003).

Stable isotope approaches have been used widely in food-web applications (e.g., Post 2002, Akamatsu et al. 2004, Kato et al. 2004, Tillberg et al. 2006, Ottonetti et al. 2008, Gibb and Cunningham 2011) and in investigating trophic traits of ecological communities (e.g., Kelly 2000, Post 2002, Ratnayake et al. 2006, Tillberg et al. 2006, Wang and Pataki 2010). Stable isotopes have been used also to investigate the functional role of organisms (e.g., Post 2002, Ratnayake et al. 2006) as well as flow and cycling of nutrients (e.g., Mizutani et al. 1992, Schumacher and Platner 2009).

Arthropods in riverine landscapes

Arthropod generalist predators, such as ground beetles (Carabidae), rovebeetles (Staphylinidae), ants (Formicidae), and spiders (Arachne) are common in riverine landscapes, where they depend on a mixture of terrestrial and aquatic food resources (Collier et al. 2002, Akamatsu et al. 2004, Paetzold et al. 2005, Paetzold et al. 2008). In a functionally intact system, these taxa typically display lateral distributional patterns from the stream edge correlated with gradients in temperature, humidity, and inundation frequency, as well as variations in the degree of vegetation cover and shading (Henschel et al. 2001, O'Callaghan et al. 2013).

Ants are nearly ubiquitously distributed across terrestrial environments (Fisher and Cover 2007). About 30,000 ants species are found on every landmass on Earth except

Antarctica, although only about 12,000 ant species have been named and described (Fisher and Cover 2007, Lach et al. 2010). The global population of ants at any one time is approximately 10 trillion individuals and constitutes about 15-20% of all non-plant biomass on Earth (Aiello 1994). Trophically, ants are remarkably diverse including herbivores, highly specialized predators, and omnivores (Tillberg et al. 2006), although most ant species are holometabolous omnivores (Lach et al. 2010). In addition to representing a wide array of feeding guilds, ants also fill other important functional roles including plant seed dispersal (Gomez and Espadaler 2013), and ecological engineers (Kalule-Sabiti 1980, Risch and Carroll 1982, Philpott and Armbrecht 2006, Underwood and Fisher 2006, Lach et al. 2010). Particularly by moving food materials through scavenging and hunting, ants redistribute nutrients and thus influence the patchiness of resources. For example Whiles and Charlton (2006) show that soil C, N, and phosphorus (P) concentrations increased near ant nests. Ant species richness and functional groups have also been used as ecological indicators of environmental disturbance (Gollan et al. 2011, Diamond et al. 2012, Ellison 2012).

There are 178 species of ants found in Ohio (Coovert 2005). Riparian ants in Ohio are dominated by Formicidae species: *Aphaenogaster tennesseensis, Formica subsericea* and *Tapinoma sessile* (Coovert 2005, Fisher and Cover 2007). Like other arthropods, ants are attracted to riparian areas partly by the presence of food resources in the form of both aquatic emergent insects and arthropod prey (Naiman et al. 1993, Hering and Plachter 1997, Framenau et al. 2002, Sadler et al. 2004, Paetzold et al. 2005). The interplay of

social behavior and ability to actively construct nests enables many ant species to move their homes to the proximity of their preferred food resources. Thus, ants are able to utilize diverse habitats, select among patch types, and to respond to disturbance at finer scales, making them an appropriate model taxon for this study (Holway and Suarez 2006, Underwood and Fisher 2006).

Riparian spiders of the family Tetragnathidae are common spiders with a broad geographic distribution. Riparian tetragnathids inhabit stream and lake margins and build weak, horizontal orb webs (Gillespie 1987, Walters et al. 2008). By relying on the consumption of aquatic emergent insects, tetragnathids are classified as subsidized stream consumers (Laeser et al. 2005). A critical habitat requirement for the tetragnathids is the presence of substrate overhanging above the water surface where orb webs can be built to capture emerging adults of aquatic insects (Gillespie 1987). Therefore, there is potential for habitat variation to affect the predation efficiency of the spiders (Laeser et al. 2005). Because tetragnathids are also common prey for a suite of terrestrial predators such as ants, bats, and birds, they represent a key trophic linkage between aquatic and terrestrial food webs (Kato et al. 2004).

The Scioto River system

The Scioto River in central Ohio (Figure 2) is a major tributary of the Ohio River with a total length of 371 km. Drainage area of the catchment is 16,900 km² and the Scioto flows primarily through agricultural land in its upper reaches (Lyons et al. 2006). Land
use and land cover (LULC) in the basin is dominated by cropland and pasture (59% by area) but supports multiple other types: 23% deciduous forest, 12.8% urban, 1.4% grassland, 0.7% evergreen forest, 0.8% open water, and 0.7% shrubland (derived from NLCD 2006). The Scioto River basin lies predominantly in a humid continental climatic region. The region in and around the Scioto River, on average, receives about 90-120 cm of precipitation annually. The average annual temperature of the region is 12°C (average high: 29.7°C; average low: -9.3°C).

The river and its tributaries first flow through the Quaternary Tills Plains and subsequently through the Glaciated Allegheny and Appalachian Plateaus before reaching the Ohio River at Portsmouth. The river flows through Columbus (the capital of Ohio) where it collects its largest tributary, the Olentangy River. Other significant tributaries of the Scioto are Big Walnut, Darby, and Paint Creeks, which collectively drain large proportions of the southern part of the Scioto River's catchment. There are multiple lowhead dams and reservoirs in and around the city of Columbus on the Scioto and Olentangy Rivers. Approximately 30% of drinking water for the city of Columbus comes from these reservoirs. Downstream of Columbus to the confluence with the Ohio, the Scioto is free-flowing. The Ohio Environmental Protection Agency describes the mainstem of the upper Scioto River as a river with moderate water quality problems with a high vulnerability to stressors.

Dominant tree species in forested and urban riparian zones of the area include American elm (*Ulmus americana* L.), American hackberry (*Celtis occidentalis* L.), black walnut (*Juglans nigra* L.), boxelder (*Acer negundo* L.), eastern cottonwood (*Populus deltoides* Bartr.), honey locust (*Gleditsia tricanthos*), silver maple (*Acer saccharinum* L.), sycamore (*Plantanus occidentalis* L.), sugar maple (*Acer saccharum* Marsh.), and white ash (*Fraxinus Americana* L.). Common woody understory vegetation includes common spicebush (*Lindera benzoin* L.), dogwood (*Cornus spp.*), hawthorn (*Crataegus spp.*), honeysuckle (*Lonicera* spp.), multiflora rose (*Rosa multiflora* Thumb), Ohio buckeye (*Aesculus octandra* Marsh.), tall paw paw (*Asimina triloba* L.), and saplings of overstory trees (Borgmann and Rodewald 2004, Leston and Rodewald 2006). Herbaceous vegetation is dominated by stinging nettle (*Urtica dioica* L.), pig weed (*Amaranthus palmeri* Wats.), cup plant (*Silphium perfoliatum* L.), and a variety of *Rumex* species. Riparian zones characterized in agricultural areas are also characterized by row crops (corn and soybean).



Figure 2. The Scioto River basin in central and southern Ohio, USA.

The mainstem channel has a generally low gradient profile ranging from 2m/km to 5m/km and characterized by pool-riffle morphology. Flashy peaks characterize the river's flow regime. The long-term (1920-2011) annual discharge displays high variability (m^3s^{-1}): max = 73.0, min = 8.5, μ = 42.0, SD = 14.4 (USGS 2012). The short-term average (2001-2011) annual discharge varies from a minimum of 28.9 m³ s⁻¹ to a maximum of 73.0 m³ s⁻¹. The varied flow regime and land-management practices associated with a riverine landscape complex that contains a suite of geomorphic and vegetation succession features including levee banks, swamps, islands, gravel bars, mudflats, and patches of forests, shrub land, grassland and emergent herbaceous plants

distributed along urban and rural (agricultural, forested) landscapes makes the Scioto River an appropriate study system for this dissertation research.

Summary and objectives

The primary goal of this research is to investigate the role of riverine landscape pattern and composition on ecosystem structure and function. To do this, I worked at 12 riverine landscapes distributed along an urban-rural gradient of the Scioto River (Ohio, USA). Initially, I focused on multiscale environmental associations with riverine landscape heterogeneity in order to understand how riverine landscape patchiness relates to both external (land use and land cover of the adjacent terrestrial landscape) and internal (river size and fluvial connectivity) factors (Chapter 2). I then consider riverine landscape patchiness as it relates to the distribution and trophic dynamics of riparian arthropods, using riparian ants and spiders of the family Tetragnathidae as model organisms. Thus, in Chapter 3, I address several potential mechanisms underlying the associations between riverine patch characteristics and the density of ants using Maximum Entropy (MaxEnt), Non-Metric Multidimensional Scaling (NMDS) and Analysis of Variance (ANOVA). In Chapter 4, I use ANOVA and linear regression with Principal Component Analysis (PCA) to examine the influence of patch composition on trophic position and reliance on aquatically-versus terrestrially-derived nutrients of ants. Similarly, I investigate the influence of nearshore habitat characteristics on the trophic dynamics (trophic position and aquatic C assimilation) of riparian tetragnathid spiders in Chapter 5 using a modelselection approach. Chapters 2-5 represent manuscripts that will be submitted for publication in ecological journals. All chapters are formatted in the same style with the exception of Chapter 2, which has been submitted for publication to *Environmental Management* (and thus follows the formatting requirements of the journal).

Worldwide, riparian corridors are increasingly impaired by urbanization and agriculture. As the footprint of human development expands, remnant riparian corridors become important reserves for biological organisms. As a result, a more comprehensive understanding of the factors that relate to diverse, functional riparian areas is necessary to appropriately protect these critical systems. I anticipate that this work, therefore, will help resolve unknown relationships related to both the maintenance and function of riverine landscapes. Additionally, it is my hope that this research will contribute to an improved understanding of the distribution and trophic dynamics of arthropods in riparian areas associated with large streams and rivers.

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Chapter 2: Environmental predictors of riverine landscape patches in a multiuse river system: evidence from the Scioto River, USA

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Submitted to Environmental Management, 01/2014

Abstract

Associations between riverine landscapes (the integrated ecological unit including the riverscape and the floodplain) and their surrounding catchment landscapes remain largely unresolved. We investigated relationships between site-specific riverine landscape patterns and catchment land use and land cover (LULC) at twelve reaches distributed along a rural-to-urban gradient of the Scioto River, OH, USA. We calculated patch metrics (area, edge, diversity, shape, and density) for each riverine landscape and measured LULC (% agriculture, forest, open water, and urban) of the catchment landscape at three nested spatial extents (1,000, 3,000, and 6,000 m) representing local, intermediate, and broad scales of environmental influence, respectively. To consider potential internal drivers of riverine landscape patchiness, we estimated drainage area (as a proxy for river size) and proximity to the nearest impoundment (as a proxy for flow heterogeneity). Drainage area ($R^2 = 0.46$, negative relationship) and proximity to impoundment ($R^2 = 0.67$, positive relationship) were strong predictors of patch area and shape, respectively. However, evidence was almost equally as strong for catchment LULC predictors of both of these patch metrics at the 1,000 and 3,000-m extents: forest for patch size, urban and agriculture for patch area. Higher patch diversity was related to greater catchment forest coverage at 3,000 and 6,000-m extents. These observations implicate both external (LULC characteristics) as well as internal (flow dynamics) controls as important environmental determinants of riverine landscape patchiness. Thus, management approaches that integrate both aquatic and terrestrial factors across a range

of spatial extents will appreciably benefit conservation of riverine landscapes, which are critical to both riverine ecosystem productivity and diversity.

Key words: Akaike Information Criterion, catchment landscape, patch metrics, riverine landscape pattern

Introduction

Although scientists have recognized for some time that fluvial systems are uniquely embedded in and highly influenced by their surrounding landscapes (Gregory et al., 1991; Hynes, 1975), rivers have largely been considered as simply one of the many elements that comprise the landscape mosaic (Wiens, 2002). Recently, a more holistic and detailed ecological view of river ecosystems has emerged – one that reflects the diversity of spatiotemporal and ecological dimensions (i.e., vegetation and physical habitat patches along the river-floodplain-riparian gradient) that constitute a river. The complex relationships among these dimensions have, in part, led to the application of principles and approaches of landscape ecology to aquatic ecosystems and to "riverscape" (sensu Fausch et al., 2002; Wiens, 2002) and "riverine landscape" (sensu Thorp et al., 2006; Ward et al., 2002) perspectives that recognize rivers as both internally heterogeneous and tightly linked to their surrounding landscapes via boundary dynamics (Fausch et al., 2002; Malard et al., 2000; Sullivan et al., 2007; Ward, 1997).

As river ecosystems increasingly become recognized as complex landscapes in their own right, identifying those environmental factors responsible for regulating riverine landscapes will be critical for their conservation and management (Ward et al., 2002; Wiens, 2002; Wu & Loucks, 1995). Conceptual advances in spatial ecology (Levin, 1992; Wiens, 1989) prominently figure in this discussion and have spurred considerable investigation of the relative influences of catchment landscape characteristics on rivers across spatial scales (e.g., Allan, 2004; Lowe et al., 2006; Townsend et al., 2003; Ward, 1989). Because river systems are widely understood to be hierarchically structured (Frissel et al., 1986; Wiens, 1989), patterns at one scale may be influenced or generated by processes operating at a different scale, or even at multiple spatial scales (Parsons & Thoms, 2007). Thus, hierarchical systems can be conceptualized as a series of organizational levels, each of which is constrained within a nested vertical structure (O'Neill, 1989). The spatial extent of each hierarchical level can be identified by functional or structural properties (Dollar et al., 2007; Goebel et al., 2006; O'Neill et al., 1989; Palik et al., 2000; Parsons & Thoms, 2007). For example, Thorp (2006) present a conceptual understanding of the effects of terrestrial conditions on biocomplexity within functional process zones (i.e., the ecological analog to hydrogeomorphic patches) as mediated by discharge of water, sediments, inorganic nutrients, and organic matter. Riverine landscapes – consisting of the riverscape, the subbankfull inundation areas, and the supra-bankfull inundation areas and permanently wetted floodplain waterbodies (following Thorp et al., 2006) – might be expected to respond to both broader terrestrial (i.e., from the surrounding uplands) and aquatic (upstream river parameters including flow, sediment, and size) domains.

Multiscale investigations improve our ability to target scale-dependent patterns and aid in the interpretation of these patterns, and may be particularly useful in understanding environmental controls on riverine landscapes. For example, Notebaert and Piegay (2013) present a conceptual model that identifies lithology and parameters that influence the river profile (e.g., base changes and tectonics, sediment load, discharge) as principal environmental drivers of floodplain width of the Rhone catchment river network. Eros et al. (2011) propose a network-based analysis, emphasizing how riverscape connectivity can provide a quantitative and spatially-implicit model with direct implications to conservation applications. Widespread changes in land use and land cover (LULC) can also have dramatic cumulative impacts to riverine ecosystems (Allan, 2004), including significant consequences for riverine landscapes. For instance, urbanization leads to increased impervious surface area and changes in drainage density and discharge resulting in increased rates of hydrogeomorphic change via disturbances in flow, erosion, and sediment regimes (Paul & Meyer, 2001; Walsh et al., 2005). Collectively, these changes might be expected to alter the spatial organization and function of riverine landscape patches (e.g., Marchetti & Acenolaza, 2011; Molnar et al., 2002).

Thus, although solid theoretical underpinnings relating to broad-scale controls on riverine landscapes are emerging, empirical evidence is currently lacking, particularly relative to how catchment landscape perturbations may alter riverine landscapes (Molnar et al., 2002). Recently developed methods in remote sensing have potential to increase our ability to empirically test conceptual riverine landscape models (Carbonneau et al., 2012). As an initial step in this direction, the objective of the current study was to use a combination of both remotely-sensed and field data to explore relationships between riverine landscape pattern and catchment LULC at multiple spatial scales. We also considered fluvial-floodplain dynamics (as captured through drainage area and proximity to nearest impoundment) given their importance in maintaining riverine landscapes

(Ibisate et al., 2013; Junk et al., 1989; Magilligan & Nislow, 2005; O'Hanley, 2011; Thorp et al., 2006).

To that end, we investigated relationships between riverine landscape patch metrics and catchment LULC at three hierarchically-nested spatial scales (1,000 m, 3,000 m, and 6,000 m) of twelve river reaches distributed along an urban-rural gradient of the Scioto River, OH, USA, a multiuse river typical of the American Midwest. We focused on a suite of patch metrics representing area, density, diversity, edge and shape that have been shown to be related to both ecosystem structure and function (Fletcher et al., 2007; Orrock et al., 2011; Ries et al., 2004). Because these patch metrics are expected to be governed by both external (catchment landscape features) and internal (fluvial dynamics), we anticipated that they would be sensitive to alterations in LULC and flow, as outlined in our conceptual model (Figure 1).

Methods

Study area and reach selection

The Scioto River is a mixed-use, 6th-order tributary of the Ohio River that drains a 16,882-km² basin. Typical valleys within the basin span ~2.5 km and form rich agricultural plains (Scheifer, 2002). Mean channel gradient in free-flowing sections is low (4 m/km), with pool-riffle morphology dominant in unmodified sections (Scheifer, 2002). The Scioto River lies predominantly in a humid continental climate (Karl & Koss, 1984), receiving 900-1,100 mm of precipitation/year on average (Rogers, 1993). LULC

in the basin is dominated by cropland and pasture (59% by area) but supports multiple other LULC types: 23% deciduous forest, 12.8% urban, 1.4% grassland, 0.7% evergreen forest, 0.8% open water, and 0.7% shrubland (NLCD, 2006). The Scioto River flows through multiple urban centers, including Columbus, OH with a population of 787,000 (US Census Bureau, 2011).

Riparian zones in the study area are dominated by sugar (*Acer saccharum* Marsh.), silver (*A. saccharinum* L.), and boxelder (*A. negundo* L.) maple; eastern cottonwood (*Populus deltoides* Bartr.); American elm (*Ulmus Americana* L.); northern catalpa (*Catalpa speciosa* Warder.); American sycamore (*Platanus occidentalis* L.); and common pawpaw (*Asimina triloba* L.). Common invasive tree and shrub species include Amur honeysuckle (*Lonicera maackii* Rupr.) and a variety of willows (*e.g., Salix nigra* Marsh, *S. purpurea* L.). Grass species are dominated by barnyard grass (*Echinochloa crus-galli* L.), Johnson grass (*Sorghum halepense* L.), and the invasive reed canary grass (*Phalaris arundinacea* L.). Sedges mainly include fragrant flatsedge (*Cyperus odoratus* L.). Herbaceous plants such as stinging nettle (*Urtica dioica* L.), pig weed (*Amaranthus palmeri* Wats.), cup plant (*Silphium perfoliatum* L.), and a variety of *Rumex* species and creeping plants such as poison ivy (*Toxicodendron radicans* L.) and hedge binder (*Calystegia sepium* L.) are also common.

The study area encompassed twelve, 1,500-m riverine landscapes along approximately 200 km of the Scioto and its major tributary, the Olentangy River, of central and southern Ohio (Figure 2). We first used the US Geological Survey (USGS) National Land Cover Data (NLCD) 2006 maps (NLCD, 2006) in ArcGIS 10.1 (ESRI, Redlands, CA, USA) to characterize LULC within a 500-m buffer from both sides of the main channel. Subsequently, we selected study reaches that represented the gradient in land cover found from urban to rural areas (i.e., developed/urban to forested and agricultural). Study reaches were separated by an average distance of 18.3 river km, although there was significant variability ($\sigma = 15.4$ km).

Riverine landscape patch metrics

To delineate riverscape patches and their configuration, we used a combination of field observations and the 2006, 30.48-cm resolution, natural color Digital Orthophoto Quarter Quadrangles (OSIP, 2012) with ArcGis 10.1 and ArcPad 8.0 1 (ESRI, Redlands, CA, USA). Using modified guidelines from Holmes and Goebel (2011) and Johansen et al. (2010), we obtained land-cover (patches) data at each of the twelve reaches by digitizing the orthophotos on a desktop computer, then checking for accuracy using a Personal Digital Assistant (Pharos 565 PDA, Pharos Science & Applications, Inc., CA, USA) with ArcPad 8.0 in the field. This approach enabled us to identify and digitize patch boundaries of fifteen patch types (Table 1, Figure 3) within our riverine landscapes. We then used the Patch Analyst extension in ArcGis 9.3.1 (Elkie et al., 1999) to compute seventeen patch metrics that characterized the landscape patterns at each of the twelve study reaches (Table 2). Detailed explanations and formulae for each metric are provided by McGarigal et al (2012).

Catchment landscape

We compiled our catchment LULC data from the USGS 2006 1:250,000 land-cover data (NLCD, 2006), which provides fifteen Anderson Level 2 classes (Andersen et al., 1976). We then used ArcGIS 10.1 to aggregate the NLCD 2012 data to seven Anderson Level I classes [Table 3; see (Homer et al., 2007) for detailed NLCD class definitions]. (Note that although eight Level 1 classes exist for our study catchment, because herbaceous was synonymous with pasture in our study system we aggregated herbaceous and cropland to form an "agriculture" class.) We also obtained % imperviousness data for our study area from the NLCD 2006 data archive (NLCD, 2006). We then used ArcGIS 10.1 to measure percent land cover for each of the seven classes and percent imperviousness at three nested spatial extents of radii 1,000 m, 3,000 m, and 6,000 m extending out from and upstream of the twelve study reaches (Figure 4). These spatial extents represent local, intermediate, and broad scales of environmental influence. The broadest scale was constrained to 6,000 m because at >6,000 m catchment LULC was overwhelmed by agricultural land use. The spatially-nested sectors are such that each larger landscape domain (e.g., 6,000-m) contains all smaller domains (e.g., 1,000 m and 3,000 m). Shrub, wetland, and barren classes represented only a small fraction of the overall landscape (collectively, 1.69% for 1,000 m, 0.42% for 3,000 m, and 0.66% for 6,000 m), so we excluded these LULC types from further analysis.

Drainage area and distance from impoundment

Because of the strong relationships between artificial impoundments and channelfloodplain connectivity (Ibisate et al., 2013; Magilligan & Nislow, 2005) and river size and floodplain development (Salisbury, 1980; Vannote et al., 1980), we used drainage area and proximity of the study reach from the nearest impoundment/dam as proxies for river size and lateral flow heterogeneity. Dams alter river flow regimes (Csiki & Rhoads, 2010; Nilsson et al., 2005) by reducing flood-pulse variability. Because floodplains are typically more developed in larger rivers, river size is linked to lateral flow connectivity between the main channel and the floodplain with consequences for vegetation patches in floodplains (Hughes & Rood, 2003; Junk et al., 1989; O'Hanley, 2011).

We used the hydrology tools in ArcGis 10.1 to delineate catchments of each of the twelve reaches from a 10-m resolution digital elevation model (DEM) of the Scioto River's catchment. We used the approximate location of the thalweg at the downstream end of each reach as the pour point, thereby including the study reach in the calculation of drainage area. We used the linear referencing tools in ArcGis 10.1 to estimate the distance (river km) of each reach's centroid to the nearest upstream dam.

Statistical analysis

Our primary statistical analysis was based on a theoretic model selection approach using the Akaike Information Criterion (AIC) (Burnham & Anderson, 2002, 2004). To identify candidate predictor variables, we used a correlation matrix to examine potential correlations among independent variables (% urban, % forest, % agriculture, % open water) at each of the three spatial extents. No variables with $|r| \ge 0.80$ were included in the same model (Sullivan et al., 2007) (Table 4). To constrain the analysis, we selected five patch indices that we considered adequately representative the seventeen patch descriptors (Table 2), and subsequently used these as dependent variables.

For each competing model set, AIC with correction for small sample size (Burnham & Anderson, 2002, 2004) was calculated:

$$AIC_{c} = N \ln\left(\frac{SSE}{N}\right) + 2K + \frac{2K(K+1)}{N-K-1}$$
(1)

where AIC_c is the sample size corrected AIC; SSE is the error sum of squares from the linear regression; *N* is the total number of data points; and *K* is the total number of estimated parameters (including the intercept and the error term). We also calculated the difference between the model with the AIC_c and each of the supported models (i.e., Δ_i):

$$\Delta_i = AIC_i - AIC_{\min} \tag{2}$$

where AIC_{*i*} is the AIC_{*c*} for the given model *i* and AIC_{min} is the AIC_{*c*} for the best model (i.e., minimum AIC_{*c*}). The model with the lowest AIC_{*c*} is considered the strongest model in its set. However, any model with $\Delta_i < 2$ is considered to be strongly supported (Burnham & Anderson, 2000). We also calculated each model's Akaike weight (*w_i*), or normalized model likelihood (i.e., *w_i*):

$$w_{i} = \frac{\exp\left(-\Delta_{i}/2\right)}{\sum_{r=1}^{R} \exp\left(-\Delta_{r}/2\right)}$$
(3)

where $\sum_{r=1}^{R} \exp(-\Delta_r/2)$ is the sum of Δ_i across all *R* competing models. The Akaike weight w_i represents a probability of a particular model being the best model. All variables were tested to meet parametric statistical assumptions and were transformed if necessary. We performed all analyses using JMP 9.0 (SAS Institute Inc., Cary NC).

Results

Percent agricultural land was invariant across the spatial extents. We observed that % forest increased from finer to broader spatial extents whereas % urban exhibited the converse pattern (Figure 5). Drainage area of the study reaches ranged from 1348.1 to 14676.3 km² and three of the twelve study reaches were within 100 m of upstream impoundments. We observed substantial variability in both riverine landscape patchiness and adjacent landscape characteristics along the urban-rural gradient. Patches described as open water and woody vegetation were found at all study reaches; cropland, grassland, fallow, and shrubland were present only in riverine landscapes embedded in agricultural landscapes; while grass (lawn) occurred only in urban reaches. Patch metrics varied widely: SEI – $\mu = 0.76$, $\sigma = 0.8$; AWMSI – $\mu = 3.07$, $\sigma = 0.6$; ED – $\mu = 157.1$ m, $\sigma = 63.1$ m; MedPs – $\mu = 17.4$ ha, $\sigma = 10.1$ ha; and TLA – $\mu = 544.6$ m², $\sigma = 333.3$ m².

The best-supported models were represented by single-variables only ($\Delta_i < 2$, Table 5; although multiple-predictor models received moderate support, $\Delta_i = 2$ -4, models
not displayed). Internal drivers related to flow variability and river size constituted the top models for the patch size and patch shape model sets, respectively. However, the weight of evidence suggested that for both of these variables, external LULC-drivers were equally plausible models (Table 5). Urban land cover was a key predictor for patch shape and edge metrics, whereas forest best predicted patch size and diversity. The null model was the strongest model in its set for patch area, indicating that our predictor variables inadequately captured variation in the total area of riverine landscape patches.

Land-use and land-cover predictors at the 1,000- and 3,000-m spatial extents were equally represented (by number of supported models) in the model sets, whereas predictors at 6,000 m were least represented and received the weakest support (Table 5). For example, urban land emerged as a predictor of edge density across all three spatial extents, with urbanization at 6,000 m ($\Delta_i = 1.86$, $w_i = 0.15$) receiving considerably less support than at 1,000 m ($\Delta_i = 0.00$, $w_i = 0.39$). Overall, LULC variables at fine and intermediate extents received the greatest model support for patch size, edge, and density; whereas patch diversity was best predicted at the intermediate and broad extents.

Discussion

Recent studies have shown that the spatial organization of riverine landscape patches influences the overall productivity of the river system as well as the flux of materials within and between the river channel, the riparian zone, and the adjacent terrestrial landscape (Moore & Thorp, 2008; Southwell & Thoms, 2011). Therefore, although

riverine landscape patchiness may be a key factor regulating both biodiversity and function in river corridors, our understanding of how environmental perturbations (e.g., land-use and land-cover change, flow alterations) influence riverine landscapes is lacking. An additional challenge is to disentangle the patterns and processes in hierarchical river systems into spatial domains of influence. Although largely exploratory, our study presents initial evidence that multiple catchment landscape variables operating across local, intermediate, and broad scales (e.g., 1,000 m, 3,000 m, and 6,000 m) can explain patterns in riverine landscape patch characteristics. In our study system, urban development best predicted patch edge and shape, while forest coverage predicted patch diversity and size. Our models also point to differences in operational spatial extents of LULC influences. For example, the influence of urban and agricultural land cover appeared to be most relevant at local to intermediate spatial extents (1,000 and 3,000 m in our study), whereas forest was influential at intermediate to broader extents (3,000 and 6,000 m). Our models also confirm the internal influence of flow dynamics on floodplain systems, pointing to both the impact of dams (e.g., on patch size) and river size (e.g., on patch shape) on riverine landscape patchiness. Collectively, our results may be used as a basis to investigate potential mechanisms driving riverine landscape patterns and make predictions relative to riverine responses to LULC change.

Internal and external drivers of riverine landscape configuration

Known relationships among sediment, flow, and riverine landscape patches (Benda et al., 2004; Church, 2002; Ward et al., 2002) suggest that internal processes related to fluvial dynamics are critical in shaping patchiness and support our finding that flow variability was an important driver of patch size and shape within our study reaches (Table 5). Multiple mechanisms have been postulated to explain how flood disturbances affect riparian vegetation structure and by extension, patchiness. Flooding can saturate the root zone (Bendix, 1999; Kozlowski, 1984), thereby removing or destroying vegetation cover. Because plant species vary in their resilience to flood disturbance, flood events differentially affect vegetation structure and ground cover, leading to a mosaic of vegetation patches across the riverine landscape (Bendix, 1999; Goebel et al., 2012). In addition to removing vegetation, flood pulses also deposit patches of fresh alluvial surfaces, woody debris, and other organic matter in riparian zones resulting in patchy vegetative growth (Auble & Scott, 1998; Malanson & Butler, 1990). These mechanisms act in concert to influence the distribution, diversity, and size of patches via the interaction between fluvial and successional dynamics.

Because over half of the large rivers in the world are affected by dams (Nilsson et al., 2005) the impacts of impoundments on riverine landscapes is a globally-common conservation and management concern. The physical influences of dams on river can be profound, both within the impounded area as well as downstream, whereby channel morphology, flow and sediment regimes, and longitudinal (upstream to downstream) and

lateral (overbank flows onto riparian areas) connectivity are altered (Baxter, 1977; Csiki & Rhoads, 2010). For example, in our study we generally observed a more complex mosaic of patches, both in terms of patch type and distribution, at reaches where floodplains were wider and overbank flows more common. Increasing distance from an upstream impoundment was strongly associated with greater patch size, and in fact represented our strongest model ($R^2 = 0.69$). Thus, dam removal (as well as other mechanisms of reestablishing environmental flows) – which is becoming an increasingly popular restoration method to reestablish connectivity of upstream and downstream streamflow, sediment regimes, and movement of organisms (Poff & Hart, 2002) – might be expected to be of appreciable benefit to riverine landscape patch dynamics as well.

Our findings also suggest that riverine landscape patchiness is also influenced by external factors related to catchment LULC, thereby supporting the notion that riverine landscapes are tightly linked to their surrounding landscape (Fausch et al., 2002; Mertes et al., 1995; Ward, 1989; Wiens, 1989). LULC dynamics (% urbanization, % forest, % agriculture) in the catchment landscape potentially influence the composition of the riverine patch mosaic partly via adjustments in overland flow and sediment entrainment from the catchment. For example, Kim (2011) showed that doubling urban imperviousness in the White Rock Watershed, TX, USA, increased precipitation runoff by 26%, and Nelson (2002) showed that urbanization was related to a ~50% increase in sediment yield in the Issaquah Creek Watershed, WA, USA. Given that the transportation and storage of river sediment and water are important hydrogeomorphological elements

that shape riverine landscapes (Hudson & Heitmuller, 2003), it is not surprising that we found positive associations between urban land and both patch shape and patch edge. High runoff rates, altered flow regimes (increased frequency and flashiness), and increased flood peaks that follow an increase in catchment imperviousness (Walsh et al., 2005; White & Greer, 2006) can lead to increased homogenization of the riverine landscape through changes in vegetation coverage and type. For example, White and Greer (2006) found that the area occupied by riparian vegetation doubled along an urban California stream as a result of a combination of increased flow rates from imported municipal water supplies and increases in flood size. Consistent with these results, patch shape increased with catchment imperviousness in our study (Figure 6). In particular, urban reaches in our study system are characterized by high density, non-native Amur honeysuckle, an invasive woody shrub in the region that outcompetes native vegetation and form large, homogenous patches.

Agricultural activities on the landscape can similarly alter runoff patterns, typically generating more surface flow and sediment yield than natural landscapes because tillage and grazing deplete the protective effects of vegetation cover and reduce the infiltration rate of precipitation (Knox, 2001). The increased yield may lead to analogous amplification of sedimentation in the riparian zone that can bury surface organic horizons and result in a loss of hydric soils (Groffman et al., 2003). Channelization is also typical of agricultural rivers, limiting natural flood pulses and the development of a diverse riverine landscape (Vought & Lacoursiere, 2010). Thus, implications for riverine patchiness may include an increase of upland plant species (Groffman et al., 2003) and a homogenization of the riparian zone. In our study, increasing % agriculture was associated with simple patch shapes (those that were closer in resemblance to circles and squares) and decreasing patch edge, although these models were not the strongest in their respective sets (Table 5). Moreover, non-obligate riparian species (e.g., *A. palmeri*, *T. radicans*, *U. dioica*) were prolific in agricultural riverine landscapes whereas more natural landscapes were dominated by obligate riparian flora (e.g., *Carex spp.*, some *Rumex spp.*).

Scale matters

The inherent associations among patch metrics and LULC measured at local and broad scales have been emphasized in recent studies (e.g., Burnett et al., 2006; Wang et al., 1997) and are consistent with our findings that underscore the influence of multiscale LULC characteristics on riverine landscape configuration. This observation generally aligns with the hierarchical nature of river systems, whereby physical and biological features are spatially nested from smaller to larger units (Allen & Starr, 1982; Frissel et al., 1986).

Identifying the land-use variables that strongly influence riverine landscape pattern and determining the most appropriate scale at which to draw inference are key steps in developing effective and sustainable conservation and management strategies. For instance, in our study system, managers may benefit from understanding that the influence of urban and agricultural land cover appears to be most relevant at local to intermediate extents, whereas forest was most predictive at broader spatial extents. In tangent with established theories of river system organization, which regard riparian areas as ecotones between terrestrial and aquatic systems (Decamps & Naiman, 1990) or littoral zones created by the flood pulse (Junk et al., 1989), these relationships also support the contention that catchment landscape influences the configuration of the riverine landscape at multiple spatial extents, implicating scale-dependent mechanisms in patch regulation (Wiens, 2002) and suggesting that management efforts at the local scale alone, may prove ineffective. For example, increases in runoff and sediment attributed to LULC change in the headwaters may lead to appreciable effects on low-gradient, downstream reaches (Parsons & Thoms, 2007) where they may influence riverine landscape configuration. Thus, the cumulative nature of the effects of LULC on riverine landscape pattern calls for management at both fine and broad spatial extents.

Conclusions

Consistent with our conceptual model (Figure 1), we found compelling evidence that riverine landscape patch patterns were related to gradients in both river size and flow variability as well as in LULC, and that these relationships were spatially-dependent. Thus, our approach represents an initial step in predicting how LULC interacts with fluvial action to generate patterns of patches in riverine landscapes. Understanding environmental controls on riverine landscapes extends beyond the physical habitat. In natural settings, riverine landscapes are comprised of a complex mosaic of patches characterized by high levels of spatio-temporal heterogeneity (Ward et al., 2002). Habitat heterogeneity influences biodiversity (MacArthur et al., 1966; Tews et al., 2004) as greater variety in habitat leads to greater variety in species. Alterations in both internal (e.g., fluvial dynamics) and external factors (e.g., LULC) can fundamentally alter riverine landscape heterogeneity with serious consequences to river-riparian biodiversity. For example, Salek et al. (2007) found that diversified riparian habitat (relic meanders) supported significantly higher bird community diversity and richness than homogenous (secondary) riparian forests. Because complex ecological processes are intimately linked to intact riverine landscapes, the ecological ramifications of river regulation and landscape change have important restoration and management implications for river corridors.

Although we did not test the influence of underlying landscape features (e.g., gradient, elevation, valley geomorphic properties) on riverine landscape patch patterns, we recognize their potential role in shaping habitat heterogeneity (Benda et al., 2004; Bendix, 1999; Goebel et al., 2012). Additionally, explicit investigation of the landscape-level mechanisms that drive riverine landscape configuration will be an important step in informing conservation and management approaches.

Acknowledgements

Research support was provided by state and federal funds appropriated to The Ohio State University, Ohio Agricultural Research and Development Center. We would like to thank Adam Kautza and Jeremy Alberts for their help in the field. Additionally, we extend our gratitude to Dr. Katie Hossler for her careful critiques of draft manuscript versions.

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Table 1. Summary of riverine landscape patch types at the twelve study reaches along the Scioto River based on authors' interpretation of field and remote-sensing data, adapted from Johansen et al. (2010).

Patch Type	Description
Barren land (gravel har	Bare soil gravel or sand
Barren land (mudflat)	Exposed mud (wet soil), particularly at the edges of open water
Cropland Herbaceous vegetation Grassland	Land tilled for crops Erect, rooted vegetation with herbaceous stems Pasture
Grass (lawn)	Managed ornamental grass, particularly in recreational parks
Fallow	Uncultivated cropland
Island	Terrestrial landscape patches bordered by open water
Open water (stream)	Water of the main channel or with direct surface connection to the stream
Open water (artificial)	Water in artificial waterbodies
Open water (floodplain waterbody)	Water in natural floodplain waterbodies
Shrub	Shrubs and young trees <6m in height
Urban/built-up land	Urban, residential, commercial, transportation or industrial land cover
Swamp	Herbaceous and wooded swamps
Woody vegetation	Trees >6m in height

Table 2. Metrics used to quantify the composition and configuration of riverine landscapes of Scioto River study reaches, Ohio, USA. Metric descriptions are adapted from McGarigal et al (2012). Italicized font denotes metrics used in the statistical analysis to represent their respective descriptors.

Descriptor	Abbrev- iation	Units	Description						
Area	TLA	На	Total Landscape Area: Total area encompassed by the riverin landscape.						
Edge	ED	m/ha	Edge Density: The length of patch edge per unit area.						
	MPE	m	Mean Patch Edge: Average edge length of all patches.						
	TE	m	Total Edge: Total edge length of patches.						
	MPAR	-	Mean Perimeter Area Ratio: Average perimeter to area ratio for all patches.						
Richness	SEI	-	Shannon Evenness Index: Patch evenness within the riverine landscape (i.e., relative abundance and distribution of patch types).						
	SDI	-	Shannon Diversity Index: Patch diversity within the riverine landscape.						
Shape	AWMSI	-	Area Weighted Mean Shape Index: Average perimeter-to-area ratio for a landscape, weighted by the size of its patches.						
	MSI	-	Mean Shape Index: Compares the patch shape to a square standard.						
	MPAR	-	Mean Perimeter Area Ratio						
	MPFD	-	Mean Patch Fractal Dimension						
	AWMPFD	-	Area Weighted Mean Patch Fractal Dimension						
Size	MedPS	ha	Median Patch Size: The median patch size in the landscape.						
	MPS	На	Mean Patch Size: Average of the size of all patches.						
	NP	Num	Number of Patches: Total number of patches in the landscape.						
	PSCoV	%	Patch Size Coefficient of Variation: Population coefficient of variation in patch size relative to the mean patch size for a landscape						
	PSSD	На	Patch Size Standard Deviation: Population standard deviation for patch sizes of a landscape.						

Table 3. Summary of land-use and land-cover classes used to characterize the surrounding catchment landscape at the twelve study reaches along the Scioto River. The National Land Cover Data (NLCD 2006) available in 15 Anderson Level 2 classes was aggregated to seven Anderson Level 1 classes adapted from the NLCD 2006 legend.

Level 1 Class	Level 2 Class
Water	Open Water
Urban	Developed, Open Space Developed, Low Intensity Developed, Medium Intensity Developed, High Intensity
Barren	Barren Land (Rock/Sand/Clay)
Forest	Deciduous Forest Evergreen Forest Mixed Forest
Shrub	Shrub/Scrub
Agriculture	Pasture/Hay Cultivated Crops Grassland/Herbaceous
Wetlands	Woody Wetlands Emergent Herbaceous Wetlands

	Agr_1	For_1	Urb_1	Wat_1	AGR_3	FOR_3	Urb_3	Wat_3	Agr_6	For_6	Urb_6	Wat_6	Area Dist
Agr_1	1.00												
For_1	0.29	1.00											
Urb_1	-0.95	-0.55	1.00										
Wat_1	-0.11	0.09	-0.04	1.00									
Agr_3	0.93	0.33	-0.91	-0.05	1.00								
For 3	0.51	0.79	-0.67	-0.10	0.39	1.00							
Urb 3	-0.93	-0.56	0.98	0.02	-0.94	-0.68	1.00						
Wat 3	0.09	0.03	-0.20	0.94	0.13	-0.01	-0.16	1.00					
Agr ⁶	0.84	0.25	-0.78	-0.13	0.94	0.24	-0.83	-0.01	1.00				
For 6	0.55	0.61	-0.65	-0.01	0.40	0.94	-0.70	0.14	0.20	1.00			
Urb 6	-0.91	-0.53	0.95	0.07	-0.92	-0.70	0.99	-0.11	-0.84	-0.70	1.00		
Wat ⁶	0.15	0.38	-0.33	0.77	0.25	0.24	-0.34	0.87	0.05	0.36	-0.27	1.00	
Area	0.64	0.64	-0.76	0.14	0.61	0.85	-0.82	0.30	0.42	0.91	-0.82	0.53	1.00
Dist	0.56	0.67	-0.68	0.02	0.52	0.89	-0.75	0.16	0.34	0.93	-0.77	0.42	0.97 1.00

Table 4. Correlation matrix of independent variables. Bold font indicates r > |0.8|.

Agr = Agriculture, For = Forest, Urb = Urban, Wat = Water, Area = Catchment area, Dist = Distance from nearest impoundment; _1, _2 and _3 = 1,000 m, 3,000 m and 6,000 m spatial extents, respectively.

Patch Metric	Model	AIC _c	Δ_i	<u><i>W_i</i></u>	R^2
Median Patch Size (size)	Dist (+)	86.46	0.00	0.50	0.69
	For_3 (+)	86.49	0.03	0.49	0.56
	Null	93.88	7.42	0.01	0.00
Area Weighted Mean Shape	Area (-)	21.95	0.00	0.26	0.46
Index (shape)	Urb_1 (+)	21.98	0.03	0.25	0.46
	Agr_1 (-)	22.20	0.25	0.23	0.45
	Urb_3 (+)	22.24	0.29	0.22	0.44
	Null	25.60	3.65	0.04	0.00
Edge Density (edge)	Urb_1 (+)	134.16	0.00	0.39	0.46
	Urb_3 (+)	135.45	1.29	0.20	0.39
	Agr_1(-)	135.57	1.41	0.19	0.39
	Urban_6 (+)	136.02	1.86	0.15	0.37
	Null	137.81	3.65	0.06	0.00
Shannon Evenness Index	For_3 (+)	-23.56	0.00	0.37	0.39
(diversity)	Null	-23.30	0.26	0.33	0.00
	For_6 (+)	-23.12	0.44	0.30	0.37
Total Landscape Area (area)	Null	178.12	-	-	0.00

Table 5. Riverine landscape pattern model sets ($\Delta_i < 2$) and AIC_c statistics.



Figure 3 (Chapter 2 Figure 1). A conceptual model of external and internal drivers of riverine landscape patch heterogeneity. Wedges represent hypothesized gradients (thick side, high; thin side, low). Urbanization and agriculture are anticipated to limit riverine landscape patchiness, whereas larger river size and increased lateral flow connectivity are expected to augment patchiness. 1000, 3000, and 6000 m represent the nested spatial extents of land use and land cover (LULC) considered in this study. Adjacent LULC at 1000 m is expected to have the greatest impact on riverine landscape patchiness. Stylized riverine landscape patch metrics are presented in order of hypothesized sensitivity to influences of river size and flow heterogeneity.



Figure 4 (Chapter 2 Figure 2). The Scioto River basin (Ohio, USA) with the locations of the twelve study reaches.



Figure 5 (Chapter 2 Figure 3). An example of riverine landscape patches delineated at one of the study reaches.



Figure 6 (Chapter 2 Figure 4). Riverine landscape of an example study reach showing the three spatial extents (1,000, 3,000 and 6,000m) used to quantify the adjacent catchment landscape.



Figure 7 (Chapter 2 Figure 5). Proportion of primary land use and land cover types by spatial extent.



Figure 8 (Chapter 2 Figure 6). Relationship between catchment imperviousness (%) and Area Weighted Mean Shape Index ($R^2 = 0.50$, p = 0.002). Dashed lines represent confidence curves at $\alpha = 0.05$.

Chapter 3: Riverine landscape patch heterogeneity drives riparian ant assemblages along an urban-rural gradient

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Abstract

Although the principles of landscape ecology are increasingly extended to include freshwater systems, explicit applications are few. We investigated associations between patch heterogeneity and riparian ant assemblages at 12 riverine landscapes of the Scioto River, OH, that represented urban, agricultural, and mixed (primarily forested, but also wetland, grassland/fallow, and exurban) land-use settings. Using remotely-sensed and ground-collected data, we delineated riverine landscape patch types (crop, forest, grass, gravel, herbaceous, mudflat, open water, shrub, and swamp), computed patch metrics (area, density, edge, richness and shape), and conducted coordinated sampling of Formicidae assemblages. Ant density in agricultural riverine landscapes was ~3.5 times less than in mixed or urban reaches (ANOVA: F = 17.39, p < 0.0001; Tukey HSD: p < 0.0001; 0.0001), whereas ant diversity (Simpson's D) was higher in agricultural (0.54 ± 0.45) than either in mixed (0.45 ± 0.36) or urban (0.39 ± 0.36) riverine landscapes (ANOVA: F = 3.89, p = 0.02; Tukey HSD: p < 0.05). Patch area, edge, and shape emerged as important predictors of ant diversity ($R^2 = 0.53$, p = 0.01) whereas patch area, edge, and density were strongly related to ant density ($R^2 = 0.65$, p < 0.03). Non-metric multidimensional scaling (stress = 0.29) separated ant density between forest and the other patch types. However, MaxEnt modeling, however indicated that patch-type influenced ant habitat choice less than either gradients of elevation or distance from surface water. These findings provide evidence that spatial habitat patterns within

riverine landscapes can influence assemblage characteristics of riparian arthropods and lend insight into the utility of landscape ecology to river science.

Key words: landscape configuration, landscape heterogeneity, MaxEnt modeling, nonmetric dimensional scaling, patch metrics, principal component analysis, riverine landscape

Introduction

Spurred in part by Wiens (2002) guiding thesis that landscape ecology has important insights to offer aquatic ecology, the principles of landscape ecology have increasingly been applied to riverine systems (Poole 2002, Ward et al. 2002a, Ward et al. 2002b, David and Thompson 2006). In particular, the central role of patch dynamics (i.e., quality, connectivity, boundaries, context) can be aptly applied to riverine systems, whereby the interaction of hydrology, sediment, and biotic factors form a rich mosaic of interconnected patches (Ward et al. 1999, Ward and Tockner 2001, Latterell et al. 2006). Riverine ecosystems can exhibit a heterogeneous amalgam of patches including active and relict river channels, point bars, oxbow lakes, meander scrolls, natural levees, backwater sloughs, swamps, mud flats, and terraces, each representing a diversity of spatiotemporal dynamic successional stages. These spatiotemporal dynamics contribute to both lateral and longitudinal variation in biogeochemical processes, sedimentation, soil moisture, and subtle shifts in elevation associated with riverine landscapes (Johnston et al. 2001).

Hydrologic dynamics are of particular significance to riverine landscapes, where water movement represents a formative process linking aquatic and terrestrial "landscape" elements in both space and time (Church 2002, Church and Hassan 2002). For example, the dynamic flooding regime inherent to semi- or unregulated riverfloodplain ecosystems is critical for patch heterogeneity (Junk et al. 1989, Richards et al. 2002). Rising floodwaters connect the main channel to floodplain waterbodies (e.g., ponds, wetlands, slackwaters, etc.) and promote exchanges of aquatic biota, thereby homogenizing aquatic communities (Bayley 1995, Wiens 1995). Conversely, a mosaic structure is reestablished as floodplain waters recede, floodplain waterbodies are isolated, and aquatic communities become more heterogeneous. For terrestrial biota, flooding events reduce connectivity among patches and may increase within-patch heterogeneity as populations become isolated (Ballinger et al. 2007, Goebel et al. 2012). For high terrestrial biotic diversity to persist, a heterogeneous patch structure must remain after floodwaters have receded and connectivity has been reestablished.

In particular, terrestrial floodplain areas can be important habitats for riparian arthropods, including spiders, ground beetles, and ants (Hering and Plachter 1997, Framenau et al. 2002, Sadler et al. 2004). Many riparian invertebrates have speciesspecific adaptations to disturbances associated with flooding, including timing of lifecycle stages and movement in and out of floodplain habitats (Hammond 1998). Riparian invertebrate communities are often organized along both longitudinal and lateral gradients of soil moisture and elevation associated with floodplains (Lambeets et al. 2008). For example, Paetzold et al. (2008) and Ballinger et al. (2007) found that habitats that were affected by frequent flood inundation were almost devoid of arthropods immediately after flooding events. Thus, changes in flooding frequency and magnitude can cause filtering of variability in abundance and composition assemblage (Hering et al. 2004). As such, the complex interconnectivity of in-channel, riparian, and floodplain
zones is thought to structure riparian arthropod communities (Ward et al. 2002b, Burt and Pinay 2005).

The notion that rivers are both internally heterogeneous and tightly linked to their surrounding landscapes has been conceptualized in "riverscape" (sensu Wiens 2002b) and "riverine landscape" (sensu Ward et al. 2002b, Thorp et al. 2006) perspectives. However, in spite of these significant conceptual advances, explicit applications of riverine landscape ecology are few (Latterell et al. 2006, but see Ballinger et al. 2007, Sullivan et al. 2007). In this study, we used a patch metrics approach to investigate patterns of density and diversity of ground-dwelling ant (Hymenoptera: Formicidae) assemblages within riverine landscapes in urban, agricultural, and "mixed" (primarily forested, but also wetland and grassland/fallow, and exurban) areas of the Scioto River basin, OH, USA. Because of the documented associations between arthropod assemblages and floodplains, we anticipated that ant density and diversity would be higher in patches that experience reduced flood disturbances (e.g., forested patches) than in patches that experience more frequent and intense flood events (e.g., gravel bars, mudflats, swamps). At a broad spatial resolution, we expected that urban and agricultural riverine landscapes, characterized by low hydrological connectivity between the floodplain and the main channel due to impoundments and or/channelization, would support low patch heterogeneity and low ant diversity. At a finer level of resolution, we hypothesized that specific patch types and characteristics within the riverine landscape (e.g., shape, size, connectivity, etc.) would influence ant assemblage density and

diversity. We used a suite of analytical tools [Analysis of Variance (ANOVA), principal component analysis (PCA), regression analysis, non-metric multidimensional scaling, and Maximum Entropy Modeling (MaxEnt)] to explore relationships between riverine patches and ant assemblages. This study represents an important proof of concept for the application of the principles of landscape ecology to riverine landscapes.

Methods

Study area and site selection

The Scioto River is a 6th-order, mixed-use river draining a 16,882-km² catchment from its headwaters in central Ohio to its confluence with the Ohio River. The catchment intersects three physiographic regions including the Till Plains, the Glaciated Appalachian Plateau, and the Unglaciated Allegheny Plateau (ODGS 1998, White et al. 2005). Typical valleys of the Scioto River in our study area span ~2.5 km and form rich agricultural plains (Scheifer 2002). Channel gradient is typically low (~4 m/km), with pool-riffle morphology dominant in unmodified sections (Scheifer 2002). The Scioto River basin lies predominantly in a humid continental climate (Karl and Koss 1984), receiving 900-1100 mm precipitation/year on average (Rogers 1993). Land use and land cover in the basin are dominated by cropland and pasture, which collectively comprise 59% of the catchment area (NLCD 2006). However, the river also flows through multiple urban centers, including Columbus, OH with a population of 787,000 (US Census Bureau 2011) as well as areas of mixed landscapes comprised of primarily deciduous forests but

with minor percentages of small urban centers/towns, grassland, shrubland, forest, and wetland (NLCD 2006). The Olentangy River is the largest tributary of the Scioto River, joining the Scioto River in Columbus from the north.

Our study included twelve, 1,500-meter (m) riverine landscapes along \sim 200 km of the Scioto and Olentangy Rivers (Figure 1). To select study reaches, we first used the National Land Cover Database (NLCD 2006) land-use maps in ArcGIS 10.1 (ESRI, Redlands, CA, USA) to characterize land use/land cover (LULC) within a 500-m buffer of the main channel following Alberts et al. (2013). Subsequently, we stratified adjacent landscapes (to the main channel) within the 500-m buffer into two land-use categories (urban and agriculture) that represented the predominant [> 66% of total LULC by area, after Kawula (2009)] LULC classes. Those riverine landscapes that had no predominant LULC were classified as "mixed". Within each of the three land-use classifications (i.e., urban, agriculture, mixed), we then systematically selected five urban, five mixed and two agricultural reaches. We were unable to attain a balanced design because of accessibility including road network and access permits. Although the study reaches were distributed along the length of the river, LULC patterns in the watershed and limited access to some stretches precluded equidistant sampling and led to an unavoidable clustering of study reaches by land-use classes. Study reaches were separated by distance of 18.3 river km on average, although there was high variability (SD = 15.4 km).

Riverine landscape patch metrics

We delineated the riverine landscapes following Thorp et al. (2006) including the riverscape [main channel and slackwaters; *sensu* Wiens (2002)], the sub- and suprainundation areas of the riparian zone, and permanent floodplain waterbodies. We then used a combination of remotely-sensed and field-collected data to characterize the terrestrial patches within the riverine landscape, as our focus was on ants. Specifically, we used a combination of on-screen digitizing in ArcGIS 10.1 and Arc Pad 8.0 (Environmental Systems Research Institute: Redlands, CA, USA) on a desktop computer and on a Personal Digital Assistant (Pharos 565 PDA, Pharos Science and Applications Inc, CA, USA), respectively. The principal source of remotely-sensed data was the 2006, 30.48-cm resolution, natural color Digital Orthophoto Quarter Quadrangles (DOQQs) of the study area obtained from the Ohio Statewide Imagery Program (OSIP 2012). Using this approach and guidelines adapted from Holmes and Goebel (2011) and Johansen et al. (2010), we identified and digitized nine patch types in the riverine landscape (Table 1). We then used Patch Analyst software (Elkie et al. 1999) within a GIS to compute seventeen patch metrics from which we selected ten that we deemed to be adequate representatives of overall patch patterns in order to characterize and quantify habitat patches at each of the riverine landscapes (Table 2).

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Ant surveys

Terrestrial taxa that inhabit floodplain environments are often ubiquitous opportunists with general habitat requirements and the capacity to quickly recolonize after a disturbance event (Lambeets et al. 2008). In particular, ants represent an excellent model taxon for this study because they respond rapidly to environmental change, represent a variety of trophic levels, are important ecosystem engineers and agents for plant seed dispersal, and have been used effectively as ecological indicators (Holway and Suarez 2006, Underwood and Fisher 2006, Gollan et al. 2011, Gomez and Espadaler 2013). We conducted detailed surveys of ground-dwelling ant assemblages in June, July, and August of 2010-2012, focusing on ants of the family Formicidae, as this group is common in riparian areas of the region, found in a diverse array of riparian patch habitats, and known to utilize a mixture of aquatic and terrestrial food resources in the study system (Alberts and Sullivan, unpublished data). First, we established five longitudinal transects that were \sim 250 m apart and ran perpendicular to the main channel. Transects extended to the end of the riverine landscape, which we visually assessed primarily by riparian to upland changes in vegetation and soils. Along each transect we used a quadrat method (460 quadrats in total; Thompson and McLachlan 2006) to survey ant assemblages at 3-m² georeferenced plots distributed at the edge of the main channel and at locations within riverine landscape patches (Figure 2). Depending on transect length (which varied with width of riverine landscape) and the number of distinct patches along each transect, we sampled from two to seven quadrats along each of five transects per reach. We also

sampled additional quadrats at the centroids of distinct ecological patches (e.g., islands) that may have been missed by the systematic transect approach. We counted and identified to species all ants that we observed within or entering the quadrat in a 10-minute period (Ward 2008). Any ants that were difficult to identify in the field were collected, dispatched, and identified in the lab following (Fisher and Cover 2007), consulting experts when necessary.

Numerical and statistical approach

We calculated Simpson's Diversity Index (D) for each quadrat using the following formula: $D = 1 - [\sum n(n-1)/N(N-1)]$, where 'N' is the count of all ants; and 'n' is the count of ants of a particular species per quadrat. D measures the probability that two individual ants randomly selected from a sample will belong to the same species; 1.0 represents infinite diversity and 0.0 represents no diversity. We also calculated ant density as the number of ants m⁻². Because the raw patch metrics were at different scales of measurement, we standardized them to per unit variance (i.e., dividing each score by the standard deviation of each respective patch metric) and used the standardized scores in the statistical analysis (Baxter 1995).

We used ANOVA followed by Tukey-Kramer honestly significant difference (HDS) ($\alpha \le 0.05$) to test for differences in patch metrics as well as ant diversity among agricultural, urban, and mixed riverine landscapes. We used non-metric multidimensional scaling (NMDS) to analyze the partitioning of ant density by patch type using a matrix comprising eight patch types (note that we excluded open water from all ant-patch analyses) and the ant densities of the three most abundant species *(F. subsericea, A. tennesseensis, and T. sessile)* in our study system. We employed Principal Component Analysis (PCA) to reduce dimensionality in the riverine landscape metric dataset and retained principal components with eigenvalues >1 as predictors of ant density and diversity in subsequent mixed stepwise linear regression models (Rencher 1995, Sullivan and Watzin 2008). ANOVA, PCA, and regression analyses were run in JMP 10.0 (SAS Institute Inc., Cary, NC); NMDS was run using R Software (R Development Core Team 2010).

We then used MaxEnt version 3.3.3

(http://www.cs.princeton.edu/~schapire/maxent/, accessed 7/2013) to generate probability maps of occurrence based on environmental conditions with presence-only data (geographic coordinates of recorded presence) for our three most abundant ant species (*F. subsericea*, *A. tennesseensis*, and *T. sessile*). This analysis complemented our primary tests by incorporating not only patch type (Table 1), but also key gradients of environmental change in riverine landscapes [distance from surface water (m) and elevation (m)] (Figure 3). We randomly selected 70% of the presence data for each of the species (Matawa et al. 2012) for training purposes. We then ran one MaxEnt model for each of the three species separately (three models total) using the jackknife approach within a logistic format (Baldwin 2009). Finally, we generated the threshold-independent receiver operating characteristic curve (ROC) in order to test the accuracy of the models (Phillips et al. 2006) and mapped the probability distributions in ArcGIS.

Results

In total, we delineated 253 riverine landscape patches across the eight patch types across all study reaches. The distribution of the patches was uneven across the twelve reaches and the three LULC classes, with forest numerically dominant across LULC classes (Figure 4). Shrub and swamp patches also occurred in all three LULC classes but collectively constituted only ~12% of the 253 patches (Figure 4). We identified grass patches only in urban reaches, although they represented a small percentage of the total number of patches in urban riverine landscapes.

Patch metrics were highly variable both within and across land-use classes (Table 3). Total Landscape Area (TLA) was 166% greater in agricultural than in urban reaches (ANOVA: F = 6.23, p = 0.02; Tukey HSD: p = 0.02). A number of other notable, although non-significant relationships emerged. Mean Patch Size (MPS) – another metric describing patch area – was 46% greater in agricultural reaches than in urban. Likewise, TLA and MPS were 3% and 83% greater in agricultural than mixed reaches. Patch density [(represented by Number of Patches (NP)] was ~1.4 times greater in urban reaches than in either mixed or agricultural reaches (Table 3). Diversity metrics (Shannon Diversity Index (SDI) and Shannon Evenness Index (SEI) were comparatively higher in mixed and urban reaches than in agricultural reaches (Table 3).

Relationships between riverine landscape LULC and ant assemblages

We surveyed 8,278 ants at 460 quadrats representing thirteen genera and 23 species. The most numerically dominant species (from greatest to least) were: T. sessile (3.393), A. tennesseensis (2,024), and F. subsericea (1,925), which collectively represented 89% of the ant community. We observed marked variability in ant abundance, density, and diversity both within and among riverine landscapes (Table 4). Of all ants surveyed, abundance was greatest in mixed riverine landscapes (54%), followed by urban (41%), and agricultural (5%). Mean ant density was ~ 3.5 times lower at agricultural reaches (1.54 ± 1.33) than mixed (5.50 ± 2.00) and urban (5.32 ± 2.16) riverine landscapes (ANOVA: F = 17.39, p < 0.0001; Tukey HSD: p < 0.0001). In contrast, diversity was 26% and 13% higher in agricultural than in urban and mixed riverine landscapes, respectively (ANOVA; F = 3.89, p = 0.02; Tukey HSD: p < 0.05; Table 4). We observed no differences in either diversity or density between mixed and urban riverine landscapes (p > 0.05). Generally, we observed the highest abundance of ants in forest patches regardless of LULC class, followed by (from highest to lowest) crop, grass, lawn, swamp, mudflat, shrub and gravel (Table 4).

Influence of patch metrics on ant assemblages

PCA identified four indices (eigenvalues >1) that accounted for ~97% of the variation in the patch-metric dataset (Table 5). Metrics representing patch area and edge [ED(-), MPS(+), TLA(+) and MPAR(-)] loaded heavily on PC1 so we labeled it 'Area/Edge

Axis'. Likewise, metrics describing patch density [NP(+) and MPE(-)] strongly influenced PC2, thus we labeled it 'Density Axis'. Patch shape [MSI(+)] controlled PC3 (thus, 'Shape Axis') and PC4 was driven primarily by metrics representing patch diversity [SDI(-) and SEI(-)] (thus, 'Diversity Axis') (Table 5).

Linear regression yielded two significant models. One of the models included both the Area/Edge and the Density Axes to explain 65% of the variation observed in ant density (F = 7.46; p = 0.01). In the second model, both the Area/Edge and the Shape Axes jointly accounted for 53% of the variation observed in ant diversity (F = 5.28; p = 0.03).

Associations between patch type and ant density

NMDS ordination distinguished ant density in forest from other patch types along the first axis (NMDS1) (stress = 0.29, $R^2 = 0.80$; Figure 5). However, there was also minor separation between ant density observed in lawn and shrub vs. crops, mud flats, and swamps (Figure 5). The three MaxEnt models with the greatest predictive power [Area Under Curve (AUC) = 0.82 for *A. tennesseensis*, AUC = 0.81 for *F. Subsericea*, and AUC = 0.78 for *T. sessile*] showed that the probability of encountering the three ant species was driven more by distance from surface water than by either patch type or elevation (Figure 6). The jackknife test of variable importance showed that of the three modeled variables (distance from water, elevation, and patch type), patch type was the least predictive of habitat selection by ants (Figure 7).

Discussion

This study represents one of the few explicit applications of landscape ecology to ecological communities in river corridors. Our exploration of riverine landscape patch dynamics revealed the importance of both landscape composition (e.g., LULC) as well as patch characteristics to ant assemblages. We found that riverine landscape patch composition and configuration influence the abundance, density, and diversity of ant communities in the Scioto River corridor. However when compared to other environmental gradients (distance from water and elevation), riverine landscape composition likely plays a secondary role.

Influence of land use and land cover on ant assemblages

The significantly higher ant assemblage density and lower ant diversity observed in both urban and mixed reaches as compared to agricultural reaches are consistent with results of past studies. For example, Lessard and Buddle (2005) observed higher ant abundance in urban areas than in protected forests in Quebec, Canada. Additionally Buczkowski and Richmond (2012) report the loss of 17-20 ant species after the urbanization of West Lafayette, Indiana, USA. Our findings, however, contradict other research. Thompson and McLachlan (2006) found a positive correlation between ant assemblage diversity and increasing urbanization rates in Manitoba, Canada whereas Ives et al. (2013) observed no significant difference in riparian ant assemblages between urban and rural catchments in Sydney, Australia. Variability in LULC relationships with ant assemblages likely points

to the geographic reduction of some species (losers) and the expansion of others (winners) as landscapes are transformed from rural to urban (McKinney and Lockwood 1999).

Associations between ant abundance and density are likely related to multiple mechanisms. Firstly, ecological theory suggests that species abundance and density should increase with increasing structural complexity of the environment (MacArthur and MacArthur (1961). As such, disturbances such as periodic inundation in riverine landscapes often produce patches with dissimilar habitat characteristics, e.g., soil moisture and soil temperature (Jarolimek et al. 1999, Hufkens et al. 2009), which can lead to filtering of riverine arthropod abundance and composition assemblage (Hering et al. 2004). Thus, the relatively high ant density observed in our urban and mixed reaches may be driven by the high patch diversity observed (Table 3). Secondly, although our study did not directly investigate temperature, the concept of urban heat gradients is well established (e.g., Kim 1992), and may implicate temperature as a driver of high ant density in our study system. Riparian environments in urban and mixed landscapes may be more attractive to ants because of greater light availability and relatively high soil temperature (Menke et al. 2011). Because ants are generally thermophilic (Andersen 1997), their abundance often increases with increasing temperature (Kaspari et al. 2000), which could partly explain why some ant species – including F. subsericea and T. sessile, together representing 41% of the urban ant fauna in our study – tend to be closely associated with human activities (McGlynn (1999). These species can affect community

ant diversity through competitive or exploitative interactions (Sanders et al. 2003), which also might be a factor contributing to the higher ant diversity we observed in agricultural than in either urban or mixed riverine landscapes. Lastly, the lower abundance of ants in riverine landscapes embedded in agricultural landscapes confirms the observation by Petal (1976) that fertilization of farmland can lead to a reduction in ant density as mineral fertilizers and chemicals that are toxic to ants are commonly used in agricultural practices in the Scioto River basin (USEPA 1999).

Effects of patch composition on ant assemblages

The significant partitioning of ant density in forested patches vs. the other seven patches, in addition to the separation of ant density between lawn and shrub vs. crop, mudflat, and swamp (Figure 5) confirms findings of past research. For example, forests can provide favorable habitat and refuge for many arthropods including ants (Yasuda and Koike 2009). The most dominant ant species we sampled *(T. sessile, A. tennesseensis, F. subsericea)* prefer to nest in vegetated habitats (Scheifer 2002, Coovert 2005) with snags and tree cavities (Yasuda and Koike 2009), which were more ubiquitous in forest patches than the other patch types. Moreover, the frequent and stochastic flooding typical of mudflats, swamps and gravel bars limits high density of ants (Lude et al. 1999). Microclimatic conditions – particularly as pertains to high temperature extremes – of gravel bars may also be limiting to many species of ants, whereas agricultural chemicals

and tillage activities might be responsible for reduced density (Petal 1976) in cropland patches.

Our examination of gradients in elevation, distance from water, and patch composition using MaxEnt indicated that patch type likely plays a secondary role in contributing to habitat choice by ants (Figure 7). Although ants are less susceptible to flood disturbance on higher ground farther away from the shoreline (Adis and Junk 2002, Lambeets et al. 2008), we strongly suspect that the intersection of both aquatic (e.g., aquatic emergent insects) and terrestrial food resources (e.g., terrestrial insects, riparian vegetation) may make the riverine shoreline attractive to ants.

Effect of patch configuration on ant communities

In our study, metrics quantifying patch area, edge, shape, and density resulted in models that explained >50% of the variations in ant density and ant diversity. Pluralistic explanations for the relationships between patch configuration and ant assemblage characteristics are likely. Patch edges can alter the flows of energy and organisms (Ries et al. 2004) and lead to changes in ant density gradients near/along edges (Retana and Cerda 2000). Edges also often have dissimilar soil moisture and soil temperature regimes from those of core areas (Ries et al. 2004, Fletcher et al. 2007). Thus, patch geometry and amount of edge might be expected to be important in structuring the distribution of arthropods (Stamps et al. 1987, Orrock et al. 2011). Patch density (a proxy for habitat diversity) may influence ant density and diversity via the mechanisms suggested by the hypothesis of habitat heterogeneity (MacArthur and MacArthur 1961), whereby high habitat heterogeneity leads to high density and diversity of species. Because larger area usually facilitates greater density and diversity of organisms (MacArthur and Wilson 1967, Mitchell et al. 2002), it is not surprising that larger patches were associated with higher ant density and diversity than smaller patches in our study system.

Conclusions

Our results indicate that the composition and configuration of patches within riverine landscapes can strongly influence both the density and diversity of ant assemblages. However, when compared to gradients of both subtle elevation and distance from open water, the influence of patch composition appears to be of lesser importance in ant habitat selection. We recognize that other variables (e.g., soil moisture and soil temperature, cross-boundary food subsidies) may also be important in governing ant assemblage characteristics. As such, future studies should assess variables including micro-climatic conditions and analyze these against ant assemblage characteristics. Nevertheless, this research advances our understanding of the utility of landscape ecology in river-riparian contexts, illustrating that patch context (i.e., land-use class) and patch quality (e.g., size, shape, edge characteristics) have important ecological implications. For example, because ants may also be agents in the propagation of plants via seed dispersal (Gomez and Espadaler 2013), the influence of patchiness on ant distribution may constrain antmediated plant seed dispersal. Our findings represent an important step in integrating river science with landscape ecology and provide insight into riverine landscape conservation in managed landscapes.

Acknowledgements

We would like to thank Adam Kautza, Jeremy Alberts, and Lars Meyer for their help in the field. Research support was provided by state and federal funds appropriated to The Ohio State University, Ohio Agricultural Research and Development Center.

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Table 6 (Chapter 3 Table 1). Riverine landscape patch types at the twelve Scioto and Olentangy River study reaches delineated from field and remotely-sensed data. Patch classification was adapted from Johansen et al. (2010).

Patch Type	Description
Crop	Land tilled for crops including fallow areas.
Forest	Land covered by trees >6m in height.
Grass	Grazed pasture.
Gravel	Bare/exposed soil, sand, or gravel along the main channel.
Lawn	Managed grass, particularly in recreational parks.
Mudflat	Exposed mud (wet soil) particularly along the main channel.
Open water	Surface water in main channel, floodplain waterbodies, and artificial impoundments (i.e., dams).
Shrub	Shrubs and young trees <6m in height.
Swamp	Herbaceous and woody marshes.

Table 7 (Chapter3 Table 2). Patch metrics, measures, units, and descriptions used to quantify riverine landscape composition and configuration of the twelve study reaches of the Scioto and Olentangy Rivers, Ohio, USA. Detailed metric descriptions and formulas are provided in McGarigal and Marks (2012).

Patch Metric	Measure	Unit	Description
Area	Total Land Area (TLA)	ha	Total area encompassed by riverine landscape.
	Mean Patch Size (MPS)	m^2	Average size of all patches.
Density	Number of Patches (NP)	Num	Total number of patches.
Edge	Edge Density (ED)	m/ha	The length of patch edge per unit area.
	Mean Patch Edge (MPE)	m	Average edge length of all patches.
	Total Edge (TE)	m	Total edge length of patches.
	Mean Perimeter Area Ratio (MPAR)	-	Average perimeter-to-area ratio for all patches.
Richness	Shannon Diversity Index (SDI)	-	Patch heterogeneity/diversity.
	Shannon Evenness Index (SEI)	-	Patch evenness (i.e., relative abundance and distribution of patch types).
Shape	Mean Shape Index (MSI)	-	Compares the patch shape to a square standard.

Table 8 (Chapter 3 Table 3). Summary statistics for patch metrics for all study reaches as well as broken out by the three land-use and land-cover classes (LULC) for the twelve study reaches. Note that values for MPE and TE were scaled down by a factor of 1,000.

Patch Metric	Overall		Agriculture		Mixed		Urban	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Area metrics								
Total Landscape Area (TLA)	47.02	25.31	85.54	18.67	46.57	12.96	32.05	21.98
Mean Patch Size (MPS)	31.87	12.70	37.29	17.14	36.12	6.77	25.42	15.31
Density metrics Number of Patches (NP)	14.50	6.20	12.50	7.80	12.40	6.20	17.40	5.90
<i>Edge metrics</i> Edge Density (ED)	157.09	63.08	129.70	50.20	128.10	24.20	197.00	79.40
Mean Patch Edge (MPE)	5.30	1.36	5.28	0.42	5.61	1.81	5.01	1.26
Total Edge (TE)	73.62	31.53	67.60	46.29	62.09	9.76	87.55	0.41
Mean Perimeter Area Ratio (MPAR)	345.40	164.90	279.30	20.30	243.30	52.90	473.90	189.80
Diversity metrics Shannon Diversity Index (SDI)	1.39	0.28	1.21	0.47	1.44	0.20	1.43	0.32
Shannon Evenness Index (SEI)	0.76	0.08	0.69	0.08	0.80	0.06	0.75	0.10
Shape metrics Mean Shape Index (MSI)	2.90	0.71	2.43	0.00	2.76	0.87	3.20	0.63

Table 9 (Chapter 3 Table 4). Summary statistics of ants surveyed by riverine land-use class (agriculture, mixed, urban), including ant abundance, density, and diversity by patch type. Note that not all patch types were observed in all three riverine land-use classes.

Land Use	Patch Type	Abundance	Density (m ⁻²)	Diversity (Simpson's 1-D)
Agriculture		406	1.65 ± 2.86	0.52 ± 0.45
	Crop	141	0.13 ± 2.16	0.46 ± 0.46
	Forest	206	1.37 ± 2.06	0.51 ± 0.46
	Grass	26	1.33 ± 2.11	0.44 ± 0.49
	Gravel	0	0.00 ± 0.00	0.00 ± 0.00
	Shrub	23	0.95 ± 1.41	0.62 ± 0.49
	Swamp	10	1.36 ± 2.33	0.60 ± 0.54
Mixed		4472	7.27 ± 9.96	0.45 ± 0.36
	Crop	663	6.13 ± 6.47	0.55 ± 0.37
	Forest	3265	7.51 ± 11.5	0.45 ± 0.37
	Grass	238	7.21 ± 6.32	0.37 ± 0.33
	Gravel	4	0.92 ± 6.36	0.10 ± 0.30
	Lawn	6	2.00 ± 0.02	0.01 ± 0.00
	Mudflat	65	1.66 ± 0.02	0.01 ± 0.00
	Shrub	62	5.16 ± 6.42	0.75 ± 0.26
	Swamp	169	7.04 ± 4.11	0.29 ± 0.22
Urban		3400	6.55 ± 9.65	0.39 ± 0.36
	Forest	2002	6.81 ± 12.2	0.36 ± 0.36
	Gravel	5	0.02 ± 0.01	0.41 ± 0.10
	Lawn	635	5.46 ± 4.59	0.54 ± 0.37
	Mudflat	220	3.66 ± 2.91	0.36 ± 0.36
	Shrub	149	5.27 ± 5.81	0.38 ± 0.34
	Swamp	389	5.18 ± 5.20	0.41 ± 0.32
All reaches		8278	5.99 ± 10.05	0.44 ± 0.38

Table 10 (Chapter 3 Table 5). Eigenvalues (>1.0) and the percent variance captured by the principal components (PCs) along with the loadings. Bold print represents the most influential loadings for each eigenvector. Names assigned to each PC axis represent these influential loadings.

Patch Metric	PC-1	PC-2	PC-3	PC-4	
	Area/Edge Index	Density Index	Shape Index	Diversity Index	
Edge Density	-0.41	0.19	0.30	0.07	
Mean Patch Size	0.42	-0.30	0.08	0.16	
Mean Perimeter Area Ratio	-0.37	0.24	0.31	0.12	
Total Land Area	0.45	0.17	0.08	0.26	
Number of Patches	0.18	0.57	0.06	0.12	
Mean Patch Edge	0.15	-0.45	0.37	0.31	
Total Edge	0.32	0.33	0.30	0.32	
Mean Shape Index	-0.27	-0.15	0.54	0.20	
Shannon Diversity Index	0.23	0.30	0.31	-0.57	
Shannon Evenness Index	0.18	-0.22	0.03	-0.56	
Eigenvalue	4.07	2.54	2.03	1.06	
% variance	40.66	25.38	20.34	10.60	



Figure 9 (Chapter 3 Figure 1). The Scioto and Olentangy Rivers of the Scioto River basin along with the twelve riverine landscape study reaches in agriculture, urban, and mixed (forested, grassland, fallow, exurban) land-use classes.



Figure 10 (Chapter 3 Figure 2). Example of experimental design at one of the study reaches including riverine landscape patches as well as transects and quadrats where ants were surveyed.



Figure 11 (Chapter 3 Figure 3). A representation of environmental variables in the MaxEnt model: (a) Euclidean distance from open water (m), (b) elevation/altitude (m) and (c) riverine landscape patch type (red dots represent 70% of the training samples for *F. subsericea*).



Figure 12 (Chapter 3 Figure 4). Frequency histogram showing the distribution of the eight patch types at riverine landscapes embedded in (a) agriculture, (b) mixed and (c) urban land use/land cover classes. N = the number of patches in each land-use/land-cover class.


Figure 13 (Chapter 3 Figure 5). Non-metric multidimensional scaling (NMDS) plots showing dissimilarity matrices of the collective density of the three most abundant ant species: *F. subsericea*, *A. tennesseensis*, and *T. sessile* (stress value = 0.29). The ellipses indicate 95% confidence intervals for clusters of each patch type and clearly show separation between ant density of forest and all other patch types.



Figure 14 (Chapter 3 Figure 6). A representation of MaxEnt models for one of the study reaches showing the probability of occurrence based on gradients of elevation, distance from open water, and patch type for (a) *A. tennesseensis* (AT); (b) *F. subsericea* (FS) and (c) *T. sessile* (TS). Hot colors (reds) show high probability while cooler colors (blues) show low probability.



Figure 15 (Chapter 3 Figure 7). The jackknife test for variable importance in MaxEnt: (a) distance yields the highest gain when used in isolation for *A. tennesseensis*; (b) distance has the highest gain when used in isolation as well as the least gain when omitted for *F. subsericea*; and (c) distance has the highest gain when used in isolation for *T. sessile*. After distance, patch type is the second most influential variable in the three models.

Chapter 4: Riverine landscape patches influence trophic dynamics of riparian ants

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Abstract

The influence of riverine landscape pattern on trophic dynamics of riparian consumers remains largely unknown. We used naturally abundant stable isotopes to compare trophic position (TP) of riparian ants (Formicidae) as well as their reliance on aquatic carbon (C_A) among riparian patch types (e.g., forest, grass, gravel bar, herbaceous, mudflat) at 12 riverine landscapes along an urban-rural gradient of the Scioto River, OH. We found that TP of ants ranged from 0.27 to 2.25 across all study sites. TP was higher in crop patches $(\mu = 1.79, \sigma = 0.48)$ than in forest ($\mu = 1.20, \sigma = 0.39$), gravel bar ($\mu = 1.05, \sigma = 0.17$), and herbaceous ($\mu = 0.88$, $\sigma = 0.18$) patches. TP of ants in herbaceous patches was also distinct from TP of ants in swamps ($\mu = 1.34$, $\sigma = 0.27$) and mudflats ($\mu = 1.51$, $\sigma = 0.32$) (F = 5.57, p < 0.0001). Ants in crop patches exhibited greater C_A ($\mu = 0.91$) than at any of the other seven patches ($\mu = 0.41$ to 0.44). Across all patch types, ant TP was weakly related to their reliance on aquatic C. The number of canopy layers and urban development in the riparian zone were positively correlated with TP of ants ($R^2 = 0.58$), pointing to the role of habitat structure in mediating TP. These findings provide evidence that riverine landscape pattern can strongly influence trophic dynamics of riparian arthropods.

Key words: aquatic carbon, ants, patch metrics, riverine landscape, stable isotopes, trophic position

Introduction

Understanding how landscape characteristics influence trophic dynamics, which are central to ecosystem function and stability (McCann 2000, van der Putten et al. 2004), is of growing importance given the alarming rate of global land-use and land-cover change (Vitousek et al. 1997, Foley et al. 2005). Trophic position (TP), a key measure of trophic structure, continues to provide insight into the functioning of ecological communities by allowing estimates of energy or mass flow (Scotti et al. 2009, Ozersky et al. 2012) and by describing the functional role of organisms (e.g., omnivory; Sprules and Bowerman 1988, Thompson et al. 2007). However, integrating landscape pattern with food-web dynamics remains a challenge, in part because environmental determinants of trophic position remain unclear (Rooney et al. 2008, Tunney et al. 2012).

In fluvial systems, food-web research has largely been constrained to discrete communities in specific habitats but needs to be considered in a broader landscape context and across the aquatic-terrestrial boundary (Polis et al. 1997, Woodward and Hildrew 2002, Sullivan et al. Submitted). A growing body of literature suggests that streams and their adjacent riparian zones are tightly linked through energy exchanges (e.g., prey items), and reciprocal transfers of energy are essential to maintain ecosystem functions (Likens and Bormann 1974, Cloe and Garman 1996, Baxter et al. 2005, Sullivan and Rodewald 2012). Many riparian organisms, for example, rely on a combination of both aquatic and terrestrial food resources. In particular, aquatic insects that emerge from streams as adults (hereafter, "emergent insects") represent a critical

prey subsidy for multiple riparian consumers including bats, birds, lizards, and invertebrates (Murakami and Nakano 2002, Baxter et al. 2005). For instance, Sanzone et al. (2003) found that riparian orb-weaving spiders obtained 100% of their carbon (C) and 39% of their nitrogen (N) from in-stream sources whereas ground-dwelling hunting spiders obtained 68% of their C and 25% of their N from in-stream sources. For riparian spiders, declines in the diversity of emergent insects have been shown to prompt not only reductions in abundance and diversity, but also diet shifts to less preferred terrestrial prey (Kennedy and Turner 2011). Thus, shifts in nutrient and energy subsidies via emergent insects have been implicated as primary mechanisms related to terrestrial consumer responses. However, the role of riverine landscape pattern in mediating trophic dynamics remains unresolved.

Riverine landscapes (*sensu* Thorp et al. 2006) are characterized by spatial patterning of patches and variability in patch content, size, distribution, density, diversity, structure, and boundary characteristic (Levin 1992, Wu 1995). Patches, which are largely created by disturbance agents including the flow and deposition of sediments (Ward 1998), in turn may influence riparian biota by influencing population growth, foraging patterns, competition, and trophic dynamics (Wiens 1976, Mangel and Clark 1986). Food chains have also been related to patch size (e.g., Schoener 1989, Post et al. 2000, McHugh et al. 2010). Trophic dynamics of riparian fauna may shift relative to riverine landscape pattern because of multiple mechanisms, including shifts in primary productivity and disturbance (Lawton 1989, Schoener 1989, Hoeinghaus et al. 2008, Takimoto and Post 2013). For example, disturbance-induced invasive plant invasions have been associated with declines in arthropod diversity in riverine landscapes (Herrera and Dudley 2003, Greenwood et al. 2004). Declines in arthropod diversity may lead to consequential shifts in the trophic dynamics of riparian fauna (Albrecht et al. 2007).

In most temperate riverine ecosystems, ants of the family Formicidae are ubiquitous, common generalist consumers (feeding on a mixture of both plant and animal food sources) (Tillberg et al. 2006, Sanders and Platner 2007, Lach et al. 2010), thus making them valuable model organisms through which to understand trophic dynamics in riverine landscapes. Ants are depredated by a suite of terrestrial consumers, including salamanders, bats, and birds and thus represent an essential aquatic-to-terrestrial trophic pathway (Anderson and Mathis 1999). In riparian zones, Formicidae may feed on a combination of both aquatic and terrestrial resources (Paetzold et al. 2008), suggesting that riparian patches may influence their reliance on aquatic food sources. Because vegetation density and canopy structure can potentially affect the foraging of ants (Sanders et al. 2008), riparian patches may be an important environmental driver of ant trophic dynamics. Resasco et al. (2012), for instance, found that TP of upland fire ant (Solenopsis invicta) colonies in isolated patches was lower than TP in similar connected patches, implicating increased plant richness in connected patches as a potential mechanism.

The analysis of stable isotope ratios of carbon (δ^{13} C) and nitrogen (δ^{15} N) is a well-established approach for investigating trophic structure (Post 2002, Akamatsu et al.

2004, Tillberg et al. 2006, Gibb and Cunningham 2011). The concentration of the heavy nitrogen isotope ¹⁵N increases from food sources to consumers by 3-4‰ (Post 2002), thus enabling the use of δ^{15} N to trace trophic position (Deniro and Epstein 1978, Hood-Nowotny and Knols 2007). In contrast, concentrations of ¹³C increase from only 0.0 to 0.4‰ (Kelly 2000, Inger and Bearhop 2008) from diet to consumer, thereby reflecting the signature of the basal food source/s for the consumer (Deniro and Epstein 1978, Peterson and Fry 1987, Post 2002). Thus, the variance of stable isotope signatures is considered as a measure of the dietary niche of consumers (Bearhop et al. 2004).

In this study, we used naturally abundant stable isotopes of C and N to compare TP and the reliance on aquatic C (C_A) of ants among riverine landscape patch types (e.g., forest, grass, gravel bar, herbaceous, mudflat, etc.). We also explored potential site-level mechanisms related to resource abundance and habitat structure in driving observed differences in TP and C_A . Our results provide novel evidence that riverine landscape pattern may influence the trophic dynamics of riparian arthropod consumers in river systems.

Materials and methods

Study system and site selection

We conducted the study at 12, 1,500-m reaches (hereafter "sites") along the Scioto River, a 6th-order river in central and southern Ohio, USA (Figure 1). In the Scioto River basin (16,882 km²), ~72% of the land is agricultural (cropland and pasture) or urbanized (NLCD 2006). As a result, riverine landscapes in the basin are often bands of remnant riparian forests flanked by agriculture and urban landscapes. The Scioto River flows through multiple urban centers, including Columbus, OH (population: 787,000; US Census Bureau 2011). The river basin experiences a humid continental climate with hot summers and cold winters (Karl and Koss 1984) and receives 900-1100 mm of precipitation per year on average (Rogers 1993).

Quantifying riverine landscape pattern

Details relative to riverine landscape patch surveys can be found in Tagwireyi and Sullivan (Submitted). Between May 2010 and September 2012, we delineated landscape patches within the riparian zone at each of the 12 study sites using a combination of remotely-sensed data and field surveys. We identified 8 patch types (gravel bar, crop, forest, grass, herbaceous, mudflat, shrub, and swamp) using guidelines adapted from Holmes and Goebel (2011) and Johansen et al. (2010). We used the 2006, 30.48-cm resolution, natural color Digital Orthophoto Quarter Quadrangles (OSIP 2012) as base maps to identify and digitize patch boundaries for each of the 12 study sites. We also compiled % imperviousness and % urban land use for the study sites from NLCD (2006) data using ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, CA, USA). We then used air-borne light detection and ranging (LiDAR) data obtained from the Ohio Statewide Imagery Program (OSIP 2012) to estimate canopy height and % tree density for the study area (Akay et al. 2012, Mueller et al. 2014). We also visually estimated the number of tree canopy layers, % small trees and shrubs (< 6 m), % large trees (\geq 6 m) and used a GIS to estimate the average riverine landscape width at each of the study sites as determined by vegetation vigor (e.g., "greenness" data) as well as ground-truthed surveys of changes from riparian to upland plant communities.

Biotic sampling

Between June and August of 2009-2012, we sampled *Formica subsericea*, as this species is common in riparian areas of the study system, found in a diverse array of riparian patch habitats, and known to utilize a mixture of aquatic and terrestrial food resources in the study system (Alberts and Sullivan, unpublished data). We sampled ants at each study site using the quadrat sampling method (Thompson and McLachlan 2006). First, we established 5 longitudinally-equidistant transects (250 m apart) that ran perpendicular to the main channel and extended to the boundary of the riparian zone. We then collected 5-8 ants at 3-m² georeferenced plots distributed along the edge of the main channel, within riverine landscape patches along each transect, and within distinct ecological patches (e.g., islands) that were not otherwise captured in our survey (Figure 2).

We collected 5 on-the-tree leaf samples (3 from the dominant tree species and 2 from the dominant species of shrubs, grasses, herbs and sedges) along each transect established for the ant surveys. Across the study sites, dominant species included maple (*Acer*) and willow (*Salix*) trees, honeysuckle (*Lonicera*), barnyard (*Echinochloa*) and reed canary (*Phalaris*) grass, stinging nettle (*Urtica*), and goldenrod (*Salidago*).

Following Alberts et al. (2013), we sampled aquatic primary producers (periphyton) by scrubbing 25-cm² of the dominant in-stream substrate (e.g., cobble) at each of the 5 transects.

Sample processing and analysis

In the lab, ants were rinsed in distilled water, oven-dried at 50°C for 48 hours, and subsequently freeze-dried (Lyophilizer, Labconco Corporation, Kansas City, MO, USA) for 48 hours. Tissue from 3-5 individuals was then homogenized by grinding into a fine powder using a mortar and pestle, and then packed into tin capsules for stable isotope analysis. Periphyton was picked of detrital material and invertebrates, rinsed with distilled water, and oven-dried. Periphyton from each subsample was combined per site and ground and packed for subsequent stable-isotope analysis. Terrestrial vegetation leaves were also picked for invertebrates, rinsed, oven-dried, and then homogenized to a fine powder using a Pica Blender Mill (Cianflone Scientific Instruments Corporation, Pittsburgh, PA, USA) before packing composite samples per site for isotope analysis.

All samples were analyzed for C and N by continuous flow isotope-ratio mass spectrometry (EA-IRMS). The results are reported in δ (‰) notation:

 δ^{13} C or δ^{15} N = [($R_{\text{sample}}/R_{\text{standard}}$)-1] * 100

where *R* is ${}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. Typical analytical precision was 0.08‰ for $\delta^{15}N$ and 0.19‰ for $\delta^{13}C$ determination.

Estimating food sources and trophic positions

We used linear mixing models to estimate food sources and trophic position of the ants following Post (2002). C_A in ants was calculated as follows:

$$C_{A} = (\delta^{13}C_{pred} - \delta^{13}C_{ter})/(\delta^{13}C_{per} - \delta^{13}C_{ter}),$$
(1)

where $\delta^{13}C_{pred}$ is the carbon isotope signature of ant samples, $\delta^{13}C_{ter}$ represents terrestrial leaves, and $\delta^{13}C_{per}$ represents periphyton. We computed TP as follows:

$$TP = \lambda + (\delta^{15}N_{pred} - [\delta^{15}N_{per} * C_A + \delta^{15}N_{ter} * (1 - C_A)])/\Delta_{N,}$$
(2)

where $\lambda = 1.0$ is the trophic position of the baseline; $\delta^{15}N_{pred}$ represents ants, $\delta^{15}N_{per}$ and $\delta^{15}N_{ter}$ represent periphyton (per) and terrestrial vegetation (ter) baselines, respectively; $\Delta_N = 3.4$ is the trophic fractionation for $\delta^{15}N$ (Post 2002), and C_A is derived from the periphyton baseline (Eq. 1).

Statistical analysis

We used analysis of variance (ANOVA) and post-hoc Tukey-Kramer honestly significant difference (HSD) tests to assess potential differences between C_A and TP of ants among the 8 patch types ($\alpha = 0.05$). To examine potential site-level mechanisms related to habitat structure driving observed differences in TP and C_A , we used Principal Component Analysis (PCA) followed by linear regression. Specifically, we entered 8 measures of riverine landscape pattern (# canopy layers, % shrub cover, % tree cover, riparian width, mean tree height, % tree density, % urban development, and % impervious surface) in a PCA and used those axes with eigenvalues >1.0 as predictors of TP and C_A, in the regression models. All data were tested for normality and homogeneity of variance before analysis and log-transformed if necessary. We used JMP 10.0 (SAS Institute Inc., Cary NC) for all statistical analyses.

Results

We found ants at 182 of the 253 patches delineated across all 12 study sites (Table 1). Of all ants surveyed, 68% were found in either forest or swamp patches. The distribution of patches was uneven across the 12 study sites. Forested patches occurred at all sites; mudflats and grass patches were found only in the five highly urbanized sites; crop, herbaceous and shrub were associated with only highly agricultural landscapes; and gravel bars were present at the four principally forested sites. Metrics describing riverine landscape pattern (i.e., those used in the PCA) also varied across the study sites. For example, canopy height and tree density ranged from ~10m to 67m ($\mu = 25.4m$, $\sigma = 16.7m$) and from 16% to 62% ($\mu = 35\%$, $\sigma = 14\%$), respectively.

Trophic position and reliance on aquatic C among patch types

Across all 12 study sites, δ^{13} C of ants ranged from -27.79‰ to -20.26‰ (μ = -25.07‰, σ = 0.89‰) whereas δ^{15} N ranged from 3.44‰ to 10.73‰ (μ = 7.05‰, σ = 1.22‰). For ants, δ^{13} C also varied widely across the 8 patch types (Figure 3). In general, δ^{13} C of ants in crop patches was the most enriched, whereas δ^{13} C of ants in herbaceous patches was most depleted. Ants in gravel bar and shrub patches exhibited the narrowest (-26.31‰ to

-24.32‰) and widest (-26.76‰ to -20.32‰) ranges in δ^{13} C, respectively. Among the 8 patch types, ants in both forest and mudflats exhibited comparatively wider ranges in δ^{15} N than ants in the other 6 patch types. Ants in gravel bars and herbaceous patches exhibited relatively narrow δ^{13} N ranges (Figure 3).

The TP of ants was higher in crop patches ($\mu = 1.79$, $\sigma = 0.48$) than in forest ($\mu = 1.20$, $\sigma = 0.39$), gravel bar ($\mu = 1.05$, $\sigma = 0.17$) and herbaceous ($\mu = 0.88$, $\sigma = 0.18$) patches whereas TP of ants at herbaceous patches was lower than those in both swamps ($\mu = 1.34$, $\sigma = 0.27$) and mudflats ($\mu = 1.51$, $\sigma = 0.32$) ($F_{(7,182)} = 5.57$, p < 0.0001; Figure 4).

Values of δ^{13} C showed clear partitioning between aquatic primary producers (periphyton) and terrestrial primary producers (riparian vegetation) (Figure 5). C_A varied for ants (42% ± 19%) across the study system. ANOVA revealed a significant effect of patch composition on C_A among the 8 patch types ($F_{(7, 182)} = 12.50$, p < 0.0001). Post-hoc comparisons indicated that C_A for the crop patches (91% ± 4%) was more than twice the C_A for any of the other 7 patch types (forest, grass, gravel bar, herbaceous, mudflat, shrub, and swamp; p < 0.05; Table 1). However, C_A did not significantly differ among the 7 other patch types (p > 0.05). Both TP and C_A decreased with distance from the river's edge (Figure 6). We also found a weak relationship between C_A and TP across all patch types (Figure 7).

Influence of riparian vegetation structure

PCA of 10 measures of riparian vegetation yielded 3 axes with eigenvalues >1 (Table 2). PC1 explained ~51% of the variance and was primarily driven by three characteristics related to canopy layers: number of canopy layers, % shrub and small trees (< 6 m) cover, and % trees (≥ 6 m) cover (+ correlations). Thus, we labeled this axis the "Canopy Layer Axis". PC2 explained ~21% of the variance; its dominant loadings were variables describing tree characteristics including density and canopy height (both with + correlation). Accordingly, we labeled this axis the "Tree Axis". PC3 was driven by % urban (- correlation) and % impervious surface (+ correlation). We labeled it the "Urbanization Axis". The Canopy Layer and Urbanization Axes accounted for 37% and 21% of the variation in TP of ants, respectively (full model: R^2 =0.58, $F_{(2,9)}$ = 6.12, p <0.02). None of the PCs successfully predicted C_A.

Discussion

This study represents one the few direct applications of landscape ecology to trophic dynamics in river corridors (but see Hagen and Sabo 2011). Our results suggest that riverine landscape patch patterns influence ant TP and relative reliance on aquatically- vs. terrestrially-derived C. Riparian vegetation structure emerged as a likely mechanism driving TP, but was not linked to C_A . Taken as a whole, our results indicate that riparian patchiness – which is a largely a function of disturbance – may influence flows of energy

and nutrients among aquatic and terrestrial components of the riverine landscape, thus supporting fundamental tenets of landscape ecology related to the importance of patch context, quality, and connectivity (see Wiens 2002). Results also highlight the complexity of relationships that exists between landscape pattern, habitat connectivity, and trophic dynamics in riverine landscapes.

Patchiness and aquatic-terrestrial trophic relationships

The wide range of resources consumed by *F. subsericea* suggests that dietary changes likely are a result of local trophic structure of the riparian habitat patches of our study system (see Layman et al. 2007). Although the complexity in trophic interactions is difficult to represent with food-web linkages alone (Polis and Strong 1996), variability in patch composition may lead to heterogeneity in trophic characteristics of ants of the same species through multiple potential mechanisms. In our study, structural vegetation characteristics related to the number and structure of canopy layers was positively related to TP. In temperate forests, the vertical stratification of arthropod assemblages has long been established (e.g., Nielsen 1978, Lawton 1983, Sobek et al. 2009). Forest systems with greater canopy layers have been related to higher arthropod diversity (Tews et al. 2004, Ulyshen 2011), which potentially provision greater food resources for ants [assuming that ground dwelling ants hunt and scavenge on arthropod prey including prey "raining" from tree canopies (Chan et al. 2008)]. In turn, this may subsequently lead to the increased TP with increasing canopy layers, as observed in our study.

Urban development and impervious surfaces also were related to TP. Both direct and indirect processes are likely at play. Directly, urban imperviousness in parts of the riparian zone represents habitat loss leading to the increased biodiversity of remaining non-impervious patches, which effectively become refuges for organisms (Naiman et al. 1993, Lees and Peres 2008). It is therefore plausible that the observed direct correlation between urban imperviousness and TP of ants could be a reflection of amplified food chains in biological refuges. Indirectly, urbanization has been shown to be associated with the development and distribution of riverine landscape patches (Tagwireyi and Sullivan, Submitted). Thus, relationships between TP and urbanization may also be artifacts of the patch types found in urbanized environments. For example, mudflats were primarily found in urban sites and may trap and expose aquatic food sources (e.g., emerging adults of aquatic insects, fish, mussels, etc.) during low flow periods, thereby providing additional food subsidies to ants (Hering and Plachter 1997). Reinforcing this explanation is the finding that TP was higher for ants closer (distance wise) to open water (Figure 6) and that mudflats were the patch type closest to the river.

We did not find evidence to support the role of vegetation structure in driving the comparatively high TP for ants in cropland patches. However, we speculate that ant TP in crop patches could be higher because of the presence of crop pests (e.g., aphids) and their predators (e.g., ladybird larvae) that are attracted to crops and are available as prey for ants (Sloggett et al. 1999).

Aquatic-to-terrestrial energy fluxes

Forty-two percent of *F. subsericea* tissue was derived from aquatic C in our study system. Paetzold (2008) also found that riparian ants along the Tagliamento River of Italy obtained a considerable proportion of their C from aquatic sources. Emergent insects, known prey of riparian ants (Hering and Plachter 1997, Sanzone et al. 2003, Chan et al. 2007), represent the most likely vector of aquatic C. Likewise, Huryn and Wallace (2000) suggest that >80% of the biomass of emergent insects is supplied to riparian food webs, where ants are important invertebrate predators.

The variability in C_A among patch types in our study system (Table 1) indicates that riparian habitat patches may exert a strong control on the aquatic-to-terrestrial transport of C. For example, ants in crop patches, which were characterized by homogenous, relatively short vegetation (largely soybean and corn) with no canopy cover derived almost all their C from aquatic sources. Crop patches may be disproportionately attractive to emerging aquatic insects because of favorable microclimatic conditions relative to increased temperature and humidity, although additional research would be necessary to test this hypothesis (Wickham et al. 2012). Conversely, ants in gravel bars only obtained 30% of their C from aquatic sources in spite of their proximity to the water, perhaps because of stochastic environments of gravel bars [e.g., temperature extremes, unpredictable flooding; (Hassan 2005)] constrain foraging by ants (Lude et al. 1999). Although the mechanism driving these patterns among patch types is unclear, the declining reliance on C_A by ants with increasing distance from the river's edge indicates that the distance emergent insects disperse into riparian zones is likely a key factor. Raikow et al. (2011) suggest that transfer of contaminants from aquatic to terrestrial systems via emergent insect subsidies was mostly constrained to within ~5 m, of the shoreline. Despite being weak, the positive relationship observed between ant C_A and TP (Figure 7) is suggestive that the addition of aquatic prey into ant diet likely increases TP. The introduction of new taxa has been also proposed as a mechanism driving increases in food-chain length in streams (Power and Dietrich 2002, Post and Takimoto 2007). Although we did not find any significant relationships between our quantitative habitat characteristics and ant C_A , it is likely that the interaction of riparian vegetation structure and dispersal dynamics of aquatic insects is important to the reliance of riparian ants on aquatic C.

In our study, we used a common ant species representing a ubiquitous, general consumer as a model organism to understand trophic position and energetic linkages between land and water. Our results indicate that riparian patchiness may be an important environmental determinant of trophic dynamics, with likely implications for ecosystem stability and diversity (Holt 2002, Brose et al. 2004). Thus, our results have relevance in the context of land management and river restoration, represent an important step in integrating river science with landscape ecology, and provide insight into riverine landscape conservation in managed landscapes.

Worldwide, urbanization and agriculture have transformed landscapes and threaten riparian ecosystems (Ives et al. 2013), which can be important biological reserves (Naiman et al. 1993, Lees and Peres 2008). Understanding the ecological functions of riverine landscapes is critical to effective conservation and management efforts. Therefore, we advocate for additional research that addresses the linkages between patchiness and spatially explicit food-webs in riverine landscapes. Research that considers mechanisms driving trophic dynamics across spatial and temporal scales will be of particular merit considering the multidimensional nature of rivers (Ward 1989). Insights gained from our current work also support the notion that river corridors are internally heterogeneous landscapes (Wiens 2002, Sullivan et al. 2007), thus advocating that management and conservation approaches not only consider the extent of the riparian zone but also its composition.

Acknowledgements

We would like to thank Adam Kautza, Jeremy Alberts, and Lars Meyer for their help in the field. Research support was provided by state and federal funds appropriated to The Ohio State University, Ohio Agricultural Research and Development Center.

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Patch characteristics		% aquatic carbon				
Patch type	Frequency	Min	Max	μ	σ	
Crop	6	0.19	0.98	0.91	0.04	
Forest	100	0.09	0.99	0.44	0.11	
Grass	14	0.23	0.48	0.37	0.08	
Gravel bar	7	0.16	0.44	0.30	0.12	
Herbaceous	11	0.19	0.46	0.35	0.08	
Mudflat	13	0.23	0.78	0.41	0.15	
Shrub	7	0.16	0.86	0.40	0.24	
Swamp	24	0.05	0.91	0.41	0.24	

Table 11 (Chapter 4 Table 1). Summary statistics of the distribution of patch types and % aquatic carbon for ants by patch type, along with means (μ) and standard deviations (σ).

Table 12 (Chapter 4 Table 2). Principal components analysis (PCA) of riverine landscape pattern including principal components (PC) with eigenvalues >1, % variance captured, and each PC's loadings and variances (r^2) for each variable shared with the PCA axis. Bold font represents the loadings driving the axis.

	Canopy Layers Axis PC1		Tree Axis PC2		Urbanization Axis PC3	
	Loading	r^2	Loading	r^2	Loading	r^2
Riverine Landscape Metrics	_		_		_	
# Canopy Layers	0.41	0.70	0.05	0.00	-0.24	0.07
% Shrub cover (<6m)	0.46	0.85	-0.21	0.07	0.17	0.03
% Tree cover (>6m)	0.41	0.70	-0.32	0.17	0.25	0.07
Riparian width (m)	-0.35	0.49	-0.03	0.00	0.38	0.17
Mean canopy height (m)	0.32	0.41	0.55	0.50	0.07	0.01
% Tree density	0.19	0.14	0.70	0.81	0.07	0.01
% Urban development	0.24	0.24	-0.20	0.06	-0.68	0.54
% Impervious surface	0.37	0.55	-0.17	0.05	0.49	0.28
Eigenvalue	4.07		1.67		1.18	
Variance	50.9		20.9		14.8	


Figure 16 (Chapter 4 Figure 1). The Scioto River basin with locations of the 12 study sites.



Figure 17 (Chapter 4 Figure 2). An example of the sampling design at one of the sites. Ants were sampled at the shaded circles; dotted lines represent vegetation transects.



Figure 18 (Chapter 4 Figure 3). Descriptive statistics of δ^{13} C and δ^{15} N for ants grouped by patch type. Black dots and the numerical labels stand for the mean, and error bars symbolize ± 1SD from the mean.



Figure 19 (Chapter 4 Figure 4). Box plots showing the distribution of trophic position of ants at each of the 8 patch types. Boxes represent the interquartile range, whiskers stand for the range, horizontal lines inside boxes represent the median, and the dotted line represents the grand mean.



Figure 20 (Chapter 4 Figure 5). Biplots of carbon and nitrogen stable isotope signatures of periphyton (n =12), riparian vegetation (n = 12), and *Formica subsericea* (n = 182). Error bars represent \pm 1SD from the mean.



Figure 21 (Chapter 4 Figure 6). Relationship between distance from open water and % aquatic carbon (C_A) and trophic position (TP) of ants (+ = ant C_A, • = ant TP; dotted and continuous lines represent linear regression fit for C_A and TP respectively). The negative correlation was significant for C_A (y = -0.0011x +1.2546, R^2 = 0.21, p = 0.0001). The relationship was weak, but also significant for TP (y = -0.0005x + 0.4658, R^2 = 0.11, p = 0.0001).



Figure 22 (Chapter 4 Figure 7). The relationship between % aquatic carbon and trophic position of ants was significant, but weak across all study sites (y = 0.13x + 0.26, $R^2 = 0.14$, p = 0.0001).

Chapter 5: Distribution and trophic dynamics of riparian tetragnathid spiders in a large river system

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Abstract

Urbanization and agriculture are increasingly encroaching into riparian areas, which can be highly productive and biodiverse. Although these globally-common land uses result in appreciable alterations to riparian habitat, the influence of nearshore environmental change on riparian arthropod consumers remains largely unknown. We investigated the influence of riparian land-use change on the distribution of nearshore riparian spiders of the family Tetragnathidae at 12 riverine landscapes along an urban-rural gradient of the Scioto River, Ohio. We also estimated trophic position (TP) as well as tetragnathid reliance on aquatic carbon (C_A) using naturally abundant carbon (C) and nitrogen (N)stable isotopes. Model selection results revealed that tetragnathid density, which ranged from 1.57 to 3.8 individuals per meter of shoreline ($\mu = 2.48$, $\sigma = 0.68$ individuals m) was more sensitive to differences in overhanging vegetation than to food resources (i.e., aquatic emergent insects). However, tetragnathid TP, which averaged 2.45 across all study reaches, was largely driven by emergent insect density. Likewise, the model with emergent insect density was the strongest for tetragnathid C_A, which ranged from 4 to 54% ($\mu = 24\%$). Collectively, our findings provide evidence that both terrestrial (habitat) and aquatic (food resources) are important environmental determinants of riparian tetragnathid distribution, trophic dynamics, and the capacity of spiders to ecologically link aquatic and terrestrial ecosystems. These results contribute to a growing understanding of the impacts of landscape change in river corridors, and suggest that

conservation at the aquatic-terrestrial interface will be an important step in maintaining diverse, functional river-riparian ecosystems.

Key words: Akaike Information Criterion, aquatic emergent insects, riparian, stable isotopes, tetragnathid spiders

Introduction

Global landscape change is widely recognized as a major threat to biodiversity (Vitousek et al. 1997, Secretariat of the Convention on Biological Diversity 2010). Although remnant riparian corridors often function as important biological reserves, providing refuge from the heavily-modified broader landscape matrix (Naiman et al. 1993, Lees and Peres 2008), increasing agricultural and urban incursion into riparian zones is causing rapid changes in riparian vegetation and structure (Tockner and Stanford 2002, Ferreira et al. 2005, Jones et al. 2010). Vegetation loss can destabilize riverbanks and lead to increased inputs of sediment and pollutants, decrease shading that moderates river temperature, and reduce inputs of large wood and organic material that are critical to aquatic consumers (Gregory et al. 1991, Studinski et al. 2012, Houghton and Wasson 2013). Changes in vegetation composition and structure also have multiple impacts including erosion, increased sediment loads, and increased flooding, which collectively can affect water quality and river health (Osborne and Kovacic 1993, Hupp and Osterkamp 1996, Bunn et al. 1999). Additionally, changes in leaf fall and composition can affect the breakdown of detritus in streams, with implications to the aquatic food web (Lagrue et al. 2011, Gurnell 2014). Collectively, these alterations may severely influence both the availability of food resources and habitat of riparian organisms (Wootton 2012, Toft et al. 2013).

A growing body of literature supports the importance of reciprocal aquaticterrestrial energy exchanges in maintaining ecosystem function (Baxter et al. 2005,

Ballinger and Lake 2006). Although transfers of energy between terrestrial and aquatic ecosystems are often seen as unidirectional pathways in which terrestrially-derived organic matter, nutrients, and biota fuel aquatic consumers (Covich et al. 1999, Power et al. 2004), reverse flows of energy exchanges (aquatic-to-terrestrial) also provide important subsidies to riparian and terrestrial food webs (Power and Rainey 2000, Henschel et al. 2001, Baxter et al. 2005). In particular, aquatic insects that emerge from streams as adults (hereafter, "emergent insects") represent a critical prey source for riparian consumers (Murakami and Nakano 2002, Baxter et al. 2005). Riparian spiders of the family Tetragnathidae (hereafter, "tetragnathids") have been shown to be highly dependent on emergent insects, which they capture in horizontal orb webs constructed in nearshore vegetation (Gillespie 1987, Collier et al. 2002, Kato et al. 2004, Iwata 2007). For example, Collier et al. (2002) found that tetragnathids derived 61% of their energy from emergent insects in New Zealand forested streams. Important spatial associations between tetragnathids and emergent insects have also been documented (e.g., Akamatsu et al. 2007, Burdon and Harding 2008). Thus, aquatic food resources have been cited as a key determinant of both tetragnathid abundance and distribution.

Riparian tetragnathids are thought to also respond to changes in vegetation characteristics (Henschel et al. 2001, Kato et al. 2004, Power et al. 2004, Laeser et al. 2005, Chan et al. 2009). For example, Laeser et al. (2005) observed that loss of riparian vegetation severely reduced tetragnathid abundance by reducing web-building substrate. By filtering solar radiation (both diffuse and direct) and reducing wind, forest canopy structure (height and density) can moderate riparian microclimatic conditions including temperature and humidity (Weiss et al. 1991). Because tetragnathids are particularly sensitive to variation in humidity, temperature, and wind (Cushing and Opell 1990), variation in tree canopy structure may lead to shifts in spider abundance and distribution. Changes in habitat structure (bank composition and height, shoreline complexity, overhanging vegetation, etc.) at the aquatic-terrestrial interface are likely to be particularly important to tetragnathids given their reliance on emergent insects (Akamatsu et al. 2004, Kato et al. 2004).

Thus, tetragnathid spiders are subject to both direct disturbance of riparian habitat and to indirect mechanisms of riparian habitat alteration via changes in the availability and/or accessibility of emergent insects (Laeser et al. 2005). In this study, we explored the influences of riparian habitat alteration on spider abundance along an urban-rural gradient of the Scioto River, Ohio, USA. Because tetragnathids are essential prey for ants, bats, and birds (Polis et al. 1997, Burdon and Harding 2008), they constitute an important trophic linkage between aquatic and terrestrial systems. Therefore, using naturally abundant stable isotopes of carbon (C) and nitrogen (N), we derived trophic position (TP) of tetragnathids, a key measure of the function of ecological communities (Scotti et al. 2009, Ozersky et al. 2012), and the reliance of tetragnathids on aquatic carbon (C_A) to elucidate how riparian habitat change may relate to shifts in river-riparian food webs. We provide evidence that both nearshore habitat and aquatic food resources can strongly influence the distribution and trophic dynamics of riparian tetragnathids.

Methods

Study system

We conducted our study along 12, 1,500-m river reaches distributed across ~200 km of the Scioto River, a 6th-order tributary of the Ohio River (Figure 1). Although 24% of the basin is forested, typical riparian zones are composed of remnant forest patches surrounded by agriculture and urban matrices (NLCD 2006). The Scioto River basin is set in a humid continental climate with hot summers and cold winters (Karl and Koss 1984). The Olentangy River, the largest tributary of the Scioto River, joins the Scioto River in Columbus [population size: 787,000; (US Census Bureau 2011)] from the North.

Tetragnathid surveys and resource availability

We surveyed tetragnathids in July of 2010-2012 when spider abundance tends to be at its peak in temperate regions (Williams et al. 1995). We focused our surveys at 5, 30-m transects on each bank distributed along the length of each study reach (Figure 2). (Note that canopy height, canopy density, Direct Site Factor (DSF), Indirect Site Factor (ISF), and % overhanging vegetation were estimated at the center of each of these transects – see below for details.) At each transect, we counted all individuals ≤ 2 m from the ground for 15 minutes between dusk and midnight. Our tetragnathid surveys were consistent with past studies (e.g., Williams et al. 1995, Benjamin et al. 2011, Meyer and Sullivan 2013). We collected 3-5 individuals from each transect for stable isotope analysis.

We collected on-the-tree vegetation samples (for baseline signatures to estimate TP): 3 samples from the dominant tree species [silver maple (*Acer saccharinum* L.) and black willow (*Salix nigra* Marsh.)] and 2 samples from the dominant species of shrubs and herbaceous plants [e.g., Amur honeysuckle (*Lonicera maackii* Rupr.), barnyard (*Echinochloa crus-galli* L.) and reed canary (*Phalaris arundinacea* L.) grass, stinging nettle (*Urtica dioica* L.), and goldenrod (*Salidago canadensis* L.)]. We sampled for aquatic primary producers (periphyton) by scrubbing a 25-cm² section of the dominant hard substrate (e.g., cobble) at 5 in-stream locations distributed along the reach length following Alberts et al. (2013). Data relative to emergent insect density and mean body size were collected in a companion study at the same study reaches (Kautza and Sullivan Submitted, see Appendix S1).

Nearshore habitat characteristics

To capture variability in nearshore canopy structure across the study reaches, we used hemispherical (fisheye) photography (Bunnell and Vales 1990, Fiala et al. 2006) at the center of each of the spider transects (i.e., 10 photographs per study reach). The photographs were taken in July 2012 using a Nikon Digital Coolpix 950 with a Sigma 8mm hemispherical lens (180° field of view). The camera was held in a custom-made mount that held the lens level and oriented the picture to magnetic North, allowing simulation of solar path during analysis. The photographs were taken at 1.5m above the water surface at the channel's shoreline at near sundown to prevent direct sunlight in the field of view.

Using Arc GIS 10.1 (Environmental Systems Research Institute: Redlands, CA), we estimated canopy height and tree density along the spider transects from the 2006 Ohio Statewide Imagery Project (OSIP 2012) digital air-borne light detection and ranging (LiDAR) data. LiDAR.las data are available in binary format containing the aboveground and bare-earth LiDAR features in addition to first and last return and intensity values, with an average resolution of 2.1m (OSIP 2012).

Because the density of some arthropods are thought to respond predictably to habitat geometry (Collinge and Palmer 2002, Orrock et al. 2011), we mapped the boundary of the shoreline at each reach using a combination of on-screen digitizing in ArcGIS 10.1 on a desktop and in-the-field digitizing in Arc Pad 8.0 (Environmental Systems Research Institute: Redlands, CA) on a Personal Digital Assistant (Pharos 565 PDA, Pharos Science and Applications Inc, CA, USA). Remotely-sensed data were derived from 2006, 30.48-cm resolution, natural color Digital Orthophoto Quarter Quadrangles (DOQQs) (OSIP 2012). We then used Patch Analyst 5.1 in ArcGIS 10.1 to compute the Mean Shape Index (MSI) – a measure of the complexity of average patch shape in the landscape compared to a standard shape. MSI is based on perimeter-area relationships and ranges between 1.0 (for a perfect circle) and infinity (for convoluted shapes). We also visually estimated the % of vegetation cover overhanging the water.

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Sample processing and analysis

We rinsed tetragnathids in distilled water, oven-dried at 60°C for 48 hours, and subsequently freeze-dried using a Lyophilizer (Labconco Corporation, Kansas, Missouri, USA) for 48 hours in the lab. Tissue was then homogenized from 3-5 individuals, ground into a fine powder using a mortar and pestle, and packed into tin capsules for stable isotope analysis. Periphyton and terrestrial vegetation was sorted from other materials (e.g., detritus, invertebrates, etc.), rinsed with distilled water, and oven-dried. We combined subsamples of periphyton and terrestrial vegetation per site, respectively, and then homogenized them into a fine powder using a Pica Blender Mill (Cianflone Scientific Instruments Corporation, Pittsburgh, PA, USA) before packing composite samples per study reach for isotope analysis.

All samples were analyzed for C and N by continuous flow isotope-ratio mass spectrometry (EA-IRMS) at the Washington State University's Stable Isotope Core Laboratory, Pullman, WA). The results are reported in δ (‰) notation defined as:

$$\delta^{13}$$
C or δ^{15} N = [($R_{\text{sample}}/R_{\text{standard}}$)-1] * 100

where *R* is ${}^{13}C/{}^{12}C$. Typical analytical precision was 0.08‰ for $\delta^{15}N$ and 0.19‰ for $\delta^{13}C$ determination.

Estimating food sources and trophic positions

We used linear mixing models to estimate C_A and TP of the tetragnathids following Post (2002), as follows:

$$C_{A} = (\delta^{13}C_{pred} - \delta^{13}C_{ter})/(\delta^{13}C_{per} - \delta^{13}C_{ter}), \qquad 1$$

where $\delta^{13}C_{pred}$ is the carbon isotope signature of tetragnathids samples, $\delta^{13}C_{ter}$ represents terrestrial leaves, and $\delta^{13}C_{per}$ represents periphyton.

$$TP = \lambda + (\delta^{15}N_{pred} - [\delta^{15}N_{per} * C_A + \delta 15N_{ter} * (1 - \alpha)])/\Delta_{N_s}$$
 2

where $\lambda = 1.0$ is the trophic position of the baseline; $\delta^{15}N_{pred}$ represents tetragnathids, $\delta^{15}N_{per}$ and $\delta^{15}N_{ter}$ represents periphyton (per) and terrestrial vegetation (ter) baselines, respectively; $\Delta_N = 3.4$ is the trophic fractionation for $\delta^{15}N$ (Post 2002), and C_A is derived from the periphyton baseline.

Numerical analysis

We used HemiView 2.1 (Delta T Devices Burwell, Cambridge, UK) to extract Indirect Site Factor (ISF) and Direct Site Factor (DSF) indices. These indices represent the potential of solar radiation (indirect or direct) to reach a given point (Anderson 1964), which has been shown to influence arthropod abundance (Babin et al. 2010). Both indices range between 0.0 (fully obscured sky) and 1.0 (completely open sky). ISF is the portion of indirect solar radiation that penetrates the tree canopy from any direction (Warren 1985). Assuming that ISF is uniform across the sky, ISF is a measure of canopy openness weighted equally across all directions (Englund et al. 2000). ISF is a proxy for microclimatic conditions such as heat balance, rate of radiative heat loss, humidity and wind penetration (Marinsek and Diaci 2011). In contrast, DSF is the potion of direct solar radiation that penetrates the canopy (Anderson 1964). Because the solar radiation-angle changes with seasonality (Warren 1985), we used HemiView to adjust ISF by the angular coordinates (azimuth direction) depending on the date we took the hemispheric photograph.

Statistical analysis

We modeled our data using Akaike Information Criterion (AIC) adjusted for small sample size (AIC_c) (Burnham and Anderson 2002, 2004). We first examined potential correlations among independent variables (canopy density, canopy height, ISF, DSF, % overhanging vegetation, MSI, density and body size of emergent insects). No variables with $|r| \ge 0.80$ were included in the same model (Sullivan et al. 2007) (Table 1). AIC selects the "best inference", model according to the data available. We ranked all candidate models according to their AIC_c values and the best model (i.e., the most parsimonious) was the model with the smallest AIC_c value (Burnham and Anderson 2000). We considered plausible models as those that were within 4 AIC units from the best model (Burnham and Anderson 2002). We then calculated Akaike weights (w_i) to determine the weight of evidence in favor of each model (Burnham and Anderson 2002). We performed all analyses using JMP 10.0 (SAS Institute Inc., Cary NC).

Results

We surveyed 892 tetragnathids across the 12 study reaches, ranging from 47 to 114 individuals per reach (μ = 74.3 individuals, σ = 20.4 individuals) or 1.57 to 3.8

individuals per meter of shoreline ($\mu = 2.48$ individuals, $\sigma = 0.68$ individuals). Predictor variables describing shoreline habitat varied across the study reaches (Table 2) and were related to landscape context in some cases. For instance, % overhanging vegetation was generally higher in urban reaches ($\mu = 77$, $\sigma = 12$) than in rural reaches ($\mu = 47$, $\sigma = 12$) due to the prevalence of the invasive Amur honeysuckle in the urban landscape. Likewise, predictor variables describing potential food sources for tetragnathids (e.g., density and body size of emergent insects) varied widely across the study sites (Table 2). On the whole, body size of emergent insects was relatively higher in rural (0.26 mg, $\sigma = 0.11$) than in urban ($\mu = 0.21$ mg, $\sigma = 0.17$) reaches. In contrast, emergent insect density was greater in urban ($\mu = 1004$, $\sigma = 600$) than in rural ($\mu = 783$, $\sigma = 740$) reaches.

Tetragnathid distribution and trophic dynamics

We observed substantial separation between δ^{13} C values of periphyton ($\mu = -16.90 \ \delta^{13}$ C, $\sigma = 3.70 \ \delta^{13}$ C) and terrestrial vegetation ($\mu = -30.18 \ \delta^{13}$ C, $\sigma = 1.41 \ \delta^{13}$ C), thus allowing us to use mixing models with confidence (Figure 4). Periphyton exhibited the greatest range in δ^{15} N values (Figure 4), and was significantly higher in rural ($\mu = 9.5\delta^{15}$ N, $\sigma = 1.5 \ \delta^{15}$ N) than in urban ($\mu = 7.2\delta^{15}$ N, $\sigma = 0.8 \ \delta^{15}$ N) reaches (t = 3.33, p = 0.008, df = 10). The alignment of tetragnathid and terrestrial vegetation δ^{15} C values in isotopic space indicated that tetragnathids typically derived the majority of their C from terrestrial plants. Mixing models confirmed these results (tetragnathid C_A: range: 4% -

54%, $\mu = 24\%$, $\sigma = 16\%$). Tetragnathid TP displayed a 2.42 range across the study sites ($\mu = 2.45$, $\sigma = 0.58$).

Model-selection resulted in the majority of the best supported models ($\Delta_i < 4$) being represented by a single variable (Table 3). Percent overhanging vegetation most strongly predicted tetragnathid density ($w_i = 0.85$). Emergent insect density and % overhanging vegetation (combined) were also plausible predictors of tetragnathid density with 11% of the support (Table 3). Predictor variables related to food sources of tetragnathids (i.e., density and body size of emergent insects) received 58% of the support for the C_A model sets, collectively. Shoreline habitat descriptors (i.e., % overhanging vegetation and canopy density) were also reasonable predictors of C_A, although jointly they received only 24% of the support. Emergent insect density was a key predictor of TP receiving 75% of the support. Likewise, emergent insect density + % overhanging vegetation were also plausible predictors of TP (Table 3).

Discussion

The importance of riparian corridors in maintaining species presence and preserving riverine ecosystem function is considerable (Osborne and Kovacic 1993, Rios and Bailey 2006). Because riparian organisms can be strongly related to both aquatic and terrestrial environmental characteristics (Sabo and Power 2002, Paetzold et al. 2005, Sullivan et al. 2007), it is important to integrate these components into explanations of distribution patterns of riparian arthropods. Consistent with this notion, we have shown that the

distribution and trophic position of riparian tetragnathid spiders were related to both terrestrial habitat structure and aquatic food resources at the aquatic-terrestrial interface, although there was greater weight of evidence for vegetation structure driving distribution and aquatic emergent insects driving TP. As might be expected, tetragnathid reliance on aquatic C was most strongly related to characteristics of the aquatic emergent insect community, reinforcing the importance of aquatic insects to terrestrial food webs (reviewed in Fausch et al. 2002a, Baxter et al. 2005, Sullivan and Rodewald 2012). These findings suggest that nearshore physical and biological changes can lead to significant alterations in riparian spiders and their capacity to serve as a functional linkage between aquatic and terrestrial ecosystems.

We found that tetragnathid density was positively related to % overhanging vegetation (Figure 5), and that the density of tetrgnathids was more sensitive to variation in shoreline habitat structure than to variation in aquatic food resources. This finding supports Chan et al. (2009), who found that substrate availability was more important than aquatic insect abundance in the distribution of riparian orb-web spiders in Hong Kong. Tetragnathids that spin horizontal webs (Gillespie 1987, Iwata 2007) on vegetation overhanging the water may improve the efficiency of trapping emergent insects as well as terrestrial insects that "rain" from the tree canopy (Kato et al. 2004, Chan et al. 2008). Thus, the predictive nature of % overhanging vegetation in the best supported tetragnathid density model (Table 3) indicates that habitat availability for web building is a key environmental determinant of riparian tetragnathid distribution, a finding also

supported by Laeser et al. (2005) in Japanese streams. In contrast to our hypotheses, tetragnathid density was not predicted by shoreline habitat geometry or microclimatic conditions that were represented by ISF and DSF, although theses parameters maybe important to other organisms and systems via species-specific microclimatic preferences (Collinge and Palmer 2002, Cobbold and Supp 2012).

Consistent with past research (e.g., Collier et al. 2002, Kato et al. 2004), our study provides further evidence that tetragnathids obtain their food from both aquatic and terrestrial sources. However we found that tetragnathids obtained $\sim 24\%$ of their C from aquatically-derived resources in the Scioto River system, less than half of the 61% reported by Collier et al. (2002), but still consistant other studies (e.g., Akamatsu et al. (2004) who documented a 58% proportion of emerging insects in the diet of many riparian spiders). In the Scioto system, which is intermediate in size as compared to the smaller headwater streams of Collier et al. (2002) and the large river system of Akamatsu et al. (2004), our results suggest that tetragnathid food sources may be predominantly aquatic insects deriving the majority of their energy from allochthonous leaf inputs. Composition of the Scioto emergent insect community (Kautza and Sullivan, Submitted) supports a detrital-based energy pathway, as the communities in the system were typically dominated by shredders (e.g., Leptoceridae, Limnephelidae) and collectors (e.g., Chironomidae, Ephemeridae) that rely on terrestrial leaf inputs. The predominance of shredders and collectors that rely on allochthonous food sources likely also explains the negative relationship we observed between emergent insect density and C_A (Table 3).

Terrestrial vegetation supplies more carbon per unit of tissue material (46%) than periphyton (12%), hence spider reliance on terrestrial C could also be related to the partitioning of the web-catch between aquatic prey and terrestrial prey falling from the canopy. Tree canopy density has also been shown to be related to density of arthropods in other systems (Spanhoff 2005, Banks et al. 2007).

Enriched consumer isotopic signatures have been associated with emergent insects in multiple studies (Gillespie 1987, Nakano and Murakami 2001, Iwata 2007). Tetragnathid TP in our study averaged 2.45, which was slightly lower than wolf spider TP of ~2.6 reported by Newman et al. (2011). Emergent insect density was negatively related to TP and represented the strongest model ($w_i = 0.57$, Table 3, Figure 6), likely because the high dominance of a few families (e.g., Chironomidae) within the emergent community at many reaches may lead to tetragnathids feeding across a limited trophic range of prey. However, TP was associated with C_A across all reaches (Figure 7), indicating that increases in tetragnathid TP is strongly linked to algal-based energy pathways. The wide range of resources [i.e., both terrestrial and aquatic (Williams et al. 1995)] consumed by tetragnathids suggest that dietary changes likely are a result of local trophic structure of the aquatic and the canopy systems, which are the primary potential sources of the prey (Chan et al. 2007, 2008). Pecent overhanging vegetation was also represented in alternativel models for TP (Table 3), which is likely related to a mechanistic relationship between inceasing web-building substrate and the efficiency of tetragnathids ability to capture a diverse array of prey of aquatic origin. For example we

observed that tetragnathid TP at our urban reaches (which were densely populated with Amur honeysuckle) was approximately 1.3 times greater than TP at rural reaches without honeysuckle in the nearshore environment.

The importance of the body size of emergent insects to C_A of tetragnathids (Table 3) is consistant with findings by Akamatsu et al. (2007), who also reported that C_A of spiders increased with body size of prey insects. In general, increases in body size enhance the ability of predators to capture prey (Newman 1999). Many studies have demonstrated body size-trophic linkages (e.g., Cohen et al. 2003, Thierry et al. 2011). Liza et al. (2009) reported that spiders increase the mesh size of their webs with increasing prey-size of available prey, which may lead to 'prey size specialization''. Thus, individual trait characteristics of emergent insects appear to be important relative to cross-ecosystem movements of nutrients and the energetics of riparian tetragnathids. That these traits may discrimate by landscape context – body size of emergent insects was higher in urban ($\mu = 0.21$ mg, $\sigma = 0.17$ mg) than in rural ($\mu = 0.26$ mg, $\sigma = 0.11$ mg) reaches in our study – and be related to aquatic-terrestrial C pathways (Table 3) via riparian spiders is a novel contribution to our understanding of riparian ecosystem

Worldwide, urbanization and agriculture continue to threaten riparian areas (Ives et al. 2013). The need for an improved understanding of drivers of riparian ecosystem structure and function is critical in both informing basic science as well as the most effective conservation schemes. Our results showed that nearshore habitat characteristics and food resources may be important determinants of the distribution and trophic dynamics of riparian spiders, highlighting the importance of both aquatic and terrestrial resources for riparian arthropods and endorsing management and restoration efforts at the aquatic-terrestrial interface. Because of the linkages we found between these factors and trophic position of riparian tetragnathids, this work has important implications for ecosystem stability, as more complex food webs are often considered as proxies for community and ecosystem resilience (Peterson et al. 1998, Aoki and Mizushima 2001). Although tetragnathid density and trophic dynamics were not sensitive to microclimatic conditions represented by ISF and DSF or to habitat geometry in our study, we recognize that these parameters maybe important to other arthropods and other systems (Collinge and Palmer 2002, Cobbold and Supp 2012). Lastly, consideration of both urban and rural riparian corridors in our study encourages a landscape, macroscale approach to river research and management (Thorp 2014).

Acknowledgements

We appreciate the field help we received from Adam Kautza, Jeremy Alberts, and Lars Meyer. Federal funds appropriated to The Ohio State University, Ohio Agricultural Research and Development Center provided research support.

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Supplementary material for this article is found in Appendix S1

Table 13 (Chapter 5 Table 1). Correlation matrix of independent variables. Bold font indicates r > |0.8|.

	MBS	CD	CH	ISF	DSF	OV	MSI	EAID
MBS	1.00							
CD	0.08	1.00						
CH	-0.02	0.63	1.00					
ISF	-0.30	-0.19	-0.11	1.00				
DSF	-0.24	-0.35	-0.35	0.85	1.00			
OV	0.31	0.60	0.18	-0.47	-0.52	1.00		
MSI	-0.53	0.55	0.34	0.38	0.19	-0.07	1.00	
EID	-0.23	-0.29	-0.10	-0.10	-0.18	-0.27	-0.01	1.00

MBS = Mean Body Size of Emergent Insects, CD = Canopy Density, CH = Canopy Height, ISF = Indirect Site Factor, DSF = Direct Site Factor, OV = Overhanging Vegetation, MSI = Mean Shape Index, and EID = Emergent Insect Density.

Table 14 (Chapter 5 Table 2). Summary statistics for independent variables considered in

Predictor variable	Min	Max	Mean	Std
Canopy Density (%)	20.0	67.4	41.3	12,1
Tree Height (m)	14.6	84.5	41.3	18.3
Indirect Site Factor (%)	29.3	89.5	51.7	17.2
Direct Site Factor (%)	25.8	81.6	49.5	15.9
% Overhanging Vegetation	36.9	86.2	60.1	17.4
Mean Shape Index	2.44	4.21	3.12	0.69
Emergent Insect Density (# m ⁻²)	255.0	2,335.0	893.0	652.0
Emergent Insect Body Size (mg)	0.07	0.61	0.25	0.17

the Akaike Information Criteria (AIC) modeling.

Table 15 (Chapter 5 Table 3). Results of model selection for models with $\Delta_i < 4$ explaining the density, trophic position, and reliance on aquatic carbon (C_A) of tetragnathids.

Ecological trait	Model	AIC _c	Δ_i	w_i	R^2
Aquatic carbon (C_A) (%)	Emergent insect density (-)	-6.43	0.00	0.42	0.28
	Null	-6.00	0.43	0.34	0.00
	Mean body size (+)	-4.77	1.65	0.16	0.18
	% overhanging vegetation (+)	-4.26	2.17	0.14	0.15
	Canopy density (+)	-3.55	2.88	0.10	0.09
Trophic position (TP)	Emergent insect density (-)	20.86	0.00	0.57	0.48
	Emergent insect density (-), % overhanging vegetation (+)	23.81	2.95	0.17	0.56
	Null	25.24	4.38	0.08	0.00
Tetragnathid density	% overhanging vegetation (+)	103.84	0.00	0.85	0.58
	Canopy density (+), % overhanging vegetation (+)	107.84	4.00	0.11	0.60
	Null	110.68	6.84	0.03	0.00



Figure 23 (Chapter 5 Figure 1). The Scioto River catchment with location of the 12 riverine landscape study reaches.



Figure 24 (Chapter 5 Figure 2). An example of the tetragnathid spider sampling design at one of the Scioto River system study reaches.



Figure 25 (Chapter 5 Figure 3). Descriptive statistics of (a) δ^{13} C and (b) δ^{15} N for tetragnathids, periphyton, and terrestrial/riparian vegetation grouped by rural and urban land uses. Lines in boxes are medians, box ends are quartiles, and whiskers show minimum and maximum values. "Terrestrial" stands for terrestrial/riparian vegetation.



Figure 26 (Chapter 5 Figure 4). Biplots of carbon (C) and nitrogen (N) stable isotope signatures of periphyton (n = 12), riparian vegetation (n = 12), and Tetragnathidae (n = 12). Error bars represent ± 1 SD from the mean.



Figure 27 (Chapter 5 Figure 5). The relationship between tetragnathid density and % vegetation cover overhanging the water surface was significant (y = 0.0297x + 0.6913, $R^2 = 0.58$, p = 0.004). Dashed lines represent confidence curves at $\alpha = 0.05$.



Figure 28 (Chapter 5 Figure 6). The negative relationship between tetragnathid trophic position and aquatic emergent insect density was significant across all study reaches (y = -43.879x + 148.82, $R^2 = 0.71$, p = 0.0038). Dashed lines represent confidence curves at α = 0.05.



Figure 29 (Chapter 5 Figure 7). The positive relationship between % aquatic carbon and trophic position of tetragnathids was significant (y = 0.029x + 1.75, $R^2 = 0.48$, p = 0.02). Dashed lines represent confidence curves at $\alpha = 0.05$.

Supporting information

Appendix S1 {Aquatic emergent insect surveys}

From 2010-2013, emergent insects were sampled with pyramidal floating emergence traps (1-m² surface area) following Alberts *et al.* (2013). The sampling effort involved two 10-day sampling periods: once in early summer and once in late summer. Six traps were deployed in the predominant flow habitats (e.g., pool, riffle, and run) represented in each study reach. The sampling protocol was consistent with other studies that measured aquatic insects emergence (e.g., Alberts et al. 2013) The captured invertebrates were enumerated, dried for 48-hours in a drying oven (60° C) and weighed for each reach (to the nearest 0.1 mg) (Akamatsu et al. 2007). These data were used to calculate total mean body size of individuals (following Meyer and Sullivan 2013), and emergent density (no m⁻² day⁻¹).

Chapter 6: Conclusions and future research

Increasingly, tenets in landscape theory have been incorporated into theoretical constructs of river ecology. However, explicit applications are few. This dissertation highlights the significance of riverine landscape pattern (i.e., patchiness) to the structure and function of riparian ecosystems, using riparian ants and spiders as model organisms. Carried out along an urban-rural landscape gradient, the implications of this work extend beyond basic science, with applications to conservation of management of riparian corridors in highly-modified regions. This is particularly important given that anthropogenic alterations of riverine landscapes may have serious consequences to river-riparian biodiversity.

In the first field investigation, I focused on riverine landscape patchiness. I found that both external environmental factors related to catchment LULC interacts with internal river features including fluvial action and ecosystem size to generate patterns of patches in riverine landscapes. Somewhat surprisingly, evidence was almost equally as strong for catchment LULC predictors of both patch area and shape at the immediate and intermediate scales (1,000 and 3,000-m extents). I recognize the potential influence of underlying landscape features that were not measured (e.g., gradient, elevation, valley geomorphic properties) on shaping riverine landscape pattern and therefore advocate for

additional, explicit investigation of additional landscape-level mechanisms that may drive riverine landscape pattern to inform conservation and management approaches.

In Chapters 3-5, I investigated the influence of riverine landscape pattern and structure on the distribution, diversity, and trophic dynamics of riparian arthropods (riparian ants and spiders of the family Tetragnathidae). In Chapter 3, I found that the composition and configuration of patches within riverine landscapes can strongly influence both the density and diversity of riparian ants, albeit with less strength than gradients of both subtle elevation and distance from open water. For example, I observed that the probability of encountering ants decreased with increasing distance from the shore. Involving microclimatic-arthropod assemblage relationships should be a priority in future studies.

In Chapter 4, I found that riparian patchiness may be an important environmental determinant of trophic dynamics of a common riparian ant species, *Formica subsericea*. Habitat factors (e.g., number of canopy layers in the riparian zone, urban development) were positively correlated with trophic position of ants, thereby implicating habitat structure in mediating trophic position of riparian arthropods.

My results from Chapter 5 showed that nearshore habitat characteristics and aquatic food resources are important drivers of the distribution and trophic dynamics of shoreline tetragnathid spiders. This finding highlights the importance of the contribution of aquatic energetic fluxes to terrestrial food webs and endorses management and restoration efforts at the aquatic-terrestrial interface. These results have important implications for ecosystem stability, as more complex food webs are often considered as proxies for community and ecosystem resilience (Peterson et al. 1998, Aoki and Mizushima 2001).

Overall, my study represents an important step in integrating river science with landscape ecology, and provides insight into riverine landscape conservation in managed landscapes. Results from this work advances our understanding of the utility of landscape ecology in river-riparian contexts, illustrating that patch context (i.e., surrounding land use) and patch quality (e.g., size, shape, edge characteristics) have important ecological implications. Fundamentally, this study supports the notion that river corridors are internally heterogeneous landscapes (Wiens 2002b) and that, therefore, management and conservation approaches must not only consider the extent of the riparian zone but also its composition and its structural and functional connectivity with the river. Additionally, the inclusion of both urban and rural riparian corridors in my study encourages a landscape, macroscale approach to river research and management (Thorp 2014). As urbanization and agriculture continue to threaten riverine landscapes worldwide (Ives et al. 2013), results from this dissertation may contribute to an improved understanding of the drivers of riparian ecosystem structure and function, improve our ability to anticipate responses of riverine landscapes to landscape alterations, and aid in targeting the most effective conservation schemes.

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Appendix A. Riverine landscape study reaches of Scioto River system, Ohio, USA. Longitude and latitude units are in decimal degrees, locations represent centroids of each of the 12, 1,500-m reaches.

Site Name	Latitude	Longitude
Site 1	40.0194	-83.0154
Site 2	40.0000	-83.0235
Site 3	39.9249	-83.0068
Site 4	39.7251	-83.0045
Site 5	39.6680	-82.9879
Site 7	39.3410	-82.9717
Site 8	39.2870	-82.9278
Site 9	39.1849	-82.8462
Site 10	39.0702	-83.0171

Site #	Species
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Camponotus
	subbarbatus, Formica exsectoides, Formica subsericea, Tapinoma sessile,
1	Tetramorium caespitum
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Camponotus
	subbarbatus, Cryptopone gilva, Formica exsectoides, Formica subsericea,
2	Tapinoma sessile, Tetramorium caespitum
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Formica
3	exsectoides, Formica obscuripes, Formica subsericea, Tapinoma sessile
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Camponotus
	subbarbatus, Crematogaster pilosa, Formica subsericea, Tapinoma
4	sessile, Tetramorium caespitum
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Crematogaster
	pilosa, Cryptopone gilva, Formica densiventris, Formica exsectoides,
	Formica obscuripes, Formica subsericea, Tapinoma difficillis, Tapinoma
5	sessile, Tetramorium caespitum
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Camponotus
	subbarbatus, Crematogaster cerasi, Crematogaster pilosa, Formica
6	densiventris, Formica subsericea, Tapinoma sessile
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Camponotus
_	subbarbatus, Crematogaster pilosa, Formica densiventris, Formica
7	exsectoides, Formica obscuripes, Formica subsericea, Tapinoma sessile
_	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Cryptopone
8	gilva, Formica subsericea, Tapinoma sessile
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Crematogaster
_	pilosa, Cryptopone gilva, Formica exsectoides, Formica subsericea,
9	Tapinoma sessile
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Cryptopone
10	gilva, Formica densiventris, Formica subsericea, Tapinoma sessile
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Camponotus
	subbarbatus, Crematogaster cerasi, Crematogaster pilosa, Formica
11	densiventris, Formica subsericea, Tapinoma sessile
	Aphaenogaster tennesseensis, Camponotus pennsylvanicus, Formica
12	exsectoides, Formica subsericea, Tapinoma sessile

Appendix B. Ants species observed at each riverine landscape study reach.

Appendix C. Mean stable isotope signatures of carbon (δ^{13} C) and nitrogen (δ^{15} N) for ants per quadrat (georeferenced waypoint), study reach, and patch type. Ordered by waypoint number (lowest to highest).

Site #	Patch type	Waypoint	Ant δ ¹³ C	Ant δ ¹⁵ N
4	Forest	001	-26.25	8.23
4	Forest	002	-25.14	7.56
4	Forest	004	-25.78	6.77
4	Swamp	011	-25.74	8.05
4	Mudflat	012	-25.38	7.84
4	Mudflat	013	-25.76	7.98
4	Swamp	014	-25.53	8.52
7	Grass	039	-25.66	7.16
7	Grass	042	-24.55	5.20
9	Herbaceous	044	-24.90	7.00
7	Grass	052	-24.86	7.23
7	Forest	054	-24.47	5.54
8	Forest	056	-23.82	6.71
8	Forest	058	-24.68	7.18
8	Herbaceous	059	-25.51	6.19
8	Forest	063	-24.43	6.94
8	Forest	064	-26.6	6.99
4	Swamp	066	-26.82	9.21
4	Swamp	067	-26.8	8.30
4	Forest	070	-26.87	7.52
4	Swamp	071	-25.37	7.97
4	Forest	072	-25.26	6.08
4	Forest	073	-25.40	7.76
4	Forest	074	-25.91	7.91
4	Forest	075	-26.00	8.58
4	Forest	076	-26.06	7.27
4	Forest	078	-25.92	8.42
9	Forest	081	-24.63	7.61
7	Swamp	088	-24.43	7.94

Site #	Patch type	Waypoint	Ant δ ¹³ C	Ant δ ¹⁵ N
7	Gravel bar	090	-24.85	5.74
7	Swamp	095	-27.44	7.28
7	Mudflat	098	-25.74	7.80
8	Gravel bar	099	-25.81	7.34
9	Forest	106	-25.25	7.31
9	Swamp	108	-25.59	6.55
4	Forest	112	-24.63	7.66
4	Forest	113	-25.13	7.51
4	Forest	115	-25.86	8.06
4	Forest	116	-23.95	5.09
4	Swamp	124	-26.06	7.34
4	Forest	126	-25.89	6.62
7	Forest	128	-25.79	5.90
7	Forest	129	-25.9	5.80
7	Swamp	134	-26.65	7.22
11	Forest	136	-26.69	7.23
11	Forest	147	-25.41	4.29
12	Herbaceous	152	-24.88	6.62
12	Herbaceous	153	-24.42	7.13
12	Forest	155	-23.60	6.94
12	Forest	157	-24.41	6.68
7	Swamp	159	-26.47	7.16
7	Forest	160	-26.06	5.79
7	Swamp	163	-26.52	6.95
7	Grass	164	-25.71	6.63
10	Forest	166	-24.60	6.99
10	Crop	168	-22.64	6.36
10	Forest	169	-24.99	6.14
12	Forest	172	-24.62	6.51
8	Forest	175	-24.49	6.88
8	Forest	177	-23.85	8.23
8	Forest	182	-24.05	8.82
8	Forest	183	-25.4	6.55
8	Forest	185	-23.93	6.88
10	Forest	187	-24.98	7.62

Site #	Patch type	Waypoint	Ant δ ¹³ C	Ant δ^{15} N
10	Forest	188	-24.49	6.55
10	Forest	189	-24.55	5.93
10	Forest	191	-25.24	6.91
12	Forest	194	-24.66	6.04
12	Forest	198	-25.32	6.75
8	Gravel bar	202	-24.81	7.54
8	Forest	204	-24.93	6.78
8	Forest	206	-25.33	7.46
8	Gravel bar	208	-25.90	7.04
8	Forest	210	-25.23	6.30
8	Swamp	211	-24.96	8.40
12	Forest	237	-27.79	6.58
12	Forest	239	-24.68	6.27
12	Crop	241	-27.32	8.93
11	Herbaceous	248	-23.81	6.72
11	Herbaceous	249	-25.24	5.91
11	Gravel bar	251	-24.32	7.05
11	Forest	252	-24.68	5.70
11	Herbaceous	253	-25.15	6.58
11	Forest	254	-25.34	5.98
11	Forest	255	-24.75	6.47
11	Herbaceous	257	-25.66	5.83
11	Forest	258	-25.27	7.62
11	Forest	263	-24.64	6.16
11	Herbaceous	264	-26.66	6.06
11	Herbaceous	265	-24.90	6.94
8	Forest	272	-24.87	6.99
8	Swamp	274	-23.99	6.04
8	Forest	282	-25.09	5.74
9	Forest	287	-24.53	7.70
9	Forest	288	-23.93	7.15
10	Swamp	291	-24.44	6.53
10	Forest	292	-23.75	5.77
10	Swamp	293	-26.14	6.80
10	Swamp	294	-24.68	6.89

Site #	Patch type	Waypoint	Ant δ ¹³ C	Ant δ ¹⁵ N
10	Swamp	295	-24.44	6.76
10	Forest	303	-24.51	8.54
10	Forest	305	-25.00	6.57
9	Gravel bar	310	-25.44	7.85
9	Shrub	311	-25.06	8.40
9	Forest	312	-26.6	7.32
9	Shrub	316	-25.45	6.03
9	Forest	318	-25.18	8.41
10	Forest	319	-25.15	9.61
3	Grass	325	-24.31	6.61
3	Grass	328	-25.94	6.04
3	Grass	329	-24.68	7.68
3	Grass	334	-24.48	6.86
3	Grass	335	-24.98	6.21
3	Grass	337	-25.24	6.91
3	Grass	339	-26.16	5.06
3	Grass	340	-26.48	7.76
3	Forest	341	-26.31	6.92
3	Forest	342	-26.80	6.52
3	Forest	345	-25.63	6.53
3	Forest	348	-25.62	9.07
7	Mudflat	352	-24.44	7.10
7	Grass	353	-24.79	7.26
6	Forest	363	-24.39	7.46
6	Forest	364	-24.84	6.74
6	Shrub	365	-23.90	7.08
6	Forest	368	-24.08	6.95
6	Forest	369	-24.87	5.82
6	Forest	370	-24.68	7.41
6	Forest	371	-23.68	7.37
6	Forest	372	-24.64	8.32
6	Shrub	373	-24.93	6.18
6	Forest	375	-26.02	7.67
6	Forest	376	-24.13	6.15
6	Herbaceous	383	-23.98	7.15

Site #	Patch type	Waypoint	Ant δ ¹³ C	Ant δ ¹⁵ N
6	Forest	391	-25.08	7.38
6	Forest	392	-23.69	6.76
6	Shrub	395	-23.32	7.87
6	Forest	401	-24.16	7.31
5	Forest	407	-25.66	7.56
5	Forest	409	-25.92	8.55
5	Crop	410	-24.59	8.04
5	Crop	411	-24.02	9.86
5	Mudflat	412	-25.33	9.09
5	Forest	414	-25.02	7.25
5	Forest	416	-24.97	7.45
5	Forest	417	-24.29	8.43
5	Forest	418	-25.87	6.60
5	Swamp	422	-24.28	7.95
5	Crop	435	-24.46	9.50
5	Swamp	438	-24.52	7.41
5	Forest	440	-25.45	8.39
5	Crop	442	-23.75	10.26
2	Forest	444	-25.40	4.72
2	Mudflat	445	-25.00	6.17
2	Forest	446	-25.45	5.67
2	Swamp	452	-25.33	7.76
2	Shrub	453	-20.26	5.63
2	Swamp	454	-23.27	6.51
2	Forest	455	-24.72	6.48
2	Mudflat	457	-24.74	4.71
2	Forest	458	-24.56	4.46
2	Swamp	461	-24.75	5.11
2	Forest	462	-25.94	6.37
2	Mudflat	463	-25.11	5.68
2	Forest	464	-25.09	5.26
2	Shrub	465	-26.76	5.96
2	Swamp	466	-24.9	6.90
2	Forest	467	-24.65	6.14
2	Mudflat	469	-24.9	6.72
Site #	Patch type	Waypoint	Ant δ^{13} C	Ant δ^{15} N
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2	Mudflat	476	-25.19	7.02
2	Mudflat	477	-24.86	6.86
1	Mudflat	486	-26.67	9.52
1	Forest	488	-25.1	5.86
1	Forest	489	-24.62	6.04
1	Mudflat	492	-25.58	10.73
1	Forest	499	-24.26	7.65
1	Forest	500	-26.02	7.76
1	Forest	501	-24.01	5.50
1	Forest	502	-25.72	8.05
1	Forest	503	-24.21	7.94
1	Forest	504	-23.96	8.14

Appendix C cont'd

Site	Spider	Spider	Periphyton	Periphyton	Terr.	Terr.
	δ ¹³ C	δ ¹⁵ N	$\delta^{15}N$	δ ¹³ C	Vegetation	Vegetation
					$\delta^{15}N$	δ ¹³ C
1	-27.74	10.64	7.02	-15.94	4.50	-29.89
2	-27.24	11.85	6.88	-18.49	2.72	-30.95
3	-26.56	14.12	6.14	-17.69	3.08	-30.36
4	-26.55	13.02	7.35	-11.26	3.92	-31.00
5	-27.79	11.69	8.85	-23.56	5.58	-31.53
6	-27.28	11.73	8.42	-18.79	4.68	-28.06
7	-27.55	12.10	7.19	-18.51	4.18	-27.91
8	-27.69	12.39	8.93	-17.13	4.75	-30.84
9	-27.31	12.71	12.39	-11.74	3.73	-28.00
10	-25.95	12.47	8.66	-21.46	4.52	-31.52
11	-26.94	12.24	8.78	-14.82	3.26	-31.52
12	-27.33	12.59	9.64	-13.41	2.89	-30.56

Appendix D. Tetragnathid spider, periphyton, and terrestrial vegetation stable isotopes of carbon (δ^{13} C) and nitrogen (δ^{15} N) of each of the 12 riverine landscape study reaches.

Appendix E. The MaxEnt Receiver Operating Characteristic (ROC) curves for

Aphaenogaster tennesseensis, Formica subsericea, and Tapinoma sessile. Area Under the

Curve (AUC) of 1.0 represents a perfect test; an area of 0.5 represents a worthless test.



Appendix F. MaxEnt models predicting the probability of occurrence based on gradients of distance from open water, patch type and elevation for *Aphaenogaster tennesseensis, Formica subsericea,* and *Tapinoma sessile* at 11 study reaches that were not presented along with Chapter 3 results. The color gradient represents probability of occurrence, i.e., increasing from blue to red.







Appendix F (Continued)



Appendix F (Continued)

