



Shifts in attributes along agriculture–forest transitions of two streams in central Ohio, USA



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ABSTRACT

Riparian forests are strongly linked to stream ecosystems, and the creation and/or conservation of riparian forests can mitigate the influence of agriculture on streams. Although riparian forest buffers are commonly advocated as best management practices, the extent of forest necessary to effectively mitigate upstream agricultural effects on streams remains unresolved. To determine how soon agricultural streams exhibit detectable effects after entering forest fragments, we surveyed sixteen sites distributed across two 2nd-order headwater streams in agricultural landscapes of central Ohio that exhibit abrupt transitions as they flow from upstream agricultural land up to 1 km into downstream forest fragments. Along these transitions we measured leaf-colonizing benthic macroinvertebrate assemblages, leaf-litter breakdown, and physicochemical habitat. Our results indicated that forest fragments can rapidly alter physicochemical and biological attributes of agricultural streams. At both study streams, daily maximum temperature declined within the first 200 m of entering forest fragments. Changes in water quality were more variable, but there was evidence of a strong decline in NO₃-N along an agriculture–forest transition. There was also evidence of a decline in fine sediment with distance into the forest at one stream. Aquatic macroinvertebrate assemblages exhibited strong changes in composition ranging from the forest edge up to 324 m into forest fragments. Taxa that declined after entering forests were generally more tolerant of anthropogenic disturbance and/or those that rely on in-stream primary productivity (i.e., scrapers) whereas most of the taxa that increased after entering forests were relatively sensitive to disturbance and rely on allochthonous organic matter inputs from the forest (i.e., shredders). Collectively, the rapid changes in biological and physicochemical attributes that we observed suggest that even relatively small forest fragments may be able to markedly influence impaired streams and that conservation and restoration of small, discontinuous forest fragments may be important for maintaining stream ecosystem integrity in agricultural landscapes.

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1. Introduction

Land-use and land-cover change has resulted in the widespread replacement of natural ecosystems with intensive agricultural and urban land uses (Foley et al., 2005). As streams and rivers are located at catchment low-points, they integrate land-use activities across catchments and thus are particularly vulnerable to anthropogenic disturbance. In the US, it has been estimated that over 40% of the nations' streams are in poor condition (US EPA, 2006), and a major driver of this impairment is agricultural land use. Agricultural practices (e.g., crop and livestock production)

have a variety of effects on streams including increased erosion and deposition of fine sediment, nutrient enrichment (i.e., nitrogen (N) and phosphorus (P)), and disturbances to the riparian area (Quinn, 2000; Allan, 2004). Agriculture is the dominant land use in the Midwestern US (Lubowski et al., 2006), and agricultural effects on streams and rivers in the Midwest have been implicated as drivers of water-quality problems in downstream receiving waterbodies including Lake Erie (Myers et al., 2000) and extending to the Gulf of Mexico (Mitsch et al., 2001).

In an effort to minimize the effects of agricultural land use on aquatic systems, forested riparian buffers are often advocated as effective best management practices (Lowrance et al., 1997; Sweeney et al., 2004). Riparian forest buffers have been shown to decrease sediment inputs (Zaimis et al., 2004; Wynn and Mostaghimi, 2006), and reduce concentrations of N (Lowrance

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et al., 1984; Osborne and Kovacic, 1993) and P (Cooper and Gilliam, 1987; Borin et al., 2005) through bank stabilization, nutrient uptake, and settling of sediment-bound nutrients. Riparian forests also regulate stream temperatures, provide food resources and habitat for aquatic biota (Gregory et al., 1991; Naiman and Decamps, 1997), and can strongly influence stream ecosystem processes such as the breakdown of leaf litter (e.g., Paul et al., 2006). Although numerous studies have described the influence of riparian buffer characteristics (e.g., width and composition) on the relative capacity of buffers to ameliorate agricultural effects on streams (Osborne and Kovacic, 1993; Broadmeadow and Nisbet, 2004), studies addressing the extent of forested buffer necessary to mitigate upstream agricultural effects are rare.

In pastoral catchments of New Zealand, Storey and Cowley (1997) and Scarsbrook and Halliday (1999) observed that in small headwater streams (both 2nd-order, ranging from a maximum width of 0.6 m (Storey and Cowley) to ~1.8 m (Scarsbrook and Halliday)), reaches in forest fragments downstream of agricultural land attained reference conditions for a variety of attributes within the first several hundred meters of entering a forest. The distance at which streams began to recover was contingent on the attribute considered and the responses were not always consistent between studies. For example, both Storey and Cowley (1997) and Scarsbrook and Halliday (1999) found evidence for aquatic macroinvertebrate recovery after entering forests, whereas only Storey and Cowley found evidence for an appreciable influence of forests on $\text{NO}_3\text{-N}$. In larger streams of New Zealand (3rd-order, up to 5.4 m wide), the influence of forest fragments on agricultural stream attributes was largely undetectable (Harding et al., 2006). Whereas the effects of forest fragments on agricultural streams have also been observed in South America (Suga and Tanaka, 2013) and Africa (Chakona et al., 2009), information on how agricultural streams respond after entering forests in the US is largely lacking (but see Houghton et al., 2011). Therefore, a general understanding of the influence of forest fragments on agricultural streams and the distance at which stream conditions can be expected to recover remains elusive.

In the current study, we explored the potential of forest fragments to mitigate land-use effects on streams draining agricultural landscapes in the US Midwest. To this end, we established longitudinal transects along agriculture-to-forest

transitions in two central Ohio headwater streams (Fig. 1). Along these transitions we measured a variety of stream attributes that are often used as indicators of land-use effects including: physical habitat, stream temperature, nutrient concentrations (N and P), leaf-colonizing aquatic macroinvertebrate assemblages, and leaf-litter breakdown. Based on previous studies of forested and agricultural stream reaches (Quinn et al., 1997; Storey and Cowley, 1997; Scarsbrook and Halliday, 1999), we expected that as agricultural streams transition into forests they become wider, have coarser surficial sediment, have lower temperature and nutrient concentrations, and are increasingly dominated by macroinvertebrate assemblages characterized by taxa sensitive to disturbance (e.g., EPT taxa and shredders). We also expected there to be a shift in leaf breakdown, however, the expected direction of land-use effects on breakdown was uncertain as evidence to date is equivocal (for decreases: Sponseller and Benfield, 2001; for increases: Paul et al., 2006). Our results provide initial evidence of the potential for forest fragments to mitigate agricultural influences on streams in midwestern US agricultural landscapes.

2. Methods

2.1. Study area

We sampled eight sites within each of two study streams, Fox Creek and Wilkin Run in the Sugar Creek and Mohican River watersheds, respectively (Fig. 1). The study streams are located in the headwaters of the Ohio River basin and the Low Lime Drift Plain ecoregion in central Ohio (Omernik and Griffith, 2013), and represented appropriate model systems for our study as common features of these catchments include a dominance of agricultural land use with small fragments of forest scattered across the landscape. Both Fox Creek and Wilkin Run are 2nd-order headwater streams, and at the site furthest into the forest they drain 740 and 700 ha, respectively. At Wilkin Run the dominant local land use upstream of the forest 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. The forest fragment is over 20 ha in area and the most

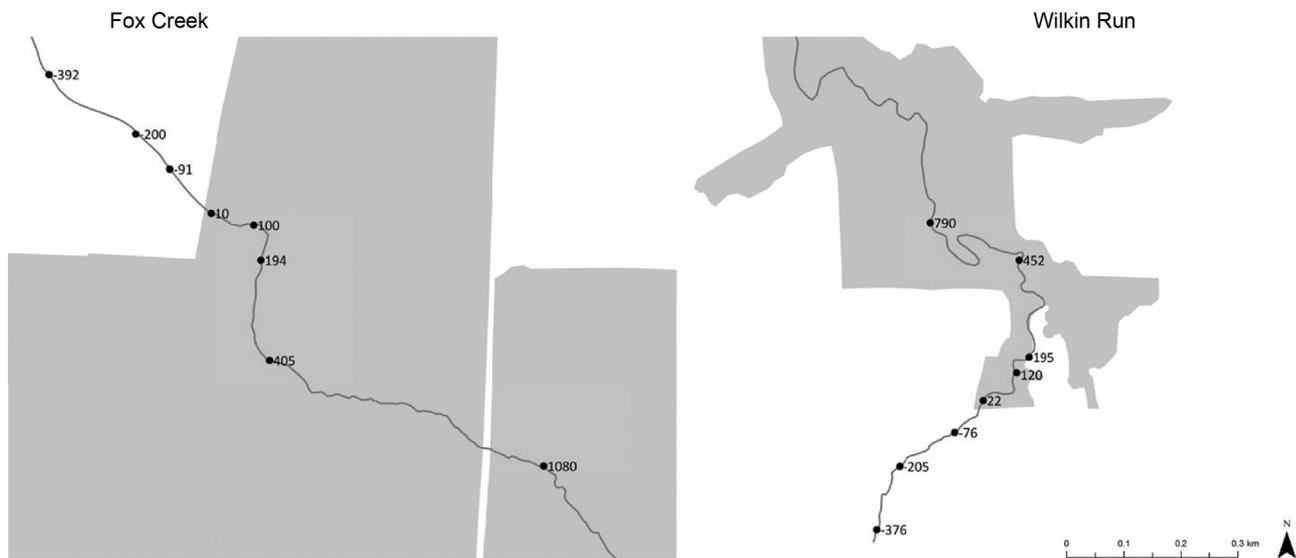


Fig. 1. Illustrations of sampling design at Fox Creek (left) and Wilkin Run (right). Grey shading corresponds to forest fragments (woody and herbaceous vegetation, and other natural areas); white areas are predominantly agricultural land (active or retired), but also correspond to residential areas and roads. The numbers correspond to the distance from the forest edge (m) with negative numbers signifying upstream of the forest (agriculture) and positive numbers indicating the forest interior. See methods for more details.

downstream sampling site drains ~7 ha of this forest. 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 downstream and upstream of the 120 and 452 m study sites, respectively (adjacent to the 195 m study site). Land use at Fox Creek is more mixed: immediately upstream of the forest, 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 (surrounding site 392 m upstream of forest) there is pasture where cattle have access to the stream. The forest fragment is over 150 ha in area and the most downstream sampling site drains ~87 ha of this forest. The forest is dominated by woody vegetation with areas of herbaceous vegetation and other aquatic ecosystems (e.g., wetlands) 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.

2.2. Leaf breakdown and macroinvertebrate assemblages

In the fall of 2010 (October through December), we assessed changes in leaf-litter breakdown and leaf-colonizing benthic macroinvertebrate assemblages along transitions between agricultural land and forests, 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 streams. 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 scour pools of the study streams (Bisson et al., 2006) where there was evidence of natural leaf accumulations. To obtain an estimate of changes in leaf breakdown and macroinvertebrate assemblages 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, and 1080 m into the forest at Fox Creek. In all of our analyses, distances were 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 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 h). Prior to drying, we washed the leaves clean of sediment, extraneous organic matter, and macroinvertebrates over a 250 μm sieve. Macroinvertebrates washed from the leaves were picked out of the 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*).

The washed leaves were put into brown paper bags and placed in drying ovens at 40–50 °C for ≥ 48 h. After drying, the leaves were

weighed and subsequently ground in a Wiley mill and stored in a drying oven at 40–50 °C until estimation of ash free dry mass (AFDM). Percent organic matter composition of the leaves was estimated by weighing out subsamples (mean between 0.26–1.0 g) and placing the samples in a muffle furnace at 500 °C for ~4 h. 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 dry mass of individual leaf bags by the percent organic matter estimates (Benfield, 2006).

2.3. Environmental conditions

We estimated variation in temperature throughout the study with Hobo[®] data loggers (Onset Computer Corporation, Massachusetts) that were centrally located at the bottom of the pool at each of the 16 study sites (8/stream). The data loggers were set to record temperature every 5 min for the duration of the 42-day experiment. 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 ($\text{NO}_3\text{-N}$, $\text{NH}_3\text{-N}$, total N) and phosphorus ($\text{PO}_4\text{-P}$ and total P) using the QuikChem[®] 8500 Series 2 Flow Injection Analysis System (Hach Company, Colorado). All water samples were stored in a dark location and then filtered using 0.45 μm mixed cellulose filters in the lab 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 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. As a rough characterization of sediment composition, we assigned each particle to one of 3 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 data 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. The physical characteristics, however, of most of the sites appeared to be unaffected by this flood and we interpret data collected in the summer of 2011 accordingly.

2.4. Statistical analyses

We used a suite of methods to explore the distance at which aquatic macroinvertebrates, leaf-litter breakdown, and environmental conditions exhibited shifts 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). Although TITAN is typically used for larger datasets (e.g., King et al., 2011; Bernhardt et al., 2012), we explored its use for detecting shifts in aquatic macroinvertebrate assemblages as an initial step towards determining how quickly these assemblages shift after entering forests. This method uses an indicator species analysis (Dufrene and Legendre, 1997) to obtain 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 scores after reaching the threshold) along

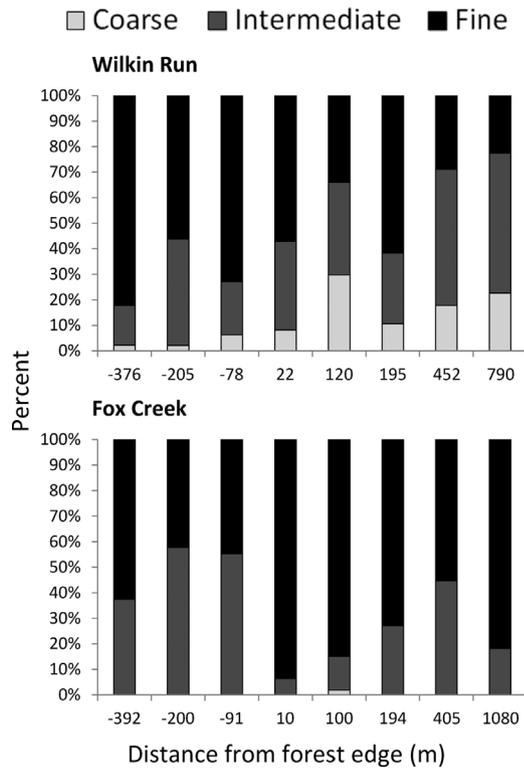


Fig. 2. Bar graphs of sediment composition collected from a 10 meter area surrounding the center of pools at Wilkin Run (top) and Fox Creek (bottom). Each particle was assigned to one of 3 relative size classes: fine (<4 mm), intermediate (4–45 mm), and coarse (>45 mm).

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 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 and determining where the maximum value occurs at a particular location along the environmental gradient. The response variables used for the TITAN analyses were the mean number of macroinvertebrates collected at a given site/date resulting in 4 observations at each site along our sampling transects. We removed taxa with less than five values (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 change points 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 1000 bootstrap replicates to generate 90% bootstrap percentile confidence intervals. In addition to the TITAN analysis, we plotted shredder (family level shredder designations obtained from Barbour et al., 1999) and stonefly (Capniidae was the only stonefly family captured in this study)

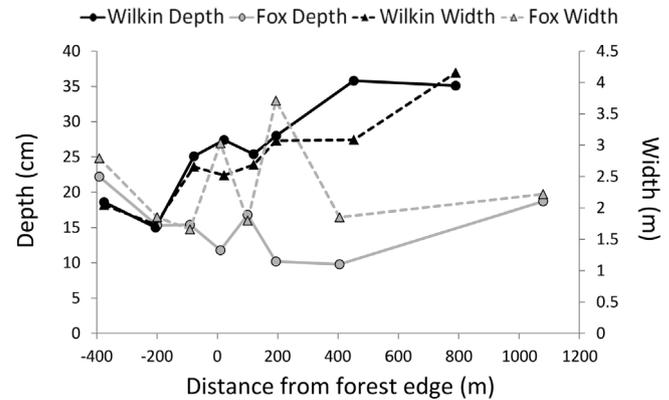


Fig. 3. Line graphs of mean pool depth and width at Wilkin Run (black) and Fox Creek (grey).

density along the distance gradient as taxa in these groups are often good indicators of stream quality.

As a complement to TITAN, we analyzed environmental conditions and leaf breakdown using two different threshold models. The first model 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 from the forest edge) 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 linear 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 the step function and piecewise models fit better than models assuming no shift in relationship, we also modeled the data using a simple linear regression and an intercept-only model. We assessed model fit by calculating the Akaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham and Anderson, 2002). 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 $\beta_0 + \delta + \text{error}_2$ if $x \geq \text{threshold}$ (Qian and Cuffney, 2012); and six for the piecewise linear regression: $\beta_0 + \beta_1 x + \beta_2 (x - \text{threshold}) + \gamma I(x > \text{threshold}) + \text{error}$, where $I(A)$ is an indicator function and equals 1 if A is true, and γ is a parameter that estimates the gap between the 2 regression lines at the threshold (Muggeo, 2008). Although our modelling effort was more exploratory than confirmatory (Burnham and Anderson, 2002), we interpreted models with an AICc of ≥ 2 less than all other models as the best model in the set; models that had AICc values within 2 of the best model were interpreted as having equal empirical evidence.

Our response variables for these analyses included temperature, nutrients ($\text{NO}_3\text{-N}$, $\text{NH}_3\text{-N}$, total N, $\text{PO}_4\text{-P}$, and total P) and the proportion of leaf mass remaining at the end of the study (natural log transformed ash-free dry mass). Overall leaf-litter breakdown rates showed similar patterns to the proportion of leaf mass remaining at the end of the study (data not shown), and we used the latter in our analysis because it allowed us to incorporate intra-site variation into our statistical analyses. For temperature, leaf-fall and colder temperatures generally caused convergence in temperature among the sampling sites; in order to determine whether the forest had any effect on stream temperature we restricted our analyses to those days that exhibited the largest range among sites in the daily maximum temperatures (i.e., only those data in the 35th percentile

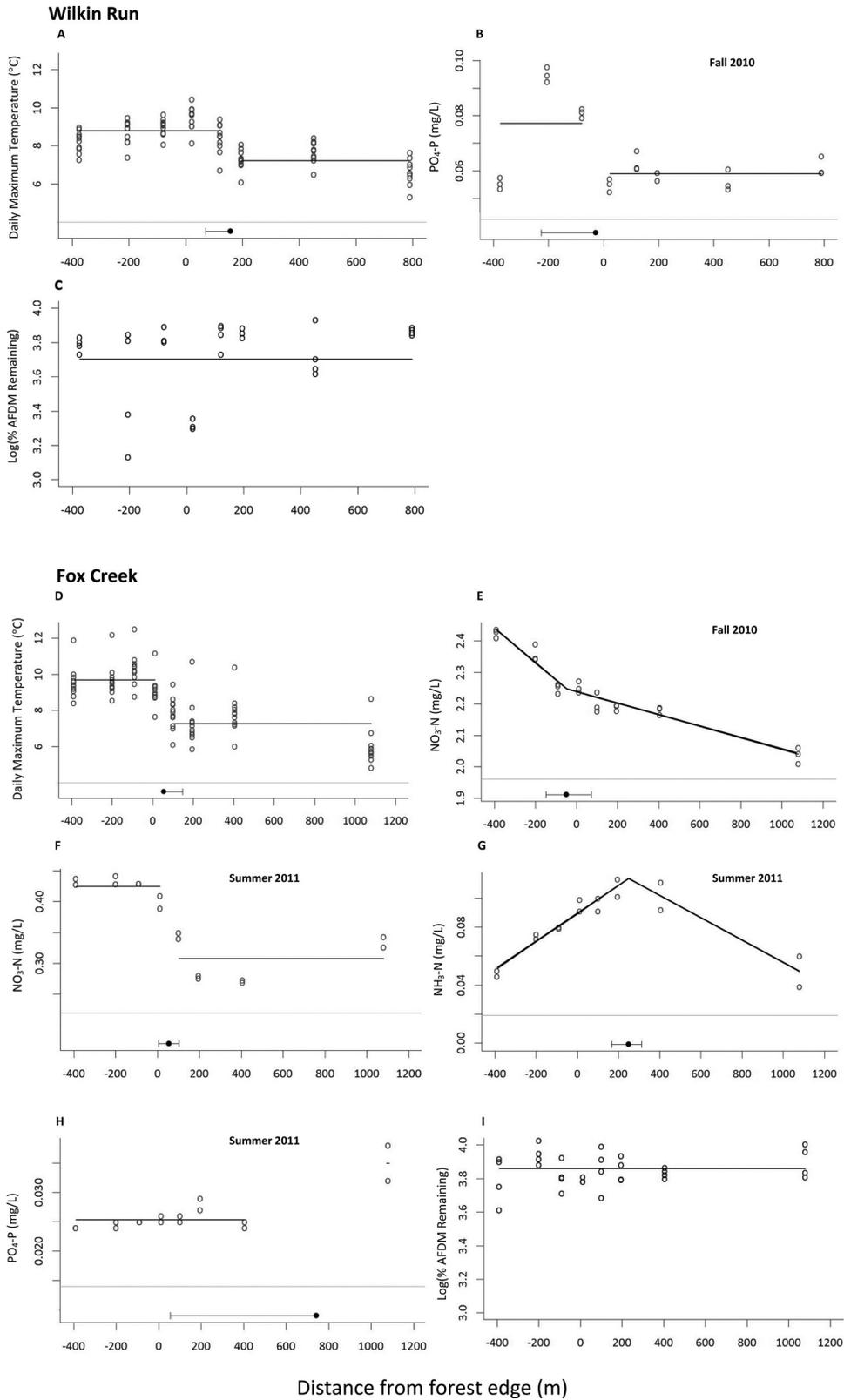


Fig. 4. Plots of the model fit (solid line) overlaid on the observed data (open circles) from the multimodel threshold analysis for fall daily maximum water temperatures (A and D; see Section 2 for more details on daily maximum water temperature estimates), PO₄-P (B and H), NO₃-N (E and F), NH₃-N (G), and %AFDM remaining (C and I). 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.

Table 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 (rounded to the nearest integer). 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 Section 2 for more details.

Wilkin Run					
Parameter	Model				
	Intercept	Linear	Step	Piecewise	Threshold
Leaf Mass	-80.54*	-79.74*	-79.43*(71)	-74.16(0)	No
Temperature	12.64	-21.15	-38.47*(158)	-37.82*(-71)	Yes
NH ₃ -N 2010	-140.52*	-142.18*	-138.45(-142)	-134.7(-35)	No
NH ₃ -N 2011	-22.94*	-22.77*	-17.18(-142)	DNC	No
NO ₃ -N 2010	-130.27*	-129.81*	-126.65(-291)	DNC	No
NO ₃ -N 2011	-41.10*	-39.21*	-33.58(-142)	DNC	No
PO ₄ -P 2010	-201.01	-201.29	-205.1*(-28)	DNC	Yes
PO ₄ -P 2011	-79.04	-86.41	-98.5*(-142)	-79.03(22)	No
Total N 2010	-46.08*	-47.48*	-44.02(324)	-38.63(123)	No
Total N 2011	-2.35*	-2.61*	2.91(-142)	DNC	No
Total P 2010	-170.14	-172.54*	-167.55(621)	DNC	No
Total P 2011	-73.99	-83.92	-93.14*(-142)	-77.39(10)	No

Fox Creek					
Parameter	Model				
	Intercept	Linear	Step	Piecewise	Threshold
Leaf Mass	-143.69*	-141.96*	-137.64(-296)	DNC	No
Temperature	92.25	29.02*	30.81*(55)	33.47(146)	Yes
NH ₃ -N 2010	-179.01*	-180.05*	-174.38(743)	DNC	No
NH ₃ -N 2011	-117.01	-114	-112.13(-296)	-139.74*(249)	Yes
NO ₃ -N 2010	-100.7	-146.12	-116.72(-146)	-161.92*(-49)	Yes
NO ₃ -N 2011	-82.92	-87.98	-100.61*(55)	-93.68(399)	Yes
PO ₄ -P 2010	-294.55	-296.85*	-297.17*(-146)	-288.69(188)	No
PO ₄ -P 2011	-175.09	-190.38*	-189.28*(743)	DNC	Yes
Total N 2010	-57.86	-91.73*	-86.36(743)	DNC	No
Total N 2011	-53.95	-57.93*	-53.47(147)	-47.78(-118)	No
Total P 2010	-243.68*	-242.52*	-240.77(-146)	-235.11(14)	No
Total P 2011	-139.47*	-136.43	-134.38(-41)	-129.51(368)	No

of the maximum range in daily maximum temps at a stream (10–11 obs./site)). For our analysis of nutrients, the observations included 1–3 samples taken at each site (taken in 2010 and 2011) and for leaf mass our observations included 4 leafbag samples/site. By analyzing multiple observations at a single site through time

(macroinvertebrates and temperature) or space (nutrients and leaf mass), we acknowledge that the response variables used in our analyses violate assumptions of independence typical of most statistical models. However, our study design precluded replication across streams as the distances and local conditions are not replicable among streams. Nonetheless, this approach is consistent with other studies where true replicates have been unobtainable (e.g., Davis et al., 2011).

To estimate the location of thresholds, we constrained the potential model set based on expectations that forests 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.

3. Results

3.1. Physical habitat

Both sediment composition and pool dimensions shifted as streams transitioned from agricultural land to forest fragments. At Wilkin Run sediment composition ranged from >80% fine and about 2% coarse 376 m upstream of the forest patch to ~23% for both fine and coarse after the stream had flowed 790 m into the forest patch. Alternatively, at Fox Creek, fine sediment exhibited a

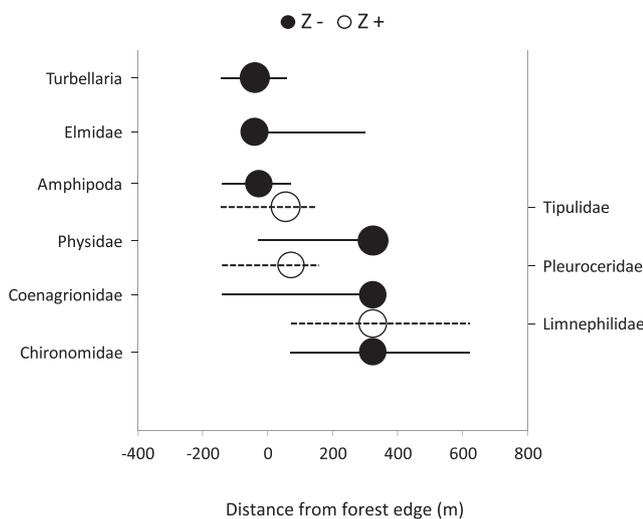


Fig. 5. 90% bootstrap percentile confidence interval estimates of the threshold distance obtained from the TITAN analysis. z- corresponds to taxa that decreased following the threshold (left axis) and z+ corresponds to taxa that increased after the threshold (right axis). The size of the dot corresponds to the relative size of the original indicator value estimate. Elmidae, Tipulidae, and Turbellaria are estimated

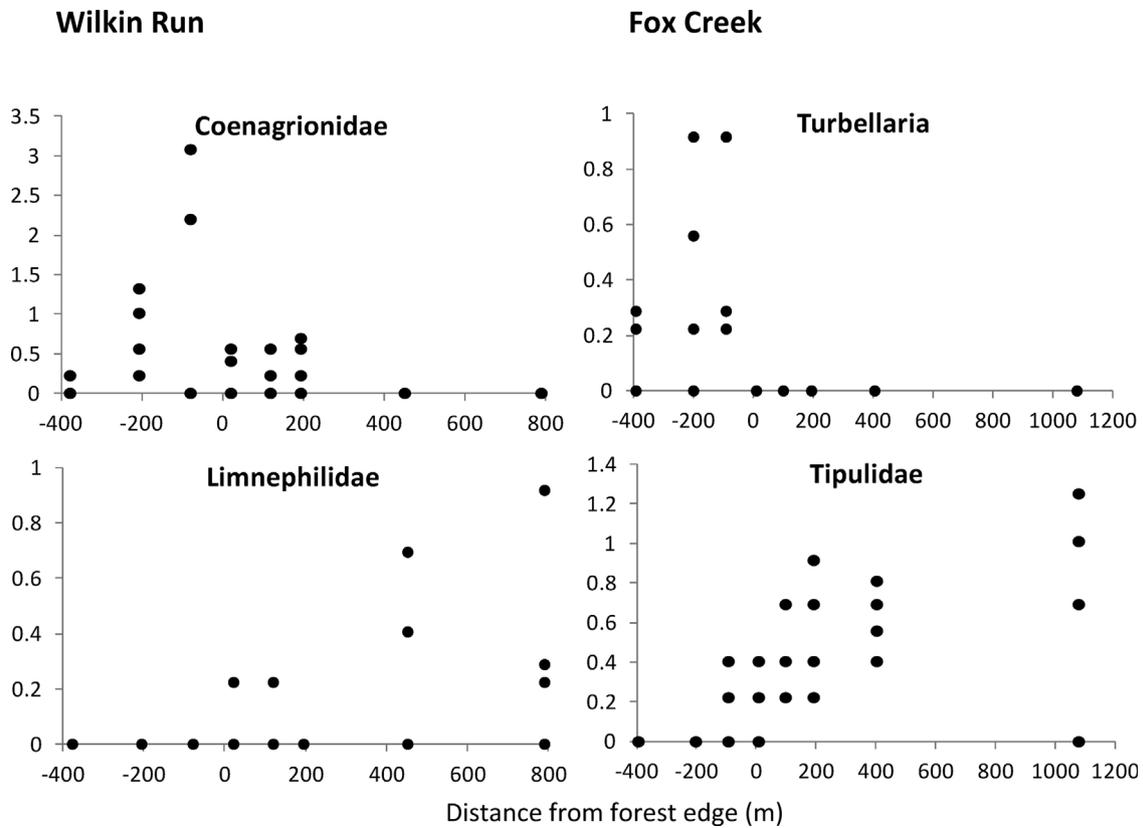


Fig. 6. Scatter plots of the mean number of macroinvertebrates sampled on each sampling date (black dots) vs distance for decreasing taxa (top) and increasing taxa (bottom) at Wilkin Run (left) and Fox Creek (right).

sharp increase at the edge of the forest and then decreased until about 405 m into the forest patch followed by another increase by 1080 m (Fig. 2). As with sediment composition, pool dimensions at Wilkin Run exhibited sharp increases in width and depth just upstream of the forest (−78 m) and then increases in depth at 452 m and width at 790 m. In contrast, the pools at Fox Creek showed no systematic changes in dimensions along the agriculture-forest transition (Fig. 3).

3.2. Multimodel threshold analysis of temperature, nutrients, and leaf-mass loss

We found evidence for strong shifts in several parameters soon after entering forest fragments (Fig. 4). In both study streams, daily

maximum temperature declined soon after entering the forest. 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 1; Fig. 4A and D). Results from our analysis of nutrient concentrations were more inconsistent. At Wilkin Run the only nutrient parameter that indicated a possible forest-mediated shift was PO₄-P in 2010 (Table 1; Fig. 4B). In Fox Creek, the threshold models were among the best models for NO₃-N in 2010 and 2011, NH₃-N in 2011, and PO₄-P in 2011 (Table 1; Fig. 4E–H). 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 1; Fig. 4C and I).

Model estimates of the threshold points indicated that shifts in environmental conditions typically occurred shortly after entering

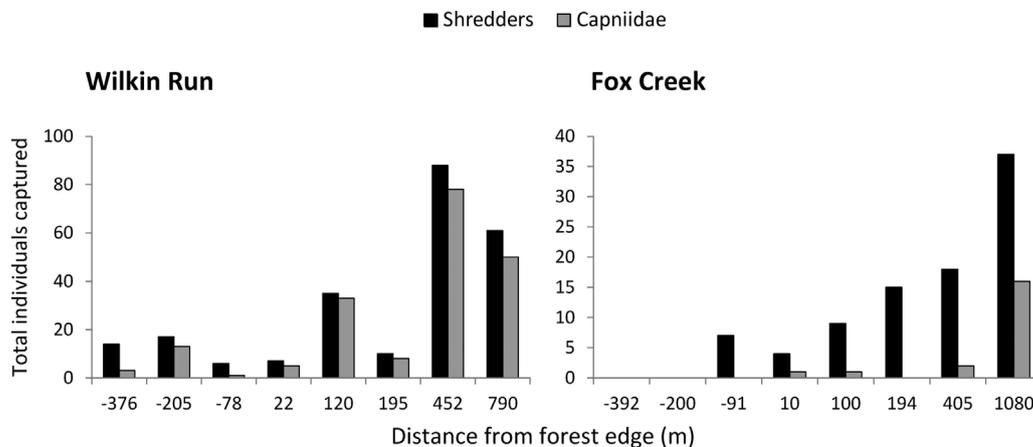


Fig. 7. Shredder and Capniidae density summed over the course of the study at Wilkin Run (left) and Fox Creek (right).

Table 2

Community wide threshold estimates (rounded to the nearest integer) for quantiles 0.05, 0.10, 0.90 and 0.95.

Site	Direction	Threshold	0.05	0.10	0.50	0.90	0.95
Wilkin Run	z–	324	–28	–28	158	324	324
	z+	324	–28	–28	324	621	621
Fox Creek	z–	–41	–146	–41	–41	55	147
	z+	300	–41	55	147	300	743

forests. At Fox Creek, NO₃–N concentrations in the fall of 2010 were negatively related to distance with a threshold approximately at the forest edge, and the model fit indicated a lower magnitude slope once the stream reaches the forest (Fig. 4E). However, the scatter plot of the observed data indicated more than one abrupt decline in NO₃–N occurring about 90 m upstream of the forest patch, and another decline by 200 m into the forest patch. Although there may have been unmeasured factors driving more complex nutrient dynamics occurring in the large spatial gap between 400 and 1080 m, there was evidence for a decline in NO₃–N between these two sites. Fox Creek daily maximum temperature and NO₃–N (summer 2011) concentrations declined after reaching a threshold 55 m downstream of the forest edge (Fig. 4D and F). NH₃–N concentrations in the summer of 2011 increased until about 249 m into the patch and decreased thereafter (Fig. 4G). Finally, summer 2011 PO₄–P concentrations at Fox Creek exhibited a shift furthest into the forest, increasing after reaching a threshold at 743 m (Fig. 4H). The threshold models for daily maximum temperature at Wilkin Run indicated a threshold near the edge of the forest (–71 m for the piecewise model) and 158 m after entering the forest (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. 4A). PO₄–P concentrations at Wilkin run exhibited a shift near the forest edge with higher concentrations upstream of the forest (Fig. 4B).

3.3. TITAN analysis of macroinvertebrate assemblages

Analysis using TITAN provided evidence for shifts in macroinvertebrate assemblages ranging from the edge to just over 300 m into forest fragments. Wilkin Run had six taxa with significant threshold estimates and at Fox Creek there were three taxa with significant thresholds. Three taxa showed a marked decrease near the forest edge (Turbellaria, Elmidae, and Amphipoda) and 3 families (Chironomidae, Coenagrionidae, and Physidae (but note that Physidae did not completely stabilize after 200,000 permutations)) showed a decrease after ~324 m into a forest (Fig. 5). Three families showed increases after reaching a threshold with distance into a forest with pleurocerids and tipulids increasing soon after entering a forest, and limnephilids showing an increase at about 324 m (Fig. 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 Limnephilidae and Chironomidae was within the forest. Consistent with the TITAN results, scatter plots of the raw density data generally showed strong changes soon after entering forests (Fig. 6). Even though we did not analyze overall shredder density and TITAN did not detect a threshold for capniid stoneflies, plots of overall shredder and Capniidae density exhibited evidence of strong, systematic changes that began at the forest edge and proceeded into the forest at both streams (Fig. 7). Additionally, TITAN revealed that community-level thresholds were consistent with the taxa-specific analyses, with thresholds ranging from near the

forest edge (between the most upstream forest site and most downstream agricultural site) to 324 m into the forest (Table 2).

4. Discussion

Although our study was limited to two streams, these model systems represent a common agricultural-forest transition of midwestern US landscapes. Our study provides initial evidence that streams draining agricultural catchments exhibit shifts in a variety of attributes soon after entering forest fragments. At both study streams, daily maximum temperature declined within the first 200 m of entering forest fragments. There was also evidence of shifts in NO₃–N (Fox Creek) and sediment size (Wilkin Run) along agricultural-forest transitions. Changes in macroinvertebrate assemblages began near the forest edge and extended up to 324 m into forests. Taxa that declined after entering forests were generally tolerant and/or those that rely on in-stream primary productivity (i.e., scrapers) whereas most taxa that increased after entering forests were relatively sensitive to disturbance and rely on allochthonous organic matter inputs from the forest (i.e., shredders). Although variation in specific attributes along agriculture-forest transitions were somewhat idiosyncratic, the rapid changes in a variety of attributes that occurred at both streams suggest that even small fragments of forest may be able to recover stream characteristics typical of more undisturbed catchments.

4.1. Variation in environmental conditions along agriculture-forest transitions

Whereas the results from our analyses of environmental conditions were variable, there was evidence of shifts 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. 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). The relatively coarse sediment upstream of the forest patch may be explained in part by the dominance of herbaceous vegetation on the banks upstream of the forest, which in some cases may provide more bank stability than woody vegetation (Lyons et al., 2000).

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. In our study, there was a shift in pool width soon after entering the forest at 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 land use in Wilkin Run but once again did not exhibit systematic trends in Fox Creek (Fig. 3). The amount of wood in forested streams is typically higher than in agricultural streams (Elosegi and Johnson, 2003), and the deeper pools in the forest of Wilkin Run may have been driven by increased presence of wood which is known to contribute to pool scour (Montgomery et al., 2003). Another potential driver of geomorphic variability at Wilkin Run between the two sites closest to the forest edge may have been the presence of a road crossing. Road crossings are known to have a variety of hydrogeomorphic effects on streams (Jones et al., 2000) and

potentially account for the observed increase in pool width and depth in the first site upstream of the forest. More comprehensive measurements of stream geomorphology in future studies will allow for increased understanding of the influences of forest fragments on the physical structure of channels in the study 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 responses we observed were consistent with these studies, and showed ~1.6–2.4 °C declines in daily maximum temperature 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 ([Fig. 4A](#) and [D](#)). Because our analysis focused on a subset of measurements of daily maximum temperatures in the fall, we expect that the temperature differences between agricultural land and forests are likely to be greater in the summer, and that shifts would perhaps occur even closer to forest edges. Further, we would expect that these changes would potentially be less rapid in larger streams which are deeper and have greater velocity leading to increasing thermal inertia with stream size (see [Rutherford et al., 1997](#) for examples of predictions under differing land cover and stream-size scenarios).

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 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, NO₃-N concentrations in Fox Creek showed strong evidence for enhanced nutrient processing in forested streams. In 2010, our data suggested a shift beginning just upstream of the forest patch ([Fig. 4E](#)); however, the scatter plots revealed that the piecewise linear regression did not capture the multiple shifts in nutrient concentrations that occurred along the agriculture-forest transition. The decline upstream of the forest may have been due to the land cover shift from active pasture (both sides of stream) to retired pasture (south side) and cropland bordered by a riparian tree buffer (north side) at the two sites immediately upstream of the forest edge, whereas subsequent declines were associated with increasing distances into the forest. The decline in the rate of change after entering the forest may have been driven by increased shading which can reduce nutrient uptake by in-stream autotrophs ([Fellows et al., 2006](#)). Alternatively, during the summer of 2011, the step function model showed that NO₃-N began to decline within the first 55 m after entering the forest patch ([Fig. 4F](#)). Previous work in agricultural catchments have found similar declines in N in streams flowing from agricultural land into forest patches ([Storey and Cowley, 1997](#)) suggesting that forest fragments may be important areas for nitrogen processing in agricultural landscapes; however, these trends did not occur in Wilkin Run in our study nor in a similar study of agriculture-forest transitions ([Scarsbrook and Halliday, 1999](#)), highlighting the potentially important role that patch context (e.g., geology, surrounding land use, forest composition) plays in regulating nitrogen cycling in streams.

We also found evidence for shifts in PO₄-P and NH₃-N at our study sites. Elevated PO₄-P concentrations immediately upstream

of the forest patch in Wilkin Run ([Fig. 4B](#)) were possibly driven by livestock access upstream of the forest and a drainage tile discharging into the stream ~200 m upstream of the forest, both of which can lead to elevated PO₄-P concentrations ([Sims et al., 1998](#); [Hubbard et al., 2004](#)). Even though our models did not detect a change prior to reaching the forest, 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 PO₄-P, the mechanisms regulating phosphate uptake are unlikely to be linked to riparian vegetation alone. Similarly, trends in PO₄-P and NH₃-N during 2011 at Fox Creek indicated that riparian vegetation was likely not the primary factor regulating nutrient dynamics at this stream.

4.2. Variation in macroinvertebrate assemblages along agriculture-forest transitions

The TITAN analysis provided strong evidence for forest-mediated shifts in macroinvertebrate assemblages. Previous analyses using TITAN have found synchronous shifts in multiple macroinvertebrate taxa along human disturbance gradients suggesting strong changes in overall macroinvertebrate community structure occur at some threshold level of human disturbance ([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. 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 3 out of the 4 estimates ([Table 2](#)). These results are consistent with previous studies that have shown recovery in macroinvertebrate assemblages within 300–600 m after agricultural streams enter forests ([Storey and Cowley, 1997](#); [Scarsbrook and Halliday, 1999](#)) suggesting that small fragments of forest may have appreciable effects on macroinvertebrate assemblages in agricultural catchments.

The changes that we observed for the macroinvertebrate assemblages corresponded to shifts 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, 1986](#)). [Hogg and Williams \(1996\)](#) showed that mean temperature changes as small as 2–3.5 °C may negatively affect aquatic macroinvertebrate assemblages. Similarly, we found that the daily maximum temperatures were about 1.6–2.4 °C lower in the forest, and we suggest that this difference is likely higher in the summer and may potentially influence thermally sensitive macroinvertebrate species. Although we did not consider fish 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 assemblages 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 with traits enabling them to exploit fine sediment (e.g., some species of Chironomidae and Oligochaeta) ([Wood and Armitage, 1997](#); [Quinn, 2000](#)). At Wilkin Run the decline in fine sediment after entering the forest may drive responses of taxa that are sensitive to sedimentation and those that are able to exploit habitats dominated by fine sediment. Alternatively, the dominance of finer sediments throughout Fox Creek may explain the more muted changes in macroinvertebrate assemblages.

In addition to the physical effects of temperature and sediment composition, shifts in macroinvertebrate assemblages suggested that basal resources supporting macroinvertebrates were influenced by the transitions from open-canopied agricultural land to more 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 by-product of agricultural land use (Carpenter et al., 1998). Our results showed 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 forests. As with most stoneflies, capniids are also highly sensitive to anthropogenic disturbance (Barbour et al., 1999) and their greater abundance in forests suggests that forests are able to mitigate upstream land-use effects on streams. TITAN's inability to detect the strong shifts in Capniidae density 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 macroinvertebrate responses. The TITAN analysis also revealed declines in the scrapers Elmidae (Fox Creek) and Physidae (Wilkin Run), suggesting that shading and lower nutrient concentrations may limit algal growth and regulate some scraper populations in forest patches.

4.3. Leaf breakdown

In contrast to the some of the results for biotic and environmental results, we found no evidence for changes in leaf breakdown along-agriculture forest transitions. 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 (Fig. 4C and I). Our results showed that agricultural land 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 reviews by Webster and Benfield, 1986; Young et al., 2008). These data are consistent with the hypothesis that leaf-breakdown rates are unaffected by land-cover 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.

4.4. Management implications, future directions, and conclusions

Although there has been considerable interest in studying the responses of streams along gradients of human disturbance

(e.g., Qian et al., 2003; Dodds et al., 2010; King et al., 2011), there has been much less focus on how streams change along impacted-to-natural gradients (but see Storey and Cowley, 1997; Scarsbrook and Halliday, 1999; Suga and Tanaka, 2013). Understanding how impaired systems respond to natural habitat is particularly important in agricultural landscapes because variation in the quality of land for cultivation as well as differences in land-use management have created heterogeneous patchworks of natural and human-dominated patches. Results from the two streams considered in this study suggest that environmental and biotic attributes of agricultural streams can rapidly change after entering forests, and that threshold models potentially provide a useful tool for estimating how much forest is necessary to mitigate upstream agricultural effects on streams. Shifts in stream attributes that have occurred at similar spatial scales in previous studies (Storey and Cowley, 1997; Scarsbrook and Halliday, 1999) lend support to the generalizability of these patterns, indicating that forests that encompass stream lengths of a few hundred meters or more may markedly improve stream conditions in agricultural catchments. It is likely, however, that the response of stream attributes to forests is contingent upon stream size (Rutherford et al., 1997; Harding et al., 2006) and geographic context (see review by Suga and Tanaka, 2013) and more research across a variety streams is necessary to obtain a broad understanding of how streams change along agriculture-forest transitions and the implications for management of these systems.

Recently, there has been increasing recognition that streams are not only influenced by fluxes of materials and organisms from terrestrial systems (e.g., leaf litter to streams), but also influence terrestrial systems via reciprocal aquatic-to-terrestrial fluxes of aquatic insects after they emerge from streams as winged adults (Baxter et al., 2005; Sullivan and Rodewald, 2012). Aquatic-to-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). Our findings that larval aquatic insects strongly shift along agriculture-forest transitions makes it likely that there is an accompanying shift in fluxes of adult aquatic insects into terrestrial systems. Exploring the implications of abrupt transitions in land cover for aquatic-to-terrestrial fluxes and the potential effects on riparian food webs would be a fruitful area of future research.

Widespread agricultural land use has been implicated in a variety of effects on stream ecosystems (Quinn, 2000; Allan, 2004). Results from the present study indicate that existing fragments of forest may be able to mitigate agricultural effects over relatively short distances. Furthermore, these results support the idea that discontinuous conservation and restoration of forest fragments may be an important strategy for managing stream integrity in agricultural landscapes (Scarsbrook and Halliday, 1999). Overall, our study indicates that fragments of forest in agricultural landscapes can strongly influence a variety of stream attributes, and that even relatively small forest fragments may be able to recover a variety of stream characteristics.

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