Influence of forest fragments on headwater stream ecosystems in agricultural landscapes

DISSERTATION

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

By
Charles William Goss

Graduate Program in Environment and Natural Resources

The Ohio State University

2014

Dissertation Committee:
Dr. P. Charles Goebel, Advisor
Dr. S. Mažeika P. Sullivan, Advisor
Dr. Peter S. Curtis
Abstract

It is widely recognized that headwater stream ecosystems are intimately associated with riparian forests. Riparian forests trap sediment, filter nutrients, provide shading, and are sources of allochthonous energy for stream food webs. Reciprocally, streams fuel riparian consumers via aquatic-to-terrestrial fluxes of aquatic emergent insects. The widespread clearing of forests in agricultural landscapes, however, has led to a decoupling of forest-stream dynamics. Patches of forest in these landscapes are often small and isolated, but may retain important functional forest-stream linkages that are otherwise absent in the surrounding agricultural landscape matrix. In this dissertation I report on a series of studies with the goal of assessing the influence of forest patches on reciprocal linkages between forests and streams in agricultural landscapes.

To address this goal, I surveyed both larval and adult (emergent) aquatic invertebrate communities and estimated various physicochemical parameters in streams that exhibit abrupt transitions in land cover – agriculture-forest and agriculture-forest-agriculture – in agricultural landscapes of central Ohio, USA. My results provide evidence for threshold changes in larval aquatic invertebrate communities that were associated with strong changes in physical habitat, temperature, and nutrient
concentrations primarily occurring between the forest edge and 324 m into forest patches. Similarly, I found that community composition of aquatic emergent insects exhibited strong shifts near the upstream edge of forest patches and a subsequent shift was observed within 139 m of edges at the downstream end of forest patches. Aquatic-to-terrestrial fluxes of aquatic emergent insect biomass also strongly responded to forest patches, exhibiting particularly strong variation as a function of distance from the center of forests. At two of the three study streams, total emergence biomass was highest near the forest center and systematically declined closer to forest edges; patterns in mean aquatic emergent insect body size were more variable but similarly showed strong variation with distance from the forest center. Shifts in aquatic emergent insect communities and biomass fluxes were also linked to variation in physical habitat, water quality, and basal energy sources suggesting that spatial configuration of land cover drives environmental variation that in turn influences emergence dynamics.

A literature review revealed that results from my studies were consistent with and expanded the extant literature on the influence of forest fragments on streams in agricultural landscapes. In general, the results of the review suggest that agricultural streams rapidly change upon entering forests leading to strong shifts in physical (increased channel width, and reduced fine sediments and solar radiation) and water quality (lower N concentrations) attributes that were linked to shifts in aquatic macroinvertebrate communities that generally occurred within the first 450 m after entering forest fragments. Overall my results suggest that streams rapidly recover upon
entering forests, and that even small patches of forest may be able to restore functional linkages between forests and streams in agricultural landscapes.
Dedicated to my wife Christine and my son Matthew
Acknowledgments

First of all, I would like to thank my advisors Charles Goebel and Mazeika Sullivan. Charles, thank you for sharing your expertise and for guiding me throughout this entire process. I appreciate your willingness to meet with me on a regular basis to discuss this work and keep it moving forward. Mazeika, thank you for agreeing to come on board as my co-advisor midway through my PhD program. I really appreciate your insights into the field of stream ecology which have greatly improved this research. Thanks also to Peter Curtis for providing input on my dissertation research as well as for being my teacher during my brief foray into the field of plant ecophysiology.

I was fortunate to have been funded throughout by tenure at OSU. My dissertation work would not have been possible without support from The Ohio State University Climate, Water, and Carbon Targeted Investment in Excellence (CWC-TIE) Program, the National Science Foundation STEM Graduate Fellows in K-12 (NSF GK-12) Education Program, and the Ohio Agricultural Research and Development Center (OARDC) SEEDS grant.

This research also would not have been possible without invaluable assistance provided by technicians and fellow students working with me over the past two years.
Paul Nelson and Silvia Francis–Bongue assisted sorting macroinvertebrates under the microscope. Erin Gorrell assisted in the field and in the lab, and produced a nice project as part of the ORIP program. Leslie Rieck demonstrated how to set up emergent insect traps and Lars Meyer showed me how to process stable isotope samples. Finally, I would like to thank Nathan Rosenbaum who worked with me for two summers. I couldn’t have asked for a more diligent and hard-working employee.

The staff at the OARDC and main campus was very helpful and assisted me throughout my dissertation. Amy Schmidt and Bev Winner always managed to make themselves available to answer questions and provide assistance. Kevin Jewell gave me access to lab space and provided advice on various lab protocols. Chuck Vrotney procured hard-to-get items and provided much needed comic relief during my time at the OARDC.

All of my work was on privately owned lands and I extend my thanks to all who agreed to let me access the streams on their lands. In particular, the staff at The Wilderness Center was exceptionally helpful with providing me with additional information over the course of my work on their property.

Finally, I would like to thank God and my family without whose love and support this would not have been possible. I would particularly like to thank my parents, James and Diane Goss, and my wife’s parents, Paul and Mary Ann Hunker, who were especially helpful and supportive throughout my time as a PhD student. Thank you for being there for us when we needed you. A final thank you goes to my wife and my son. Thank you
for bearing with me through this process over the past four years. I love you both very much.
Vita

June 1998 ..............................................Troy High School

2003 ......................................................B.A. Economics and B.S. Environmental Policy and Behavior, University of Michigan

2007 ......................................................M.S. Biology, Florida International University

2009 to present .......................................NSF GK-12 Fellow and Graduate Research Associate, School of Environment and Natural Resources, The Ohio State University

Publications


Fields of Study

Major Field: Environment and Natural Resources
# Table of Contents

Abstract .......................................................................................................................... ii

Dedication ......................................................................................................................... v

Acknowledgments .............................................................................................................. vi

Vita .................................................................................................................................. ix

List of Tables ..................................................................................................................... xvii

List of Figures .................................................................................................................... xxi

Chapter 1 : Introduction .................................................................................................... 1

References ........................................................................................................................ 7

Chapter 2 : Abrupt transitions in land use and land cover lead to ecological thresholds in
stream ecosystems ........................................................................................................... 11

Abstract .......................................................................................................................... 11

Introduction ....................................................................................................................... 13

Methods ............................................................................................................................ 15

Environmental Parameters ............................................................................................. 18

xi
Statistical Analyses................................................................. 20
Results ...................................................................................... 23
Physical Habitat ........................................................................ 23
Multimodel threshold analysis of temperature, nutrients, and leaf mass loss ....... 24
TITAN analysis of macroinvertebrate communities ........................................ 25
Discussion ................................................................................ 27
Thresholds in environmental variables ..................................................... 27
Macroinvertebrate community thresholds ............................................... 31
Mechanisms regulating macroinvertebrate community structure ................. 32
Leaf breakdown ........................................................................... 34
Conclusions and implications for management and restoration of streams ........ 35
Acknowledgements ...................................................................... 38
References .................................................................................. 39
Chapter 3 : Transitions in land cover drive aquatic emergent insect communities in agricultural landscapes ........................................................................ 59
Abstract .................................................................................... 59
Introduction .................................................................................. 61
Methods ...................................................................................... 63
Site description ................................................................................................................. 63
Aquatic emergent insect sampling ..................................................................................... 64
Environmental parameters ................................................................................................. 65
Statistical analyses ............................................................................................................. 66
Results .................................................................................................................................. 68
Aquatic emergent insect communities .............................................................................. 68
Taxa-specific patterns ........................................................................................................... 69
Environmental parameters ................................................................................................. 70
Discussion ............................................................................................................................ 72
Aquatic emergent insect communities along land-cover transitions .............................. 72
Environmental drivers ........................................................................................................ 74
Linking aquatic emergent insects and environmental drivers ........................................... 76
A downstream shadow? ....................................................................................................... 78
Aquatic-terrestrial linkages and restoration ....................................................................... 79
Conclusion .......................................................................................................................... 80
Acknowledgements ............................................................................................................ 82
References ........................................................................................................................... 83
Chapter 4: Spatial configuration of land cover drives aquatic-terrestrial fluxes in agricultural landscapes

Abstract ............................................................................................................................ 100

Introduction ....................................................................................................................... 102

Methods .............................................................................................................................. 106

Site description .................................................................................................................. 106

Aquatic emergent insect sampling and environmental measurements ................... 107

Stable isotope analysis ....................................................................................................... 108

Statistical Analysis ............................................................................................................ 109

Results ............................................................................................................................... 111

Emergence flux properties ............................................................................................... 111

Spatial models .................................................................................................................... 112

Physicochemical models ................................................................................................. 113

Energy source linkages ..................................................................................................... 114

Discussion ......................................................................................................................... 115

Linking emergence to spatial patterns in land cover .................................................... 115

Linking emergence to physical habitat and water quality ............................................. 119

Linking emergence to energy sources ............................................................................. 120
Conclusion .............................................................................................................. 122
Acknowledgements ............................................................................................ 125
References ............................................................................................................ 126

Chapter 5 : Influence of forest fragments on headwater streams in agricultural landscapes: a review ............................................................ 145
Abstract .............................................................................................................. 145
Introduction ......................................................................................................... 147

Six central themes of landscape ecology: Implications for understanding the influence of forest fragments on headwater streams ........................................ 150
Patches differ in quality ...................................................................................... 150
Patch boundaries affect flows .......................................................................... 153
Patch context matters ........................................................................................ 156
Connectivity is critical ........................................................................................ 157
Organisms are important ..................................................................................... 160
Scale is important ............................................................................................... 161
Synthesis ............................................................................................................. 163
Forest fragments and stream restoration ............................................................ 164
References .......................................................................................................... 167
Chapter 6: Conclusion ........................................................................................................... 177

References ............................................................................................................................ 180

List of References ................................................................................................................ 181

Appendix A: GPS coordinates of the sites for each study. Distance from the upstream forest edge is measured in meters, and latitude and longitude are measured in decimal degrees. ...................................................................................................................... 195

Appendix B: Summary statistics for aquatic invertebrate taxa collected during each study. Count corresponds to the number of individuals collected and mass corresponds to dry mass measured in milligrams. ................................................................................................. 198

Appendix C: Estimates of the wet mass of leaves used to estimate stable isotope composition and resource quality (C:N) of terrestrial energy sources in chapter 4. Distance from the upstream edge is measured in meters and woody and herbaceous leaf mass is measured in grams. Woody leaf mass corresponds to allochthonous leaf inputs from terrestrial woody plants, and herbaceous leaf mass corresponds to allochthnous leaf inputs from terrestrial herbaceous plants. ......................................................................................... 204
List of Tables

Table 2.1. AICc statistics from each model for Wilkin Run (top) and Fox Creek (bottom). Asterisks correspond to models that are within 2 of the best model in the candidate model set. Threshold estimates are displayed in parentheses. DNC corresponds to models that did not converge. The threshold column corresponds to whether a forest-mediated threshold is present (Yes or No). Models without evidence of a threshold or where the threshold occurs outside of the forest boundaries are given a value of “No” (see methods for more details). ................................................................. 45

Table 2.2. Community wide threshold estimates (sum of the individual z- and z+ scores) for quantiles 0.05, 0.10, 0.90 and 0.95.......................................................... 47

Table 3.1. Estimates of threshold changes in community composition based on a multivariate regression tree analysis. Numbers correspond to location of the threshold relative to the upstream or downstream edge (negative numbers correspond to upstream of forest edge). .............................................................. 89

Table 3.2. Results from an indicator species analysis on the groups derived from the multivariate regression tree analysis. Land cover corresponds to the group (upstream, forest, or downstream) that had the highest indicator value for that family. .............. 90
Table 3.3. Pearson correlation coefficient estimates for the first two PCA axes and the abiotic variables at each stream. Grey shading corresponds to variables that were significantly \((P < 0.05)\) correlated with either of the PCA axes.

Table 4.1. Results from the spatial analysis of aquatic insect emergence. Response corresponds to the response variable in the analysis which was either the daily emergence rate \([\log(\text{mg DM m}^{-2}\text{ day}^{-1})]\) or the average body size \([\log(\text{mg DM})]\). The different models include a categorical land cover (LC) variable with two levels (Agriculture or Forest), a categorical land cover variable (PO) with three levels (Upstream, Forest, Downstream), and the distance from the forest center (DFC). Parameter estimates correspond to slope estimates (DFC) or least-squares means (LC and PO). The heading Agriculture/Upstream corresponds to agriculture for the LC effects and to upstream for the PO effect. \(P\)-values were estimated either from a t-distribution to measure slope significance (DFC), or from Tukey’s post-hoc tests. The superscripts next to the parameter estimates correspond to \(P\)-values (rounded to the nearest hundredth): \(\leq 0.01\) (a), \(\leq 0.05\) (b), and < 0.10 (c). For the categorical variables, only those estimates that are different from each other \((P \leq 0.05)\) have a superscript.

Table 4.2. Results from the analysis linking physicochemical habitat to aquatic insect emergence Response corresponds to the response variable in the analysis which was either the daily emergence rate \([\log(\text{mg DM m}^{-2}\text{ day}^{-1})]\) or the average body size \([\log(\text{mg DM})]\). The parameters are either the physical habitat PCA axes or water quality PCA axes. Estimate corresponds to the slope estimate and the b superscript corresponds to a
Table 4.3. Eigenvector estimates from PCA analyses of physical habitat variables (BA) and water quality variables (CA). The PCA eigenvectors at BA represent the first physical habitat PCA axis (proportion of variance = 0.47) and those at CA represent the second water quality PCA axis (proportion of variance = 0.23).

Table 4.4. Results from the analysis linking energy sources to aquatic insect emergence. Response corresponds to the response variable in the analysis which was either the daily emergence rate [log(mg DM m⁻² day⁻¹)] or the average body size [log(mg DM)]. The parameters are the stable isotope composition (δ¹³C and δ¹⁵N) of the energy sources (terrestrial leaves and periphyton) and the quality (C:N ratio) of the energy sources. Estimate corresponds to the slope estimate and b superscript corresponds to a P-value of ≤ 0.05 and the c superscript corresponds to a P-value of < 0.10 (rounded to the nearest hundredth).

Table 5.1. Themes of landscape ecology as they relate to FFS. For each category "Yes" and "No" corresponds to whether or not there were observed differences in between fragment and agricultural streams (upstream or downstream of the forest fragment). Yes* corresponds a study where larval macroinvertebrate richness upstream and within forest was greater than richness downstream of the forest. Dashes correspond to parameters that were not estimated in that study. For the estimates of distance under scale category only those estimates where a statistical test was done are reported.
the Boundary heading, PLR = piecewise linear regression, NPDR = nonparametric deviance reduction analysis, and TITAN corresponds to Threshold Indicator Taxa Analysis........................................................................................................................................... 174
List of Figures

Figure 2.1. Bar graphs of sediment composition collected from a 10 m area surrounding the center of pools at Wilkin Run (top) and Fox Creek (bottom). ........................................ 48

Figure 2.2. Line graphs that correspond to the mean pool depth and width at Wilkin Run (black) and Fox Creek (grey). ........................................................................................................ 49

Figure 2.3. Plots of the model fit (solid line) overlaid on the observed data (open circles) for the multi-model threshold analysis. 90% bootstrap percentile confidence interval estimates and the original threshold estimate (black dot) are displayed at the bottom of the graphs. Nutrient samples were collected in both the fall of 2010 and the summer of 2011 to capture seasonal variation in nutrient dynamics ................................................................. 50

Figure 2.4. Mean and 95% confidence interval estimates for NO₃-N concentrations during the fall of 2010 at Fox Creek ........................................................................................................ 54

Figure 2.5. 90% bootstrap percentile confidence interval estimates of the threshold distance obtained from the TITAN analysis. Z- corresponds to taxa that decreased following the threshold (left axis), and Z+ correspond to taxa that increased after the threshold (right axis); the size of the dot corresponds to the relative size of the original indicator value estimate. Elmidae, Tipulidae and Turbellaria are estimated from Fox
Creek; the rest of the taxa, Physidae, Coenagrionidae, Chironomidae, Amphipoda, Pleuroceridae, and Limnephilidae, are from Wilkin Run.

**Figure 2.6.** Scatter plots of macroinvertebrate density vs distance for decreasing taxa (top) and increasing taxa (bottom) at Wilkin Run (left) and Fox Creek (right).

**Figure 2.7.** Shredder and Capniidae density summed over the course of the study at Wilkin Run (left) and Fox Creek (right).

**Figure 3.1.** Diagrams of forest patch area for each site in the study: BA (Left), CA (Middle), WA (Right). The grey area corresponds to forest patches, and the white area surrounding patch is primarily cropland. Numbers correspond to distances (m) from the upstream edge of a forest (negative numbers correspond to sites upstream of the edge).

**Figure 3.2.** 90% confidence interval estimates illustrating threshold uncertainty at our study sites. Upstream (black circles) and downstream (grey circles) were estimated using a multivariate regression tree analysis and percentile confidence intervals (horizontal lines) were estimated using a bootstrap procedure. The long black vertical line corresponds to the upstream edge (0 m) and the small black vertical lines correspond to the downstream edges for each of the forests in the study.

**Figure 3.3.** Plots of the overall aquatic insect density for each site at CA. The primary y-axis corresponds to Chironomidae density, the secondary y-axis corresponds to the remaining families, and the black vertical lines correspond to the upstream and downstream edges.
**Figure 3.4.** Plots of the overall aquatic insect density for each site at BA. The secondary y-axis corresponds to Sciomyzidae density, the primary y-axis corresponds to the remaining families, and the black vertical lines correspond to the upstream and downstream edges.

**Figure 3.5.** Bar graphs of Trichopterans and Heptageniids summed across all sites for each land use category.

**Figure 3.6.** PCA axes for each of the study streams plotted vs distance from the upstream edge. The black vertical lines correspond to the upstream and downstream edge.

**Figure 3.7.** Plots of abiotic variables vs distance from the upstream edge. The long black vertical lines correspond to the upstream edge and the short black vertical lines correspond to the downstream edges of the forest patches.

**Figure 4.1.** A-C: Bar graphs representing the proportion of biomass attributable to different families at each stream. Only those families are shown that accounted for ≥ 1% of the total biomass from each stream. Distance corresponds to the distance from the center of the forest and the bar graphs are ordered from upstream to downstream sampling sites. Dashed vertical grey lines correspond to the upstream and downstream edges of the forest patch. D: line plot of the maximum body size estimate at a given location across all sites. Three letter codes on the x-axis correspond to the different taxa: CAL = Calopterygidae, STR = Stratiomyidae, SCI = Sciomyzidae, HEP = Heptageniidae, SCA = Scathophagidae, TRI = Trichoptera, TIP = Tipulidae, EPH = Ephydridae, DOL =
Dolichopodidae, CUL = Culicidae, PSY = Psychodidae, CHI = Chironomidae, PHO = Phoridae, CER = Ceratopogonidae, EMP = Empididae.

Figure 4.2. Plots illustrating spatial model fits. Observed data (black dots) are overlaid with the predicted data (grey line). For figure 4.3C, an outlier was removed prior to fitting the model, but it remains in the graph (open circle).

Figure 4.3. Plots illustrating physicochemical model fits. Observed data (black dots) are overlaid with the predicted data (grey line).

Figure 4.4. Plots illustrating variation in $\delta^{15}$N of terrestrial leaves and periphyton as a function of distance from the forest center. Grey and black lines correspond to leaves and periphyton, respectively, and dashed and solid lines correspond to BA and WA, respectively.

Figure 5.1. Conceptual model of the changes in stream ecosystems as they transition from agricultural land into forest fragments, and the implications of for stream conservation and restoration.
Chapter 1: Introduction

Forest ecosystems are one of the dominant ecosystems worldwide, comprising ~1/3 of the Earth’s land surface (FAO 2010). Because trees exert strong biophysical effects on the surrounding environment, forests are important both for trophic processes (e.g., as primary producers) as well as for generating habitat (e.g., shade, roots, large wood) (Jones et al. 1997) that drive forest ecosystem dynamics. Although studies of forest ecosystems often focus on within-forest dynamics (Barnes et al. 1998), the effects of forests can extend beyond forest boundaries into a variety of non-forest ecosystems.

One of the most well studied cross-boundary influences of forests are the effects of forests on headwater stream ecosystems. Although headwater streams are the smallest streams within a given watershed, they comprise the majority of stream length (Leopold et al. 1964), can harbor appreciable amounts of biodiversity (Meyer et al. 2007), and can strongly influence larger streams and rivers via downstream transport of water, nutrients, and organic matter (Wipfli et al. 2007). The small size of headwater streams makes them intimately linked to the catchments that they drain, and these linkages are predicted to be particularly strong in forested catchments (Vannote et al. 1980). Riparian forests influence streams in myriad ways including filtering nutrients, trapping sediment and
stabilizing stream banks; providing shading and thus moderating in-stream temperatures; and provisioning of large wood and leaf litter which can serve both as habitat and energy sources for stream food webs in the form of allochthonous plant material (Gregory et al. 1991, Naiman et al. 2005). Riparian forests also provide habitat for terrestrial invertebrates that fall into streams that can be an important resource for top consumers such as fish (Nakano et al. 1999, Baxter et al. 2004).

In addition to the strong effects of riparian forests on streams, reciprocal effects of streams on forests have important implications for riparian food webs. One of the most widely studied stream-to-forest linkages is the flux of aquatic insects into terrestrial systems after they emerge from streams as winged adults (Baxter et al. 2005, Sullivan and Rodewald 2012). Adult aquatic insects are often important components of terrestrial consumer diets (Henschel et al. 2001, Iwata et al. 2003, Iwata 2007) that can lead to numerical responses across a range of invertebrate (Paetzold and Tockner 2005, Iwata 2007) and vertebrate taxa (Iwata et al. 2003, Fukui et al. 2006). These strong reciprocal exchanges have in part led to the notion that streams and riparian forests should be considered as a single ecological entity (Sullivan et al. 2007, Fausch et al. 2010).

Although strong linkages may persist between streams and riparia regardless of the dominant land cover, large-scale clearing of forests in agricultural landscapes has markedly changed the nature of the linkages between streams and riparian systems. As a consequence of human settlement and land-use processes, many forested landscapes have given way to dominance by agricultural practices, resulting in ~ 40% of the Earth’s land
surface covered by agricultural land (Foley et al. 2005). Land-use effects associated with agricultural landscapes include the alteration of physicochemical (e.g., sediment composition, nutrient concentrations, temperature) and biological properties (e.g., species composition, trophic pathways) of stream ecosystems (Quinn 2000, Allan 2004). In turn, the effects of land use on in-stream processes can be translated to terrestrial systems via fluxes of adult aquatic insects (Laeser et al. 2005, Davis et al. 2011).

Even though large-scale forest clearing has marginalized forest cover in agricultural landscapes, patches of forest that persist may retain important functional forest-stream linkages that are otherwise absent in these landscapes. There is an expanding body of literature indicating that forest patches in agricultural landscapes can strongly influence the characteristics of headwater stream ecosystems. For example, studies of forest patches in pastoral catchments of New Zealand (Storey and Cowley 1997, Scarsbrook and Halliday 1999) have indicated that agricultural streams undergo rapid changes in abiotic and biotic conditions upon entering forest patches, and can converge on reference conditions within 300 m of entering forest patches. It has also been hypothesized that the effects of forests on headwater streams can extend into downstream agricultural reaches (Harding et al. 2006). These studies suggest that conserving and/or restoring discontinuous patches of forests may be able to restore water quality and biotic integrity to impaired headwater streams (discussed by Scarsbrook and Halliday 1999), which would ultimately be transported downstream to larger streams and rivers. Results from studies documenting the influence of forest patches on headwater
streams, however, suggest that there are inconsistencies in both the presence and
direction of forest patch effects (Suga and Tanaka 2013), and it is unclear whether there
are general effects of these patches on headwater stream ecosystems.

To further investigate the influence of forest patches on stream ecosystems, I
conducted three field studies that focused on the implications of transitions between
agricultural land and forest patches for headwater stream ecosystems in agricultural
landscapes of central Ohio. In the first field study (currently in review at Freshwater
Science), I focused on agriculture-forest transitions to determine the distance at which
biological and physicochemical attributes of streams shift after entering forest fragments.
Based on previous studies of the influence of forest patches on streams (Storey and
Cowley 1997, Scarsbrook and Halliday 1999), I expected that stream ecosystem
attributes would undergo abrupt shifts soon after entering forest patches (i.e., reach an
ecological threshold, Groffman et al. 2006). To investigate possible forest-mediated
threshold responses I surveyed headwater streams beginning in upstream agricultural land
and proceeding downstream into forest patches (16 sites at 2 headwater streams). I used
leaf bags to estimate macroinvertebrate community structure and leaf breakdown, and
measured various physicochemical parameters that I expected to vary along agriculture-
forest transitions. Further, I employed a suite of threshold detection analyses—piecewise
linear regression (Muggeo 2003), nonparametric deviance reduction analysis (based on
univariate regression tree analysis) (Qian et al. 2003), and Threshold Indicator Taxa
ANalysis (TITAN) (Baker and King 2010)—to estimate the distance at which biological and physicochemical parameters changed after entering forests.

In the second study, I examined how land-cover transitions influence stream-to-forest fluxes of aquatic emergent insects. This project is an important extension of the first study because it enables a test of whether the effects of land cover transitions on in-stream processes are transmitted to terrestrial systems via aquatic emergent insects. I also extended the sampling design in this study to encompass agriculture-forest-agriculture transitions at 28 sites distributed across three headwater streams. Such a sampling design enabled me to determine how rapidly streams change after both entering and leaving forest patches. Similar to the first study, I used an analytical approach based on multivariate regression tree analysis to determine where threshold changes in aquatic emergent insect community composition occurred. I also measured a variety of physicochemical habitat variables in an effort to link changes in aquatic emergent insect community composition with changes in environmental variables.

In addition to examining transitions in aquatic emergent insect communities, in the third study I quantified fluxes of aquatic emergent insect biomass and in-stream energy sources along agriculture-forest-agriculture transitions. Specifically, I focused on how the spatial configuration and composition of land cover influenced aquatic emergent insect flux properties (biomass and mean body size) and physicochemical habitat. I also linked aquatic emergent insect flux properties to energy sources supporting aquatic insect food webs by measuring stable isotope composition (δ^{13}C and δ^{15}N) and resource quality.
(C : N ratio) of aquatic (periphyton) and terrestrial (detritus) energy sources. This study complements the second study by providing an estimate of the overall quantity of aquatic emergent insect biomass available to riparian food webs as well as the traits of these fluxes (e.g., mean body size) which have been shown to have important implications for riparian food webs (Davis et al. 2011, Meyer and Sullivan 2013).

In the final chapter, the results of my dissertation research are placed in the context of the larger literature by reviewing studies on the influence of forest fragments on headwater streams in agricultural landscapes. I used the central themes of landscape ecology as outlined by Wiens (2002) as a framework for this review which emphasizes the response of ecological processes to patch quality, boundaries among patches, context, connectivity, organisms, and scale. Using this framework I extended a previous review of forest fragment effects on aquatic macroinvertebrate communities (Suga and Tanaka 2013) to both include three additional studies (including two from this dissertation) and the effects of forest patches on physicochemical habitat and basal resources in streams. I reviewed the pertinent literature in the context of each landscape ecology theme and conclude by synthesizing the results and discussing the implications of forest fragments for restoration of streams in agricultural landscapes.
References


Chapter 2: Abrupt transitions in land use and land cover lead to ecological thresholds in stream ecosystems

Abstract

Ecological thresholds correspond to abrupt changes in ecosystem attributes along environmental gradients and may be particularly important for understanding the effects of land-use and land-cover change on stream ecosystems. In agricultural landscapes, streams and forests have largely been decoupled, but remnant patches of forest may still maintain forest-stream linkages that are otherwise absent in these landscapes. However, the effects of remnant forest patches on stream characteristics are largely unknown. Our primary objectives were to determine whether streams exhibit threshold changes as they transition from the agricultural matrix to forest patches, and if so, to identify where these changes occur within forest patches. To address our objectives, we surveyed macroinvertebrate communities, monitored leaf breakdown, and collected physicochemical data at 16 study sites in 2 headwater streams along transects running from upstream agricultural land through downstream forest patches in central Ohio, USA. Using a suite of threshold indicator techniques including the Threshold Indicator Taxa Analysis (TITAN) to model biotic thresholds and nonparametric deviance and piecewise
linear regression within an AIC approach to model abiotic thresholds, our results show that the study streams changed rapidly after entering forest patches. The total distance into forest patches ranged from 10 to 1080 m, and we found evidence for threshold changes in physical habitat, temperature, nutrient concentrations, and macroinvertebrate communities primarily occurring between the forest edge and 324 m into forest patches. We found no evidence, however, for threshold changes in leaf-mass loss along this gradient, suggesting that processes unrelated to land use may be driving leaf breakdown in this system. We conclude that even relatively small patches of forest may be able to markedly influence stream dynamics, and that conservation and restoration of small, discontinuous patches of forest may be important for maintaining stream integrity in agricultural landscapes.
Introduction

Land-use and land-cover (LULC) change is one of the most ubiquitous and influential processes influencing stream and river ecosystems worldwide (Paul and Meyer 2001, Allan 2004). The conversion from natural land cover to human land uses (primarily agricultural and urbanization) leads to widespread stream impairment (US EPA 2006), which commonly results in homogenization of stream habitat (Wood and Armitage 1997, Lester and Boulton 2008), loss of water quality (Osborne and Kovacic 1993, Carpenter et al. 1998), and reductions in biodiversity (Allan and Flecker 1993, Rahel 2002) via mechanisms such as sedimentation, loss of large wood, nutrient enrichment, and species introductions.

Recently, the notion of ecological thresholds has emerged as an important consideration for understanding stream responses to gradients in land use. An ecological threshold can be defined as the point at which an ecological system exhibits an abrupt shift in ecological attributes along an environmental gradient (Groffman et al. 2006). Many studies have documented ecological thresholds along gradients of human disturbance (e.g., Qian et al. 2003, Radford et al. 2005, Dodds et al. 2010), and recent findings suggest that thresholds in streams can occur at very low levels of catchment disturbance (King et al. 2011, Bernhardt et al. 2012). These results indicate that threshold changes along human disturbance gradients may be common, even in minimally impacted landscapes.
Although there has been progress in our understanding of land-use effects on streams, there is still considerable uncertainty as to the best methods for restoring degraded streams, and whether streams reach thresholds as they recover to more natural conditions. The strong linkages between forests and streams have long been recognized (Hynes 1975, Vannote et al. 1980) and riparian forest restoration is often an integral component of stream restoration projects. However, the scale of riparian restoration is often small relative to the scale of land-use impacts on streams, which can frustrate stream restoration efforts (e.g., Moerke and Lamberti 2003). Even though numerous studies in terrestrial systems have examined the threshold distance from forest edges at which natural forested conditions are restored (i.e., edge effects) (e.g., Palik and Murphy 1990, Cadenasso et al. 1997, Gehlhausen et al. 2000, Li et al. 2007), similar studies of how soon streams recover after entering forest patches are rare (but see Storey and Cowley 1997, Scarsbrook and Halliday 1999, Suga and Tanaka 2013). Understanding potential threshold changes in streams and at what distance thresholds occur after entering forest patches could provide valuable information for stream conservation and restoration efforts, especially in regions where reference conditions are unavailable.

In this study, we examined how remnant forest patches embedded in agricultural landscapes influence stream characteristics. Our objectives were to assess whether streams exhibit threshold changes as they flow from agricultural land into forest patches, and if so, how long a stream must flow through a forest prior to reaching a threshold. To address these objectives, we studied 16 sites at two headwater streams in central Ohio.
that flowed through abrupt transitions in LULC from agricultural land into downstream forest patches. We focused on macroinvertebrate communities and leaf breakdown, but also measured various environmental parameters (habitat, temperature, and nutrients) that we expected to change along this transition, thereby influencing changes in stream ecosystem function and structure.

**Methods**

In our study, we sampled eight locations within each of two study streams, Fox Creek and Wilkin Run, in the Sugar Creek and Mohican River watersheds, respectively. The study streams are located in the headwaters of the Ohio River basin and the Low Lime Drift Plain ecoregion (Omernik and Griffith 2013), and represented appropriate model systems for our study as common features of these watersheds include a dominance of agricultural land use with small patches of remnant forest scattered across the landscape. Both Fox Creek and Wilkin Run are relatively small headwater streams that drain 7.82 km² and 8.37 km² at the site furthest into the forest, respectively. At Wilkin Run the dominant land use upstream of the forest patch is pasture where cattle have direct access to the stream; tree cover is very sparse and is limited to scattered woody vegetation along the banks of the stream, and a two-lane road separates agricultural land from the downstream forest patch. The forest patch is ~ 27 hectares in area and canopy cover is predominantly composed of mature trees, and within the forest there is a residence where trees on the east side (adjacent to the stream) were cleared over
a small section. Land use at Fox Creek is more mixed: immediately upstream of the forest patch, the land use is dominated by retired pasture on the south side of the stream; on the north side of the stream there is a narrow buffer of riparian trees (~25 m wide) that separates the stream from cropland. Further upstream there is pasture where cattle have access to the stream. The forest patch is ~160 hectares in area and dominated by woody vegetation with areas of herbaceous vegetation and other aquatic ecosystems (e.g., wetlands) are also present. The site furthest into the patch is located downstream of a two-lane road that divides the eastern and western portions of the forest.

In the fall of 2010 (October through December), we assessed changes in leaf-litter breakdown and macroinvertebrate communities along transitions between agricultural and forested streams, using a leaf litter bag method similar to that detailed in Benfield (2006). We collected recently abscised tuliptree leaves (*Liriodendron tulipifera* L.) from the forest at Fox Creek, as these trees are present in the riparian area at both sites. These leaves were spread out on tables in the lab and air dried for 6-8 days. After air drying the leaves, a mean of 4 g (range from 3.79 to 4.20 g) of leaves were weighed and placed in mesh produce bags (mesh size = 11 mm) and sealed with cable ties. After leaves were weighed, placed in bags, and tagged, we transported and placed them in the streams, specifically in scour pools (Bisson et al. 2006) where there was evidence of natural leaf accumulations. To obtain an estimate of changes in leaf breakdown and macroinvertebrates along agriculture-forest transitions, we placed leaf bags in pools 376, 205, and 76 m upstream of the forest edge at Wilkin Run, and 392, 200, and 91 m
upstream of the forest at Fox Creek; leaf bags were placed at 22, 120, 195, 452, and 790 m into the forest at Wilkin Run, and 10, 100, 194, 405, 1080 m into the forest at Fox Creek. In all of our analyses, distances are determined by position relative to the forest edge (distance = 0) with upstream sites having negative numbers and sites downstream of the edge (in the forest) having positive numbers. In each pool, leaf bags were secured to the substrate in 4 groups of 5 using gutter nails. After the bags were nailed to the substrate, handling correction bags, which are used to adjust the initial weights for leaf mass loss due to travel to and from site, were immediately removed from the stream and returned to the lab for processing.

At each sampling interval (7, 14, 31, and 42 days), one leaf bag was collected from each group (4 groups/pool) within a pool making sure to remove most of the leaves from the outside of the bags to minimize collection of macroinvertebrates that did not colonize the leaves inside the bag. Leaf bags were returned to the laboratory on ice and refrigerated until processing (within ~ 24 hours). Prior to drying, we washed the leaves clean of sediment, extraneous organic matter, and macroinvertebrates over a 250 µm sieve. Leaves were subsequently put into brown paper bags and placed in drying ovens at 40-50 °C for ≥ 48 hours. After drying, the leaves were weighed and subsequently ground in a Wiley mill (all four samples were either pooled prior to grinding or ground separately) and stored in a drying oven at 40-50 °C until estimation of ash free dry mass (AFDM). All samples were not pooled because we suspected there may be within-site heterogeneity of AFDM. Although there was some heterogeneity among pooled and
non-pooled AFDM estimates, after examining both the AFDM and dry-mass data we concluded that the differences were not appreciable, so for all of our analyses we treated estimates of AFDM from the pooled and the mean of four individual samples as equivalent. After the study was completed, we measured the percent organic matter composition of the leaves by weighing out either an average of ~1 g (pooled samples) or an average of ~ 0.26 g (individual samples), and placed the samples in a muffle furnace at 500 °C for approximately 4 hours. Samples were left overnight in the muffle furnace and then reweighed the following morning to determine the percent organic matter composition of the samples. AFDM was estimated by multiplying the leaf dry mass by the percent organic matter in the sample.

Macroinvertebrates washed from the leaves were picked out of a 250 µm sieve using forceps and subsequently preserved in 95% ethanol until further processing. All individuals were then separated from inorganic and organic material, enumerated, and identified to family for aquatic insects and snails or to higher levels for other macroinvertebrates (e.g., oligochaetes).

Environmental Parameters

We estimated variation in temperature throughout the study with Hobo® data loggers that were placed at the bottom of the pool in the center of each of our 16 study sites (8/stream). The data loggers were set to record temperature every five minutes for the duration of the experiment. Because the onset of winter generally caused
convergence in temperature among the sampling sites, we only analyzed the data that correspond with large discrepancies in the maximum daily temperatures among sites (i.e., >65% of the maximum range). At each study site, we measured the wetted width and water depth (~0, 25, 50, 75, and 100% of the wetted width) of a 10-m area at 2.5-m intervals (5 transects) surrounding each site. We examined patterns in width and depth by estimating the overall mean width at each pool and the mean of the maximum depths (1 value/transect) at each pool.

To capture seasonal variation in nutrient dynamics, we collected water samples in the fall of 2010 and summer of 2011. Water samples (49 ml water preserved with 1 ml sulfuric acid) were analyzed for nitrogen and phosphorous (NO$_3$-N, NH$_3$-N, Total N, PO$_4$-P, and Total P) using the QuikChem® 8500 Series 2 Flow Injection Analysis System. All water samples were stored in a dark location prior to analysis, although due to a procedural error, only samples from the summer of 2011 were refrigerated. We also estimated the surficial substrate composition in the summer of 2011 by using a gravelometer to measure median axis of 10 particles at approximately equally-spaced intervals across the wetted width of the channel resulting in ~50 particles at each site. We then assigned each particle to one of three relative size classes [fine (< 4 mm), intermediate (4 - 45 mm), and coarse (＞ 45 mm)] and estimated the proportion of sediment that fell within each class. Prior to collection of nutrient or sediment composition in 2011, Wilkin Run experienced a flood event that caused a channel avulsion between 455 and 795 m into the forest and may have shortened the total distance.
the stream flowed. However, the physical characteristics of most of the sites appeared to be unaffected by this flood and we interpret data collected in the summer of 2011 accordingly.

Statistical Analyses

We used a suite of methods to detect thresholds in aquatic macroinvertebrates, leaf litter breakdown, and environmental data along a gradient of distance from the forest edge. To analyze macroinvertebrates we used the Threshold Indicator Taxa ANalysis (TITAN) developed by Baker and King (2010). This analysis uses an indicator species analysis to generate species scores which are standardized by randomized permutations to generate z-scores; the z-scores are then used to estimate both the threshold location and the response direction (higher or lower values after reaching the threshold) along environmental gradients for a particular taxon. A bootstrapping procedure is used to generate confidence intervals around the threshold. Two metrics are used to determine the response strength of a particular taxon: (1) purity – the proportion of bootstrap samples that have the same direction of change as the original response; and (2) reliability - the proportion of bootstrap samples with indicator value score p-values < 0.05 based on a permutation analysis. We deemed taxa as “significant” if the purity and reliability were ≥ 0.95. A community-level threshold estimate is also generated by summing the standardized indicator scores across taxa responding in the same direction at a particular location along the environmental gradient. We removed taxa that occurred in
less than five samples (Baker and King 2010) at a given stream, and transformed the data (natural log + 1) prior to analysis.

Because the TITAN program does not appropriately handle datasets with multiple observations at a given point along an environmental gradient (Cuffney and Song 2013), we modified the program such that it only considered those samples that included all observations at a given distance along the gradient. Analysis of these data revealed that a large number of permutations were required to obtain stable threshold estimates across runs, and found that 100,000 and 200,000 permutations for Fox Creek and Wilkin Run, respectively, were able to generate more stable threshold estimates. Uncertainty in threshold estimates was estimated using a total of 1,000 bootstrap replicates to generate 90% bootstrap percentile confidence intervals. In addition to the TITAN analysis, we plotted shredder abundance (family level shredder designations obtained from Barbour et al. 1999) and Plecoptera (Capniidae was the only plecopteran family captured in this study) density along the distance gradient as taxa in these groups are often good indicators of stream integrity.

As a complement to TITAN, we analyzed abiotic data using a model selection approach to model threshold responses (e.g., Qian and Cuffney 2012). To identify potential thresholds, we analyzed the data using two different threshold approaches. The first approach is based on the nonparametric deviance reduction method (Qian et al. 2003) which can also be termed a step function model. In this method a regression tree analysis is used with one predictor variable (in our case, distance) and the split that
results in the greatest reduction in deviance (i.e., the error sums of squares) is chosen.

We also used a piecewise linear regression (Muggeo 2008) to estimate whether there was a change in the relationship between distance and abiotic variables at our study sites. Estimates of uncertainty in the change point were made for both models using nonparametric bootstrapped percentile confidence intervals methods (Qian et al. 2003, Toms and Lesperance 2003). To determine whether these models fit better than models assuming no threshold response, we also modeled the data using a simple linear regression and an intercept-only model. We assessed model fit by calculating the AICc statistic for each model. The number of parameters used in the AICc calculation were two for the intercept only model: $\beta_0 + \text{error}$; three for the linear regression model: $\beta_0 + \beta_1 x + \text{error}$; five for the nonparametric deviance reduction model: $\beta_0 + \text{error}_1$ if $x < \text{threshold}$, and $\beta_0 + \beta_1 x + \text{error}_2$ if $x \geq \text{threshold}$ (Qian and Cuffney 2012); and six for the piecewise linear regression: $\beta_0 + \beta_1 x + \beta_2 (x - \text{threshold}) + \gamma \text{I}(x > \text{threshold}) + \text{error}$, where $\text{I}(A)$ is an indicator function and equals 1 if $A$ is true, and $\gamma$ is a parameter that estimates the gap between the two regression lines at the threshold (Muggeo 2008). Any model with an AICc of $\geq 2$ less than all other models was interpreted as the best model in the set; models that had AICc values within two of the best model were interpreted as having equal empirical evidence (Burnham and Anderson 2002). Our response variables for these analyses included temperature, nutrients ($\text{NO}_3$-N, $\text{NH}_3$-N, $\text{PO}_4$-P, Total N and Total P), and the proportion of leaf mass remaining at the end of the study (natural log transformed ash-free dry mass).
We constrained the potential model set based on a priori expectations that forest patches would cause shifts in ecological and environmental parameters. Therefore, we interpreted a model as having evidence of a forest-mediated threshold only if the threshold estimate was within the forest patch (this includes estimates that occurred between the first site within the forest and the first site upstream of the forest, resulting in a negative distance value) and threshold models were within 2 AICc of the best model. If the threshold was not within the forest patch and/or the intercept only model was within 2 AICc of the best model (indicating poor overall model fit) then we deemed that there was no evidence for a forest-mediated threshold.

**Results**

*Physical Habitat*

Both sediment composition and pool dimensions showed strong changes as streams transitioned from agricultural land to forest patches. At Wilkin Run, sediment composition ranged from >80% fine and about 2% coarse 376 m upstream of the forest patch to ~23% fine and coarse after the stream had flowed 790 m into the forest patch. Alternatively, at Fox Creek, fine sediment exhibited a sharp increase at the edge of the forest and then decreased until about 405 m into the forest patch followed by another increase 1080 m into the patch (Fig. 2.1). As with the sediment composition, at Wilkin Run the pool dimensions showed strong changes exhibiting a sharp increase in width and depth just upstream of the patch (~78 m) and then another strong increase was observed.
for the depth at 452 m and for the width at 790 m. In contrast, the pools at Fox Creek showed no systematic changes in dimensions along the transition from agricultural land to the forest patch (Fig. 2.2).

*Multimodel threshold analysis of temperature, nutrients, and leaf mass loss*

We found strong evidence for threshold changes in multiple parameters soon after entering forest patches (Fig. 2.3). In both study streams, temperature showed evidence of a threshold. At Wilkin Run, the step function and the piecewise regression models best described temperature variation, and at Fox Creek the step function model was among the best candidate models (Table 2.1; Figs 2.3A and 2.3D). Results from our analysis of nutrient concentrations were more heterogeneous. At Wilkin Run, the only nutrient parameter that indicated a possible forest-mediated threshold was PO$_4$-P in 2010 (Table 2.1; Fig. 2.3B). In Fox Creek, the threshold models were among the best models for NO$_3$-N in 2010 and 2011, NH$_3$-N in 2011, and PO$_4$-P in 2011 (Table 2.1; Figs 2.3E – 2.3H). The analysis of leaf mass loss indicated no evidence of a threshold, with both streams having the lowest AICc value for the intercept only model (Table 2.1; Figs 2.3C and 2.3I).

Confidence interval estimates for the multimodel threshold analysis suggested that thresholds typically occurred shortly after entering forest patches. At Fox Creek, NO$_3$-N concentrations in the fall of 2010 were negatively related to distance with a threshold ~ the forest edge, and the model fit indicated a lower magnitude slope once the
stream reaches the forest patch (Fig. 2.3E). To explore these patterns in NO$_3$-N further, we estimated the mean and 95% confidence intervals for each location and found that there was an abrupt decline 100 m upstream of the forest patch, another decline occurred between 200 and 400 m into the forest patch, and a final decline occurred after the stream had flowed 1080 m into the forest (Fig. 2.4). Fox Creek temperature and NO$_3$-N (summer 2011) concentrations declined after reaching a threshold 55 m after entering the forest (Fig. 2.3D and 2.3F). NH$_3$-N concentrations in the summer of 2011 increased until about 249 m into the patch and decreased thereafter (Fig. 2.3G). Finally, summer 2011 PO$_4$-P concentrations at Fox Creek exhibited a threshold the furthest into the forest, increasing after reaching a threshold at 743 m (Fig. 2.3H). The threshold models for temperature at Wilkin Run indicated a threshold near the edge of the forest patch (-71 m for the piecewise model) and 158 m after entering the forest patch (step function model). Examination of temperature scatter plots at Wilkin Run showed that the temperature was still increasing after the stream flowed 22 m into the forest indicating that the step function model provided the most reasonable estimate of the threshold distance (Fig. 2.3A). PO$_4$-P concentrations at Wilkin Run had a threshold near the edge of the forest patch with higher concentrations upstream of the patch (Fig. 2.3B).

**TITAN analysis of macroinvertebrate communities**

Analysis using TITAN provided evidence for threshold changes in macroinvertebrate communities occurring relatively soon after entering forest patches.
Wilkin Run had 6 taxa that exhibited a threshold and at Fox Creek, 3 taxa exhibited threshold responses. Threshold decreases with distance into a forest patch was the most common response with three taxa showing a marked decrease near the forest edge (Turbellaria, Elmidae, and Amphipoda), and three families [Chironomidae, Coenagrionidae, and Physidae (but note that Physidae did not completely stabilize after 200,000 permutations)] showing a decrease after reaching a threshold about 324 m into a forest (Fig. 2.5). Three families showed threshold increases with distance into a forest patch with Pleurocerids and Tipulids increasing soon after entering a forest patch, and Limnephilids showing a threshold increase at about 324 m (Fig. 2.5). Uncertainty estimates were relatively low for 6 taxa with bootstrap percentile estimates spanning less than 352 m. Three families had larger uncertainty estimates ranging from 465 to 550 m, but the entire interval for Limnephilids and Chironomids occurred within the forest patch. Consistent with the TITAN results, scatter plots of the raw data generally showed strong changes soon after entering forests (Fig. 2.6). Even though we did not analyze overall shredder abundance and TITAN did not detect a threshold in Capniidae abundance, we plotted the overall shredder and Capniidae abundance and found evidence for strong, systematic changes beginning at the forest edge and proceeding into the forest at both sites (Fig. 2.7). Additionally, TITAN revealed that community level thresholds were consistent with the taxa-specific analyses, with thresholds ranging from near the forest edge (between first forest site and last agricultural site) to about 324 m into the patch (Table 2.2).
Discussion

Our study provides strong evidence that streams draining agricultural land exhibit abrupt threshold changes after entering forest patches. Both the TITAN and the multi-model threshold analyses showed threshold changes in biotic and abiotic parameters primarily ranging from the forest edge to 324 meters into forest patches. However, leaf-mass loss was relatively invariant and did not exhibit a forest-mediated threshold. Overall, our results demonstrate that streams rapidly change upon entering forest patches, and that even small patches of forest may be effective in restoring functional linkages between forests and streams in agricultural landscapes.

Thresholds in environmental variables

Although the results from our analyses of environmental variables were heterogeneous and depended on the specific variable of interest, there was evidence for abrupt changes in habitat (sediment and pool dimensions), temperature, and nutrient concentrations. There is appreciable evidence that agricultural land use can lead to erosion and deposition of fine sediment in streams (Wood and Armitage 1997, Quinn 2000). We observed this trend in Wilkin Run where the relative dominance of fine sediment in the agricultural section gave way to coarser sediment with increasing distance into the forest patch. However, at Fox Creek the benthic sediment composition was generally coarser in the agricultural section, followed by increased fine sediment
near the forest edge that gave way to coarser sediment further into the forest (Fig. 2.1). The relatively larger sediment upstream of the forest patch may be explained in part by the dominance of herbaceous vegetation on the banks upstream of the forest patch, which in some cases may provide more bank stability than woody vegetation (Lyons et al. 2000), resulting in reduced erosion and associated deposition of fine sediment.

Many studies have also shown marked differences in channel dimensions between forested and agricultural reaches. In streams where the riparian area is dominated by herbaceous vegetation, streams are often narrower than forested streams (Davies-Colley 1997, Scarsbrook and Halliday 1999, Sweeney et al. 2004), which is driven by the ability of herbaceous vegetation to trap sediment and stabilize stream banks (Lyons et al. 2000). In our study, we found a strong shift in pool width soon after entering the forest patch in Wilkin Run, but the trends were much less clear in Fox Creek. Similarly, we found that pools were generally deeper in the forest than in the pasture in Wilkin Run but once again did not exhibit systematic trends in Fox Creek (Fig. 2.2). The deeper pools in the forested stream segments of Wilkin Run may have been driven by the larger number of pool forming structures (e.g., large wood, tree roots) present in the forested patch. More comprehensive geomorphic measurements would be necessary to make additional conclusions about the effects of forest patches on pool structure in this system.

Stream temperature is an important parameter influencing stream biota, and can be markedly influenced by forest cover. In the Hubbard Brook Experimental Forest, Burton and Likens (1973) found that stream temperatures declined 4-5 °C approximately...
50 m after transitioning from clear cuts to forested stream sections. Similarly, Storey and Cowley (1997) found that stream temperatures showed a sharp decline in pastoral streams within 300 m after entering a forest patch. The threshold responses we observed were consistent with these studies, and showed ~ 1.6 to 2.4 °C declines occurring between 0 and 200 m after entering forests. Additionally, our models were able to elucidate the nature of the response: a sharp drop in the mean (as opposed to a change in slope) that stabilized soon after entering the forest (Figs 2.3A and 2.3D). Because our analysis focused only on the maximum daily temperatures in the fall, we expect that the temperature differences between agricultural land and forest patches are likely to be greater in the summer, and that thresholds would perhaps be reached even closer to forest edges.

Riparian forests have long been known to influence nutrient concentrations in streams by filtering catchment water prior to reaching the stream (Lowrance et al. 1984). Additionally, forests can enhance in-stream nutrient processing through an increased benthic surface area (Sweeney et al. 2004), accumulations of large wood which can increase retentiveness of streams (Bilby and Likens 1980), and large wood biofilm can enhance local uptake of nutrients (Ashkenas et al. 2004). In our study, nitrogen concentrations in Fox Creek showed strong evidence for enhanced nutrient processing in forested streams. In 2010, our data suggested a threshold just upstream of the forest patch (Fig. 2.3E); however, plots of the mean and 95% confidence intervals showed that the piecewise linear regression did not capture the multiple, strong shifts in nutrients that
occurred along the agriculture-forest transition (Fig. 2.4). During the summer of 2011, the step function model showed a clear threshold in NO$_3$-N that occurred almost immediately after entering the forest patch (Fig. 2.3F). Previous studies in agricultural catchments have found similar declines in N in streams flowing from agricultural land into forest patches (Storey and Cowley 1997, Houghton et al. 2011) suggesting that remnant forest patches may be important areas for nitrogen processing in agricultural landscapes; however, these trends did not occur in Wilkin Run, highlighting the potentially important role that patch context (e.g., surrounding land use, geology, forest composition, etc. Wiens 2002) plays in regulating nitrogen cycling in streams.

We also found evidence for threshold changes in phosphate and ammonia at our study sites. Elevated phosphate concentrations immediately upstream of the forest patch in Wilkin Run (Fig. 2.3B) were possibly driven by livestock access upstream of the forest and a drainage tile discharging into the stream ~200 m upstream of the forest patch, both of which can lead to elevated phosphate concentrations (Sims et al. 1998, Hubbard et al. 2004). Even though the threshold model did not detect a change prior to reaching the forest patch, there was clearly a spike (~200 m) and subsequent decline prior to reaching the forest patch (~100 m) suggesting that while the stream may quickly process phosphate, the mechanisms regulating phosphate uptake are unlikely to be linked to riparian vegetation alone.

In 2011 at Fox Creek, an increase in phosphate occurred after reaching a threshold at 743 m into the forest (Fig. 2.3H). An inverse pattern was observed for ammonia,
peaking about midway through the forest patch, and then sharply declining after 249 m (Fig 2.3G). These patterns may be explained, at least in part, by a wetland adjacent to the stream that occurred between 400 and 1080 m into the forest, which may have been a phosphorous source but a nitrogen sink (Mitsch and Gosselink 2000 and citations therein). Overall, our nutrient results suggest that forest patches can have an important role in regulating nutrient dynamics of streams in agricultural landscapes, although additional research will be necessary to further quantify these relationships.

Macroinvertebrate community thresholds

The TITAN analysis yielded strong evidence for forest-mediated threshold changes in macroinvertebrate communities. Previous analyses using TITAN have suggested that synchronous threshold changes in multiple macroinvertebrate taxa in response to disturbance provide evidence for community-level thresholds (King et al. 2011, Bernhardt et al. 2012). Although we only detected a total of nine taxa exhibiting a threshold response across both study streams, the responses were relatively synchronous, generally occurring within a narrow range of distance from the forest edge (~ edge to 324 m; Fig. 2.5). Further, all of the community-level threshold estimates occurred within 324 m of entering a forest patch, and the uncertainty estimates were within the bounds of the forest patch for three out of the four estimates (Table 2.2). These results are consistent with previous studies that have shown recovery in macroinvertebrate communities within 300 to 600 m after a stream enters a forest patch (Storey and Cowley 1997, Scarsbrook
and Halliday 1999). Because TITAN enabled us to disaggregate macroinvertebrate community data, our results yielded additional insight into individual taxon responses showing that several of the taxa exhibited threshold changes almost immediately after entering a forest patch that persisted into the patch interior. These results support our contention that even very small patches of forest may be able to recover linkages between forests and streams.

**Mechanisms regulating macroinvertebrate community structure**

The threshold changes that we observed for the macroinvertebrate communities corresponded to strong changes in temperature, sediment composition, nutrients, and forest cover. Water temperature is important for regulating growth, development, and survivorship of aquatic macroinvertebrates (Sweeney and Vannote 1984, Sweeney and Vannote 1986). Hogg and Williams (1996) showed that temperature changes as small as 2 to 3.5 °C may negatively affect aquatic macroinvertebrate communities. We found that the maximum daily temperatures were about 1.6 to 2.4 °C lower in the forest, and we suggest that this difference is likely higher in the summer and may potentially influence thermally sensitive invertebrate species. Although we did not consider fishes in this study, there are multiple lines of evidence showing that fish life history is dramatically affected by temperature (reviewed in Caissie 2006), suggesting that fish communities may have similar responses to abrupt changes in forest cover as exhibited by macroinvertebrates in our study.
In stream ecosystems, it is widely known that erosion and deposition of fine sediment can adversely affect habitat and food resources of aquatic biota. In particular, sedimentation can have a variety of effects on aquatic macroinvertebrates including filling interstitial spaces, reducing food quality, and favoring species adapted to fine sediment (e.g., some species of Chironomidae and Oligochaeta) (Wood and Armitage 1997, Quinn 2000). At Wilkin Run, the strong changes in fine sediment after entering the forest may drive responses of taxa that are sensitive to sedimentation and those that may use fine sediment for habitat or tube building (e.g., Chironomidae). Alternatively, the dominance of finer sediments throughout Fox Creek may explain the more muted changes in macroinvertebrate community composition.

In addition to the physical effects of temperature and sediment composition, shifts in macroinvertebrate community composition suggested that basal resources supporting these communities were influenced by the transitions from open-canopied agricultural land to shaded forest patches. There is considerable evidence that forested reaches have lower algal biomass and higher allochthonous organic material (e.g., leaf litter) than more open reaches of streams draining agricultural land (Delong and Brusven 1992, Delong and Brusven 1994, Quinn et al. 1997). Furthermore, nutrients (N and P) can regulate stream primary productivity and nutrient enrichment is often a byproduct of agricultural land use (Carpenter et al. 1998). Our results showed threshold increases in the shredders Limnephilidae (Wilkin Run) and Tipulidae (Fox Creek) soon after entering forest patches suggesting increased availability of leaf litter in forest patches. Although not detected by
TITAN, we also found evidence for systematic increases in the shredder Capniidae, and overall shredder abundance with distance into forest patches. TITAN’s inability to detect the strong changes in Capniids is consistent with studies that have found that TITAN may be unable to detect threshold changes that are more complex than simple step functions (Cuffney and Song 2013), and suggests that supplementary exploratory analysis may be necessary more fully understand threshold dynamics. The TITAN analysis also revealed threshold declines in the scrapers Elmidae (Fox Creek) and Physidae (Wilkin Run), suggesting that shading and lower nutrient concentrations may limit algal growth and regulate scraper populations in forest patches.

Leaf breakdown

In contrast to the other biotic and abiotic results, we found no evidence for threshold changes in leaf breakdown. We expected that our sampling design would enable us to detect shifts in leaf breakdown as streams transition from agricultural to forest patches; however, the relatively stable mass loss that we observed suggests that land use did not alter leaf breakdown rates in these streams (Figs 2.3C and 2.3I). Our results showed that agricultural patches had evidence of higher nutrient concentrations and temperatures, which are often associated with elevated activity of microorganisms and increased rates of leaf breakdown. However, there were also marked increases in shredder densities in the forest patches that have also been associated with higher breakdown rates (see Webster and Benfield 1986, Young et al. 2008 for a review of the
mechanisms influencing leaf breakdown). These data are consistent with the hypothesis that leaf breakdown rates are unaffected by LULC changes because as shredders are lost due to declining forest cover there can be a compensatory increase in microbial breakdown (Hladyz et al. 2010). Another possible explanation for our results could be that the effects of agricultural land use are only manifest over longer temporal scales during which the leaves would experience a greater range of agricultural effects than during the course of a six week study. Some of the previous studies that have found land use effects on breakdown left leaves in streams for greater than 100 days (Young et al. 1994, Sponseller and Benfield 2001, Niyogi et al. 2003), which may partly explain why a land-use effect was observed in these studies.

**Conclusions and implications for management and restoration of streams**

Although there has been considerable interest in identifying ecological thresholds along gradients of human disturbance recently (e.g., Qian et al. 2003, Dodds et al. 2010, King et al. 2011), there has been much less focus on potential thresholds along impacted-to-natural gradients (but see Storey and Cowley 1997, Scarsbrook and Halliday 1999, Suga and Tanaka 2013). Our results suggest that streams rapidly reach a threshold in both abiotic and biotic parameters after entering forest patches in agricultural landscapes, and that threshold modeling techniques may provide a viable method to quantify how much forest is necessary to recover historical structure and function to impaired streams. Because of patterns in land ownership and the costs of retiring entire catchments from
agricultural production, restoration of discontinuous forest patches provides a possible alternative that may help sustain forest-stream linkages in human-dominated landscapes (Scarsbrook and Halliday 1999). Recovery of streams as indicated by our threshold estimates occur at similar scales as previous studies (Storey and Cowley 1997, Scarsbrook and Halliday 1999), which supports the generalizability of these patterns and indicates that forests that encompass stream lengths of a few hundred meters or more can maintain strong linkages between forests and streams.

While our study provides strong evidence for forest-mediated thresholds, our sample size and sampling time periods are limited and more research is necessary to obtain a general understanding how streams change along agriculture-forest transitions and the implications for management of these systems. This study and previous studies of agriculture-forest transitions in streams primarily focus on the influence of forests located downstream of agricultural land; however, the effects of forests on streams may also cascade into downstream stream sections draining agricultural land (i.e., a downstream shadow, Harding et al. 2006), and future studies should explore this to more fully understand the role of forest patches in human-dominated landscapes.

Furthermore, there is increasing recognition that streams are not only influenced by fluxes of materials and organisms from terrestrial systems, but also influence terrestrial systems via reciprocal aquatic-to-terrestrial fluxes of organisms (Baxter et al. 2005, Sullivan and Rodewald 2012). These aquatic-terrestrial linkages can strongly influence the ecology of riparian areas by providing energy subsidies to terrestrial
consumers and potentially acting as vectors of contaminants (Sullivan and Rodewald 2012); however, the implications of abrupt transitions in LULC for aquatic-terrestrial linkages is at present not well understood and further study is needed. Although the value of ecological thresholds and how best to model them is a hotly debated topic (King and Baker 2011, Cuffney et al. 2011), our study shows that the threshold concept is useful for understanding the effects of agriculture-forest transitions on stream ecosystems, and can provide an important tool for prioritizing conservation and restoration of streams in managed landscapes.
Acknowledgements

This work was supported by The Ohio State University Climate, Water, and Carbon Targeted Investment in Excellence (CWC-TIE) Program and the National Science Foundation STEM Graduate Fellows in K-12 (NSF GK-12) Education Program, Grant No. 0638669. N. Rosenbaum and S. Francis–Bongue assisted with macroinvertebrate identification. J.R. Holomuzki and M.J. Paul contributed insightful comments on the initial study design. Finally, we would like to thank The Wilderness Center and other land owners for their cooperation and permission to conduct this study on their property.
References


Table 2.1. AICc statistics from each model for Wilkin Run (top) and Fox Creek (bottom). Asterisks correspond to models that are within 2 of the best model in the candidate model set. Threshold estimates are displayed in parentheses. DNC corresponds to models that did not converge. The threshold column corresponds to whether a forest-mediated threshold is present (Yes or No). Models without evidence of a threshold or where the threshold occurs outside of the forest boundaries are given a value of “No” (see methods for more details).

Wilkin Run

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Intercept</th>
<th>Linear</th>
<th>Step</th>
<th>Piecewise</th>
<th>Threshold</th>
<th>Evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf Mass</td>
<td>-80.54*</td>
<td>-79.74*</td>
<td>-79.43*(71)</td>
<td>-74.16(0)</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>12.64</td>
<td>-21.15</td>
<td>-38.47*(158)</td>
<td>-37.82*(-71)</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td>NH₃ 2010</td>
<td>-140.52*</td>
<td>-142.18*</td>
<td>-138.45(-142)</td>
<td>-134.7(-35)</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>NH₃ 2011</td>
<td>-22.94*</td>
<td>-22.77*</td>
<td>-17.18(-142)</td>
<td>DNC</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>NO₃ 2010</td>
<td>-130.27*</td>
<td>-129.81*</td>
<td>-126.65(-291)</td>
<td>DNC</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>NO₃ 2011</td>
<td>-41.1*</td>
<td>-39.21*</td>
<td>-33.58(-142)</td>
<td>DNC</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>PO₄ 2010</td>
<td>-201.01</td>
<td>-201.29</td>
<td>-205.1*(-28)</td>
<td>DNC</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td>PO₄ 2011</td>
<td>-79.04</td>
<td>-86.41</td>
<td>-98.5*(-142)</td>
<td>-79.03(22)</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Total N 2010</td>
<td>-46.08*</td>
<td>-47.48*</td>
<td>-44.02(324)</td>
<td>-38.63(123)</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Total N 2011</td>
<td>-2.35*</td>
<td>-2.61*</td>
<td>2.91(-142)</td>
<td>DNC</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Total P 2010</td>
<td>-170.14</td>
<td>-172.54*</td>
<td>-167.55(621)</td>
<td>DNC</td>
<td>No</td>
<td></td>
</tr>
<tr>
<td>Total P 2011</td>
<td>-73.99</td>
<td>-83.92</td>
<td>-93.14*(-142)</td>
<td>-77.39(10)</td>
<td>No</td>
<td></td>
</tr>
</tbody>
</table>

continued
Table 2.1 continued

Fox Creek

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Intercept</th>
<th>Linear</th>
<th>Step</th>
<th>Piecewise</th>
<th>Threshold Evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf Mass</td>
<td>-143.69*</td>
<td>-141.96*</td>
<td>-137.64(-296)</td>
<td>DNC</td>
<td>No</td>
</tr>
<tr>
<td>Temperature</td>
<td>92.25</td>
<td>29.02*</td>
<td>30.81*(55)</td>
<td>33.47(146)</td>
<td>Yes</td>
</tr>
<tr>
<td>NH₃ 2010</td>
<td>-179.01*</td>
<td>-180.05*</td>
<td>-174.38(743)</td>
<td>DNC</td>
<td>No</td>
</tr>
<tr>
<td>NH₃ 2011</td>
<td>-117.01</td>
<td>-114</td>
<td>-112.13(-296)</td>
<td>-139.74*(249)</td>
<td>Yes</td>
</tr>
<tr>
<td>NO₃ 2010</td>
<td>-100.7</td>
<td>-146.12</td>
<td>-116.72(-146)</td>
<td>-161.92*(-49)</td>
<td>Yes</td>
</tr>
<tr>
<td>NO₃ 2011</td>
<td>-82.92</td>
<td>-87.98</td>
<td>-100.61*(55)</td>
<td>-93.68(399)</td>
<td>Yes</td>
</tr>
<tr>
<td>PO₄ 2010</td>
<td>-294.55</td>
<td>-296.85*</td>
<td>-297.17*(-146)</td>
<td>-288.69(188)</td>
<td>No</td>
</tr>
<tr>
<td>PO₄ 2011</td>
<td>-175.09</td>
<td>-190.38*</td>
<td>-189.28*(743)</td>
<td>DNC</td>
<td>Yes</td>
</tr>
<tr>
<td>Total N 2010</td>
<td>-57.86</td>
<td>-91.73*</td>
<td>-86.36(743)</td>
<td>DNC</td>
<td>No</td>
</tr>
<tr>
<td>Total N 2011</td>
<td>-53.95</td>
<td>-57.93*</td>
<td>-53.47(147)</td>
<td>-47.78(-118)</td>
<td>No</td>
</tr>
<tr>
<td>Total P 2010</td>
<td>-243.68*</td>
<td>-242.52*</td>
<td>-240.77(-146)</td>
<td>-235.11(14)</td>
<td>No</td>
</tr>
<tr>
<td>Total P 2011</td>
<td>-139.47*</td>
<td>-136.43</td>
<td>-134.38(-41)</td>
<td>-129.51(368)</td>
<td>No</td>
</tr>
</tbody>
</table>
Table 2.2. Community wide threshold estimates (sum of the individual z- and z+ scores) for quantiles 0.05, 0.10, 0.90 and 0.95.

<table>
<thead>
<tr>
<th>Site</th>
<th>Direction</th>
<th>Change Point</th>
<th>0.05</th>
<th>0.10</th>
<th>0.50</th>
<th>0.90</th>
<th>0.95</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilkin Run</td>
<td>Z-</td>
<td>323.5</td>
<td>-28</td>
<td>-28</td>
<td>157.5</td>
<td>323.5</td>
<td>323.5</td>
</tr>
<tr>
<td></td>
<td>Z+</td>
<td>323.5</td>
<td>-28</td>
<td>-28</td>
<td>323.5</td>
<td>621</td>
<td>621</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Z-</td>
<td>-40.5</td>
<td>-145.5</td>
<td>-40.5</td>
<td>-40.5</td>
<td>55</td>
<td>147</td>
</tr>
<tr>
<td></td>
<td>Z+</td>
<td>299.5</td>
<td>-40.5</td>
<td>55</td>
<td>147</td>
<td>299.5</td>
<td>742.5</td>
</tr>
</tbody>
</table>
Figure 2.1. Bar graphs of sediment composition collected from a 10 m area surrounding the center of pools at Wilkin Run (top) and Fox Creek (bottom).
Figure 2.2. Line graphs that correspond to the mean pool depth and width at Wilkin Run (black) and Fox Creek (grey).
Figure 2.3. Plots of the model fit (solid line) overlaid on the observed data (open circles) for the multi-model threshold analysis. 90% bootstrap percentile confidence interval estimates and the original threshold estimate (black dot) are displayed at the bottom of the graphs. Nutrient samples were collected in both the fall of 2010 and the summer of 2011 to capture seasonal variation in nutrient dynamics.
Figure 2.3

Wilkin Run

Distance from forest edge (m)

continued
Figure 2.3 continued

Distance from forest edge (m)
Figure 2.3 continued

Distance from forest edge (m)
Figure 2.4. Mean and 95% confidence interval estimates for NO$_3$-N concentrations during the fall of 2010 at Fox Creek.
Figure 2.5. 90% bootstrap percentile confidence interval estimates of the threshold distance obtained from the TITAN analysis. $Z^{-}$ corresponds to taxa that decreased following the threshold (left axis), and $Z^{+}$ correspond to taxa that increased after the threshold (right axis); the size of the dot corresponds to the relative size of the original indicator value estimate. Elmidae, Tipulidae and Turbellaria are estimated from Fox Creek; the rest of the taxa, Physidae, Coenagrionidae, Chironomidae, Amphipoda, Pleuroceridae, and Limnephilidae, are from Wilkin Run.
Figure 2.5
Figure 2.6. Scatter plots of macroinvertebrate density vs distance for decreasing taxa (top) and increasing taxa (bottom) at Wilkin Run (left) and Fox Creek (right).
Figure 2.7. Shredder and Capniidae density summed over the course of the study at Wilkin Run (left) and Fox Creek (right).
Chapter 3: Transitions in land cover drive aquatic emergent insect communities in agricultural landscapes

Abstract

It is widely recognized that headwater stream ecosystems are intimately associated with riparian forests. Aquatic insects that emerge from streams as adults fuel terrestrial food webs, thus representing a key aquatic-terrestrial linkage. The widespread clearing of forests for agriculture, however, has led to a decoupling of forest-stream dynamics. At 28 sites distributed across three central Ohio headwater streams, we examined how remnant forest patches in agricultural landscapes influenced aquatic emergent insect community composition. We observed consistent shifts in aquatic emergent insect community composition near the upstream edge of forest patches and again within 139 meters of downstream edges of forests. These shifts were associated with insect families that were predominantly found in either agricultural (e.g., Culicidae and Psychodidae) or forested (e.g., Polycentropodidae and Psychomyiidae) sites. Shifts in insect communities were linked to abiotic conditions (e.g., nutrients, channel width and solar radiation) that changed over similar spatial extents. Our results also suggested that decreased N concentrations observed in forests extended into downstream agricultural
areas. Our study yields evidence that patches of forest can rapidly recover aquatic-to-terrestrial insect fluxes between forests and streams, but that these effects may not extend beyond forest boundaries.
Introduction

Among the most important factors influencing stream dynamics are the linkages with the catchments that they drain (Hynes 1975). These linkages are especially apparent in forested headwater streams, where shade and seasonal pulses of allochthonous organic matter can fuel headwater stream food webs and drive community structure (Vannote et al. 1980, Wallace et al. 1997, Wallace et al. 1999). Changing land use and land cover (hereafter land cover), however, can decouple streams and from adjacent riparian forests leading to widespread stream impairment (US EPA 2006), spurring considerable interest of the effects of land-cover change on stream ecosystems (Quinn 2000, Paul and Meyer 2001, Allan 2004).

In general, studies of the effects of land-cover change on streams have focused on in-stream processes; however, it is increasingly recognized that streams and riparia may best be viewed as integrated, holistic systems (Sullivan et al. 2007, Fausch et al. 2010), thus comprehensive evaluations of the effects of land-cover change on these linked systems could benefit from further consideration of reciprocal aquatic-terrestrial exchanges. Because of their complex life-cycles, aquatic insects are particularly important components of linked stream-riparian ecosystems. As aquatic larvae, they mediate basal resources (e.g., leaf litter) to higher aquatic consumers, and as winged terrestrial adults they transport energy derived from streams (both terrestrial and aquatic in origin) to terrestrial food webs (reviewed in Baxter et al. 2005, Sullivan and Rodewald 2012). The importance of adult aquatic insects to terrestrial systems varies, but they
often make substantial contributions to the diets of terrestrial consumers and can elicit numerical responses in a diverse array of taxa including spiders, lizards, birds, and bats (Henschel et al. 2001, Sabo and Power 2002, Iwata et al. 2003, Fukui et al. 2006).

Although recent studies have greatly advanced our understanding of the role of aquatic insects in linking aquatic and terrestrial systems, the effects of spatial heterogeneity in land cover on aquatic-terrestrial linkages is not well understood. In particular, quantifying the influence of transitions in land cover on linked stream-riparian ecosystems and whether impaired streams can recover after flowing through forest patches may be critical to develop a more complete understanding of stream-riparian function in fragmented landscapes. Although not widely investigated, some studies (Storey and Cowley 1997, Scarsbrook and Halliday 1999) suggest that in-stream abiotic and biotic conditions can change rapidly within the first few hundred meters after entering forest patches, and may eventually converge upon reference conditions. It has also been hypothesized that the effects of forests on streams can extend beyond forest boundaries and create a “downstream shadow” effect (Harding et al. 2006). However, very few studies have investigated the effects of agriculture-forest-agriculture land cover transitions on streams, and the implications of these transitions for aquatic-to-terrestrial insect fluxes remains largely an open question.

In the present study, we sought to determine the effects of land-cover transitions on aquatic-to-terrestrial invertebrate fluxes in agricultural landscapes with scattered patches of forest. Specifically, our objectives were to: 1) describe shifts in aquatic
emergent insect communities in response to land-cover transitions, 2) estimate the
distance at which aquatic emergent insect community composition shifts after entering
and leaving forest patches, and 3) to determine whether these shifts corresponded to shifts
in environmental drivers along these transitions. In order to address our objectives, we
sampled aquatic emergent insect communities and various environmental variables in
headwater streams that undergo abrupt agriculture-forest-agriculture transitions (Fig. 3.1)
in agricultural landscapes of central Ohio.

Methods

Site description

We sampled 28 locations in three streams draining agricultural landscapes in the
Low Lime Drift Plain ecoregion in central Ohio (Omernik and Griffith 2013). The study
streams are located in Baughman Township, Canaan Township, and Wayne Township
and are named BA, CA, and WA accordingly. All study streams are small headwater
systems that undergo abrupt transitions in land cover and have watershed areas of 1.27
km² (BA), 1.24 km² (CA), and 1.22 km² (WA) (estimated at the most downstream site).
To address our objectives we studied scour pools (Bisson et al. 2006) located upstream,
within, and downstream of forest patches (Fig. 3.1). Study sites that were upstream and
downstream of forest patches primarily flowed through cropland and were bordered by a
mixture of herbaceous plants and shrubs, or a single line of trees on the banks of the
streams (upstream at WA and downstream at BA). The forested sites were generally
dominated by mature, second-growth forest with a contiguous forest area of ~ 19, 31, 11 ha for BA, CA, and WA, respectively.

*Aquatic emergent insect sampling*

We sampled aquatic emergent insects from pools along a continuum beginning upstream of forest patches, proceeding through the forests, and continuing downstream of the forest patches (Fig. 3.1). We focused on pools (i.e., sites) because there is evidence that insect emergence from pools can be substantially higher than riffles (Iwata 2007) and are less prone to drydowns. To sample emerging aquatic insects, we used 1-m² floating emergent insect traps which consisted of a pyramidal shaped wooden frame covered in window screen which tapers into a sample jar following Alberts et al. (2013). These traps were placed in a central position within pools and surrounded with rebar ensure that they sampled the same area throughout the study. At each site, we collected a total of two samples over an eight day period (1 sample every four days). At two sites (905 and 1000 m at BA), the sampling jar fell off and was replaced after 1 day, resulting in seven-day collection periods. At another site (840 m at BA), the jar fell off the trap prior to collecting the first sample, resulting in only one sample collected at this site. At CA 22 meters downstream of the forest, the pool completely dried out prior to sampling, so we moved the trap to a nearby pool (764 m) resulting in only one sample collected at this site as well. To minimize seasonal effects, all insect samples were collected during the summer (2012) dry season in Ohio (July-August). All samples were preserved in 70%
ethanol and non-parasitoid aquatic insects were identified to family under a dissecting microscope using Merritt et al. (2008) and Triplehorn and Johnson (2005). Individuals from the family Muscidae were not included in our analyses because the characteristics that differentiate aquatic and terrestrial species were ambiguous on our specimens.

*Environmental parameters*

In addition to sampling aquatic emergent insects, we measured pool dimensions, sediment composition, water chemistry, and canopy cover. At each pool, we established five equidistantly-spaced transects running across the stream where we measured wetted width and water depth (five equally-spaced measurements at each transect) at low flow. Along these transects, sediment composition (20 particles/transect for a total of ~100/pool) was measured using a gravelometer (≤ 2 and 4 – 180 mm; the longest axis was measured for embedded rocks). We collected water samples within 21 m of each pool (49 ml water preserved with 1 ml sulfuric acid) and analyzed the samples for nitrogen and phosphorous (NO$_3$-N, NH$_3$-N, total N, PO$_4$-P, and total P) using a QuikChem® 8500 Series 2 Flow Injection Analysis System. Conductivity and pH were estimated using a YSI™ water quality sonde (6920 V2) at each pool. We used digital hemispherical photographs to obtain estimates of canopy cover set at the minimum tripod height (~85 cm above the stream bottom) and positioned within each pool to acquire an estimate of canopy cover close to the stream surface. We used WinSCANOPY™ (Regents
Instruments, 2006) to estimate the daily total (direct + diffuse) photosynthetically active radiation (PAR) calculated over the growing season (May through September).

Statistical analyses

To detect shifts in aquatic emergent insect community composition, we used a multivariate regression tree (mvrt) analysis (De'ath 2002). We modeled our approach after similar univariate threshold detection methods (Qian et al. 2003), and we used a mvrt analysis with one predictor variable (distance) and chose the two splits that resulted in the greatest reduction in the deviance (i.e., the sum of the squared errors). Prior to analysis, data were transformed using a log$_{10}$ transformation, which deemphasizes abundant species so that the resultant analysis more accurately reflects changes in community composition rather than the most abundant taxa (Anderson et al. 2006). We then calculated a Bray-Curtis dissimilarity matrix, which was subsequently analyzed using the mvpart package in R (De'ath 2013). We estimated uncertainty in threshold estimates using a bootstrapping procedure where we sampled the data with replacement 10,000 times, and calculated the 90% percentile confidence intervals. These estimates were plotted for each site for visual interpretation of threshold uncertainty. Because a regression tree analysis will partition the data regardless of whether a split is significant, we tested whether differences among groups were significant using a permutational multivariate analysis of variance (perMANOVA, Anderson 2001). At streams where the perMANOVA yielded significant effects ($P < 0.05$), we analyzed family composition.
data using an indicator species analysis. This analysis uses pre-defined groups (in our case defined by the mvrt) to generate indicator species values for each group based on the relative abundance and presence of taxa within the community. The group with the maximum indicator species value is chosen as the final indicator value for that species (or family in the present study). Indicator species are deemed as significant if the observed maximum indicator value is greater than or equal to 95% of the indicator values generated by random permutations of the data (we used 10,000). After determining significant families, we plotted the data to examine trends along agriculture-forest transitions.

To examine environmental trends in response to land cover, we used a principal components analysis (PCA). Physical habitat variables used in the PCA included pool length, mean pool width and depth, the proportion of benthic sediment composition [proportion of fines (< 2 mm), coarse sediment (> 64 mm), or bed/hardpan], and PAR. Water-quality variables included in the PCA were: \( \text{NO}_3-N \), \( \text{NH}_3-N \), total N, \( \text{PO}_4-P \), total P, pH, and conductivity. Prior to analysis, each variable was first standardized by subtracting the column mean and dividing by the standard deviation. After ordination of the physical habitat and water-quality parameters, we estimated Pearson correlations between the PCA axes and the abiotic variables to determine those variables that had significant correlations \((P < 0.05)\). PCA axes and variables with significant correlations across all sites were further interpreted using plots of the data as a function of distance from forest edges.
Results

Aquatic emergent insect communities

The multivariate regression tree analysis and the perMANOVA indicated that land-cover transitions lead to strong changes in aquatic emergent insect community composition. The multivariate regression tree revealed that sites commonly had breaks in the data near forest edges. All streams exhibited transitions in aquatic emergent insect community composition at ~ the upstream edge of forest patches (Table 3.1 and Fig. 3.2). Both BA and CA also had transitions near the downstream edge of the forest, with CA transitioning ~ downstream edge, and BA transitioning 139 m prior to leaving the patch. WA had the most centrally located transition which was about 260 m downstream of the edge (Table 3.1). For both BA and CA, the main effect from the perMANOVA confirmed that the model generated by the multivariate regression tree was significant ($P < 0.001$), whereas the WA perMANOVA analysis did not yield a significant effect ($P = 0.12$). Pairwise comparisons showed that all land-cover categories (i.e., upstream, forest, downstream) were different from each other at BA ($P < 0.05$), and at CA the upstream and downstream sections were different from the forest ($P < 0.05$), but not from each other ($P = 0.22$).

Although there was considerable variability in the threshold estimates, our estimates of threshold uncertainty were consistent with the regression tree and perMANOVA results. At WA, the 90% confidence intervals in both the upstream and
downstream thresholds exhibited the greatest overlap of any of the sites, suggesting weak (if any) transitions in community composition (Fig. 3.2). Alternatively, BA had the lowest overlap in threshold estimates of any of the streams. The downstream threshold estimate had a very narrow confidence interval indicating a high probability that the threshold occurred just prior to the downstream edge of the forest. The upstream threshold estimate at this stream indicated more uncertainty spanning ~ 500 m into the forest, but the bulk of the bootstrap replicates (>80%) occurred within 100 m of the upstream edge of the forest. At CA, the upstream threshold estimate had the lowest uncertainty of any of the sites spanning from near the forest edge to 180 m into the forest. The downstream estimate was much more variable at this site, and the 90% confidence interval almost spanned the entire forest patch. Nevertheless, over half of the bootstrap replicates occurred within 100 m of the downstream edge.

**Taxa-specific patterns**

The indicator taxa analysis identified a total of three forest indicator taxa, five upstream agricultural indicator taxa, and no downstream agricultural indicator taxa (Table 3.2); Tipulidae was the only family that emerged as an indicator for more than one stream system (upstream for BA and CA). Forest indicator taxa exhibited strong increases in density after entering and/or leaving forest patches (Figs 3.3 and 3.4). At CA, both of the forest indicator families (Chironomidae and Polycentropodidae) showed an abrupt increase and subsequent decrease soon after entering and leaving the forest,
respectively. The agricultural indicator families at this stream (Tipulidae and Culicidae) sharply declined both after entering and upon leaving the patch, and were not present in the forest. At BA, the only forest indicator taxa (Psychomyiidae) were only present at one agricultural site and showed a systematic increase in density with distance into the forest, declining to zero near the downstream forest edge. All of the agricultural indicator taxa exhibited a decline in density upon entering the forest at BA, and Sciomyzidae was the only agricultural indicator that was not present at any of the forest sites. Although not indicator taxa, Heptageniidae and Trichoptera showed markedly higher density in the forest than in the upstream or downstream sites (Fig. 3.5).

Environmental parameters

The analysis of nutrient concentrations resulted in most of the samples having a lower total N than the sum of NO$_3$-N and NH$_3$-N and/or a lower total P than PO$_4$-P. We are uncertain why this occurred (possibly instrument or personnel error), and assume that the errors did not affect the relative values of the nutrient concentrations at each stream. Therefore, we interpret the trends along the sampling continuum, but caution interpretation of the absolute values of nutrient concentrations.

Similar to the results from the aquatic emergent insect community and taxa-specific analyses, the environmental data showed strong changes in response to land cover. Results of the PCA analyses showed that the first two axes captured much of the variation in the data with 65% at CA and WA, and 70% at BA. When we plotted PCA
axis scores versus distance we found that almost all of the axes exhibited sharp changes occurring near the edges of forest patches (Fig. 3.6).

Correlation analyses between the original data and the PCA axes showed that a range of parameters were strongly related to either the first or second PCA axis (Table 3.3). At WA, the first PCA axis was most strongly related to a combination of physical habitat and water quality variables, whereas variation in the second axis was primarily correlated to water-quality parameters. Similar to the first axis at WA, the first axis at CA was most strongly related to a combination of physical and water quality parameters. The second axis at CA did not exhibit significant correlations with any of the abiotic variables. At BA, the significant correlations showed that the axes primarily represented water quality (axis 1) or physical habitat (axis 2).

The correlation analyses revealed seven parameters that were significantly correlated with PCA axes across all streams. Plots of total N and NO$_3$-N versus distance from the upstream forest edge generally showed strong declines after entering forests (Figs 3.7A and B), while total P and phosphate increased after entering forests (Figs 3.7C and D). At all sites, pH within the forest tended to increase upon entering forests and decrease after leaving forests (Fig 3.7E). Both solar radiation and pool width showed sharp changes upon entering and/or leaving forest patches across sites (Figs 3.7F and G).
Discussion

Based on our observations from these headwater streams there is evidence that aquatic emergent insect communities in agricultural landscapes rapidly respond to transitions in land cover. Our results suggest that aquatic emergent insect community composition shifted immediately after entering forest patches, and that a subsequent shift was found near the downstream edge of the forest (within 139 m). These shifts were associated with insect families that were predominantly found in either agricultural land or forest patches. Further, insect community shifts were coupled with environmental changes that included both physical habitat (channel width and solar radiation) and water quality (NO$_3$-N, total N, PO$_4$-P, and total P). We conclude that forests embedded in agricultural landscapes rapidly alter the stream environment, driving shifts in aquatic emergent insect communities and recovering an important aquatic-to-terrestrial linkage between streams and forests.

Aquatic emergent insect communities along land-cover transitions

Regression-tree analyses revealed that aquatic emergent insect communities underwent abrupt changes as streams entered and left forest patches. Numerous studies have shown that forested streams provide distinct habitat and support different communities of macroinvertebrates than streams flowing through non-forested land (Lenat and Crawford 1994, Quinn et al. 1997, Scarsbrook and Halliday 1999, Sweeney et al. 2004). Additionally, previous work in agricultural streams indicates that the response
of macroinvertebrates to forest cover can be rapid, recovering within the first 300 to 600 m after entering forest patches (Storey and Cowley 1997, Scarsbrook and Halliday 1999). Although our study focused on aquatic emergent insect communities, which can exhibit compositional differences from larval communities (e.g., Iwata 2007), our regression tree models were consistent with these larval studies, and showed strong breaks near the upstream forest edge (all streams) and within 139 m of the downstream forest edge [two of three streams (BA and CA)], which were confirmed by significant differences between land-cover categories at two of the three streams.

In contrast to BA and CA, the high overlap in threshold estimates (Fig. 3.2) and the lack of significant effects among land-cover categories exhibited at WA suggests relatively little compositional variation can be attributed to transitions in land cover at this stream. This was likely driven by the numerical dominance of chironomids (~99% of individuals captured) and the rarity of other taxa at this stream (6 families with ≤ 2 individuals captured). Nevertheless, the consistency in threshold changes near the upstream and downstream edges of forests suggests that forest patches elicit a general response in aquatic emergent insect communities that is largely contained within the forest boundaries. Patterns in individual insect families generally support this contention (Figs 3.3 and 3.4), and suggest that certain families are associated with areas within forest boundaries whereas others are associated with areas found outside forest boundaries (i.e., agricultural land).
Environmental drivers

Agricultural land use is known to have a variety of effects on both the water quality (e.g., Lenat and Crawford 1994, Niyogi et al. 2007) and physical habitat (e.g., Roth et al. 1996, Davies-Colley 1997, Lammert and Allan 1999) of streams. Plots of the axes derived from PCA analyses in our study showed that the stream environment strongly changed after entering and leaving forests at all study streams, suggesting that multiple environmental variables respond to changes in land cover that were consistently associated with a combination of habitat and water quality variables. pH is a commonly measured water quality variable, and low pH levels can have negative effects on invertebrate communities (e.g., Cherry et al. 2001). In our study, pH showed systematic variation in response to land cover at all sites, but almost all sites were well above circumneutral and we conclude that these relatively high values likely had minimal implications for aquatic emergent insect community composition.

Nitrogen runoff is often associated with agricultural land use, and a variety of studies have shown that elevated N concentrations in streams are linked to agricultural land use (Lenat and Crawford 1994, Storey and Cowley 1997, Jones et al. 2001, Buck et al. 2004). Riparian forests provide a buffer that prevents N from entering waterways (Lowrance et al. 1984), can enhance in-stream nutrient uptake due to deposition of organic matter (Mulholland 2004), and the wider channels typical of forested streams can enhance nutrient processing relative to non-forested streams (Sweeney et al. 2004). Consistent with these studies, we found that nitrogen (NO$_3$-N and total N) strongly
declined with distance into the forest at all of the study streams, indicating that remnant forest patches provide both a buffer and promote in-stream processing of nitrogen.

Alternatively, our results indicated that P concentrations (both total P and PO$_4$-P) increased after entering forest patches. This was surprising, because many studies have shown that riparian buffers reduce concentrations of P (Cooper and Gilliam 1987, Daniels and Gilliam 1996, Lee et al. 2000, Borin et al. 2005). The effects of a riparian buffer on water chemistry, however, can depend on a variety of factors (e.g., slope, geology, season, etc.), and retention of dissolved P has been identified as the “least general” function provided by riparian forests (Lowrance et al. 1997). Previous work has shown that herbaceous plants may be more effective at retaining phosphorous than tree buffers (Osborne and Kovacic 1993), and we found among the lowest P concentrations at BA and CA occurred upstream of the forest where the stream bank was dominated by herbaceous riparian vegetation. Another potential explanation for increases P concentrations in forests is that forest patches are acting as sources rather than sinks for P. Riparian areas can become P sources when dissolved oxygen conditions are low (Mulholland 1992), or if they become saturated with P (Omernik et al. 1981). In our study, all of the forest patches were embedded within an agricultural matrix, and may have become saturated with P over time, ultimately making them sources of P for streams.

The physical habitat variables that were most consistently associated with the PCA axes were pool width and solar radiation. Previous studies suggest that herbaceous
riparian vegetation can stabilize stream banks and trap sediment which leads to narrower channels than those found in forested reaches (Davies-Colley 1997, Scarsbrook and Halliday 1999, Sweeney et al. 2004). With the exception of the section downstream of BA and upstream at WA, we found strong changes in pool width as streams transitioned between agricultural land and forest patches (Fig. 3.7G). A possible explanation for the wider channels downstream of BA is that two out of the three pools were bordered by a narrow riparian tree buffer which may have allowed the development of naturally wider channels similar to those found in forests. Similar to shifts in pool width, we found that solar radiation exhibited sharp declines after entering and leaving forests (Fig. 3.7F). These findings are consistent with previous work indicating that forests provide greater canopy cover than open agricultural reaches (Quinn et al. 1997, Davies-Colley and Quinn 1998), and studies documenting rapid changes in solar radiation near forest edges in both aquatic (Scarsbrook and Halliday 1999) and terrestrial (Cadenasso et al. 1997) systems. Our finding that narrow riparian tree buffers lead to muted or no changes in solar radiation after entering or leaving forests (upstream at WA and the first 2 downstream sites at BA), suggests that even narrow, single tree line riparian buffers may be able to provide similar levels of shading as larger patches of forest.

*Linking aquatic emergent insects and environmental drivers*

Our observation that transitions in land cover leads to simultaneous changes in multiple environmental factors may explain the taxa-specific patterns we observed at our
study sites. Trichopterans and Ephemeropterans are composed of many taxa that are sensitive to human disturbance and are often used to assess stream quality (e.g., Kerans and Karr 1994, Wallace et al. 1996). Our results show that Ephemeropterans and Trichopterans were almost exclusively found in forests (Fig. 3.5), suggesting that forests generate conditions that provide refugia for these taxa in landscapes where they are otherwise unable to persist. Among all of the study sites, the forested sites at CA had perhaps the most distinct conditions. The stream flowing through the forest at CA had the highest solar radiation of all our forested study sites, the widest channels, and the highest phosphorous concentrations of any of the streams. This combination of factors likely led to greater in-stream primary productivity which may explain the presence and high density of the scraper, Heptageniidae, in the forest at this stream when it was absent at other streams (Fig. 3.5). Additionally, the combination of high autochthonous productivity and allochthonous inputs form the surrounding forest may have generated appreciable amounts of FPOM, which could potentially explain the high numbers of collectors (Polycentropodidae and Chironomidae) in this forest patch. Surprisingly, our results show that the shredder Tipulidae was an indicator of agricultural sites at both BA and CA. Though these sites had little to no tree cover, there was a considerable amount of terrestrial grass growing on the bank and in the stream. Previous work by Menninger and Palmer (2007) demonstrated that terrestrial grasses can be an abundant resource in agricultural streams, and can support diverse shredder assemblages that may explain our observation of relatively high Tipulid abundance at agricultural sites. An alternative
explanation could be that transport and deposition of allochthonous detritus from upstream sources may have provided resources for Tipulids. This is possible at BA because there was a small patch of forest just upstream of the upstream agricultural sites. At many of the agricultural sites there were relatively high levels of fine sediment, solar radiation, and N which may explain why the moderate to highly tolerant families Sciomyzidae, Psychodidae, and Culicidae (Barbour et al. 1999) were most abundant in agricultural sites.

A downstream shadow?

It has been hypothesized that forest patches can generate a “downstream shadow” whereby the effects of forests on streams extend downstream of forest boundaries (Harding et al. 2006). Physical habitat parameters such as solar radiation and pool width did not exhibit evidence of a downstream shadow. Because these parameters are driven by the physical effects of the trees (e.g., canopy cover and root structure), once riparian trees are absent these physical characteristics should rapidly change. Alternatively, nutrient dynamics in flowing waters can operate over large spatial scales and concentrations at a given spatial location reflect the accumulation of local as well as catchment scale processes. Our finding of relatively low N concentrations downstream of forests suggests that forest effects can indeed extend downstream of forest patch boundaries. We suggest that once streams leave forests there is less efficient in-stream N processing resulting in less change per unit distance (indicated by an asymptote
downstream of forests, Figs 3.7A and B), and we expect that N concentrations increase further downstream of forest patches.

_Aquatic-terrestrial linkages and restoration_

Even though there has been increased recognition that streams and riparian forests should be viewed as an integrated system (Sullivan et al. 2007, Fausch et al. 2010), most studies largely focus on in-stream measures to quantify the effects of land cover on streams (e.g., those studies reviewed in Allan 2004). Studies of stream recovery following land-cover effects demonstrate that strong changes in in-stream processes can occur rapidly after streams enter forest patches (Storey and Cowley 1997, Scarsbrook and Halliday 1999, Suga and Tanaka 2013, Goss et al. 2013). Consistent with and expanding on this work, we observed that rapid in-stream changes that occur after streams enter and leave forest patches are translated to terrestrial ecosystems via the emergence of adult aquatic insects. The qualitative differences in aquatic emergent insect communities among agricultural and forest patches may have important implications for the assimilation emergent insects into terrestrial food webs. For example, Davis et al. (2011) found that nutrient enrichment decoupled streams and terrestrial food webs because of an increased dominance of Trichopterans which had traits (body size and wing hairs) that conferred predation resistance (e.g., large body size). In light of this study, our observation that Trichopterans and Heptageniids (also known to be large-bodied) were almost exclusively found in forest patches may have important implications for the
coupling of stream-riparian food webs in agricultural and forest patches. In order to more clearly determine the functional significance of land-cover transitions for stream-riparian food webs, further research is needed relative to the differences in the magnitude of aquatic emergent insect biomass fluxes and the response of riparian food webs to these fluxes (e.g., Baxter et al. 2004, Iwata 2007, Davis et al. 2011). As conservation and restoration efforts take a more integrated view of stream-riparian systems, studies of the recovery of aquatic-terrestrial linkages will be able to provide valuable information to those ends.

Conclusion

Our study demonstrates that forest patches in agricultural landscapes influence strongly aquatic emergent insect communities and abiotic conditions in streams. Rapid changes in aquatic insect community structure occurred near upstream and downstream forest edges and were linked to land-cover driven changes in physical habitat and water chemistry. The effects of forests on physical habitat and aquatic emergent insects were largely contained within forest boundaries, but the effects of forests on nutrient dynamics extended downstream of forest boundaries. While our results are derived from one season in a limited geographical area, they are consistent with and expand upon previous studies to include inferences about aquatic-terrestrial linkages and downstream effects. Overall, our work shows that remnant forest patches can restore key aquatic-terrestrial
connectivity and adds to a growing body of evidence that suggests that even relatively small forested areas can improve stream function in human-dominated landscapes.
Acknowledgements

This work was supported by The Ohio State University Climate, Water, and Carbon Targeted Investment in Excellence (CWC-TIE) Program and the National Science Foundation STEM Graduate Fellows in K-12 (NSF GK-12) Education Program, Grant No. 0638669. Thanks to N. Rosenbaum and E. Gorrell for assistance with field work and aquatic insect processing, and to L. Rieck for demonstrating how to set up emergent insect traps. We would also like to thank private land owners for their participation in this study. Without their cooperation this work would not have been possible.
References


Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141-156.


Table 3.1. Estimates of threshold changes in community composition based on a multivariate regression tree analysis. Numbers correspond to location of the threshold relative to the upstream or downstream edge (negative numbers correspond to upstream of forest edge).

<table>
<thead>
<tr>
<th>Stream</th>
<th>Upstream Threshold (m)</th>
<th>Downstream Threshold (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BA</td>
<td>-12.5</td>
<td>-139</td>
</tr>
<tr>
<td>CA</td>
<td>-23</td>
<td>3.5</td>
</tr>
<tr>
<td>WA</td>
<td>-14</td>
<td>-379.5</td>
</tr>
</tbody>
</table>
Table 3.2. Results from an indicator species analysis on the groups derived from the multivariate regression tree analysis. Land cover corresponds to the group (upstream, forest, or downstream) that had the highest indicator value for that family.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Stream</th>
<th>Land Cover</th>
<th>Indval</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Psychomyiidae</td>
<td>BA</td>
<td>Forest</td>
<td>61.4</td>
<td>0.024</td>
</tr>
<tr>
<td>Psychodidae</td>
<td>BA</td>
<td>Upstream</td>
<td>63.9</td>
<td>0.020</td>
</tr>
<tr>
<td>Sciomyzidae</td>
<td>BA</td>
<td>Upstream</td>
<td>50.0</td>
<td>0.033</td>
</tr>
<tr>
<td>Tipulidae</td>
<td>BA</td>
<td>Upstream</td>
<td>75.9</td>
<td>0.003</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>CA</td>
<td>Forest</td>
<td>71.8</td>
<td>0.009</td>
</tr>
<tr>
<td>Polycntrpodidae</td>
<td>CA</td>
<td>Forest</td>
<td>60.0</td>
<td>0.046</td>
</tr>
<tr>
<td>Culicidae</td>
<td>CA</td>
<td>Upstream</td>
<td>70.9</td>
<td>0.020</td>
</tr>
<tr>
<td>Tipulidae</td>
<td>CA</td>
<td>Upstream</td>
<td>81.8</td>
<td>0.009</td>
</tr>
</tbody>
</table>
Table 3.3. Pearson correlation coefficient estimates for the first two PCA axes and the abiotic variables at each stream. Grey shading corresponds to variables that were significantly ($P < 0.05$) correlated with either of the PCA axes.

<table>
<thead>
<tr>
<th>Site</th>
<th>PCA Axis</th>
<th>Pool Length</th>
<th>Pool Width</th>
<th>Pool Depth</th>
<th>Fine</th>
<th>Coarse</th>
<th>Bed</th>
<th>PO$_4$-P</th>
<th>NO$_3$-N</th>
<th>NH$_3$-N</th>
<th>Total N</th>
<th>Total P</th>
<th>Conductivity</th>
<th>pH</th>
<th>PAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>BA</td>
<td>PC1</td>
<td>-0.209</td>
<td>-0.832</td>
<td>0.558</td>
<td>-0.121</td>
<td>0.003</td>
<td>0.491</td>
<td>-0.933</td>
<td>0.927</td>
<td>-0.732</td>
<td>0.902</td>
<td>-0.922</td>
<td>-0.666</td>
<td>0.387</td>
<td>0.096</td>
</tr>
<tr>
<td></td>
<td>PC2</td>
<td>0.891</td>
<td>0.328</td>
<td>-0.210</td>
<td>-0.834</td>
<td>0.832</td>
<td>0.092</td>
<td>0.025</td>
<td>0.103</td>
<td>-0.149</td>
<td>-0.220</td>
<td>0.126</td>
<td>-0.476</td>
<td>0.834</td>
<td>-0.816</td>
</tr>
<tr>
<td>CA</td>
<td>PC1</td>
<td>-0.517</td>
<td>-0.763</td>
<td>-0.486</td>
<td>0.520</td>
<td>-0.318</td>
<td>-0.863</td>
<td>0.760</td>
<td>-0.947</td>
<td>-0.309</td>
<td>-0.929</td>
<td>0.756</td>
<td>-0.648</td>
<td>-0.679</td>
<td>0.669</td>
</tr>
<tr>
<td></td>
<td>PC2</td>
<td>0.442</td>
<td>0.584</td>
<td>-0.547</td>
<td>-0.304</td>
<td>0.200</td>
<td>-0.147</td>
<td>0.517</td>
<td>-0.076</td>
<td>-0.125</td>
<td>0.180</td>
<td>0.543</td>
<td>-0.653</td>
<td>0.374</td>
<td>-0.616</td>
</tr>
<tr>
<td>WA</td>
<td>PC1</td>
<td>0.629</td>
<td>0.631</td>
<td>-0.685</td>
<td>-0.804</td>
<td>0.646</td>
<td>0.463</td>
<td>0.128</td>
<td>0.927</td>
<td>0.261</td>
<td>0.096</td>
<td>-0.969</td>
<td>0.470</td>
<td>-0.336</td>
<td>-0.717</td>
</tr>
<tr>
<td></td>
<td>PC2</td>
<td>0.170</td>
<td>0.761</td>
<td>0.101</td>
<td>0.230</td>
<td>-0.098</td>
<td>-0.057</td>
<td>-0.728</td>
<td>0.027</td>
<td>-0.789</td>
<td>0.684</td>
<td>0.136</td>
<td>0.854</td>
<td>0.860</td>
<td>0.020</td>
</tr>
</tbody>
</table>
Figure 3.1. Diagrams of forest patch area for each site in the study: BA (Left), CA (Middle), WA (Right). The grey area corresponds to forest patches, and the white area surrounding patch is primarily cropland. Numbers correspond to distances (m) from the upstream edge of a forest (negative numbers correspond to sites upstream of the edge).
Figure 3.2. 90% confidence interval estimates illustrating threshold uncertainty at our study sites. Upstream (black circles) and downstream (grey circles) were estimated using a multivariate regression tree analysis and percentile confidence intervals (horizontal lines) were estimated using a bootstrap procedure. The long black vertical line corresponds to the upstream edge (0 m) and the small black vertical lines correspond to the downstream edges for each of the forests in the study.
Figure 3.3. Plots of the overall aquatic insect density for each site at CA. The primary y-axis corresponds to Chironomidae density, the secondary y-axis corresponds to the remaining families, and the black vertical lines correspond to the upstream and downstream edges.
Figure 3.4. Plots of the overall aquatic insect density for each site at BA. The secondary y-axis corresponds to Sciomyzidae density, the primary y-axis corresponds to the remaining families, and the black vertical lines correspond to the upstream and downstream edges.
Figure 3.5. Bar graphs of Trichopterans and Heptageniids summed across all sites for each land use category.
Figure 3.6. PCA axes for each of the study streams plotted vs distance from the upstream edge. The black vertical lines correspond to the upstream and downstream edge.
**Figure 3.7.** Plots of abiotic variables vs distance from the upstream edge. The long black vertical lines correspond to the upstream edge and the short black vertical lines correspond to the downstream edges of the forest patches.
Figure 3.7 continued

- **E**: pH plot showing data points for BA, CA, and WA.
- **F**: PAR (PAR) plot showing data points for BA, CA, and WA.
- **G**: Channel Width (m) plot showing data points for BA, CA, and WA.

**Distance from upstream edge (m)**
Chapter 4: Spatial configuration of land cover drives aquatic-terrestrial fluxes in agricultural landscapes

Abstract

Stream and riparian systems are increasingly viewed as interdependent systems linked by reciprocal exchanges of materials, organic matter, and organisms. Aquatic-to-terrestrial fluxes of aquatic emergent insects are integral to the functioning of linked stream-riparian ecosystems, and human activities on the landscape that alter this flux may have profound ecological consequences. In the present study, we investigated aquatic-to-terrestrial fluxes of aquatic emergent insects in response to variation in spatial patterns of adjacent land cover. We surveyed aquatic emergent insects at 28 sites along transects at three streams that flowed through forest patches embedded in agricultural landscapes (i.e., agriculture-forest-agriculture). Our results suggest that aquatic emergent insects were tightly linked to spatial patterns in land cover and exhibited particularly strong variation as a function of distance from the center of forest patches. At two of our study streams, total emergence was highest near the center and systematically declined closer to forest edges; patterns in mean insect body size were more variable but similarly showed strong variation with distance from the forest center. We also found initial evidence that
the configuration of agricultural patches may influence downstream emergence, such that emergence biomass in the agricultural matrix downstream of a forest patch was more similar to emergence biomass in the forest than to the upstream agricultural matrix. Shifts in aquatic emergent insect fluxes were also related to variation in physical habitat, water quality, and energy sources suggesting that spatial configuration of land cover drives environmental variation which in turn drives emergence dynamics. Overall, results from our study demonstrate that aquatic-to-terrestrial fluxes of aquatic emergent insects are strongly related to spatial patterns in land cover and represent a valuable step towards linking emergence dynamics to stressors in human-modified landscapes.
Introduction

Streams are dynamic, open systems that are functionally linked to terrestrial systems through reciprocal aquatic-terrestrial exchanges of energy, organisms, and materials. The importance of terrestrial-to-stream linkages has long been known (Fisher and Likens 1973, Hynes 1975), and has been fundamental to central paradigms of stream ecology (e.g., River Continuum Concept, Vannote et al. 1980, Flood Pulse Concept, Junk et al. 1989, Riverine Ecosystem Synthesis, Thorp et al. 2006). Subsidies from terrestrial to aquatic systems can be particularly important in forested headwater streams where fluxes of leaf litter can fuel stream ecosystems (Fisher and Likens 1973) and inputs of terrestrial arthropods can drive in-stream fish and invertebrate community structure (Nakano et al. 1999). In addition to being recipients of terrestrial subsidies, stream systems can also subsidize terrestrial systems via fluxes of aquatic emergent insects. Aquatic emergent insects often comprise a substantial portion of terrestrial consumer diets (Henschel et al. 2001, Iwata et al. 2003, Iwata 2007), and variation in emergent fluxes can drive numerical responses in both terrestrial (Sabo and Power 2002a, Baxter et al. 2004) and aerial insectivores (Iwata et al. 2003, Fukui et al. 2006). These strong reciprocal exchanges contribute to the notion that stream and riparian systems function as a single integrated ecological unit (Sullivan et al. 2007, Fausch et al. 2010).

Consequently, alterations to the stream are likely to influence the riparian area, and vice versa. Anthropogenic disturbances have a variety of effects on stream ecosystems through impacts on the physicochemical habitat and the energy sources
supporting stream food webs (Paul and Meyer 2001, Allan 2004). These in-stream effects have been shown to strongly influence fluxes of aquatic emergent insects into terrestrial systems. For example, in streams of northern Japan, Laeser et al. (2005) found that stream channelization and deforestation led to strong decreases in riparian spider abundance due to a reduction of larval aquatic insect abundance and subsequently reduced fluxes of adult aquatic insects into terrestrial systems. Similarly, Davis et al. (2010, 2011) found that applying a nutrient enrichment treatment to streams stimulated in-stream secondary production and resulted in greater aquatic emergent insect biomass. Surprisingly, the larger biomass flux reduced the dependence of terrestrial food webs on aquatic subsidies, and the authors suggest that this was driven by shifts in the quality (size structure and community composition) of the subsidy. These results suggest the effects of anthropogenic stressors on in-stream habitat and energy sources drives emergence dynamics, and can influence both the quantity and the quality of aquatic-terrestrial subsidies. Therefore, predicting emergence dynamics in human-modified landscapes may be particularly challenging because land-use often causes simultaneous changes in multiple stressors which can lead to synergistic or antagonistic effects (Folt et al. 1999) on stream-riparian ecosystems.

In human-modified landscapes, land use and land cover (hereafter land cover) are linked to anthropogenic stressors, and measures of the spatial scale, composition, and configuration of land cover are often useful for predicting ecological responses to stressors. At the catchment scale, Roth et al. (1996) found that habitat and fish
communities exhibited strong variation as a function of the land cover composition of the catchment upstream of sampling reaches (e.g., % forest and % agricultural land). Similarly, in streams of western Washington, Morely and Karr (2002) found strong associations between the percent catchment in urban land use (which was inversely related to forest cover) and benthic macroinvertebrate communities. At smaller spatial scales, studies in New Zealand (Storey and Cowley 1997, Scarsbrook and Halliday 1999) and Ohio (Goss et al. 2013a) revealed that forest patches located immediately downstream of agricultural patches undergo rapid changes in physicochemical habitat (and energy sources, Scarsbrook and Halliday 1999) as a function of distance into forests. In turn, these effects translated into shifts in biomass (Scarsbrook and Halliday 1999) and composition (Storey and Cowley 1997, Scarsbrook and Halliday 1999) of in-stream aquatic invertebrate communities. Similarly, it has been hypothesized that the effects of forests on streams can be transported into downstream agricultural patches (Harding et al. 2006). Based on studies linking larval with adult stages of aquatic insects (Baxter et al. 2004, Iwata 2007, Davis et al. 2011) we would expect that these in-stream effects would propagate to terrestrial systems via emergence. The implications of land cover configuration for aquatic emergence into terrestrial systems, however, remain largely unresolved (but see Houghton et al. 2011).

Studies of forest patches in agricultural landscapes also suggest that physicochemical habitat and energy sources may change at asynchronous spatial scales. For example, Goss et al. (2013a) found evidence for strong shifts in stream temperature
within the first 200 m of entering a forest; however, sediment size at one stream systematically changed until ~ 800 m into the forest. Similarly, Scarsbrook and Halliday (1999) found that shade, channel width and Chlorophyll a changed rapidly upon entering forests, but concluded that there was no evidence of appreciable nitrogen processing occurring within the first 300 m into forests. By coupling these asynchronous shifts in environmental variables with ecological responses, it may be possible to better determine the role of specific mechanisms regulating fluxes of aquatic emergent insects in human-modified landscapes. This information may be particularly pertinent for management of aquatic-terrestrial systems because multiple stressors are linked to emergence processes (Fausch et al. 2010), and identifying the stressors most important for regulating aquatic insect emergence will facilitate conservation and restoration efforts.

In the present study, we explored the implications of spatial patterns in land cover for aquatic-to-terrestrial linkages in agricultural landscapes. Our objectives were to quantify the effects of land-cover composition and spatial configuration on aquatic emergent insect flux properties including total emergence biomass and mean individual body size, and to assess whether variation in emergence properties were related to land-cover-driven variation in physicochemical habitat and/or the energy sources supporting aquatic insect food webs. To this end we surveyed aquatic emergent insects and estimated physicochemical habitat parameters along agriculture-forest-agriculture transitions in agricultural landscapes of central Ohio, USA (Fig. 3.1). We used naturally abundant stable isotopes (\(^{15}\)N and \(^{13}\)C) to link aquatic emergent insects to terrestrial
(detritus) and aquatic (periphyton) basal energy sources. Carbon and nitrogen isotope ratios can be used as indicators of environmental change (Kendall et al. 2010), and we used $\delta^{15}N$ and $\delta^{13}C$ to determine whether environmental variation reflected in basal energy sources was related to influence emergence dynamics. We also used the C:N ratio of aquatic and terrestrial energy sources to predict emergence, as this ratio can be indicative of resource quality and has been linked to functional processes in stream systems (e.g., Hladyz et al. 2009).

**Methods**

*Site description*

In this study we used 28 sampling locations distributed among three streams draining agricultural landscapes in the Low Lime Drift Plain ecoregion in central Ohio (Omernik and Griffith 2013). Stream names were derived from township names and are: BA (Baughman Township), CA (Canaan Township), and WA (Wayne Township). We studied small headwater systems flowing through abrupt transitions in land cover, with catchment areas of 1.27 km$^2$ (BA), 1.24 km$^2$ (CA), and 1.22 km$^2$ (WA) (estimated at the most downstream site of each study stream). We sampled scour pools (Bisson et al. 2006) located upstream, within, and downstream of forest patches (Fig. 3.1) because there is evidence that insect emergence from pools can be substantially higher than riffles (Iwata 2007), and pools are less prone to drying out than riffles. The study sites surrounding forest patches primarily drained cropland and were adjacent to mixtures of
herbaceous plants and shrubs, or single lines of riparian trees on the banks of the stream (upstream at WA and downstream at BA). Forest patches were composed of mature, secondary growth forest with areas of ~ 19, 31, and 11 ha for BA, CA, and WA, respectively.

Aquatic emergent insect sampling and environmental measurements

Our primary aim in this study was to estimate emergence properties from streams along transitions between agricultural land and forest. In the following, we briefly summarize the methods used to collect aquatic emergent insects and estimate environmental parameters. Additional details can be found in Goss et al. (2013b).

We sampled insects using ~ 1-m$^2$ aquatic emergent insect traps in pools along transects beginning upstream of forest patches, proceeding through these forests, and continuing downstream of the forest patches (Fig. 3.1). All samples were collected during Ohio’s dry season (July-August) to minimize seasonal effects. Samples were preserved in 70% ethanol and non-parasitoid aquatic insects were identified to family under a dissecting microscope using Merritt et al. (2008) and Triplehorn and Johnson (2005). Muscidae was not included in our analyses because the characteristics that differentiate aquatic and terrestrial families were ambiguous on our specimens. All samples were dried for ≥ 2 days at ~ 60°C and were subsequently weighed (mg). We also measured various environmental characteristics at each of the pools, including pool
dimensions (length, width, depth), benthic sediment composition, water chemistry (NO$_3$-N, NH$_3$-N, total N, PO$_4$-P, total P, pH, and conductivity), and canopy cover.

**Stable isotope analysis**

In order to examine variation in primary sources of energy supporting aquatic insect food webs, we analyzed the stable isotope composition of basal resources (periphyton and terrestrial leaves). Within each pool (or in a nearby pool in cases of insufficient algal mass) we scraped green/brown epilithon or epipelon off of 4-5 rocks with toothbrushes or off the surface of sediment with a razor, respectively. All periphyton samples were preserved in ~70% ethanol. Macroinvertebrates and larger plant detritus and inorganic particles were then removed from periphyton samples, which were subsequently sieved through a 1 mm sieve to separate out any remaining detrital and inorganic particles. Allochthonous resources at our study sites were primarily composed of deciduous tree leaves and/or terrestrial grasses growing along the banks and in the stream. We collected samples of submersed tree leaves and submersed grasses (mixture of live and dead based on availability) throughout each pool and preserved these samples in 70% ethanol. To estimate the stable isotope composition, basal resources were dried at ~60°C for ≥ 2 days and ground to a fine powder using a ball mill or a mortar and pestle, weighed, and placed in tin capsules. Samples were analyzed for δ$^{13}$C, δ$^{15}$N, and percent C and N at the Washington State Stable Isotope Core Laboratory in Pullman, WA. Isotopic values were estimated using a continuous flow isotope mass spectrometer and
were expressed (relative to international standards) in per mil (‰) as follows: \( \delta^{13}C \) or \( \delta^{15}N = \frac{[R_{\text{sample}} - R_{\text{standard}}]}{R_{\text{standard}}} \times 1000 \) where \( R = \frac{^{13}C}{^{12}C} \) or \( \frac{^{15}N}{^{14}N} \).

**Statistical Analysis**

Relationships between aquatic insect communities along land cover transitions are often idiosyncratic (Storey and Cowley 1997, Scarsbrook and Halliday 1999, Goss et al. 2013a). Therefore, we analyzed streams separately to explore the spatial variation in emergence and to determine whether the patterns are related to physicochemical habitat and/or variation in energy sources. We identified patterns in the data based on plots of the data as well as preliminary analysis, and the present analysis is a reduced model set based on this iterative process. The response variables for our analyses were daily rate of emergent insect flux (mg DM m\(^{-2}\) day\(^{-1}\)) and the mean body size of insects at a given site (total mg DM at a site ÷ the total no. of individuals collected). To describe variation in the response variables, we used three sets of models that included spatial, physicochemical, or energy source variables. For the spatial models, we used general linear models (GLM) that included continuous variables, categorical variables, or both. The continuous variable models included: (1) distance from the forest center (DFC) to test whether there was systematic variation (linear or quadratic) in emergence properties as a function of distance from the center and towards forest edges and agricultural patches; (2) and downstream distance (DWS), which tests whether there is a systematic change in biomass as a function of the distance downstream of the uppermost site. A
simple linear relationship is indicative of change regardless of land-cover transitions, but a second order model may indicate an effect of land cover on emergence properties. The categorical models included: (1) land cover (LC), which tests whether there was a shift in the emergence properties according to land cover (agriculture vs forest). We also tested whether agricultural land cover (1) leads to a shift in the mean in the response variable controlling for the distance from the center of the forest (DFC + LC), and whether land use predicted a shift in the DFC slope (DFC + LC + DFC x LC); (2) spatial position (PO) tests whether emergence properties differed among downstream, forest, and upstream patches. If a significant main effect of PO was detected then we used Tukey’s post-hoc tests to test for differences among means.

To test for linkages between emergence properties and potential environmental drivers we used physical habitat and water quality variables (see Goss et al. 2013b for more details on these parameters). We used PCA to distill the variation in these variables into synthetic axes for each stream. We kept only those axes that accounted for greater than ~20% of the variation at each stream (2 axes/site for both physical habitat and water quality). These axes were used as predictor variables in separate simple linear regressions to assess the relationship between emergence properties and physicochemical variation.

The third and final model set that we used was to assess whether emergence properties were linked to variation in basal energy sources. We used $\delta^{13}$C and $\delta^{15}$N of terrestrial leaves and periphyton in separate simple linear regressions to predict whether
emergence or body size were linked to isotopic variation in energy sources. We also used simple linear regressions to test whether resource quality as indicated by the C:N of leaves and periphyton were linearly related to emergence.

For all analyses, we use the $F$-statistic to generate a set of candidate models (Gotelli and Ellison 2004). We restrict our interpretation to models with overall $F$-statistic values that correspond to $P$-values less than 0.10, and that explained more than 30% of the variation in the data ($R^2 > 0.30$). Additionally, models with greater complexity but that did not significantly ($P \leq 0.05$) improve upon simpler models (e.g., non-significant second order interaction) were not considered.

**Results**

*Emergence flux properties*

Emergence flux properties showed strong variation among streams, sites, and families. Our results revealed that CA had the greatest overall transfer of aquatic emergent insect biomass to terrestrial systems (total = 316 mg DM), followed by WA (total = 261 mg DM), and finally BA had the lowest (total = 137 mg DM). Family specific patterns in aquatic insect emergence showed strong differences in the biomass composition of emergence fluxes (Fig. 4.1 A-C). Although there was some variation in the family-specific contribution to total emergence at WA, Chironomidae was dominant throughout most of the sampling continuum. Patterns at CA showed more variability, with Culicidae, Tipulidae, and Dolichopodidae in agricultural patches giving way to
dominance by Heptageniidae, Trichoptera, and Chironomidae in the forest. At BA, Sciomyzidae, Dolichopodidae, and Chironomidae were more indicative of agricultural areas (and forest edges) while Trichoptera was almost exclusively found within the forest patch. Tipulidae also comprised a substantial proportion of emergence biomass (mean of ~ 20%) at BA, but there were not clear differences in emergence between agriculture and forest (Fig. 4.1 A). Overall, Calopterygidae represented the largest mean body size across the study sites (only one individual was captured). Heptageniidae and Trichoptera also had relatively large body sizes ranking fourth and sixth overall, respectively. The rest of the taxa were dipterans which encompassed almost the entire spectrum ranging from the second highest body size estimate (Stratiomyiidae) to the smallest (Empididae) (Fig. 4.1D).

**Spatial models**

Spatial models suggested strong spatial variation in emergence and mean body size at the study streams. Across all sites, the strongest predictor of biomass and body size was the distance from the forest center (DFC). The models that best described emergence biomass at CA and BA showed a strong negative linear relationship between DFC and emergence biomass with higher biomass in the forest center giving way to lower estimates near the forest edges (Table 4.1; Fig. 4.2A and B). At BA, the systematic linear decline in biomass as a function of DFC was interrupted by an abrupt increase in the mean upon entering agricultural patches (Table 4.1; Fig. 4.2A). The significant PO
effect at BA revealed an influence of spatial configuration on agricultural patches whereby sites upstream of the forest had greater emergence biomass than the forest, but biomass at the downstream site was not different from forest (Table 4.1). We also found a weak (0.09) negative relationship between mean body size and DFC at BA (Fig. 4.2C), and a significant positive relationship between body size and DFC at WA (Table 4.1). The relationship between body size and DFC at WA was greatly strengthened ($P = 0.007$, $R^2 = 0.73$) when an exceptionally low emergence estimate in the downstream agricultural area was removed (Fig. 4.2D). A marginal LC effect ($P = 0.07$) at WA was suggestive of lower mean body size in the forest compared to agricultural patches.

*Physicochemical models*

We found evidence for linear relationships between emergence biomass and both water quality and physical habitat. At WA, the model was suggestive of a weak ($P = 0.08$) relationship between water quality and the first PCA axis (Table 4.2); however, further examination of these data revealed that this relationship is strongly driven by a single influential data point, and we did not further consider this model. At CA there was a significant negative relationship between the water quality axis (PCA 2) and total emergence (Table 4.2; Fig. 4.3A). Eigenvectors from the PCA axis indicated that larger total emergence biomass was associated with higher levels of NH$_3$-N, PO$_4$-P, Total P, and pH (Table 4.3). At BA, there was a weak ($P = 0.096$) negative relationship between the first PCA axis and biomass (Table 4.2; Fig.4.3B). Examination of the eigenvectors
associated with this axis showed that higher total emergence associated with smaller pools (length and width), more fine and less coarse sediment, and higher solar radiation.

_Energy source linkages_

Our energy source models revealed linkages between emergence properties and both the isotopic composition and the quality of energy sources. At WA, the positive \((P = 0.07)\) relationship between terrestrial N sources (leaf \(\delta^{15}\)N) and mean body size was similar to that observed for the DFC model (Table 4.4). Similarly, there was a strong positive relationship between terrestrial nitrogen sources and total biomass at BA (Table 4.4). Although aquatic N sources (periphyton \(\delta^{15}\)N) were marginal direct predictors of emergence biomass and body size \((P = 0.097 \text{ at BA}; P = 0.11 \text{ at WA})\), both aquatic and terrestrial N sources show strong changes as a function of distance from the center of the forest (Fig. 4.4) which is consistent with variation in total biomass and mean body size at BA and WA, respectively. At CA, biomass was also linked to both aquatic [periphyton \(\delta^{13}\)C \((P = 0.05)\)] and terrestrial [leaf \(\delta^{13}\)C \((P = 0.07)\)] carbon sources (Table 4.4). Aquatic and terrestrial resource quality (C:N) at CA [aquatic \((P = 0.06)\) and terrestrial \((P = 0.04)\)] and BA [aquatic \((P = 0.04)\)] showed that larger mean body size (BA) and emergence biomass (CA) were associated with poorer resource quality (higher C:N). Alternatively, at WA the regression results were suggestive \((P = 0.09)\) of a negative relationship between aquatic resource quality and body size (Table 4.4).
Discussion

The recent application of the tenets of landscape ecology to fluvial systems has contributed to a more comprehensive understanding of the influence of landscape patterns on stream processes (Wiens 2002, Poole 2002, Thorp et al. 2006, Poole 2010). In the present study, we integrate these conceptual developments (esp. Poole 2002) with recent work emphasizing the importance of aquatic invertebrate subsidies to terrestrial food webs (Baxter et al. 2005) to explore how aquatic-to-terrestrial fluxes are influenced by spatial patterns in land cover. Our results suggest that aquatic emergent insects were tightly linked to spatial patterns in land cover, exhibiting strong variation as a function of distance from the center of forest patches. Patterns at two out of our three study streams indicated that within forests the emergence biomass was highest near the center and systematically declined closer to forest edges. Patterns in mean body size were more variable but similarly showed strong variation with distance from the center of forests. Emergence properties were also linked to environmental variables, suggesting that the influence of land cover on aquatic insect emergence is likely mediated by local environmental determinants.

Linking emergence to spatial patterns in land cover

We observed that aquatic insect emergence was strongly regulated by the composition and juxtaposition of agricultural and forest patches. Previous studies suggest aquatic emergent insects are influenced by a variety of stressors than can increase
or decrease (Baxter et al. 2004, Laeser et al. 2005, Meyer and Sullivan 2013) aquatic-to-terrestrial emergence properties depending on the nature of the stressor. These variable effects may make it difficult to predict emergence dynamics in human-modified landscapes where heterogeneity in land cover results in the simultaneous effects of multiple stressors on stream-riparian systems. Our results suggest that in agricultural landscapes, aquatic insect emergence is strongly linked to spatial patterns in land cover. In two of three study systems, we found that the strongest predictor of emergence biomass was the distance from the center of forest patches, where the highest emergence occurred near the center of forest patches and systematically decreased towards the forest edges.

Based on previous work documenting the responses of terrestrial food webs to aquatic insect emergence (Henschel et al. 2001, Iwata et al. 2003, Fukui et al. 2006), our results suggest that stream-riparian food webs may be most tightly coupled near the center of forests, becoming increasingly decoupled closer to forest edges. This observation is likely the result of an ecological boundary (Cadenasso et al. 2003) created by the spatial juxtaposition of patches with dissimilar conditions (i.e., agriculture and forest). At one stream (BA), the decline in emergence biomass near the forest edge was followed by an abrupt increase upon entering agricultural patches. These results suggest that local conditions in agricultural patches stimulate emergence, but that within forest patches there are environmental gradients that result in systematic increases towards the center of forest patches. We also found evidence that the spatial position of agricultural
patches influenced total emergence at BA. It has been hypothesized that the effects of forest patches on streams can be transported into downstream agricultural patches (Harding et al. 2006). Our data are consistent with this hypothesis at one stream (BA); however, the first two sites in the downstream agricultural patch were bordered by a narrow strip of riparian trees on the banks which may have buffered the effect of agricultural land use on emergence biomass. Therefore, although our data are suggestive of a downstream effect of the forest, further work is necessary to more conclusively establish this link.

Our results also reveal that emergence traits may interact with quantity to influence terrestrial food web responses. The primary focus of emergent insect studies is often on the magnitude of aquatic emergent insect fluxes from streams to riparian consumers (Sabo and Power 2002b, Iwata et al. 2003, Iwata 2007, Benjamin et al. 2011). Taxa-specific traits of aquatic insects emerging from streams, however, can dramatically influence the quality of these subsidies to terrestrial consumers. For example, a stream enrichment study by Davis et al. (2011) revealed that emergence at an enriched site was dominated by large-bodied insects that were less vulnerable to predation by terrestrial consumers leading to a decoupling of stream-riparian systems. Consistent with these results, we found that at CA the sites with the highest total emergence were dominated by relatively large-bodied aquatic insects (Heptageniidae which was 4th overall with a mean body size of 2.2 mg DM). Alternatively, emergence biomass and mean body size at BA were somewhat decoupled, with higher biomass in the agricultural patches and mean
body size generally higher in the forest. At WA, there were not clear patterns in emergence biomass, but there was a strong increase in mean body size as a function of distance from the forest center (Fig 4.2D). This result suggests that the dominance of Chironomidae near the center of the forest at this stream (accounting for ≥ 88 % of the biomass at the three most central sites, Fig. 4.1C) drove these patterns in small body size, which shifted as larger-bodied families entered the invertebrate community near the edges and in the agricultural patches.

Our results also indicate that the taxonomic composition of biomass fluxes is strongly influenced by land cover, which may influence the incorporation of emergence into terrestrial food webs. Davis et al. (2011) found that terrestrial consumers were more decoupled from streams where caddisflies were a dominant component of emergence. They suggested that, similar to the wing scales that confer predation resistance to Lepidopterans, the hairy wings of the closely related caddisflies may function as a deterrent to predation. This inference is supported by previous findings showing that caddisflies can contribute very little to riparian arthropod diets (Williams et al. 1995, Henschel et al. 2001). In light of these studies, the relatively high contribution of caddisflies to total emergence biomass may weaken aquatic-terrestrial linkages in forests. Caddisflies were also among the larger insects that we captured (6th overall with a mean body size of 1 mg DM), which may have further conferred predator resistance to these taxa. Similarly, mayflies are relatively large insects that can be resistant to predation (Paetzold and Tockner 2005) and our results showed that they had among the highest
estimates of mean body size and were almost exclusively found in forested sites at CA. We also found that Chironomidae comprised the greatest proportion of the biomass flux within forests at all of our study streams, and previous work suggests that they can be the most important subsidy in the diet of riparian spiders (Williams et al. 1995, Henschel et al. 2001). Overall, our results suggest that while land cover strongly drives patterns in emergence biomass, the importance of these subsidies for terrestrial food webs may be largely determined by the qualitative characteristics of emergence.

**Linking emergence to physical habitat and water quality**

Our analyses revealed that variation in emergence biomass was linked to physical habitat and water quality. The relationship between biomass and the physical PCA axis at BA was suggestive that the conditions typical of agricultural patches, which included smaller pools with relatively fine sediment and high solar radiation, were linked to high emergence biomass. These results support our findings of greater biomass at agricultural sites, and indicate that higher biomass fluxes are associated with particular physical habitat characteristics. Alternatively, the strong linkages between water quality and emergence biomass at CA suggest that emergence is strongly linked to elevated NH$_3$-N and P (PO$_4$-P and total P) concentrations. P and N are well known to be important for limiting primary productivity in stream ecosystems (Dodds et al. 2002), and the relatively high concentrations of P and NH$_3$-N may have driven higher aquatic primary productivity within forest patches. Further, recent logging activity within the forest has left the
canopy of CA relatively open, which also may contribute to elevated primary production. This inference is further supported by the presence of Heptageniid scrapers in the forest, which constituted a large portion of the biomass flux.

*Linking emergence to energy sources*

Our results suggest that both stable isotope ratios and C:N ratios were indicators of environmental shifts that drove patterns in emergence properties. Isotope ratios of stream biota can be used as a metric to detect environmental responses to anthropogenic stressors (Kendall et al. 2010). Because anthropogenic sources of N often have elevated $\delta^{15}$N signatures relative to natural N sources, studies have used $\delta^{15}$N of biota to trace the impacts of anthropogenic N in aquatic food webs (Anderson and Cabana 2005, Kohzu et al. 2009). Our results show that higher $\delta^{15}$N signatures of both terrestrial and aquatic N sources were linked to higher emergence biomass and greater mean body size of aquatic emergent insects in agricultural patches, and lower total emergence biomass and mean body size in forest patches. Whereas leaf composition data (Appendix C) suggests that higher $\delta^{15}$N of terrestrial N sources was likely driven by species composition and/or differences the proportion of living and dead organic material, higher $\delta^{15}$N signatures of aquatic sources was most likely a reflection of anthropogenic N inputs in agricultural patches. This result indicates that anthropogenic N inputs may have led to the highest emergence fluxes at BA and greatest mean body sizes at WA.
Similarly, $\delta^{13}C$ of basal resources sources were correlated with emergence biomass and spatial patterns in land cover. At CA, increase in emergence biomass with decreasing terrestrial source $\delta^{13}C$ suggests that the declining $\delta^{13}C$ is likely driven by shifts in the species composition of terrestrial leaves from agricultural (primarily herbaceous) to forest patches (mixture of herbaceous and woody leaves). Aquatic $\delta^{13}C$ signatures were also linked with emergence biomass, and the relatively higher signatures within forests predicted higher emergence at CA. The cause of variation in $\delta^{13}C$ is more uncertain than $\delta^{15}N$, and may be linked to environmental effects such as changes in water velocity among forest and agricultural patches, or a change in the photosynthetic rates both of which can result in enriched algal $^{13}C$ due to fractionation effects (Finlay and Kendall 2007). Higher photosynthetic rates are a likely explanation, because although there was greater solar radiation in agricultural patches there may have been appreciable shading from terrestrial grasses. Further, the forest had relatively open canopies (due to recent logging activity) and wider channels, which may have exposed the benthos to more solar radiation and stimulated primary productivity, driving the enriched $\delta^{13}C$ signatures. The wider pools in the forest may have resulted in lower velocity than pools in agricultural patches which may have also lead to enriched $\delta^{13}C$ signatures.

Because resource quality is often linked to the C:N ratio of basal resources, we expected a negative relationship between emergence biomass and/or mean body size and C:N. However, our results suggest a positive relationship between C:N of basal energy sources and total emergence biomass (CA) and mean body size (BA), and a negative
relationship between C:N and body size at WA. Previous work has found that aquatic invertebrates exhibit preferences for and can accumulate greater biomass on food resources that are typically rich in N (Canhoto and Graca 1995). Although the regression relationship was not significant, the trend in the data suggests that at WA the higher quality periphyton was associated with larger body sizes of emergent insects. This pattern may be driven by the greater quantity of anthropogenic N inputs in agricultural patches at WA which potentially increase the body size of aquatic insect taxa. Alternatively, we found negative relationships between C:N of basal resources and body size and emergence biomass at BA and CA, respectively. At these sites the C:N ratio may be more of an environmental indicator of changing C and N in the environment, rather than an indicator of resource quality.

Conclusion

Perhaps the most influential conceptual model in stream ecology, the River Continuum Concept (RCC), predicts that the structure and function of lotic systems gradually changes along a continuum from the headwaters to larger streams and rivers. More recently, this model has been subsumed under more general models that explicitly recognize the importance of non-continuous changes in stream systems, and predict a “discontinuum” whereby the configuration of patches in space markedly influences internal patch dynamics and the variation and assimilation of C in stream food webs (Poole 2002, Sullivan 2013). Our work is consistent with these conceptual advancements.
and demonstrates the importance of the spatial juxtaposition and configuration of different land cover patch types for regulating stream-riparian function. Our finding that emergence biomass and mean body size of adult aquatic insects exhibit strong shifts from the center of forest patches extending out into the surrounding agricultural matrix suggests that the effects of agricultural land use extends into forests, and may influence the coupling of streams with terrestrial food webs. Further, these shifts in aquatic insect fluxes were somewhat linked to variation in physical habitat, water quality, and energy sources suggesting that spatial configuration of land cover drives local environmental variation that in turn drives emergence dynamics.

Increasingly, stream and riparian systems are viewed as being interdependent, linked systems (Baxter et al. 2005, Sullivan and Rodewald 2012). This notion, coupled with increased interest in stream conservation and restoration, makes understanding the mechanisms driving aquatic insect emergence imperative for more integrative management of linked stream-riparian systems. Our study demonstrates that fluxes of adult aquatic insects are strongly related to spatial patterns in land cover, and represents a critical step towards linking emergence dynamics to stressors in human-modified landscapes. This work can be further extended by exploring the implications of land-cover mediated changes in aquatic emergent insect fluxes for terrestrial food webs. Additional extensions include more detailed studies of the specific mechanisms driving aquatic insect fluxes, and investigations on the influence of both qualitative (e.g., forest composition) and quantitative (e.g., forest size) characteristics of land cover on
emergence. Overall, our work contributes to our understanding of the influence of land-cover mediated changes on linked stream-riparian systems, and improves our ability to anticipate responses of these linked systems to land-cover change.
Acknowledgements

This work was supported by The Ohio State University Climate, Water, and Carbon Targeted Investment in Excellence (CWC-TIE) Program, the National Science Foundation STEM Graduate Fellows in K-12 (NSF GK-12) Education Program, Grant No. 0638669, and the Ohio Agricultural Research and Development Center (OARDC) SEEDS grant. Thanks to N. Rosenbaum and E. Gorrell for assistance sampling and processing aquatic insects, to L. Rieck for demonstration of how to set up emergent traps, and to L. Meyer for assistance with stable isotope protocols. We would also like to thank private land owners for their willingness to participate in this study.
References


Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141-156.


Table 4.1. Results from the spatial analysis of aquatic insect emergence. Response corresponds to the response variable in the analysis which was either the daily emergence rate [log(mg DM m\(^{-2}\) day\(^{-1}\))] or the average body size [log(mg DM)]. The different models include a categorical land cover (LC) variable with two levels (Agriculture or Forest), a categorical land cover variable (PO) with three levels (Upstream, Forest, Downstream), and the distance from the forest center (DFC). Parameter estimates correspond to slope estimates (DFC) or least-squares means (LC and PO). The heading Agriculture/Upstream corresponds to agriculture for the LC effects and to upstream for the PO effect. P-values were estimated either from a t-distribution to measure slope significance (DFC), or from Tukey’s post-hoc tests. The superscripts next to the parameter estimates correspond to P-values (rounded to the nearest hundredth): ≤ 0.01 (a), ≤ 0.05 (b), and < 0.10 (c). For the categorical variables, only those estimates that are different from each other (P ≤ 0.05) have a superscript.
Table 4.2. Results from the analysis linking physicochemical habitat to aquatic insect emergence. Response corresponds to the response variable in the analysis which was either the daily emergence rate \([\log(\text{mg DM m}^{-2} \text{ day}^{-1})]\) or the average body size \([\log(\text{mg DM})]\). The parameters are either the physical habitat PCA axes or water quality PCA axes. Estimate corresponds to the slope estimate and the \(b\) superscript corresponds to a \(P\)-value of \(\leq 0.05\) and the \(c\) superscript corresponds to a \(P\)-value of \(< 0.10\) (rounded to the nearest hundredth).

<table>
<thead>
<tr>
<th>Stream</th>
<th>Response</th>
<th>Parameter</th>
<th>Estimate</th>
<th>(R^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BA</td>
<td>Emergence</td>
<td>Physical (Axis 1)</td>
<td>-0.19(^c)</td>
<td>0.31</td>
</tr>
<tr>
<td>CA</td>
<td>Emergence</td>
<td>Water Quality (Axis 2)</td>
<td>-0.612(^b)</td>
<td>0.56</td>
</tr>
<tr>
<td>WA</td>
<td>Emergence</td>
<td>Water Quality (Axis 1)</td>
<td>0.232(^c)</td>
<td>0.37</td>
</tr>
</tbody>
</table>
Table 4.3. Eigenvector estimates from PCA analyses of physical habitat variables (BA) and water quality variables (CA). The PCA eigenvectors at BA represent the first physical habitat PCA axis (proportion of variance = 0.47) and those at CA represent the second water quality PCA axis (proportion of variance = 0.23).

<table>
<thead>
<tr>
<th>Site</th>
<th>Model</th>
<th>Parameter</th>
<th>PCA Eigenvectors</th>
</tr>
</thead>
<tbody>
<tr>
<td>BA</td>
<td>Physical Habitat</td>
<td>Pool Length</td>
<td>0.51</td>
</tr>
<tr>
<td>BA</td>
<td>Physical Habitat</td>
<td>Pool Width</td>
<td>0.328</td>
</tr>
<tr>
<td>BA</td>
<td>Physical Habitat</td>
<td>Pool Depth</td>
<td>-0.252</td>
</tr>
<tr>
<td>BA</td>
<td>Physical Habitat</td>
<td>Fine Sediment</td>
<td>-0.417</td>
</tr>
<tr>
<td>BA</td>
<td>Physical Habitat</td>
<td>Coarse Sediment</td>
<td>0.455</td>
</tr>
<tr>
<td>BA</td>
<td>Physical Habitat</td>
<td>Bedrock</td>
<td>-0.009</td>
</tr>
<tr>
<td>BA</td>
<td>Physical Habitat</td>
<td>Solar Radiation</td>
<td>-0.433</td>
</tr>
<tr>
<td>CA</td>
<td>Water Quality</td>
<td>NO$_3$</td>
<td>-0.051</td>
</tr>
<tr>
<td>CA</td>
<td>Water Quality</td>
<td>NH$_3$</td>
<td>-0.555</td>
</tr>
<tr>
<td>CA</td>
<td>Water Quality</td>
<td>Total N</td>
<td>-0.16</td>
</tr>
<tr>
<td>CA</td>
<td>Water Quality</td>
<td>PO$_4$</td>
<td>-0.401</td>
</tr>
<tr>
<td>CA</td>
<td>Water Quality</td>
<td>Total P</td>
<td>-0.42</td>
</tr>
<tr>
<td>CA</td>
<td>Water Quality</td>
<td>Conductivity</td>
<td>0.108</td>
</tr>
<tr>
<td>CA</td>
<td>Water Quality</td>
<td>Ph</td>
<td>-0.561</td>
</tr>
</tbody>
</table>
Table 4.4. Results from the analysis linking energy sources to aquatic insect emergence.

Response corresponds to the response variable in the analysis which was either the daily emergence rate [log(mg DM m\(^{-2}\) day\(^{-1}\))] or the average body size [log(mg DM)]. The parameters are the stable isotope composition (\(\delta^{13}\)C and \(\delta^{15}\)N) of the energy sources (terrestrial leaves and periphyton) and the quality (C:N ratio) of the energy sources. Estimate corresponds to the slope estimate and b superscript corresponds to a P-value of \(\leq 0.05\) and the c superscript corresponds to a P-value of \(< 0.10\) (rounded to the nearest hundredth).

<table>
<thead>
<tr>
<th>Stream</th>
<th>Response</th>
<th>Parameter</th>
<th>Estimate</th>
<th>(R^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BA</td>
<td>Emergence</td>
<td>Leaf (\delta^{15})N</td>
<td>0.12(^b)</td>
<td>0.54</td>
</tr>
<tr>
<td>BA</td>
<td>Emergence</td>
<td>Periphyton (\delta^{15})N</td>
<td>0.335(^c)</td>
<td>0.31</td>
</tr>
<tr>
<td>BA</td>
<td>Body Size</td>
<td>Periphyton C/N</td>
<td>0.344(^b)</td>
<td>0.43</td>
</tr>
<tr>
<td>CA</td>
<td>Emergence</td>
<td>Periphyton (\delta^{13})C</td>
<td>0.280(^b)</td>
<td>0.44</td>
</tr>
<tr>
<td>CA</td>
<td>Emergence</td>
<td>Leaf (\delta^{13})C</td>
<td>-0.731(^c)</td>
<td>0.39</td>
</tr>
<tr>
<td>CA</td>
<td>Emergence</td>
<td>Periphyton C/N</td>
<td>0.346(^c)</td>
<td>0.41</td>
</tr>
<tr>
<td>CA</td>
<td>Emergence</td>
<td>Leaf C/N</td>
<td>0.223(^b)</td>
<td>0.48</td>
</tr>
<tr>
<td>WA</td>
<td>Body Size</td>
<td>Leaf (\delta^{15})N</td>
<td>0.089(^c)</td>
<td>0.40</td>
</tr>
<tr>
<td>WA</td>
<td>Body Size</td>
<td>Periphyton C/N</td>
<td>-1.293(^c)</td>
<td>0.35</td>
</tr>
</tbody>
</table>
Figure 4.1. A-C: Bar graphs representing the proportion of biomass attributable to different families at each stream. Only those families are shown that accounted for ≥ 1% of the total biomass from each stream. Distance corresponds to the distance from the center of the forest and the bar graphs are ordered from upstream to downstream sampling sites. Dashed vertical grey lines correspond to the upstream and downstream edges of the forest patch. D: line plot of the maximum body size estimate at a given location across all sites. Three letter codes on the x-axis correspond to the different taxa:

- CAL = Calopterygidae
- STR = Stratiomyidae
- SCI = Sciomyzidae
- HEP = Heptageniidae
- SCA = Scathophagidae
- TRI = Trichoptera
- TIP = Tipulidae
- EPH = Ephydridae
- DOL = Dolichopodidae
- CUL = Culicidae
- PSY = Psychodidae
- CHI = Chironomidae
- PHO = Phoridae
- CER = Ceratopogonidae
- EMP = Empididae.
Figure 4.1 continued

A

CA  

- Chironomidae  - Culicidae  - Dolichopodidae
- Heptageniidae  - Tipulidae  - Trichoptera

B

WA  

- Chironomidae  - Calopterygidae  - Dolichopodidae
- Stratiomyidae  - Tipulidae

C

continued
Mean body size [across all streams (mg DM)]

Aquatic insect taxa

Figure 4.1 continued
Figure 4.2. Plots illustrating spatial model fits. Observed data (black dots) are overlaid with the predicted data (grey line). For figure 4.3C, an outlier was removed prior to fitting the model, but it remains in the graph (open circle).
Figure 4.2 continued

**Log emergence biomass (mg DM m$^{-2}$ day$^{-1}$)**

Distance from forest center (m)

B

continued
Figure 4.2 continued

Log [mean body size (mg DM)]

Distance from forest center (m)
Figure 4.2 continued

![Graph showing log mean body size (mg DM) vs. distance from forest center (m). The graph includes a linear trend line.]

D
Figure 4.3. Plots illustrating physicochemical model fits. Observed data (black dots) are overlaid with the predicted data (grey line).
Figure 4.3 continued

Physical Habitat (Axis 1)

Log [emergence biomass (mg DM m\(^{-2}\) day\(^{-1}\)]
Figure 4.4. Plots illustrating variation in $\delta^{15}N$ of terrestrial leaves and periphyton as a function of distance from the forest center. Grey and black lines correspond to leaves and periphyton, respectively, and dashed and solid lines correspond to BA and WA, respectively.
Chapter 5: Influence of forest fragments on headwater streams in agricultural landscapes: a review

Abstract

Headwater streams are strongly linked to forests by a variety of processes including nutrient filtration, sediment trapping, and organic matter inputs. However, in agricultural landscapes forests have largely been cleared for human land uses that have functionally decoupled forest-stream dynamics over a range of spatial scales. In order to better understand the implications of these small fragments of forest for headwater streams, we reviewed a series of studies that examined how headwater streams change as they transition from agricultural land into forest fragments. We use the central themes of landscape ecology as outlined by J.A. Wiens as a framework to emphasize the response of ecological processes to patch quality, boundaries among patches, context, connectivity, organisms, and scale. Based on the small number of studies in this review, we have made some tentative generalizations about the effects of forest fragments on streams in agricultural landscapes. Our results suggest that as streams transition from agricultural land to forest fragments they become wider, have less benthic fine sediment and lower solar radiation, and exhibit reductions in N and increases in P concentrations. Further,
we found some evidence of increased importance of allochthonous energy sources in
forest fragments. Consistent with changes in physicochemical and basal resource
measures, macroinvertebrate communities generally exhibited rapid changes after
entering forest patches (< 450 m). Although inferences based on this review are limited
due to the small sample size, our results suggest that forest fragments can rapidly recover
water quality and biotic integrity of headwater streams in agricultural landscapes.
Introduction

The structure and function of stream ecosystems is largely driven by linkages with the catchments that they drain (Hynes 1975), and these linkages are predicted to be particularly strong for headwater streams draining forested catchments (Vannote et al. 1980). The importance of forest-stream linkages have long been recognized (Fisher and Likens 1973) and have been a focal point of conceptual frameworks in stream ecology (e.g., Vannote et al. 1980, Gregory et al. 1991) and empirical studies (Fisher and Likens 1973, Wallace et al. 1997, Wallace et al. 1999, Harding et al. 2006, Death and Collier 2010). Forest-stream linkages are manifest in a variety of ways ranging from filtering nutrients and trapping sediments to providing habitat and food resources for aquatic biota (Gregory et al. 1991, Naiman and Decamps 1997). More recently, it has been recognized that linkages between forests and streams include terrestrial invertebrate fluxes into and aquatic invertebrate fluxes out of streams leading to the suggestion that forests and streams function as integrated ecological units (Sullivan et al. 2007, Fausch et al. 2010).

However, in agricultural landscapes forests have largely been cleared for human land-uses that have functionally decoupled forest-stream dynamics over a range of spatial scales. In contemporary landscapes, agricultural land is often the dominant landscape element (i.e., the matrix) and has been estimated to cover ~ 40% of the Earth’s land surface (Foley et al. 2005). Common effects of agricultural landscapes on streams include the deposition of fine sediment, nutrient enrichment [e.g., nitrogen (N) and
phosphorus (P)], increased solar radiation, elevated temperatures, and shifts in basal resources (Quinn 2000, Allan 2004). In turn, biotic community composition can be markedly different among forested and agricultural streams (Quinn et al. 1997, Scarsbrook and Halliday 1999, Goss et al. 2013a). Although there are strong differences between streams draining forested and agricultural landscapes, scattered fragments of forest are prevalent elements of agricultural landscapes and may be able to restore linkages between forests and streams that are otherwise absent in these landscapes.

The ecological dynamics within and among forest fragments have been widely studied by terrestrial landscape ecologists, however, the implications of these patches of forest for stream structure and function are largely unknown. As a field of study, landscape ecology emphasizes the influence of landscape structure and composition on ecological processes (Turner 1989, Forman 1995, Wiens 2002a), and this approach has been especially fruitful for understanding the influence of forest fragments on terrestrial ecosystem processes. Though the principles of landscape ecology are increasingly being applied to study stream ecosystems (Poole 2002, Thorp et al. 2006, Poole 2010), the ecological consequences of forest fragments for stream ecosystems in agricultural matrices remain largely unresolved. Those studies that have focused on streams draining forest fragments (hereafter, fragment streams) indicate inconsistencies in both the presence and direction of forest fragment effects (Suga and Tanaka 2013), and it is unclear what, if any, generalities can be gleaned from the extant studies of fragment streams. The potential for forest fragments to restore water quality and biotic integrity to
streams that have been impaired by human land uses (e.g., Storey and Cowley 1997, Scarsbrook and Halliday 1999) suggests that an integrated framework to understand the effects of forest fragments on streams may be critical for stream restoration and conservation efforts.

In the following paper, we use the six central themes of landscape ecology as discussed by Wiens (2002b) as a conceptual basis to review literature and identify generalities related to the effects of forest fragments (identified by Suga and Tanaka 2013) on stream ecosystems. We also identify key knowledge gaps and suggest areas for future research. Suga and Tanaka (2013) provide a brief summary of aquatic macroinvertebrate responses to forest fragments in headwater streams, and we extend this work by: (1) considering physicochemical and basal resource responses to forest fragments; (2) including three studies not considered in the original review (however, Arnaiz et al. (2011) was not included because of the study design); and (3) providing an in-depth discussion based on the landscape ecology framework outlined by Wiens. We constrain our review to those studies identified by Suga and Tanaka (2013) because they focus on the influence of inter-patch transitions between agricultural land and forest fragments along single streams. This structure permits the assessment of the gross differences between fragment and agricultural streams (patch quality), as well as the effects of boundary dynamics, context, connectivity, and scale on fragment streams all of which comprise Wiens’ landscape ecology themes. We conclude by synthesizing the
studies in this review and discussing the implications for conservation and restoration of stream ecosystems in agricultural landscapes.

**Six central themes of landscape ecology: Implications for understanding the influence of forest fragments on headwater streams**

In his paper on the application of landscape ecology to stream ecosystems, Wiens (2002b) outlines six major themes of landscape ecology and reviews how these themes have been used to advance our knowledge of stream structure and function. The six themes are centered on an internally homogenous spatial unit termed “patch” (Forman 1995, Turner et al. 2001), and the implications of patch quality, patch boundaries, the landscape context of each patch, connectivity among patches, organisms within and among patches, and the scale of ecological processes (e.g., micro habitat vs. watershed scale) operating within and among patches. Because these landscape characteristics have been shown to be important in a range of systems (Shmida and Wilson 1985, Baltz et al. 1993, Polis and Hurd 1995, Gehlhausen et al. 2000, Palmer et al. 2000), we apply them to the effects of forest fragments on streams.

*Patches differ in quality*

Patch quality is an inherently organism-centered concept because habitat quality is dependent upon the focal organisms and whether the conditions within a patch are suitable for them to persist. Because all of the studies in our review used aquatic
macroinvertebrates as the primary biotic response variable, our discussion of patch quality is centered on how forest fragments influence the conditions that are most important for regulating aquatic macroinvertebrate communities.

Although aquatic macroinvertebrates are regulated by a variety of processes operating over multiple spatial scales (see reviews by Malmqvist 2002, Cummins et al. 2008), basic requirements for persisting in any given patch include the physicochemical conditions (physical habitat and water quality) and the presence of food resources (i.e., the fundamental niche, Hutchinson 1957). All the studies we reviewed estimated water quality parameters, and six out of eight measured at least some aspect of the physical habitat (Table 5.1). The most common physical habitat responses after entering fragments observed across the studies were decreases in fine sediments, increases in channel width, and decreases in solar radiation. All these effects potentially influence aquatic macroinvertebrates through increasing interstitial spaces available as habitat (fine sediment reduction) to lowering temperatures and altering the food base (decreased solar radiation) (Quinn 2000) to increasing the amount of benthic habitat per unit of stream length (channel width) (Sweeney et al. 2004).

Of those studies that found effects of forest fragments on water quality, the two most consistent responses were decreases in N concentrations (four total studies) and increases in P concentrations (four total studies). Riparian forests have long been known to reduce amount of terrestrially derived N entering streams (Lowrance et al. 1984), and recent work suggests that forests can also enhance in-stream N uptake (Sweeney et al. 2004).
2004). The consistent increase in P after agricultural streams entered forests was somewhat surprising given that studies often show that riparian buffers reduce P concentrations (Cooper and Gilliam 1987, Daniels and Gilliam 1996, Lee et al. 2000, Borin et al. 2005). Results from our review are consistent in part with results from Sweeney et al. (2004), which showed that P uptake per unit area was greater in non-forested than in forested stream reaches, and suggested that this was driven by greater biotic (e.g., periphyton) and sorptive uptake processes in non-forested reaches. Previous work has also shown that under certain conditions, riparian forests can function as sources of P to streams (Mulholland 1992). Overall, the water-quality results suggest that forest fragments may be efficacious for attenuating N concentrations, but may not be effective at reducing P concentrations in streams.

Of the studies we reviewed, only two out of eight had direct measurements of basal resources. Although high variability precluded a significant effect, Scarsbrook and Halliday (1999) found strong, consistent trends of lower periphyton biomass and higher CPOM biomass within forest fragments. This result is consistent with the specific research upon which this study was based (Quinn et al. 1997) as well as general headwater stream literature emphasizing the importance of forests for regulating basal resources (Fisher and Likens 1973, Vannote et al. 1980, Wallace et al. 1999, England and Rosemond 2004). In contrast, Harding et al. (2006) found no effect of forest fragments on periphyton biomass. This was surprising because it is well known that solar radiation strongly limits periphyton productivity, which Harding et al. found to be significantly
lower within forest fragments than in agricultural patches. A possible explanation for this lack of an effect could be that elevated nutrient concentrations (N and P) that often accompany agricultural land use (Carpenter et al. 1998) may have been transported from the surrounding catchment compensating for the low light levels in forest fragments.

Although basal resources were not measured directly, four studies measured shifts in macroinvertebrate functional feeding groups, which can be used as indirect measures of resource availability (Merritt and Cummins 1996). Three out of the four studies suggested that macroinvertebrate shredders increased after streams entered forest fragments (Houghton et al. 2011, Suga and Tanaka 2013, Goss et al. 2013a). Alternatively, results from Goss et al. (2013b) showed that Heptageniidae scrapers were among the most numerically dominant aquatic insect families at one of the fragments in this study. The authors attributed this effect to recent logging activity which had removed substantial amounts of mature canopy cover. This result suggests that in addition to conversion of forest to agricultural land, modification of existing forest cover may have important implications for stream ecosystems (see Meyer and Turner 1992 for a discussion of conversion vs modification).

*Patch boundaries affect flows*

Ecological boundaries correspond to areas that delimit different patches in a landscape and are often defined by steep gradients in abiotic or biotic conditions (Cadenasso et al. 2003). Perhaps the most well-known boundaries are those that occur in
terrestrial systems between forests and agricultural fields, whereby the effects of the nearby field penetrate into the forest influencing both the microclimate and species composition of the forest (i.e., an edge effect, Forman 1995). In order to detect spatial boundaries such as those exhibited at the juxtaposition of forests and fields, a variety of approaches have been used including analysis of variance (ANOVA, Gehlhausen et al. 2000), piecewise linear regression (Cadenasso et al. 1997), moving window analysis (Goebel et al. 2012), and Monte Carlo randomization analysis (Harper and MacDonald 2001). Similar to terrestrial edge effects studies, the studies in our review focused on streams that flowed through adjacent patches of agricultural land and forest. However, as opposed to the processes driving edge effects in terrestrial systems (e.g., wind), the boundaries in these studies were driven by flows of water that transport agricultural conditions into forest fragments (or vice versa). In this section, we discuss the different analytical methods that the studies in our review used to detect boundaries. Further details of boundary properties are discussed in the “scale” section.

With the exception of one study (Harding et al. 2006), all of the studies we reviewed showed evidence for strong longitudinal boundaries occurring as agricultural streams flow into forest fragments. Although the analytical approaches were variable and included ANOVA, nonlinear regression, piecewise linear regression, non-parametric threshold analyses (Qian et al. 2003), and the Threshold Indicator Taxa ANalysis (TITAN, Baker and King 2010), the results from almost all of the studies conform to the
expectation that there is a steep gradient in the study streams that is driven by the juxtaposition of forest and agricultural patches.

Recent work on ecological thresholds (spatial boundaries among patches being a special case of a threshold) suggests that threshold responses can have a variety of forms ranging from a simple shift in the mean to more complex changes such as shifts in both the mean and slope (Qian and Cuffney 2012). In our review, five studies used ANOVA to detect changes along the boundary, indicating a shift in the mean. One advantage of an ANOVA approach is that it allows the detection of the specific distance along the agriculture-forest boundary at which the stream is significantly different from the upstream agricultural patch. A drawback of this approach is that it does not generate uncertainty estimates of where this change occurs (i.e., the threshold point). While mathematically more elegant, Suga and Tanaka’s (2013) use of nonlinear regression models does not permit a statistical test to determine the location of the boundary between agricultural land and the forest fragment. Only one of the studies we reviewed explicitly modeled the data using multiple functional forms to describe differences in the response shape and location of change along agriculture-forest transitions (Goss et al. 2013a). In this study, Goss et al. found evidence that both changes in slope and changes in mean were important for explaining variation in stream dynamics along the agriculture-forest boundary. Further, their application of a community threshold analysis (TITAN) represents a unique approach to the study of spatial boundaries among patches,
and yielded evidence for strong shifts in aquatic macroinvertebrate communities after agricultural streams entered forest fragments.

*Patch context matters*

Agricultural landscapes are composed of a variety of different types of natural and anthropogenic land cover, and the matrix within which forest fragments are embedded can strongly influence stream dynamics. Although the number of studies in our review was small, they encompass a variety of different landscape contexts. All of the studies in our review took place in agricultural catchments, but the type of agriculture differed among studies and included pastoral, cropland, sugarcane, and communal farming. Most of the studies occurred in temperate regions, but the geographic location among temperate studies was substantially different with three studies occurring in the USA, and three studies occurring in New Zealand.

The studies occurring in semi-arid and tropical climates had unique land uses (sugarcane and communal farming) that did not occur in the temperate studies, which may have contributed to distinct differences in responses to forest fragments. The study that showed perhaps the largest impact of agricultural land use on the physical habitat occurred in a dry-land stream nested within a semi-arid climate zone (Chakona et al. 2009). Results of this study showed that the percent of the benthos covered in fine sediment shifted from 2% in an upstream forest fragment to a mean of > 80% after flowing through a catchment dominated by communal agriculture, and exhibited another
shift to a mean of 12% after entering a downstream forest fragment. These strong shifts suggest that within the context of communal agriculture in a semi-arid climate, local physical habitat can experience substantial degradation; however, the effects may be short-lived as indicated by the sharp decline in fine sediment in the downstream forest fragment. Of all the studies in this review, only the study by Suga and Tanaka (2013) indicated a decline in EPT taxa metrics within forest patches. The authors attributed this unexpected response to greater structural complexity and food resources upstream of the forest fragment. Further, the sampling locations upstream of the forest were adjacent to an abandoned sugarcane plantation with active sugarcane being located further upstream. These results emphasize the need for taking into account the adjacent land-use activity when making general inferences about the effects of forest fragments on streams (Suga and Tanaka 2013).

*Connectivity is critical*

Connectivity refers not only to the distance between patches, but also to the facility by which organisms, energy, and materials flow from one patch to another. In stream ecosystems, connectivity is largely driven by longitudinal, lateral, and vertical streamflow vectors (Ward 1989). The studies in our review yielded strong evidence that these three connectivity vectors are important for driving changes in stream structure and function.
In the papers we reviewed, the strong similarities between parameters estimated near the edges of forests to those estimated in upstream agricultural patches indicate that strong longitudinal connectivity drives agricultural influences on streams into downstream forest fragments. For example, Goss et al. (2013a) found evidence that temperature and nutrients near forest edges were more similar to the agricultural stream than they were to sites in the forest interior. Similarly, Suga and Tanaka (2013) found that macroinvertebrate rarefied taxon richness within the first 50 m of entering a forest fragment was more similar to the agricultural stream than it was to sites 600 m into the forest fragment. The changes observed as a function of distance from forest edges are consistent with terrestrial edge effects studies (Harper et al. 2005), and suggest that similar processes are occurring albeit driven by water flow instead of terrestrial connectivity vectors such as wind.

It has also been hypothesized that longitudinal connectivity leads to the effects of forests (e.g., leaf litter, improved water quality, sensitive taxa) on streams being transported into agricultural areas located downstream of forest fragments (Harding et al. 2006). However, only two studies that we reviewed examined the possible downstream effects of forests on agricultural streams. Though the initial hypothesis of a “downstream shadow” was put forth by Harding et al. (2006) they did not find evidence for this effect in their study. Alternatively, Goss et al. (2013b) found evidence that depressed nitrogen concentrations within forest patches were transported downstream of forests such that the downstream concentrations were lower than concentrations closer to the upstream forest.
This suggests that strategic placement of forest fragments in headwater streams of agricultural landscapes may prevent elevated N concentrations from being transported into larger streams and rivers.

In addition to the longitudinal linkages, results from our review suggest that both lateral and vertical linkages may also play an important role. During the conceptual evolution of stream ecology it has been increasingly recognized that streams are strongly structured by longitudinal, lateral, and vertical hydrologic connectivity vectors (Poole 2010). While our findings of strong similarities near forest edges suggest strong longitudinal effects, the strong changes with distance into the stream suggest the importance of vertical and lateral connectivity. After entering forest fragments, decreases in fine sediment and changes in the dominant basal resources may alter surface and subsurface (vertical) connectivity as well as the role of the hyporheos for nutrient processing (e.g., increase in anaerobic versus aerobic processes) which may account for some of the changes we observed such as the decreases in N (Triska et al. 1989). Further, wider streams in forest fragments may increase the benthic surface area and result in an increased role of lateral connectivity within the channel (Sweeney et al. 2004). Out-of-stream lateral linkages with riparian forests are well known to drive in-stream nutrient processes (Lowrance et al. 1984) as well as regulate basal resources (Vannote et al. 1980). These connectivity vectors were likely important for driving the observed physicochemical and biological patterns we observed in fragment streams, and support
the argument that riparian forests are important best management practices for protecting stream quality (Montgomery 1997).

Organisms are important

Because of their ecological importance as well as their use in biomonitoring, aquatic macroinvertebrates are often a focal point of stream studies. As larvae, aquatic macroinvertebrates primarily live in the benthos and are important for processing organic matter, nutrient cycling and making basal energy sources available to higher-level consumers (Wallace and Webster 1996). Aquatic macroinvertebrate larvae are also ubiquitous in streams, are relatively sedentary, have long life spans, and are sensitive to a range of stressors which makes them useful for assessing the effects of anthropogenic disturbance on stream systems (Rosenberg and Resh 1993). Recently, the functional significance and biomonitoring utility of aquatic macroinvertebrates has been extended to include the winged adult phase of aquatic insects that functionally links aquatic and terrestrial systems by providing subsidies to terrestrial consumers (Baxter et al. 2005), and these subsidies are regulated by anthropogenic stressors such as channelization (Laeser et al. 2005) and nutrient enrichment (Davis et al. 2011).

Almost all of the studies we reviewed investigated the response of larval aquatic macroinvertebrates to forest fragments. This response was also the most consistent, with six of the studies finding an effect (Table 5.1). Based on the summary by Suga and Tanaka (2013), the response of particular macroinvertebrate metrics were somewhat
heterogeneous, but there was evidence that three out of the four studies included in our review exhibited increases in sensitive taxa in forest fragments. Further, Goss et al. (2013a) found that Plecopterans, which are known to be highly sensitive to anthropogenic disturbance, were more abundant in forest fragments than in agricultural streams.

The only two studies in our review that examined the effects of forest fragments on adult aquatic insects both showed strong responses of aquatic emergent insect communities to forest fragments. Both Goss et al. (2013b) and Houghton et al. (2011) found evidence for strong shifts in taxa sensitive to stressors (Ephemeroptera and Trichoptera) which were either more abundant (Ephemeropterans and Trichopterans, Goss et al. 2013b) or had higher richness (Trichopterans, Houghton et al. 2011) in forest fragments. Overall, our review of macroinvertebrates suggests that forest fragments drive shifts in aquatic macroinvertebrate and adult aquatic insect community structure and may provide important refuges for sensitive taxa in human-dominated landscapes.

Scale is important

The importance of spatial scale is ubiquitous in ecology, and has important implications for fragment streams in agricultural landscapes. The scale of forest fragmentation and loss is closely linked with all of the aforementioned themes: larger scale forest clearing leads to smaller and more homogenous patches of forest that are surrounded by an increasing amount of matrix; smaller patches have relatively greater edge-area ratios and are often isolated and less connected, and contain fewer organisms.
that are typical of contiguously forested landscapes. These effects potentially have particularly important implications for the distance an agricultural stream must flow through a forest fragment before it recovers forest-stream linkages.

Almost all of the studies we reviewed examined the response of streams along sampling transects between agricultural land and forest fragments, but only a few estimated the distance at which these changes occurred. Of those studies that estimated distances, there was evidence for strong shifts in macroinvertebrate communities ranging from near forest edges (~0) up to 450 m into a forest fragment. Heterogeneity among these results may have been driven by the different macroinvertebrate response variables used as well as the different analyses (see boundary section for a more detailed discussion of analytical approaches). For example, Storey and Cowley (1997) and Scarsbrook and Halliday (1999) analyzed a multimetric macroinvertebrate index using an analysis of variance, but Goss et al. (2013a) used a threshold detection technique that targets individual taxa as well as community-wide responses. Nevertheless, these results suggest that whereas the scale (and context) of agricultural influence was likely different in each catchment, there was evidence of marked changes in macroinvertebrate communities relatively soon after agricultural streams entered forest patches. This supports the argument that even relatively small forest fragments may be able to restore/retain functional linkages between forests and streams. However, the size and/or location within forest fragments may need to be at larger scales than those in Harding et al. (2006)
(total stream length within forest ranged from 250-350, and reach placement was ~125-175 m into the forest) as they were the only study in this review that didn’t find an effect.

Also related to scale, we found that there was a relatively narrow range of stream sizes investigated in these studies. The sizes of streams included first through third order streams, and although these streams can make up the majority of stream length within a given catchment, this restricts the generality of results from these studies. In particular, as streams increase in size, riparian vegetation is expected to have increasingly smaller effects on stream structure and function (Vannote et al. 1980). Therefore, we might expect that larger streams (>3rd order) may not change as rapidly as smaller streams, and thus may require larger fragments to recover stream structure and function.

**Synthesis**

Based on the small number of studies in this review we have made some tentative generalizations about the effects of forest fragments in streams in agricultural landscapes (Fig. 5.1). Overall forest fragments strongly influenced physicochemical conditions of streams. Relative to agricultural streams, fragment streams were typically wider, had lower deposition of fine sediments, had lower solar radiation, and N concentrations decreased within forests. There was also evidence for a switch from autochthonous as the dominant resource to allochthonous, but this was somewhat idiosyncratic and depended on the integrity of the forest. Concentrations of P were generally higher in forests, suggesting less efficient P uptake and/or leaching of P from riparian forests.
Almost all studies in the review exhibited evidence of a boundary (or edge effect) and the nature of the response appeared to be an abrupt change in the mean as opposed to more gradual responses such as a shift in slope. The presence of physicochemical effects of forest fragments were generally consistent among different geographic locations and climates, but the magnitude and direction of effects may be altered by contextual factors such as the type and state (active versus abandoned) of agricultural land use. Similarities between sites near forest edges and agricultural streams suggest strong longitudinal connectivity, however lateral and vertical connectivity vectors drive processing of materials within fragments which can improve water quality and potentially transport these effects downstream of forest fragments. Patterns in macroinvertebrates (both larval and adult) reflected changes in physicochemical attributes and basal resources, and exhibited strong increases in sensitive taxa after streams entered forest fragments. The scale of change after entering forest fragments was variable, but generally was quite rapid (< 450 m) suggesting the importance of restoration and conservation of small forest fragments.

*Forest fragments and stream restoration*

In response to widespread degradation of water resources, stream and river restoration has become increasingly popular resulting in substantial amounts of money being spent on stream restoration projects (Bernhardt et al. 2005). Restoration of stream “quality” ensures that streams can provision a variety of ecosystem services such as water
quality and quantity, biodiversity conservation, and recreational opportunities. By restoring functional linkages between forests and streams, results of the present review indicate that forest fragments can provide a variety of services that are otherwise absent in agricultural landscapes (Fig. 5.1). Fine sediment and nutrient enrichment have been identified as among the most widespread stressors of stream ecosystems (US EPA 2006). Our review suggests that these stressors can be greatly attenuated by forest fragments in small headwater stream catchments resulting in improved habitat and water quality. Further, the consistent improvement in macroinvertebrate measures indicative of “biotic integrity” (sensu Karr 1991) in forest fragments suggests an overall improvement in stream quality. Because the effects of forest fragments on stream ecosystems were realized over relatively small spatial scales, improvements in stream quality may be attained by conserving and restoring relatively small fragments of forest. This approach may be particularly effective in human-dominated landscapes because patterns in land ownership likely preclude restoration of contiguous corridors of riparian forest (discussed in Scarsbrook and Halliday 1999). Moreover, strategic restoration and conservation of forest fragments near the confluence of headwater streams and larger streams and rivers may be able to prevent degradation in headwater catchments from being transported downstream. Results of our review also indicated that the in-stream effects of forests on streams are translated back into terrestrial systems via stream-to-forest fluxes of adult aquatic insects. This is consistent with the idea that streams and riparian systems are linked interdependent systems (Sullivan et al. 2007, Fausch et al. 2010), and suggests that
studies of forest fragments effects on fluxes of adult aquatic insects can provide valuable information for integrated management of stream-riparian systems. All that being said, it is important to consider that general inferences based on this review are quite limited because of the small number of studies within limited land-use and catchment size contexts. As research on fragment streams expands to other contexts more generalizations may become evident. Nevertheless, the results of the studies in this review were generally consistent and point to the value of forest fragments of a range of sizes for conserving and restoring functional linkages between forests and streams in agricultural landscapes.
References


172
Table 5.1. Themes of landscape ecology as they relate to FFS. For each category "Yes" and "No" corresponds to whether or not there were observed differences in between fragment and agricultural streams (upstream or downstream of the forest fragment). Yes* corresponds a study where larval macroinvertebrate richness upstream and within forest was greater than richness downstream of the forest. Dashes correspond to parameters that were not estimated in that study. For the estimates of distance under scale category only those estimates where a statistical test was done are reported. Under the Boundary heading, PLR = piecewise linear regression, NPDR = nonparametric deviance reduction analysis, and TITAN corresponds to Threshold Indicator Taxa Analysis.
<table>
<thead>
<tr>
<th>Study</th>
<th>Physical Habitat</th>
<th>Water Chemistry</th>
<th>Basal Resources</th>
<th>Boundary</th>
<th>Location</th>
<th>Land-Use</th>
<th>Forest</th>
<th>Larval Aquatic Macroinvertebrates</th>
<th>Adult Aquatic Insects</th>
<th>Distance</th>
<th>Scale</th>
</tr>
</thead>
<tbody>
<tr>
<td>Storey and Cowley (1997)</td>
<td>Yes</td>
<td>Yes</td>
<td>-----</td>
<td>ANOVA</td>
<td>New Zealand</td>
<td>Pasture</td>
<td>Temperate secondary growth</td>
<td>Yes</td>
<td>------</td>
<td>350 - 450</td>
<td>2nd order</td>
</tr>
<tr>
<td>Scarsbrook and Halliday (1999)</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>ANOVA</td>
<td>New Zealand</td>
<td>Pasture</td>
<td>Temperate secondary growth</td>
<td>Yes</td>
<td>------</td>
<td>50 - 300</td>
<td>1st and 2nd order</td>
</tr>
<tr>
<td>Harding et al. (2006)</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>ANOVA</td>
<td>New Zealand</td>
<td>Dairy and beef cattle farms</td>
<td>Temperate secondary and old growth</td>
<td>No</td>
<td>------</td>
<td>-----</td>
<td>3rd order</td>
</tr>
<tr>
<td>Chakona et al. (2009)</td>
<td>Yes</td>
<td>No</td>
<td>-----</td>
<td>ANOVA</td>
<td>Zimbabwe</td>
<td>Communal agriculture</td>
<td>Semi-arid secondary growth</td>
<td>Yes</td>
<td>------</td>
<td>-----</td>
<td>1st order and ≥2nd order</td>
</tr>
<tr>
<td>Houghton et al. (2011)</td>
<td>-----</td>
<td>Yes</td>
<td>-----</td>
<td>ANOVA</td>
<td>Michigan, USA</td>
<td>Agriculture</td>
<td>Temperate secondary growth</td>
<td>Yes*</td>
<td>Yes</td>
<td>-----</td>
<td>3rd order</td>
</tr>
<tr>
<td>Suga and Tanaka (2013)</td>
<td>-----</td>
<td>Yes</td>
<td>-----</td>
<td>nonlinear regression</td>
<td>Brazil</td>
<td>sugarcane plantation; abandoned sugarcane plantation</td>
<td>Tropical secondary growth</td>
<td>Yes</td>
<td>Yes</td>
<td>-----</td>
<td>3rd order</td>
</tr>
<tr>
<td>Goss et al. (2013)</td>
<td>Yes</td>
<td>Yes</td>
<td>-----</td>
<td>PLR, NPDR, TITAN</td>
<td>Ohio, USA</td>
<td>Pasture; abandoned pasture; cropland; riparian tree-buffer</td>
<td>Temperate secondary growth</td>
<td>Yes</td>
<td>------</td>
<td>~0 to 320</td>
<td>1st and 2nd order</td>
</tr>
<tr>
<td>Goss et al. (2013)</td>
<td>Yes</td>
<td>Yes</td>
<td>-----</td>
<td>NPDR</td>
<td>Ohio, USA</td>
<td>Cropland; marginal riparian tree-buffers</td>
<td>Temperate secondary growth</td>
<td>Yes</td>
<td>Yes</td>
<td>~0</td>
<td>1st order</td>
</tr>
</tbody>
</table>
Figure 5.1. Conceptual model of the changes in stream ecosystems as they transition from agricultural land into forest fragments, and the implications of for stream conservation and restoration.
Chapter 6: Conclusion

One of the most influential conceptual frameworks in stream ecology, the River Continuum Concept (RCC), predicts that the structure and function of lotic systems gradually change along a continuum from the headwaters to larger streams and rivers. A prominent prediction of this model is that headwater stream ecosystems are strongly influenced by forest-stream linkages. However, large-scale forest clearing has led to landscapes where forests are minor components, and streams flowing through these landscapes are confronted with a heterogeneous mixture of human land-uses and forest patches. Few studies have investigated the effects of forest patches on stream structure and function in agricultural landscapes, and the research in my dissertation was aimed at providing more information to those ends.

In the first field study, I focused on how in-stream processes were influenced by forest patches in agricultural landscapes. Threshold analysis results revealed that physicochemical measures and larval aquatic macroinvertebrate communities exhibited strong shifts that primarily occurred within the first 324 m after entering forest patches. Surprisingly, we found that leaf litter breakdown did not change along after streams entered forests, suggesting that factors operating at different spatial and/or temporal scales may be influencing this process in the small headwater streams we studied.
The second and third studies extended this work to include stream-to-terrestrial fluxes of aquatic emergent (adult) insects. Similar to the first study, the second study revealed that aquatic emergent insect communities rapidly responded soon after entering forest patches. Additionally, the sampling design we employed in this study enabled us to detect a subsequent shift in aquatic emergent insect composition just prior to leaving forests. These responses were linked to land-cover-driven variation in physicochemical habitat. Additionally, results from this study revealed that the physicobiological effects of forests on streams were largely contained within forest boundaries, but the effects on water quality extended into downstream agricultural reaches.

The third study indicated that forest patches strongly influenced aquatic-to-terrestrial aquatic insect biomass fluxes which were linked to the physicochemical environment and the energy sources supporting aquatic insect food webs. The results showed that strong variation in both aquatic emergent insect biomass and mean body size were strongly linked to the distance from the center of forest patches. These results suggest that stream-riparian food webs within forests may be most tightly coupled near the center of forests, and become increasingly decoupled closer to forest edges.

Finally, the literature review revealed that results from my dissertation research are consistent with and extend our knowledge of the effects of forest fragments on stream ecosystems. General effects observed in the review suggested that relative to agricultural streams, streams draining forest fragments were wider, and had reduced solar radiation, deposition of fine sediments, and N concentrations. These physicochemical effects were reflected in macroinvertebrate communities that exhibited strong changes within the first 450 meters of entering forest fragments.
As the paradigm of streams as continua incorporates newer paradigms that view streams as discontinuous hierarchies of patches (Poole 2002, Thorp et al. 2006, Poole 2010) there is an increasing emphasis on the influence of landscape structure and composition on stream dynamics. Results from our research are consistent with these conceptual developments, and suggest that the influence of forest fragments drive reciprocal linkages between forests and streams resulting in stream-riparian systems that are distinct from the surrounding landscape. The nature of these reciprocal linkages changes rapidly after streams enter and exit forest patches, and suggests that even small patches of forest can recover functional forest-stream linkages that are otherwise absent in agricultural landscapes. The recognition that streams and riparian systems are interdependent linked systems (Baxter et al. 2005, Sullivan and Rodewald 2012), coupled with increased interest in stream conservation and restoration, makes understanding the patterns and processes driving aquatic insect emergence imperative for more integrative management of linked stream-riparian systems. My dissertation contributes to those ends and improves our ability to anticipate responses of these linked stream-forest systems to land-cover change.
References


List of References


185


Houghton, D. C., E. A. Berry, A. Gilchrist, J. Thompson, and M. A. Nussbaum. 2011. Biological changes along the continuum of an agricultural stream: influence of a


Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141-156.


Appendix A: GPS coordinates of the sites for each study. Distance from the upstream forest edge is measured in meters, and latitude and longitude are measured in decimal degrees.
<table>
<thead>
<tr>
<th>Stream</th>
<th>Distance from upstream edge</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilkin Run</td>
<td>-376</td>
<td>40.64435</td>
<td>-82.09085</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>-205</td>
<td>40.64535</td>
<td>-82.09037</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>-78</td>
<td>40.64588</td>
<td>-82.08922</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>22</td>
<td>40.64638</td>
<td>-82.08863</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>120</td>
<td>40.64682</td>
<td>-82.08793</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>195</td>
<td>40.64707</td>
<td>-82.08768</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>452</td>
<td>40.64860</td>
<td>-82.08787</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>790</td>
<td>40.64920</td>
<td>-82.08970</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>-392</td>
<td>40.68148</td>
<td>-81.64780</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>-200</td>
<td>40.68053</td>
<td>-81.64601</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>-91</td>
<td>40.67997</td>
<td>-81.64532</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>10</td>
<td>40.67926</td>
<td>-81.64447</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>100</td>
<td>40.67907</td>
<td>-81.64358</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>194</td>
<td>40.67851</td>
<td>-81.64344</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>405</td>
<td>40.67693</td>
<td>-81.64328</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>1080</td>
<td>40.67522</td>
<td>-81.63761</td>
</tr>
<tr>
<td>Stream</td>
<td>Distance from upstream edge</td>
<td>Latitude</td>
<td>Longitude</td>
</tr>
<tr>
<td>--------</td>
<td>-----------------------------</td>
<td>-----------</td>
<td>------------</td>
</tr>
<tr>
<td>BA</td>
<td>-89</td>
<td>40.89368</td>
<td>-81.69928</td>
</tr>
<tr>
<td>BA</td>
<td>-45</td>
<td>40.89368</td>
<td>-81.69870</td>
</tr>
<tr>
<td>BA</td>
<td>20</td>
<td>40.89368</td>
<td>-81.69792</td>
</tr>
<tr>
<td>BA</td>
<td>133</td>
<td>40.89348</td>
<td>-81.69701</td>
</tr>
<tr>
<td>BA</td>
<td>252</td>
<td>40.89389</td>
<td>-81.69608</td>
</tr>
<tr>
<td>BA</td>
<td>556</td>
<td>40.89437</td>
<td>-81.69373</td>
</tr>
<tr>
<td>BA</td>
<td>756</td>
<td>40.89427</td>
<td>-81.69220</td>
</tr>
<tr>
<td>BA</td>
<td>840</td>
<td>40.89390</td>
<td>-81.69144</td>
</tr>
<tr>
<td>BA</td>
<td>905</td>
<td>40.89345</td>
<td>-81.69097</td>
</tr>
<tr>
<td>BA</td>
<td>1000</td>
<td>40.89345</td>
<td>-81.69097</td>
</tr>
<tr>
<td>CA</td>
<td>-96</td>
<td>40.97822</td>
<td>-81.95302</td>
</tr>
<tr>
<td>CA</td>
<td>-61</td>
<td>40.97853</td>
<td>-81.95303</td>
</tr>
<tr>
<td>CA</td>
<td>15</td>
<td>40.97923</td>
<td>-81.95289</td>
</tr>
<tr>
<td>CA</td>
<td>104</td>
<td>40.97963</td>
<td>-81.95243</td>
</tr>
<tr>
<td>CA</td>
<td>252</td>
<td>40.98055</td>
<td>-81.95238</td>
</tr>
<tr>
<td>CA</td>
<td>520</td>
<td>40.98250</td>
<td>-81.95248</td>
</tr>
<tr>
<td>CA</td>
<td>727</td>
<td>40.98378</td>
<td>-81.95208</td>
</tr>
<tr>
<td>CA</td>
<td>764</td>
<td>40.98415</td>
<td>-81.95213</td>
</tr>
<tr>
<td>CA</td>
<td>815</td>
<td>40.98463</td>
<td>-81.95215</td>
</tr>
<tr>
<td>WA</td>
<td>-50</td>
<td>40.88697</td>
<td>-81.98217</td>
</tr>
<tr>
<td>WA</td>
<td>-33</td>
<td>40.88688</td>
<td>-81.98231</td>
</tr>
<tr>
<td>WA</td>
<td>5</td>
<td>40.88664</td>
<td>-81.98264</td>
</tr>
<tr>
<td>WA</td>
<td>126</td>
<td>40.88584</td>
<td>-81.98293</td>
</tr>
<tr>
<td>WA</td>
<td>249</td>
<td>40.88483</td>
<td>-81.98348</td>
</tr>
<tr>
<td>WA</td>
<td>510</td>
<td>40.88291</td>
<td>-81.98380</td>
</tr>
<tr>
<td>WA</td>
<td>621</td>
<td>40.88201</td>
<td>-81.98356</td>
</tr>
<tr>
<td>WA</td>
<td>702</td>
<td>40.88135</td>
<td>-81.98325</td>
</tr>
<tr>
<td>WA</td>
<td>732</td>
<td>40.88108</td>
<td>-81.98325</td>
</tr>
</tbody>
</table>
Appendix B: Summary statistics for aquatic invertebrate taxa collected during each study. Count corresponds to the number of individuals collected and mass corresponds to dry mass measured in milligrams.
<table>
<thead>
<tr>
<th>Stream</th>
<th>Family</th>
<th>Count total</th>
<th>Count mean</th>
<th>Count range</th>
<th>Count std. dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wilkin Run</td>
<td>Aeshnidae</td>
<td>2</td>
<td>0.02</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Amphipoda</td>
<td>19</td>
<td>0.15</td>
<td>5</td>
<td>0.33</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Ancyliidae</td>
<td>295</td>
<td>2.31</td>
<td>99</td>
<td>3.98</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Baetidae</td>
<td>4</td>
<td>0.03</td>
<td>1</td>
<td>0.05</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Belostomatidae</td>
<td>7</td>
<td>0.06</td>
<td>2</td>
<td>0.06</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Bivalvia</td>
<td>408</td>
<td>3.26</td>
<td>34</td>
<td>3.36</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Branchiobdellida</td>
<td>56</td>
<td>0.44</td>
<td>13</td>
<td>0.94</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Caenidae</td>
<td>6</td>
<td>0.05</td>
<td>1</td>
<td>0.06</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Calopterygida</td>
<td>26</td>
<td>0.21</td>
<td>3</td>
<td>0.14</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Capniidae</td>
<td>191</td>
<td>1.53</td>
<td>17</td>
<td>1.76</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Ceratopogonida</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Chironomidae</td>
<td>7236</td>
<td>56.96</td>
<td>774</td>
<td>47.49</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Coenagrionida</td>
<td>156</td>
<td>1.23</td>
<td>28</td>
<td>2.45</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Corixidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Dolichopodida</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Dryopidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Dytiscidae</td>
<td>2</td>
<td>0.02</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Elmidae</td>
<td>52</td>
<td>0.41</td>
<td>8</td>
<td>0.66</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Haliplidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Hirudinea</td>
<td>9</td>
<td>0.07</td>
<td>3</td>
<td>0.13</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Hydropsychida</td>
<td>7</td>
<td>0.05</td>
<td>2</td>
<td>0.08</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Isopoda</td>
<td>2</td>
<td>0.02</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Leptophlebiida</td>
<td>12</td>
<td>0.10</td>
<td>3</td>
<td>0.12</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Libellulidae</td>
<td>5</td>
<td>0.04</td>
<td>2</td>
<td>0.11</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Limnephilidae</td>
<td>18</td>
<td>0.14</td>
<td>3</td>
<td>0.23</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Lymnaeidae</td>
<td>7</td>
<td>0.05</td>
<td>1</td>
<td>0.08</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Oligochaeta</td>
<td>708</td>
<td>5.54</td>
<td>224</td>
<td>12.48</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Phryganeida</td>
<td>21</td>
<td>0.16</td>
<td>3</td>
<td>0.18</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Physidae</td>
<td>875</td>
<td>6.86</td>
<td>208</td>
<td>16.13</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Planorbidae</td>
<td>140</td>
<td>1.10</td>
<td>45</td>
<td>2.59</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Pleurocerida</td>
<td>76</td>
<td>0.60</td>
<td>37</td>
<td>1.04</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Ptychopterida</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Rhyacophilida</td>
<td>2</td>
<td>0.02</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Sialidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Tabanidae</td>
<td>6</td>
<td>0.05</td>
<td>1</td>
<td>0.06</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Tipulidae</td>
<td>8</td>
<td>0.06</td>
<td>1</td>
<td>0.06</td>
</tr>
<tr>
<td>Wilkin Run</td>
<td>Turbellaria</td>
<td>35</td>
<td>0.27</td>
<td>7</td>
<td>0.30</td>
</tr>
<tr>
<td>Stream</td>
<td>Family</td>
<td>Count total</td>
<td>Count mean</td>
<td>Count range</td>
<td>Count std. dev.</td>
</tr>
<tr>
<td>------------</td>
<td>-----------------</td>
<td>-------------</td>
<td>------------</td>
<td>-------------</td>
<td>-----------------</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Aeshnidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Amphipoda</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Ancyliidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Baetidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Belostomatidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Bivalvia</td>
<td>138</td>
<td>1.08</td>
<td>11</td>
<td>1.03</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Branchiobellida</td>
<td>4</td>
<td>0.03</td>
<td>2</td>
<td>0.05</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Caenidae</td>
<td>2</td>
<td>0.02</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Calopterygidae</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Capniidae</td>
<td>20</td>
<td>0.16</td>
<td>6</td>
<td>0.34</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Ceratopogonida</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Chironomidae</td>
<td>512</td>
<td>4.02</td>
<td>30</td>
<td>3.20</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Coenagrionidae</td>
<td>40</td>
<td>0.31</td>
<td>6</td>
<td>0.52</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Corixidae</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Dolichopodidae</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Dryopidae</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Dytiscidae</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Elmidae</td>
<td>32</td>
<td>0.26</td>
<td>5</td>
<td>0.24</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Haliplidae</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Hirudinea</td>
<td>12</td>
<td>0.09</td>
<td>2</td>
<td>0.11</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Hydropsychidae</td>
<td>2</td>
<td>0.02</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Isopoda</td>
<td>27</td>
<td>0.21</td>
<td>4</td>
<td>0.22</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Leptophlebiidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Libellulida</td>
<td>1</td>
<td>0.01</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Lymneophilidae</td>
<td>2</td>
<td>0.02</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Lymnaeidae</td>
<td>45</td>
<td>0.36</td>
<td>6</td>
<td>0.54</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Oligochaeta</td>
<td>1252</td>
<td>9.78</td>
<td>131</td>
<td>8.57</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Oligochaeta</td>
<td>6</td>
<td>0.05</td>
<td>1</td>
<td>0.06</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Physidae</td>
<td>365</td>
<td>2.90</td>
<td>27</td>
<td>1.74</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Planorbidae</td>
<td>16</td>
<td>0.13</td>
<td>3</td>
<td>0.20</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Pleuroceridae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Ptychopteridae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Rhyacophilidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Sialidae</td>
<td>2</td>
<td>0.02</td>
<td>1</td>
<td>0.03</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Tabanidae</td>
<td>2</td>
<td>0.02</td>
<td>1</td>
<td>0.04</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Tipulidae</td>
<td>61</td>
<td>0.48</td>
<td>6</td>
<td>0.48</td>
</tr>
<tr>
<td>Fox Creek</td>
<td>Turbellaria</td>
<td>22</td>
<td>0.18</td>
<td>5</td>
<td>0.27</td>
</tr>
<tr>
<td>Stream</td>
<td>Family</td>
<td>Count total</td>
<td>Count mean</td>
<td>Count range</td>
<td>Count std. dev.</td>
</tr>
<tr>
<td>--------</td>
<td>-------------------</td>
<td>-------------</td>
<td>------------</td>
<td>-------------</td>
<td>-----------------</td>
</tr>
<tr>
<td>BA</td>
<td>Calopterygidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>BA</td>
<td>Ceratopogonidae</td>
<td>59</td>
<td>2.95</td>
<td>32</td>
<td>6.05</td>
</tr>
<tr>
<td>BA</td>
<td>Chironomidae</td>
<td>1326</td>
<td>71.70</td>
<td>245</td>
<td>71.13</td>
</tr>
<tr>
<td>BA</td>
<td>Culicidae</td>
<td>2</td>
<td>0.10</td>
<td>1</td>
<td>0.21</td>
</tr>
<tr>
<td>BA</td>
<td>Dolichopodidae</td>
<td>41</td>
<td>2.70</td>
<td>13</td>
<td>4.20</td>
</tr>
<tr>
<td>BA</td>
<td>Empididae</td>
<td>4</td>
<td>0.20</td>
<td>2</td>
<td>0.48</td>
</tr>
<tr>
<td>BA</td>
<td>Ephyridae</td>
<td>6</td>
<td>0.30</td>
<td>2</td>
<td>0.42</td>
</tr>
<tr>
<td>BA</td>
<td>Helicopsychidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>BA</td>
<td>Heptageniidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>BA</td>
<td>Leptoceridae</td>
<td>1</td>
<td>0.05</td>
<td>1</td>
<td>0.16</td>
</tr>
<tr>
<td>BA</td>
<td>Molannidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>BA</td>
<td>Philopotamidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>BA</td>
<td>Phoridae</td>
<td>4</td>
<td>0.20</td>
<td>1</td>
<td>0.26</td>
</tr>
<tr>
<td>BA</td>
<td>Polycentropodidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>BA</td>
<td>Psychodidae</td>
<td>22</td>
<td>1.10</td>
<td>7</td>
<td>1.37</td>
</tr>
<tr>
<td>BA</td>
<td>Psychomyiidae</td>
<td>20</td>
<td>1</td>
<td>6</td>
<td>1.49</td>
</tr>
<tr>
<td>BA</td>
<td>Scathophagidae</td>
<td>1</td>
<td>0.05</td>
<td>1</td>
<td>0.16</td>
</tr>
<tr>
<td>BA</td>
<td>Sciomyzidae</td>
<td>2</td>
<td>0.10</td>
<td>1</td>
<td>0.21</td>
</tr>
<tr>
<td>BA</td>
<td>Stratiomyiidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>BA</td>
<td>Tipulidae</td>
<td>58</td>
<td>2.90</td>
<td>12</td>
<td>3.48</td>
</tr>
<tr>
<td>Stream</td>
<td>Family</td>
<td>Count total</td>
<td>Count mean</td>
<td>Count range</td>
<td>Count std. dev.</td>
</tr>
<tr>
<td>--------</td>
<td>-------------------</td>
<td>-------------</td>
<td>------------</td>
<td>-------------</td>
<td>----------------</td>
</tr>
<tr>
<td>CA</td>
<td>Calopterygidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>CA</td>
<td>Ceratopogonidae</td>
<td>4</td>
<td>0.33</td>
<td>2</td>
<td>0.71</td>
</tr>
<tr>
<td>CA</td>
<td>Chironomidae</td>
<td>1463</td>
<td>81.28</td>
<td>262</td>
<td>89.84</td>
</tr>
<tr>
<td>CA</td>
<td>Culicidae</td>
<td>17</td>
<td>1.06</td>
<td>8</td>
<td>1.55</td>
</tr>
<tr>
<td>CA</td>
<td>Dolichopodidae</td>
<td>22</td>
<td>1.83</td>
<td>11</td>
<td>3.49</td>
</tr>
<tr>
<td>CA</td>
<td>Empididae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>CA</td>
<td>Ephydridae</td>
<td>3</td>
<td>0.22</td>
<td>1</td>
<td>0.36</td>
</tr>
<tr>
<td>CA</td>
<td>Helicopsychidae</td>
<td>1</td>
<td>0.06</td>
<td>1</td>
<td>0.17</td>
</tr>
<tr>
<td>CA</td>
<td>Heptageniidae</td>
<td>92</td>
<td>5.11</td>
<td>34</td>
<td>8.16</td>
</tr>
<tr>
<td>CA</td>
<td>Leptoceridae</td>
<td>2</td>
<td>0.11</td>
<td>1</td>
<td>0.22</td>
</tr>
<tr>
<td>CA</td>
<td>Molannidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>CA</td>
<td>Philopotamidae</td>
<td>1</td>
<td>0.06</td>
<td>1</td>
<td>0.17</td>
</tr>
<tr>
<td>CA</td>
<td>Phoridae</td>
<td>19</td>
<td>1.11</td>
<td>10</td>
<td>1.65</td>
</tr>
<tr>
<td>CA</td>
<td>Polycentropodidae</td>
<td>10</td>
<td>0.56</td>
<td>4</td>
<td>0.73</td>
</tr>
<tr>
<td>CA</td>
<td>Psychodidae</td>
<td>8</td>
<td>0.5</td>
<td>2</td>
<td>0.66</td>
</tr>
<tr>
<td>CA</td>
<td>Psychomyiidae</td>
<td>3</td>
<td>0.17</td>
<td>2</td>
<td>0.50</td>
</tr>
<tr>
<td>CA</td>
<td>Scathophagidae</td>
<td>1</td>
<td>0.11</td>
<td>1</td>
<td>0.33</td>
</tr>
<tr>
<td>CA</td>
<td>Sciomyzidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>CA</td>
<td>Stratiomyidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>CA</td>
<td>Tipulidae</td>
<td>14</td>
<td>0.83</td>
<td>4</td>
<td>1.30</td>
</tr>
<tr>
<td>Stream</td>
<td>Family</td>
<td>Count total</td>
<td>Count mean</td>
<td>Count range</td>
<td>Count std. dev.</td>
</tr>
<tr>
<td>--------</td>
<td>------------</td>
<td>-------------</td>
<td>------------</td>
<td>-------------</td>
<td>-----------------</td>
</tr>
<tr>
<td>WA</td>
<td>Calopterygidae</td>
<td>1</td>
<td>0.06</td>
<td>1</td>
<td>0.17</td>
</tr>
<tr>
<td>WA</td>
<td>Ceratopogonidae</td>
<td>8</td>
<td>0.44</td>
<td>2</td>
<td>0.39</td>
</tr>
<tr>
<td>WA</td>
<td>Chironomidae</td>
<td>4574</td>
<td>254.11</td>
<td>978</td>
<td>254.18</td>
</tr>
<tr>
<td>WA</td>
<td>Culicidae</td>
<td>2</td>
<td>0.11</td>
<td>1</td>
<td>0.22</td>
</tr>
<tr>
<td>WA</td>
<td>Dolichopodidae</td>
<td>11</td>
<td>0.61</td>
<td>2</td>
<td>0.55</td>
</tr>
<tr>
<td>WA</td>
<td>Empididae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>Ephyridae</td>
<td>1</td>
<td>0.06</td>
<td>1</td>
<td>0.17</td>
</tr>
<tr>
<td>WA</td>
<td>Helicopsychidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>Heptageniidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>Leptoceridae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>Molannidae</td>
<td>1</td>
<td>0.06</td>
<td>1</td>
<td>0.17</td>
</tr>
<tr>
<td>WA</td>
<td>Philopotamidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>Phoridae</td>
<td>22</td>
<td>1.22</td>
<td>13</td>
<td>2.14</td>
</tr>
<tr>
<td>WA</td>
<td>Polycentropodidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>Psychodidae</td>
<td>1</td>
<td>0.06</td>
<td>1</td>
<td>0.17</td>
</tr>
<tr>
<td>WA</td>
<td>Psychomyiidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>Scathophagidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>Sciomyzidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>Stratiomyiidae</td>
<td>1</td>
<td>0.06</td>
<td>1</td>
<td>0.17</td>
</tr>
<tr>
<td>WA</td>
<td>Tipulidae</td>
<td>8</td>
<td>0.44</td>
<td>4</td>
<td>0.68</td>
</tr>
</tbody>
</table>
Appendix C: Estimates of the wet mass of leaves used to estimate stable isotope composition and resource quality (C:N) of terrestrial energy sources in chapter 4. Distance from the upstream edge is measured in meters and woody and herbaceous leaf mass is measured in grams. Woody leaf mass corresponds to allochthonous leaf inputs from terrestrial woody plants, and herbaceous leaf mass corresponds to allochthonous leaf inputs from terrestrial herbaceous plants.
<table>
<thead>
<tr>
<th>Stream</th>
<th>Distance from upstream edge</th>
<th>Woody leaf mass</th>
<th>Herbaceous leaf mass</th>
</tr>
</thead>
<tbody>
<tr>
<td>BA</td>
<td>-89</td>
<td>2.15</td>
<td>26.58</td>
</tr>
<tr>
<td>BA</td>
<td>-45</td>
<td>1.31</td>
<td>18.87</td>
</tr>
<tr>
<td>BA</td>
<td>20</td>
<td>31.34</td>
<td>0.27</td>
</tr>
<tr>
<td>BA</td>
<td>133</td>
<td>25.85</td>
<td>0.42</td>
</tr>
<tr>
<td>BA</td>
<td>252</td>
<td>18.72</td>
<td>0</td>
</tr>
<tr>
<td>BA</td>
<td>556</td>
<td>22.22</td>
<td>0</td>
</tr>
<tr>
<td>BA</td>
<td>756</td>
<td>13.24</td>
<td>0</td>
</tr>
<tr>
<td>BA</td>
<td>840</td>
<td>19.71</td>
<td>14.60</td>
</tr>
<tr>
<td>BA</td>
<td>905</td>
<td>4.08</td>
<td>27.95</td>
</tr>
<tr>
<td>BA</td>
<td>1000</td>
<td>0.05</td>
<td>35.54</td>
</tr>
<tr>
<td>CA</td>
<td>-96</td>
<td>0</td>
<td>58.35</td>
</tr>
<tr>
<td>CA</td>
<td>-61</td>
<td>0</td>
<td>51.91</td>
</tr>
<tr>
<td>CA</td>
<td>15</td>
<td>36.31</td>
<td>3.79</td>
</tr>
<tr>
<td>CA</td>
<td>104</td>
<td>8.21</td>
<td>34.04</td>
</tr>
<tr>
<td>CA</td>
<td>252</td>
<td>3.13</td>
<td>5.50</td>
</tr>
<tr>
<td>CA</td>
<td>520</td>
<td>6.42</td>
<td>10.56</td>
</tr>
<tr>
<td>CA</td>
<td>727</td>
<td>4.67</td>
<td>6.99</td>
</tr>
<tr>
<td>CA</td>
<td>764</td>
<td>0</td>
<td>41.04</td>
</tr>
<tr>
<td>CA</td>
<td>815</td>
<td>0</td>
<td>40.20</td>
</tr>
<tr>
<td>WA</td>
<td>-50</td>
<td>26.48</td>
<td>51.79</td>
</tr>
<tr>
<td>WA</td>
<td>-33</td>
<td>6.44</td>
<td>32.61</td>
</tr>
<tr>
<td>WA</td>
<td>5</td>
<td>4.58</td>
<td>25.23</td>
</tr>
<tr>
<td>WA</td>
<td>126</td>
<td>37.44</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>249</td>
<td>51.29</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>510</td>
<td>31.07</td>
<td>0.31</td>
</tr>
<tr>
<td>WA</td>
<td>621</td>
<td>28.01</td>
<td>0</td>
</tr>
<tr>
<td>WA</td>
<td>702</td>
<td>0.01</td>
<td>41.92</td>
</tr>
<tr>
<td>WA</td>
<td>732</td>
<td>3.36</td>
<td>55.10</td>
</tr>
</tbody>
</table>