RESEARCH ARTICLE

Riparian and watershed land use alters food web structure and shifts basal energy in agricultural streams

Eden L. Effert-Fanta[1,3] · Robert U. Fischer[2] · David H. Wahl[1]

Abstract

We examined food web structure in headwater streams to determine whether riparian buffers can mitigate the effects of agricultural land use on stream ecosystem function. Study sites were located in the Midwestern US and divided into three land use groups (forested, buffered, agricultural) based on the amount of riparian forest and row crop agriculture in the watershed. Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) was performed on basal energy sources and consumers (6 invertebrate groups and 7 fish species) with isotopic metrics used to assess variation in food web structure related to land use, instream environmental parameters, and food resources. Land use differences were associated with community-wide isotopic shifts with all trophic diversity metrics greater in forested compared to agricultural streams, whereas buffered streams were generally intermediate. Agricultural streams had compressed food webs with high trophic redundancy indicative of a shared resource pool for all consumers. In contrast, forested and buffered stream food webs showed larger trophic niche area due to greater utilization of detrital energy and higher variability in trophic position among invertebrates and fish. Circular statistics revealed fish communities shifted to lower trophic positions and increased dependence on periphyton production in agricultural streams. The presence of riparian forests was associated with a broader range of resources used by consumers, expanded trophic diversity, and elevated fish trophic position in buffered streams. Results suggest that riparian forests can improve food web structure in streams impacted by croplands and provide further support for restoring buffer areas to moderate adverse effects of agriculture.

Keywords Stable isotopes · Isotopic metrics · Riparian buffer · Cropland · Trophic niche

Introduction

Agriculture has caused extensive landscape changes and is the leading cause of degradation to stream ecosystems in the United States (Malmqvist and Rundle 2002). Physical and chemical stream alterations from agricultural activities, such as channelization and nutrient pollution, may be linked to declines in species diversity, changes in community composition, and loss of ecosystem integrity (Allan 2004). Forested riparian 'buffers', typically 30–50 m wide alongside streams, can improve stream water quality in agricultural areas by reducing soil erosion and filtering runoff before it enters a stream (NRC 2002; Lovell and Sullivan 2006). In addition, forested riparian zones can moderate stream water temperature through shading, supply important inputs of organic matter, and provide critical habitat that connects aquatic and terrestrial communities (Sweeney 1993; Naiman and Decamps 1997; Baxter et al. 2005). Although riparian forest buffers are promoted to improve both water quality and ecological integrity (Bernhardt et al. 2005), there has been much debate as to whether protecting relatively narrow streamside area is sufficient to mitigate large-scale watershed agricultural disturbances. Previous studies have reached conflicting conclusions and suggest that more research in needed to understand the extent to which riparian areas influence

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agricultural stream ecosystems (Marshall et al. 2008; Smiley et al. 2009; Hrodey et al. 2009; Feld 2013).

Stable isotope analysis (δ^{13}C and δ^{15}N) measures variation in food web structure and has been increasing used in stream ecosystem assessments (e.g., Anderson and Cabana 2005; Hogsden and Harding 2014; Machado-Silva et al. 2022) because food webs provide an integrated measure of stream health by combining interactions among trophic levels with ecological processes that control nutrient cycling and basal energy sources (Layman et al. 2012). Stable nitrogen isotopes have been used to track anthropogenic N loads in aquatic ecosystems (Anderson and Cabana 2005; Lee et al. 2018) and carbon isotopes used to infer human-induced changes in organic matter utilization in stream food webs (England and Rosemond 2004; Erdozain et al. 2021). Stable isotopes are particularly useful in studying aquatic ecosystems because δ^{13}C signatures of terrestrial plants are generally different than δ^{13}C signatures of aquatic primary producers (Peterson and Fry 1987). Since δ^{13}C of consumers closely match their dietary source, stable isotope analysis can be used to differentiate and trace allochthonous and autochthonous C sources in aquatic ecosystems (Finlay 2001; Post 2002). Nitrogen isotope ratios are useful estimators of trophic position because δ^{15}N increases predictably (about 3.4‰) with each trophic step (Post 2002). Therefore, inferences about a consumer's diet and trophic position can be made by comparing its isotopic ratios (δ^{13}C and δ^{15}N) with those of other taxa in its food web (Peterson and Fry 1987).

Because changes in riparian forest and agricultural land use are predicted to change basal C sources and may alter consumer trophic position, stable isotope analysis provides a powerful tool to detect differences in food web structure in agricultural headwater streams. Removal of riparian vegetation may have the greatest impact on headwater streams because earlier studies suggested that allochthonous detrital inputs from the riparian zone regularly fuel their food webs (Vannote et al. 1980; Wallace et al. 1995). Increased light levels due to an open canopy along with higher nutrient inputs from agriculture may increase algal productivity and can shift the system toward an autochthonous resource base (Wiley et al. 1990). These changes in basal energy sources may fundamentally alter food webs in agricultural streams (Hladyz et al. 2011b). More recent studies in other systems have emphasized the importance of autochthonous C to stream consumers even in small forested streams (Reis et al. 2020) because algae is a more labile and nutritional food than detritus (Brett et al. 2017; Guo et al. 2021). However, less in known about the relative importance of terrestrial inputs from riparian forests to consumers in agricultural streams because few studies have investigated the influence of cropland agricultural land use on temperate headwater food webs particularly those that encompass

multiple trophic levels (Lee et al. 2018). Most research in this area has focused on comparisons of forested versus pasture streams (Hicks 1997; Hladyz et al. 2011b; Carvalho et al. 2015), streams affected by deforestation due to logging (England and Rosemond 2004; Gothe et al. 2009; Erdozain et al. 2021), or agricultural streams in tropical regions (de Carvalho et al. 2017; Garcia et al. 2017).

Although positive correlations between the amount of watershed agriculture and δ^{15}N values of periphyton and/or aquatic consumers have been recognized (Anderson and Cabana 2005; Bergfur et al. 2009; Diebel and Vander Zanden 2009; Lee et al. 2018), limited research has been directed at detecting community shifts in C sources or alterations in food web structure in row crop agricultural streams. Bergfur et al. (2009) found no changes in δ^{13}C signatures of basal energy sources, invertebrates and fish in boreal streams with increasing agricultural nutrient enrichment. Similar results were reported in a study that sampled urban, forested, and agricultural streams and found no differences in δ^{13}C and δ^{15}N signatures of basal resources or primary consumers (Milanovich et al. 2014). Additionally, δ^{13}C signatures in mussels and fish did not correlate with the proportion of agricultural land use in their catchments (Lee et al. 2018). In contrast, food web shifts in pasture streams have been shown with invertebrates in unshaded streams utilizing more autochthonous C sources than in forested streams (Hicks 1997; Hladyz et al. 2011a). Differences in basal C sources supporting headwater food webs with different forest management practices have also been observed with levels of allochthony in streams influenced by harvesting intensity (Erdozain et al. 2021). The lack of evidence of C shifts in cropland agricultural streams may be the result of previous studies not specifically selecting sites with varying amounts of riparian forest or canopy cover thus potentially limiting differences among systems.

Here, we assessed the effects of row crop agricultural land use on stream food webs and examined whether differences in riparian forest buffer was associated with shifts in basal resources or consumer trophic position. We used stable isotope analysis to investigate food web structure in headwater streams that varied in the amount of riparian forest and row crop agriculture in the watershed. Sampling was conducted in spring and summer because seasonal variability in basal resources and terrestrial inputs has been shown to influence stream food webs (Nakano and Murakami 2001; Lau et al. 2009; Dekar et al. 2009; Woodland et al. 2012) particularly in temperate regions. We hypothesized that agricultural streams with riparian forest buffers would have higher trophic diversity and larger trophic niche than streams with low riparian forest because of greater variability in basal resource use. Conversely, we hypothesized that communities in agricultural streams with low riparian forest would shift toward increased reliance on autochthonous resources,

due to higher instream productivity and lower allochthonous resources. Finally, we predicted that periphyton and consumers in agricultural streams would have enriched $\delta^{15}N$ signatures in response to elevated nutrient levels.

Materials and methods

Study area

The study was conducted in nine headwater streams (2nd or 3rd order) located in the Embarras River Watershed in east-central Illinois, USA (Fig. 1). Streams in the watershed are low-gradient with sand as the primary substrate. Land use within the watershed is dominated by row crop (mostly corn and soybean) agriculture (73.5%) with low amounts of urban development (1.8%). Individual sites were selected from a total of 48 stream segments examined after calculating proportions of agriculture and forest in the riparian zone (land use within 30 m of the stream) and the whole watershed (the entire area upstream of each site) using ArcView GIS 9.1 (ESRI 2005). The 48 potential sampling locations were chosen following a random, stratified survey design that selected sites from all 2nd and 3rd order stream segments within the same ecoregion of the watershed (Olsen and Peck 2008). Study sites within each stream (one 100 m reach per stream) were selected to have similar channel width and watershed area (27–39 km²) to minimize differences among streams unrelated to land use (Table 1). See Effert-Fanta et al. (2019) for more details on GIS methods and habitat assessments. These locations were previously studied to examine fish and macroinvertebrate assemblages and environmental conditions at each site (Effert-Fanta et al. 2019). Stream canopy cover was measured at 10 transects across each stream using a spherical densiometer and the percent cover for each transect was averaged for each site (Table 1) to examine differences in shading that would influence basal resources.

The nine streams were equally divided into three distinct land use groups that spanned the available range of riparian forest and agricultural land use in the watershed (Online Resource Fig. S1). The land use groups (forested, buffered, and agricultural) were selected to provide streams with a gradient of impacts from cropland agriculture. Stream sites in watersheds with the highest percent forest (> 41%) and the lowest percent agriculture (≤ 51%) were classified as "Forested". For our study, forested streams had a high percent
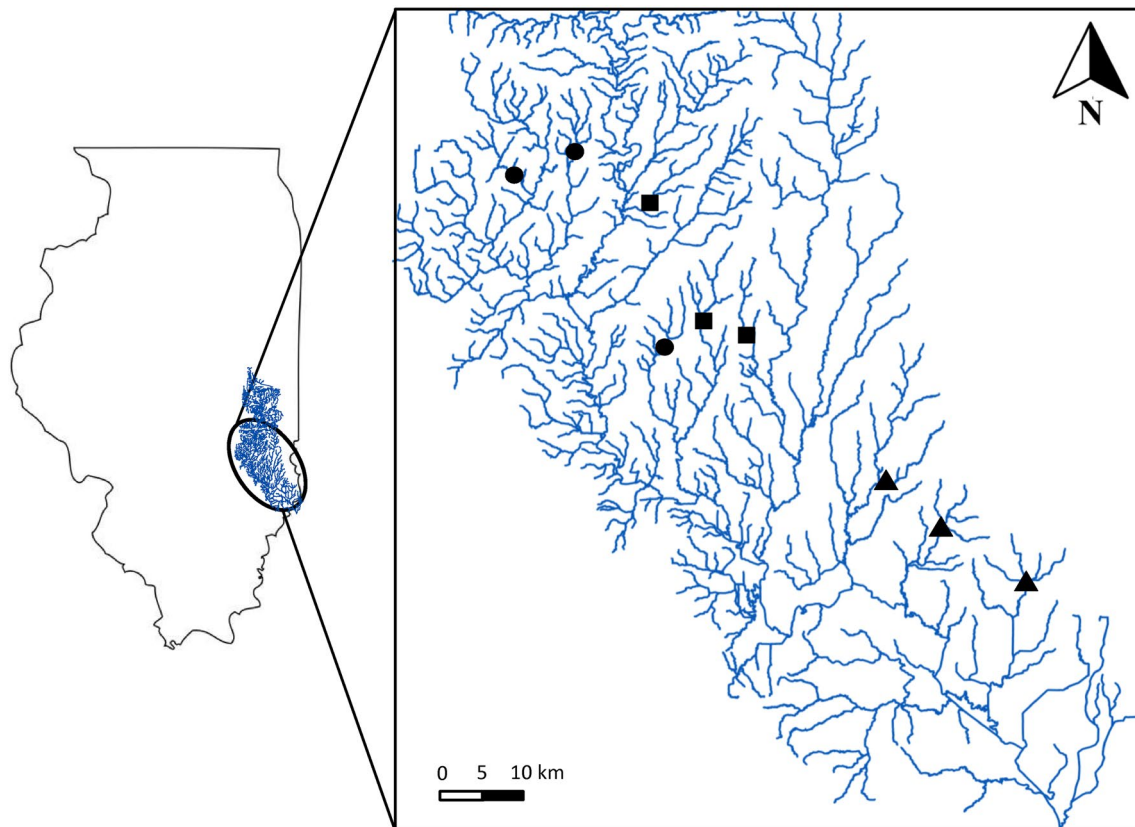

Fig. 1 Study site locations sampled in the Embarras River Watershed in Illinois, USA. Streams classified into land use groups based on the percent riparian forest buffer (30 m) and cropland agricultural land use in the watershed (Table 1). Triangles represent Forested stream sites, squares represent Buffered stream sites, and circles represent Agricultural stream sites

Table 1 Physical characteristics, land use, and canopy cover percentages for the nine headwater streams in the Embarras River Watershed, Illinois, USA

Stream Site	Land Use Group	Mean Width (m)	Mean Depth (m)	Watershed Riparian Forest %	Watershed Agriculture %	Mean Canopy Cover %
Bennett Creek	Forested 1	4.7	0.15	92.0	51.8	88.5
Brushy Creek	Forested 2	5.9	0.16	75.2	52.9	83.8
Honey Creek	Forested 3	5.1	0.21	77.5	48.2	87.0
East Crooked Creek	Buffered 1	4.8	0.18	86.5	78.7	87.4
Lost Creek	Buffered 2	4.4	0.17	73.5	76.5	77.8
Panther Creek	Buffered 3	4.7	0.19	69.5	73.4	90.4
Cottonwood Creek	Agricultural 1	4.8	0.20	15.9	79.0	5.2
Bear Creek	Agricultural 2	6.0	0.19	36.5	83.2	37.5
West Crooked Creek	Agricultural 3	3.7	0.14	38.5	88.0	44.8

Streams categorized into distinct land use groups (forested, buffered, agricultural) based on percentages of riparian forest buffer (30 m) and agriculture (mostly corn and soybean) in the watershed

riparian forest buffer (> 75%; Table 1), but had a lower percent watershed forest than temperate forested streams in other regions because agriculture is the dominant land use in the study area. Nonetheless, forested streams were expected to have the lowest influence from agriculture in the entire watershed. Stream sites in watersheds with the highest percent agriculture (> 79%) and the lowest percent riparian forest (< 39%) were classified as "Agricultural". Finally, stream sites with a high percent agriculture (> 73%) and a high percent riparian forest (> 70%) were classified as "Buffered" (Table 1). Buffered streams had similar percentages of watershed agriculture (row crops) as agricultural streams with higher levels of riparian forest to test the effectiveness of the riparian buffer. The percentages for these groups were used because they provided the largest separation between land use categories in the watershed and made it possible to independently examine the effects of riparian and watershed land use on stream communities (Effert-Fanta et al. 2019). Here, the study design created differences in basal resource availability among streams (e.g., more terrestrial inputs with greater % riparian forests) along with variation in the amount of agriculture to assess a range of potential influences on food webs.

Food web sample collection

At each site, a representative 100 m reach was selected to include two riffle-pool sequences. During spring (May-early June) and summer (August) 2009, we collected conditioned leaves (and other coarse particulate organic matter), periphyton, macroinvertebrates, and fishes over the study reach in each stream. Five replicate samples of organic matter and consumers were collected at each sampling event whenever possible. All samples were placed on ice in the field and frozen upon return to the lab. Course particulate organic matter (CPOM) was collected by hand at 5 random locations distributed across the reach. Samples were gently rinsed through a 1 mm sieve to remove invertebrates and sediment. Periphyton was collected from unglazed ceramic tiles affixed to cement blocks placed in each stream 4 weeks prior to sampling. Tiles were used because sand is the dominant substrate in all streams and most sites lacked rocks large enough to adequately sample periphyton for isotopic analyses. Because water velocity has been shown to influence periphyton isotopic signatures (Finlay et al. 1999), blocks were placed in areas with the similar flow in each stream (targeted range of 0.11–0.16 m/s) in an effort to minimize differences among sites that would be related to channel placement. When present, filamentous algae was collected from attached substrates and rinsed following CPOM methods.

Consumers were sampled from all available stream habitats (i.e., riffles, pools, debris dams) across the entire 100 m reach. Macroinvertebrates were collected using a kicknet (50 cm wide, 500-μm mesh) to capture dislodged material after disturbing the substrate with 20 kick samples (~ 0.5 m^2/sample) taken at locations in proportion to the microhabitats in each stream site (Barbour and Stribling 2006). Organisms were live sorted and identified to family or subfamily in the field. Additional kick samples were done if needed to collect enough individuals from each group for stable isotope analysis. Macroinvertebrates were combined by functional feeding group into plastic bags containing stream water and kept overnight (minimum of 8 h) to allow voiding of digestive tracts to eliminate contamination by unassimilated material. Organisms were then rinsed with distilled water and frozen. Crayfish were frozen immediately upon return to the lab. Fish were collected over the 100 m reach using a Smith-Root (LR-24) backpack electrofishing unit with a

targeted sampling of 5–10 individuals of the most abundant species. All fishes were identified to species, measured for total length (mm), and individuals collected for isotopic analysis were placed on ice and frozen upon return to the lab.

Laboratory processing

CPOM, periphyton tiles, and filamentous algae samples were carefully examined under a dissecting microscope to remove invertebrates and debris before processing for isotopic analysis. Periphyton was scrubbed off tiles, rinsed with distilled water, and then filtered through pre-combusted Whatman CF/C glass fiber filters. Samples were placed in a drying oven at 60° C for 24 h. Periphyton filters and filamentous algae were then weighed into silver capsules and placed in a desiccator for acid fumigation to remove inorganic C that may have been deposited from the stream bed (Harris et al. 2001). Dried CPOM was shredded, ground and then weighed into tin capsules.

Abundant invertebrate taxa and fish species that were common at all sites were used for food web analysis. Seven fish species and six invertebrate groups were selected to include a range in trophic levels and functional feeding groups (see Table 2). Many of these taxa are relatively omnivorous and show high dietary flexibility, and therefore have the ability to respond to changing resources. Fish and crayfish were weighed and total length measured. Individual fish were selected to fall within a similar size range for each species for all sites. Dorsal muscle was removed from 1–5 individuals of each fish species (mean = 4) from each site/season. Tail muscle was removed from 3–5 crayfish per site/season. Macroinvertebrates from three functional feeding groups (scrapers, collector-gatherers, predators) were collected from each site with an average of 2 taxa per group for each site/season. Single individuals were used for the large predatory odonates, whereas 10–25 individuals of the same taxonomic group for most macroinvertebrates were combined to achieve sufficient mass. Gastropod shells were removed and soft tissues combined for their composite sample. Invertebrate and fish samples were prepared for isotopic

Table 2 Fish species and invertebrate taxa collected at all sites for food web analysis

Common name	Scientific name	Trophic Guild/FFG	Abbreviation
Fish			
Central stoneroller	*Campostoma anomalum*	Herbviore/Detritivore	COS
Creek chub	*Semotilus atromaculatus*	Omnivore	CRC
Bluntnose minnow	*Pimephales notatus*	Omnivore	BLT
Bluegill	*Lepomis macrochirus*	Invertivore	BLG
Green sunfish	*Lepomis cyanellus*	Invertivore	GSF
Orangethroat darter	*Etheostoma spectabile*	Benthic Invertivore	ORD
Largemouth bass	*Micropterus salmoides*	Invertivore/Piscivore[a]	LMB
Invertebrates			
Snails	Gastropoda		
	Physidae	Grazers	Gas
	Planorbidae	Grazers	Gas
Mayfly larvae	Ephermeroptera		
	Baetidae	Grazers	Eph
	Heptageniidae	Grazers	Eph
Midge larvae	Chironomidae		
	Chironominae	Collector-gatherer	Chi
Caddisfly larvae	Tricoptera		
	Hydropsychidae	Collector-gatherer	Hyd
Dragonfly larvae	Odonata		
	Gomphidae	Predator	Odo
	Libellulidae	Predator	Odo
Crayfish	Decapoda		
	Cambaridae	Ominovore	Cra

Trophic guild and functional feeding group (FFG) classification according to Gerking (1994) for fish and Merritt and Cummins (1996) for invertebrate taxa. Scientific name, common name and abbreviation codes are shown

[a]Switch to piscivore at later life stages

analysis by oven drying at 60° C for 48 h and then ground to a fine powder with a mortar and pestle. The homogenized samples were weighed into tin capsules.

Prepared samples were sent to the UC Davis Stable Isotope Facility for analysis of ^{13}C and ^{15}N isotopes using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Results are expressed in delta (δ) notation and measured as parts permil (‰) relative to international standard material, Vienna Pee Dee Belemnite limestone for carbon and ambient air for nitrogen. Isotopic ratios are calculated following: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$; where $R = {}^{13}C/{}^{12}C$ or $^{15}N/{}^{14}N$. Measurement precision was determined by standard deviations from internal laboratory standards, with mean standard deviations of 0.05‰ for $\delta^{13}C$ and 0.16‰ for $\delta^{15}N$. Prior to data analysis, we corrected for lipid effects on $\delta^{13}C$ signatures following equations in Post et al. (2007) using % carbon for basal sources or C:N ratios for consumers.

Food web analysis

Analysis of $\delta^{13}C$ was used to infer differences in organic matter flow and $\delta^{15}N$ was used to infer trophic relationships among organic matter and consumers. Analysis of variance (ANOVA) was used to determine if periphyton and CPOM had distinct isotopic signatures (Peterson and Fry 1987). The relative trophic position (TP) of consumers was calculated to determine possible differences in trophic structure related to land use and season. Because basal energy sources can show high temporal variability, TP was calculated relative to a ubiquitous primary consumer, which has more stable $\delta^{15}N$ signatures due to slower nitrogen turnover rates (Cabana and Rasmussen 1996). Chironomidae larvae (mainly Chironominae) were used as our baseline $\delta^{15}N$ because they were the most abundant primary consumer at all sites and grazing taxa were not found in all sites/seasons. Using a single common taxa as a baseline instead of the mean $\delta^{15}N$ values of all primary consumers reduces the bias caused by high variability among different taxa (Anderson and Cabana 2007). Chironomid larvae generally had the lowest $\delta^{15}N$ of all primary consumers and little differences were found between chironomids and grazers at sites where they were both present (mean difference $\delta^{15}N = 0.4$‰). In addition, the preliminary gut content analysis found chironomids to be a common diet item in most fish species. TP was calculated using the equation: $TP_{consumer} = [(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/3.4] + 2$, where $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ of the taxa for which the TP is estimated, $\delta^{15}N_{baseline}$ is the baseline $\delta^{15}N$, 3.4 is the typical $\delta^{15}N$ fractionation per trophic level (Minagawa and Wada 1984) and 2 is the expected trophic position of the baseline (Cabana and Rasmussen 1996). Differences in fish TP among species, land use groups, and

seasons were examined using repeated measures analysis of variance (ANOVA) using PROC MIXED (SAS Institute Inc. 2012) with land use group as a fixed variable and season as a repeated variable. When a significant effect of land use type or season was found, pairwise comparisons were made using Tukey post hoc multiple comparison tests. Replicate samples of each species were pooled for each sampling event and the means were used to test for differences among factors.

To compare food web structure among land use groups, we used the community-wide metrics proposed by Layman et al. (2007a) and an ellipse-based metric of the stable isotope data (Jackson et al. 2011). Both metrics are based on geometric calculations of the $\delta^{13}C$ and $\delta^{15}N$ bi-plot space, referred to as isotopic niche space. Because the range in $\delta^{13}C$ of possible basal resources needs to be similar to be able to use these metrics to compare between sites or seasons (Layman and Post 2008), we used ANOVA to examine differences in $\delta^{13}C$ values of basal resources (i.e., periphyton and CPOM) among land use groups and seasons. We used baseline corrected trophic position instead of absolute $\delta^{15}N$ values in our bivariate plots to allow comparison between sites with different basal signatures (Layman et al. 2012). Only fish and invertebrate isotopic signatures were considered in these analyses because basal signatures have higher variability in space and time than consumers (Post 2002; Layman et al. 2007a; Jackson et al. 2011).

Six community-wide metrics were used that reflect different measurements of food web structure (Layman et al. 2007a). The isotopic metrics that provide information on trophic diversity and redundancy included: $\delta^{15}N$ range (NR), $\delta^{13}C$ range (CR), total area (TA), mean distance to centroid (CD), mean nearest neighbor distance (MNND), and standard deviation of nearest neighbor distance (SDNND). NR represents vertical food web structure (i.e., food chain length). CR provides information on the diversification of basal resources used by consumers. TA is the total convex hull area encompassing all species in bi-plot space and represents the total isotopic niche space of the food web. Caution should be taken when comparing TA among sites and seasons because is it sensitive to sample size and outliers (Jackson et al. 2011). However, the use of TA in our study was appropriate because our sample sizes were relatively similar and the numbers of groups and fish species were the same for all streams. CD is the average Euclidean distance of each community component to the centroid, giving a measure of the average degree of trophic diversity within the food web. MNND and SDNND are calculated from the spacing of species relative to each other with smaller values indicating a more similar and more even distribution of trophic niches (Layman et al. 2007a).

In addition to TA, the total isotopic niche space was quantified for each site and season based on standard ellipse areas (SEA) calculated using a Bayesian approach

(Jackson et al. 2011). A standard ellipse is comparable to the standard deviation for univariate data (Batschelet 1981). Bayesian SEAs include sampling error of estimates of the means of different community components with appropriate corrections possible for small samples sizes (< 10 individuals per taxa) that is insensitive to the influence of outliers and differences in sample sizes thereby overcoming criticism of previous approaches when used to compare studies or sites with different communities (Jackson et al. 2011). We used community-wide metrics and SEAs as complementary methods that may reveal different underlining characteristics of trophic structure (Layman et al. 2012). All community-wide metrics and SEAs were calculated using the SIBER package (Jackson et al. 2011) in the R computing program (R Development Core Team 2012). Data were tested for normality prior to analysis (Shapiro–Wilk test, SAS). Differences in isotopic niche width among land use groups and seasons were determined by comparing sizes and overlap of the SEAc (corrected for small sample-size) for each site/season. Community-wide metrics were compared using repeated measures ANOVA with Tukey post hoc tests. If significant land use x season interactions were found, we examined the interaction with planned Tukey comparisons between land use groups for each season.

Circular statistics (Schmidt el al. 2007) were used to quantify basal energy or trophic shifts in fish stable isotope signatures by assessing directional changes between each land use group and season. Only fish were used in directional tests because macroinvertebrate taxa varied between sites and seasons. Sites were pooled by land use group with isotopic means calculated for each fish species. Similar to the metrics analysis, we used baseline corrected trophic position for δ^{15} N values instead of raw δ^{15} N for comparison among sites. Vectors were calculated from shifts in isotopic signatures by comparing the x–y coordinates for each species in one land use group or season to another (only pairwise comparisons can be made). The length of each vector represents the distance the species moved in isotopic niche space, whereas the angle of the vector represents the directionality of that shift. Arrow diagrams were created by plotting the mean vector and angle of change to visualize the direction and magnitude of individual fish species and community-level shifts. Rayleigh's test for circular uniformity was used to determine whether the distribution of vectors from all species was significantly different from uniform (Batschelet 1981) indicating a community-wide shift in trophic position and/or basal energy use. Circular statistics and arrow diagrams were calculated using Oriana 2.0 (Kovach 2009). All statistical analyses were performed at α = 0.05.

Results

Stable isotope analysis

Periphyton (range: − 26.37‰ to − 21.37‰) and CPOM (range: − 28.26‰ to − 30.84‰) isotopic signatures were distinct at all sites and during all seasons (Fig. 2). Because periphyton δ^{13}C values had higher variance than CPOM, a Kruskal–Wallis Test on ranks was performed to test for differences between basal δ^{13}C sources. Periphyton δ^{13}C (mean = − 24.47‰) was significantly different and more enriched than CPOM δ^{13}C (mean = − 29.56‰) in all land use groups ($P < 0.001$) and seasons ($P < 0.001$). CPOM δ^{13}C values were consistent with allochthonous resources of terrestrial origin (Peterson and Fry 1987). Periphyton δ^{15} N was also significantly more enriched than CPOM δ^{15} N ($P < 0.001$). No significant differences in CPOM isotopic signatures were found among land use groups or seasons (ANOVA, $P > 0.05$). Periphyton δ^{13}C did not vary among land use groups (ANOVA, $P = 0.24$), however, periphyton δ^{15} N was significantly more enriched in agricultural streams compared to forested (Tukey, $P = 0.02$) and buffered sites ($P = 0.04$). Periphyton δ^{15} N was also more enriched in summer compared to spring (Tukey, $P = 0.006$). In sites where it was found, (agricultural streams and buffered site 2) filamentous algae δ^{13}C (mean = − 33.06) was significantly more depleted than CPOM or periphyton ($P < 0.001$, Fig. 2).

Most invertebrate and fish δ^{13}C values fell within the range of basal energy sources (Fig. 2) after accounting for 1‰ trophic fractionation (Post 2002). Exceptions were Hydropsychidae and Ephemeroptera larvae in forested site 1 in spring (Fig. 2a) and Hydropsychidae in buffered site 3 in summer (Fig. 2b), both were more δ^{13}C depleted than CPOM (Fig. 2). Hydropsychids also had the greatest δ^{13}C and δ^{15} N variability among sites and land use groups, which is indicative of an omnivorous collector-gather. In contrast, Chironominae larvae (i.e., baseline taxa) were often the most δ^{15} N depleted primary consumer and did not significantly differ from grazer δ^{15} N signatures in all streams and seasons ($P < 0.05$). As expected, crayfish and odonates were the most δ^{15} N enriched invertebrates reflecting their consumption of animal matter, and fish were the most δ^{15} N enriched of all consumers (Fig. 2). All seven fish species were collected at each site and during each season, except no largemouth bass were found during spring sampling for agricultural site 3. Largemouth bass δ^{15} N values and trophic position estimates for all sites/seasons were similar to other invertivore fish species (Fig. 2). Since largemouth bass were all small juveniles (< 90 mm, mean = 60 mm) they were unlikely to have switched to piscivory.
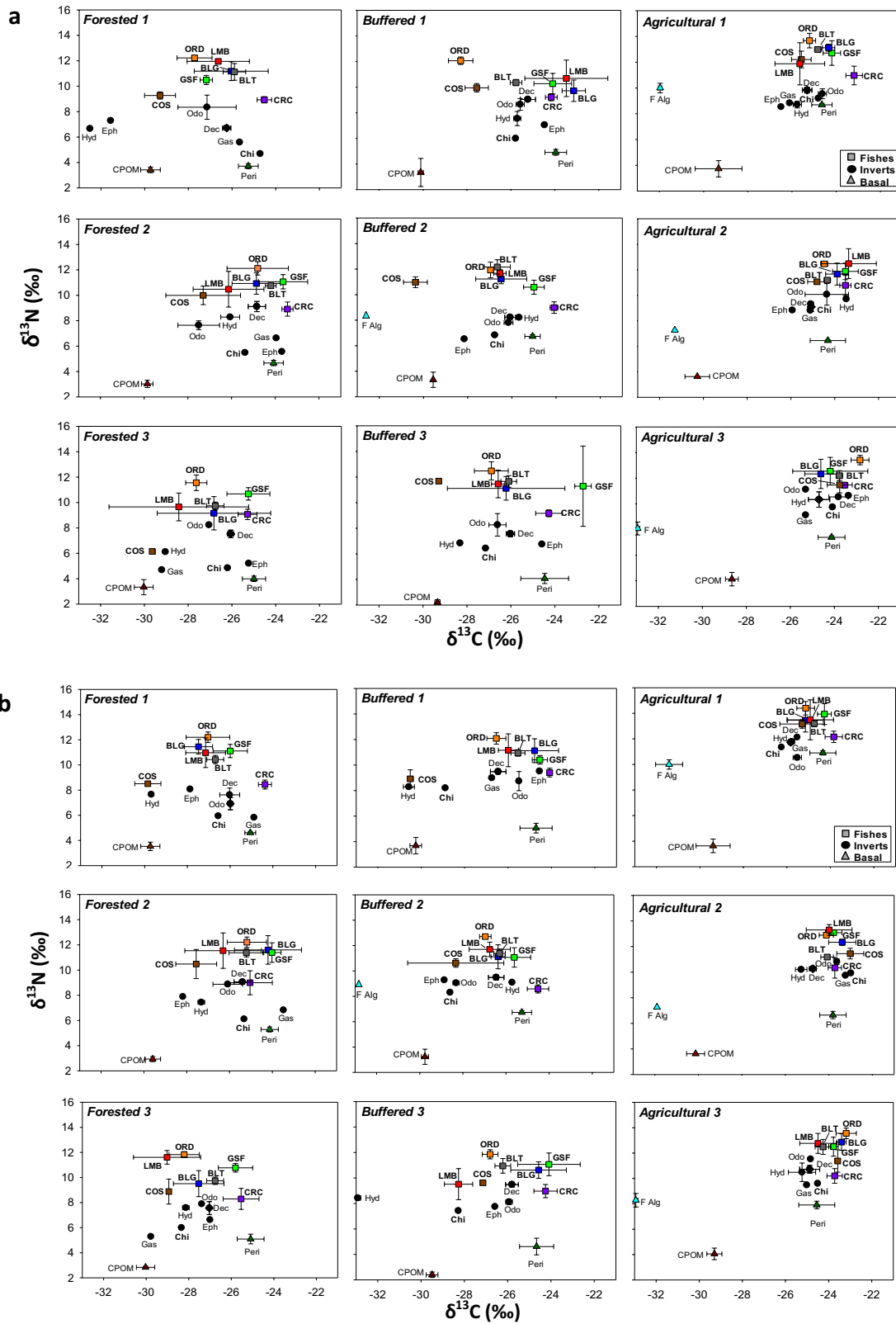
Fig. 2 Bivariate plots of mean (±SE) δ^{13}C and δ^{15}N for fish, invertebrates, and basal resources sampled in **a** spring and **b** summer at nine study sites divided into three land use groups (Table 1). Fish species (*squares* with colors specific to each species) and invertebrate taxa (*circles*) abbreviations given in Table 2. Basal resources (*triangles*): CPOM = coarse particulate organic matter, Peri = periphyton, F Alg = filamentous algae

Isotopic metrics and standard ellipse areas

Community-wide metrics revealed differences in isotopic niche space among streams in different land use groups (Fig. 3). We were able to use these metrics to compare among land use groups and seasons because the range in $\delta^{13}C$ of basal resources did not differ among groups or seasons (Fig. 2, ANOVA, all $P > 0.05$) and $\delta^{15}N$ signatures were standardized to trophic position (Post 2002; Layman et al. 2012) All trophic diversity isotopic metrics varied significantly among land use groups and seasons ($P < 0.05$), however, significant interactions between land use group and season precluded interpretation of main effects (Table 3). Pairwise comparisons indicated that all trophic diversity metrics were significantly greater in forested compared to agricultural streams in both spring and summer (Fig. 3, Tukey, all $P < 0.05$). Forested streams had food webs with higher trophic diversity than agricultural sites that included more diverse carbon sources and longer trophic lengths. Buffered stream metrics were generally intermediate (Fig. 3). The significant interactions were the result of seasonal variation in the relationship between buffered streams and the other land use groups.

Fig. 3 Mean + SE of trophic structure metrics (Layman et al. 2007a, b) total convex hull area ‰² (TA), $\delta^{13}C$ range (CR), $\delta^{15}N$ range (NR), and mean distance to centroid (CD) for streams in each land use group ($n = 3$ streams per group) for **a** spring and **b** summer. Bars with different letters indicate a significant difference between land use types ($P < 0.05$) based on repeated measures ANOVA models (see Table 3) and Tukey's pairwise comparisons
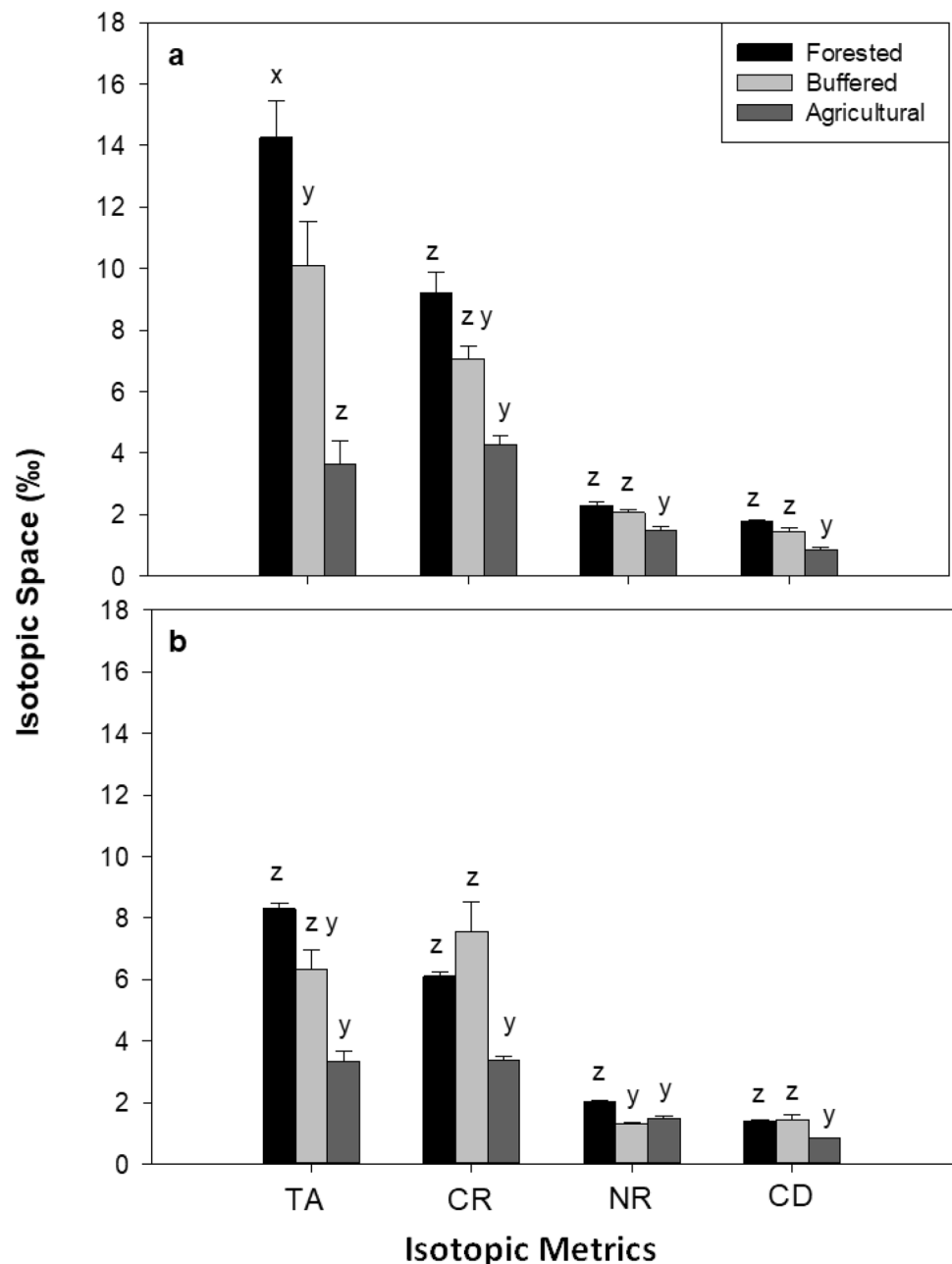
Table 3 Repeated-measures ANOVA models for the effect of land use group, season, and their interaction on Layman metrics and fish trophic position ($n=3$ for each land use group, $n=2$ for season).

Parameter	Land Use Group		Season		Land Use X Season	
	$F_{2,6}$	P	$F_{1,6}$	P	$F_{2,6}$	P
Layman Metrics						
Total Area (TA) $‰^2$	**31.01**	**< .0001**	**30.32**	**< .0001**	**7.34**	**0.022**
δ^{13}C range (CR) $‰$	**25.09**	**0.001**	**11.59**	**0.014**	**9.26**	**0.015**
δ^{15} N range (NR) $‰$	**28.79**	**< 0.001**	**17.25**	**0.006**	**7.01**	**0.023**
Mean distance to centroid (CD) $‰$	**26.51**	**0.001**	**10.76**	**0.017**	**7.41**	**0.024**
Mean nearest neighbor distance $‰$	**7.13**	**0.026**	**10.02**	**0.019**	3.73	0.088
Nearest neighbor distance $‰$	**20.82**	**0.002**	3.66	0.104	0.95	0.438
Fish Trophic Position						
Central stoneroller	2.29	0.182	3.64	0.105	4.21	0.072
Creek chub	**47.56**	**< 0.001**	**42.21**	**0.001**	0.41	0.683
Bluntnose minnow	**20.31**	**0.002**	5.39	0.059	0.62	0.570
Bluegill	**15.84**	**0.004**	3.25	0.122	0.40	0.689
Green sunfish	**66.04**	**< 0.001**	5.43	0.068	1.53	0.290
Orangethroat darter	**23.58**	**0.001**	**7.43**	**0.034**	0.88	0.463

Significant differences ($P<0.05$) in bold

Total trophic area (TA) was significantly larger in forested than agricultural streams in spring and summer (Tukey, $P \leq 0.006$). Buffered streams TA were similar to forested in spring but intermediate in summer (Fig. 3). δ^{13}C range (CR) was significantly larger in forested than agricultural streams in both spring and summer (Tukey, $P \leq 0.01$) with forested streams having more than 2 times greater CR. Buffered streams CR were intermediate in spring but similar to forested in summer (Fig. 3). δ^{15} N range (NR) was significantly larger in forested compared to agricultural streams in spring and summer (Tukey, $P \leq 0.006$) with forested streams NR almost twice as large as agricultural streams. Buffered streams NR were similar to forested streams in the spring but similar to agricultural streams in summer (Fig. 3). Mean distance to centroid (CD) was significantly larger in forested and buffered streams compared to agricultural streams in spring and summer (Tukey, all $P < 0.05$). Forested streams had larger TA, CR, and CD in spring compared to summer (Tukey, all $P \leq 0.02$), whereas buffered and agricultural streams did not significantly differ seasonally in those measurements. NR only varied seasonally in buffered streams with a larger range in spring compared to summer (Tukey, $P = 0.01$).

Community-wide metrics that measure trophic redundancy differed among land use groups and season with no significant interactions (Table 3). Mean nearest neighbor distance (MNND) and nearest neighbor distance (SDNND) were significantly lower in agricultural streams compared to forested and buffered streams (Tukey, all $P < 0.05$), indicating higher trophic redundancy in agricultural streams. MNND was also significantly lower in summer compared to spring (Tukey, $P = 0.02$), whereas SDNND did not differ among seasons (Table 3).

Bayesian standard ellipse areas (SEA) based on invertebrate and fish isotopes for each land use group varied in size and shape (Fig. 4). Differences in SEAc overlap reveal variation in isotopic niche space among land use groups and seasons. Overlap between forested and buffered sites was very high in spring (up to 95%; Fig. 4a), but much lower in summer (range 37–45%) due to a seasonal change in NR in buffered sites (Fig. 4b). SEAc overlap between forested and agricultural sites was low in both seasons with 0% overlap between forested sites and 2 of the agricultural sites (Fig. 4a and 4b). SEAc overlap between buffered and agricultural site was also low in both seasons (range 0–22%, Fig. 4a and 4b).

In spring, 100% of posterior SEAc from all forested streams were larger than all agricultural streams (Fig. 4c). All forested streams SEAc were also larger than buffered site 1 (likelihood 99%) and buffered site 2 (Fig. 4c, likelihood 98%). SEAc size did not differ among forested streams and buffered site 3 (Fig. 4c). All buffered sites SEAc were larger than agricultural sites 2 and 3 (likelihood 99%), however, only buffered site 3 was larger than agricultural site 1 (Fig. 4c, likelihood 99%). In summer, SEAc size did not differ among forested and buffered sites, whereas all SEAc in forested and buffered sites were larger than in agricultural sites (Fig. 4db, likelihood 99%).

Community isotopic shifts

Significant directional isotopic shifts occurred among fish communities in different land use groups (Fig. 5, Table 4). Circular statistics revealed that fishes from agricultural sites
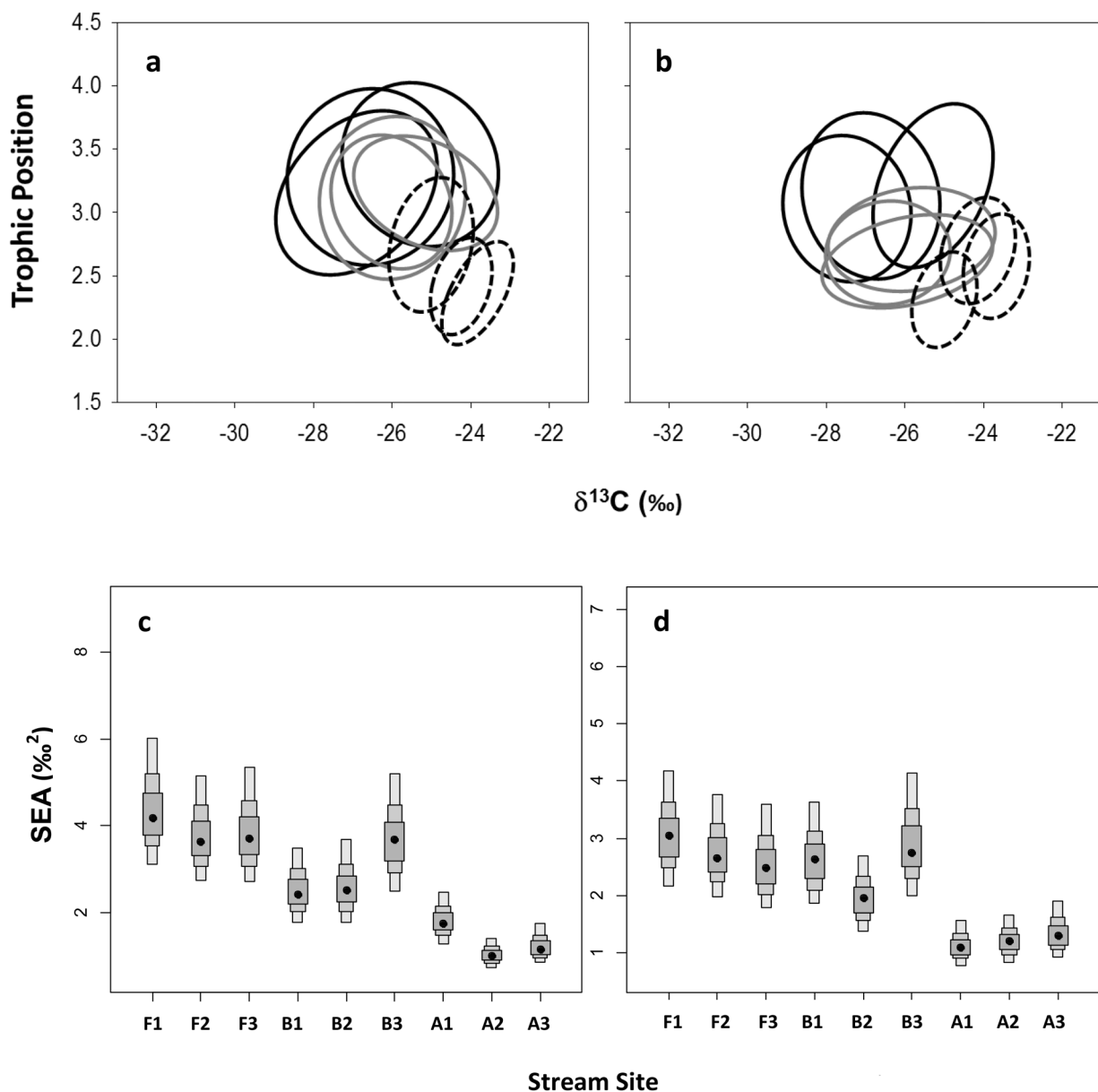
Fig. 4 Bayesian standard ellipses (SEAc) of trophic position and $\delta^{13}C$ values of fish and invertebrates from the nine study streams for **a** spring and **b** summer sampling periods. SEAc enclose the core niche width (40% of the data) for each site and season. Stream sites are identified by land use group ($n = 3$ streams per group): *solid black lines* represent forested streams, *gray lines* represent buffered streams, and *dashed lines* represent agricultural streams. Density plots showing the credibility intervals (50%, 75%, 95%) of the SEA for each of the stream sites from **c** spring and **d** summer samplings. Black dotes represent their mode. Stream sites are identified by land use group: forested (F1, F2, F3), buffered (B1, B2, B3) and agricultural (A1, A2, A3)

were more $\delta^{13}C$ enriched with lower mean trophic positions relative to fishes in forested sites in both spring and summer (Fig. 4, Table 4). Similarly, fishes shifted towards $\delta^{13}C$ enrichment and lower mean trophic positions in agricultural sites relative to buffered sites in spring (Fig. 5, Table 4). Fishes in agricultural sites were also more $\delta^{13}C$ enriched relative to buffered sites in the summer, but no differences in trophic position were found (Fig. 5, Table 4). Although the magnitude of change was much lower than comparisons with

agricultural sites, fishes decreased in mean trophic position in buffered relative to forested streams in summer (Fig. 5, Table 4). No significant shifts occurred between forested and buffered sites in spring (Fig. 5, Table 4). No significant seasonal shifts occurred for fish communities within the same land use group (Rayleigh's test, $P > 0.5$).

Individual fish species had consistent isotopic shifts between agricultural and forested or buffered streams with species in the same trophic guild having similar responses.
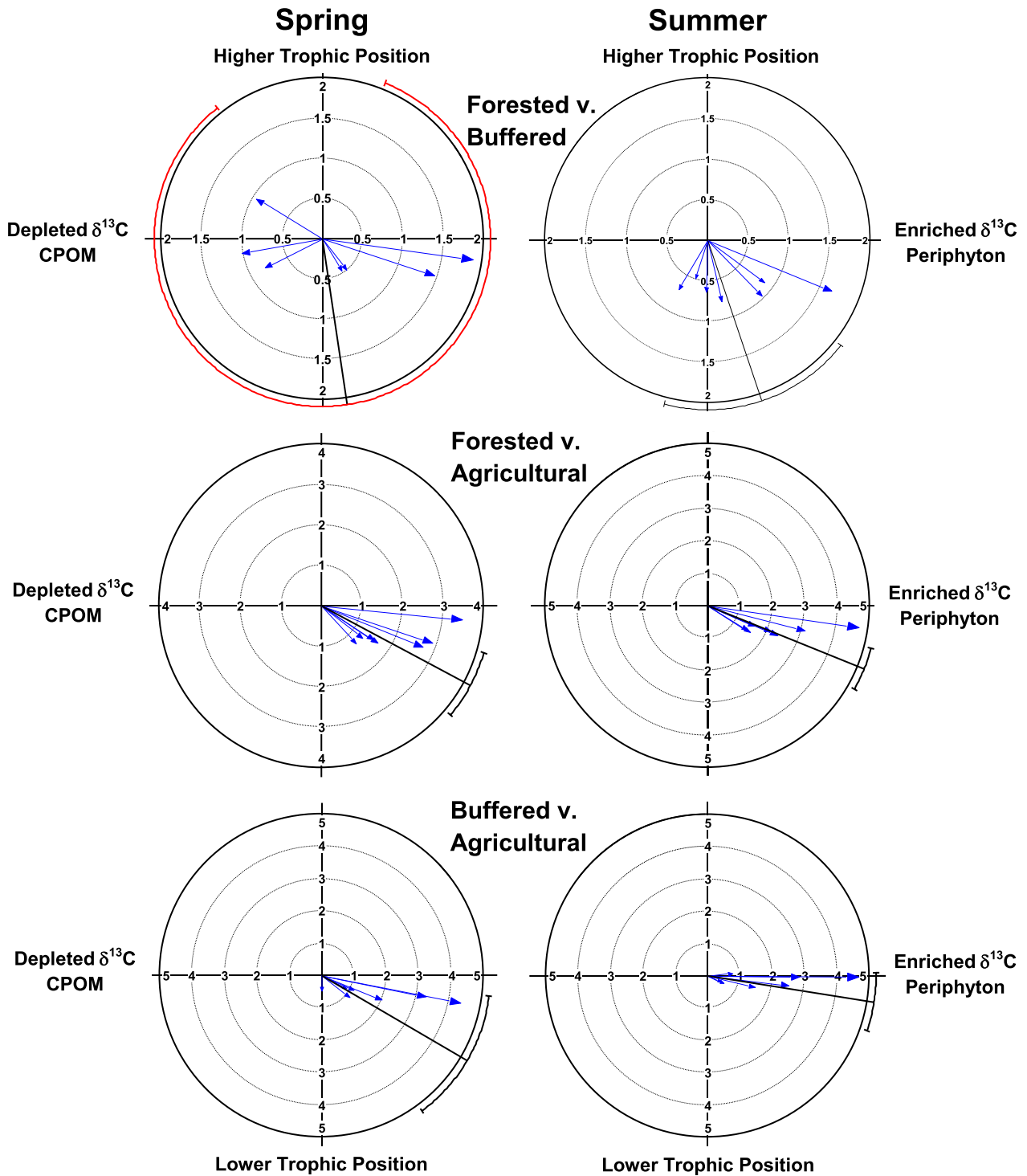
Fig. 5 Circular plots of $\delta^{13}C$ and $\delta^{15}N$ corrected baseline values (TP). Arrow diagrams show comparisons for each land use group and indicate the directionality (angle) and magnitude (arrow length) of change among fish communities. Individual arrows represent the mean of a single fish species. The vector direction indicates shifts in trophic niche space between sites in different land use groups. Num-bers in concentric circles correspond to magnitude of change, in delta units (‰). The overall mean angle of change among all species is represented by a solid straight line and the 95% confidence interval is the curved line outside the circumference with a black curved line indicating significant Rayleigh's test for circular uniformity ($P < 0.05$) and red line not significant

Table 4 Vector angle (degrees) and length for fish species used for circular statistics (Fig. 5). Paired land use comparisons for each season with significant Rayleigh's tests for circular uniformity in bold

Common name	Forested to Buffered				Forested to Agricultural				Buffered to Agricultural			
	Spring		Summer		Spring		Summer		Spring		Summer	
	Angle	Length	Angle	Length	Angle	Length	Angle	Length	Angle	Length	Angle	Length
Central stoneroller	300.76	0.96	181.77	0.63	95.10	3.81	98.19	4.69	100.95	4.37	90.42	4.66
Creek chub	148.99	0.47	126.27	0.87	127.95	1.27	121.82	1.42	116.68	0.86	114.83	0.56
Bluntnose minnow	259.86	1.02	197.37	0.49	137.00	1.26	121.73	1.54	111.72	2.00	103.11	1.50
Bluegill	142.38	0.48	112.00	1.65	122.60	1.53	112.05	2.10	114.03	1.09	112.23	0.46
Green sunfish	108.16	1.46	135.74	0.96	123.51	1.67	113.47	1.56	179.20	0.47	85.25	0.77
Orangethroat darter	243.30	0.80	210.20	0.70	112.10	2.69	113.11	2.33	101.52	3.28	97.03	2.52
Largemouth bass	97.97	1.88	167.15	0.78	108.54	2.88	104.40	3.10	126.95	1.09	90.31	2.83
Mean	171.54	0.32	161.60	0.82	118.22	0.98	112.12	0.99	120.27	0.91	99.00	0.98
Rayleigh (Z)	0.72		4.06		6.66		7.96		5.82		6.76	
Rayleigh (P)	0.506		**0.04**		**< 0.0001**		**< 0.0001**		**0.0006**		**< 0.0001**	

The herbivorous central stoneroller from agricultural sites had the smallest differences in mean trophic position and largest vector lengths (range 3.81–4.69) relative to forested and buffered streams indicating strong shifts toward periphyton δ^{13}C (Table 4). In contrast, the omnivorous creek chub and bluntnose minnow from agricultural sites showed decreased mean trophic position relative to forested sites (angles range 121.73 − 137.74), but little difference in δ^{13}C signatures (Table 4). Orangethroat darter and juvenile largemouth bass had larger magnitudes of change (i.e., vector lengths) than the other invertivores in agricultural streams relative to forested and buffered streams (Table 4).

We examined fish trophic position further to determine if individual species level shifts were significant. Fish trophic position was significantly different among land use groups for most species with the exception of central stoneroller (Table 3). In spring, all fish species, except central stoneroller, had a significantly lower trophic position in agricultural streams compared to forested and buffered streams (Tukey, all $P < 0.05$). Creek chub and green sunfish were the only species that had a significantly lower trophic position in buffered compared to forested streams in spring (Tukey, $P < 0.05$). In summer, most fish species had a significantly higher trophic position in forested than buffered and agricultural streams (Tukey, $P < 0.05$). Bluntnose minnow and orange throat darter were the only species with trophic positions that did not differ in forested compared to buffered streams in summer (Tukey, $P > 0.05$). Although there were differences in trophic position among land use groups and among species within seasons, most individual fish species trophic position did not differ among seasons (Table 3). The exceptions were creek chub and orange throat darter that both had a significantly higher trophic position in spring compared to summer (Tukey, $P < 0.05$).

Discussion

Our results suggest that headwater food webs are sensitive to differences in both riparian forest and watershed agriculture. Comparisons among streams in the three land use groups indicate that riparian forest buffers have strong associations with key instream parameters (e.g., basal energy and nutrients) that impact stream food web structure. Agricultural streams had higher nitrogen concentrations and greater periphyton biomass, whereas buffered and forested streams had greater standing stocks of CPOM associated with greater canopy cover (Effert-Fanta et al. 2019). Forested streams, which had the lowest percent row crop agriculture, had food webs with the highest trophic diversity, largest trophic niche width, and lowest trophic redundancy. Although trophic diversity measures tended to be smaller in buffered streams, δ^{15}N range (NR) in summer was the only isotopic metric that was significantly smaller in all buffered sites compared to forested streams. Thus, despite differences in watershed agricultural land use (mean 50% vs. 76%), forested and buffered streams had relatively similar food web structure in spring. In contrast, agricultural streams with a low percent forest buffer had compressed food webs exhibiting low trophic diversity and high trophic redundancy. In other studies, isotopic metrics have revealed food web changes from other anthropogenic stressors, such as decreases in food chain length in hydrologically disturbed marshes (Sargeant et al. 2010), lower δ^{13}C variability and trophic position of fish in urban streams (Eitzmann and Paukert 2010), and smaller trophic diversity in sugarcane streams (de Carvalho et al. 2017). To our knowledge, this is the first study to show community-wide isotopic differences related to alterations in riparian forest and row crop agricultural land use.

We were able to examine differences in primary resources used by consumers because basal energy sources had distinct

stable isotope signatures in all streams (Peterson and Fry 1987; Layman et al. 2007a). Periphyton $\delta^{13}C$ and $\delta^{15}N$ had greater variation and were more enriched than CPOM isotopic signatures. Periphyton and CPOM isotopic values in our study streams were similar to those reported in previous studies from open prairie and forested headwater streams (e.g., Evans-White et al. 2001; England and Rosemond 2004; Lau et al. 2009). CPOM $\delta^{13}C$ values (mean $= -29.56‰$) were consistent with allochthonous resources of terrestrial origin (Peterson and Fry 1987). Filamentous algae had the most depleted $\delta^{13}C$ values of all sources collected but was only present in agricultural streams and one of the buffered sites. Based on the relatively depleted $\delta^{13}C$ values of all consumers in agricultural sites, filamentous algae appear to be an insignificant food source in those streams. Herbivorous fish and invertebrates have been shown to prefer and select palatable algae in periphyton, such as diatoms, over unpalatable filamentous algae that may be difficult to consume (Geddes and Trexler 2003; Devlin et al. 2013).

CPOM $\delta^{13}C$ and $\delta^{15}N$ signatures and periphyton $\delta^{13}C$ were similar among all streams, whereas periphyton $\delta^{15}N$ varied among land use groups and seasons. As predicted, $\delta^{15}N$ values of periphyton were enriched in agricultural streams. Our results are consistent with previous studies that have shown increases in $\delta^{15}N$ along nutrient and agricultural gradients (Anderson and Cabana 2005; Bergfur et al. 2009; Diebel and Vander Zanden 2009; Lee et al. 2018). Enriched $\delta^{15}N$ is likely associated with increased nitrate levels that were found in agricultural sites (Effert-Fanta et al. 2019) from greater fertilizer runoff with a low percent riparian forest buffer. Changes in instream nitrification, denitrification, and assimilation following N fertilizer application are known to elevate $\delta^{15}N$ of primary producers (Kendall 1998). Periphyton $\delta^{15}N$ in agricultural streams may also be affected by increased light availability and higher algal biomass, which may cause a higher consumption of the less preferred isotope (^{15}N instead of ^{14}N) due to increased competition (Fogel and Cifuentes 1993).

All isotopic measures of trophic diversity (TA, CR, NR, CD) and isotopic niche area (SEA) were smaller in agricultural compared to forested streams. Buffered stream isotopic metrics were intermediate between agricultural and forested streams, but there was seasonal variation in the strength of the differences. Communities in agricultural streams had reduced trophic diversity compared to buffered streams in spring, whereas isotopic niche area and carbon ranges were smaller in agricultural streams in the summer. These community-wide differences were not due to differences in assemblages among sites or seasons because similar invertebrate taxa and only fish species present in all streams were included in these analyses. Instead, lower trophic diversity and smaller isotopic niche area (TA and SEA) in agricultural streams was a result of lower diversity of basal resources supporting the food web (CR), as well as lower trophic position variation (NR) among invertebrates and fish. Lower NR in marshes with high fish densities has been attributed to increased competition reducing the abundance of larger predatory invertebrates that are preferred prey forcing fish to feed on lower trophic levels (Sargeant et al. 2010). Agricultural streams in our study had the highest fish and macroinvertebrate abundance, with chironomids as the dominant invertebrate (68% of total taxa; Effert-Fanta et al. 2019). The combination of a high density of small primary consumers and increased competition for larger predatory invertebrates may have contributed to lower fish trophic position in agricultural streams. Low overlap in core isotopic niche space (SEAc) suggests that resources used by consumers in agricultural streams were different than in buffered and forested streams (Jackson et al. 2011). Low CR and high trophic redundancy suggest that all consumers are converging on the same resource pool in agricultural sites (Layman et al. 2007b). Compressed food webs (i.e., smaller TA) caused by decreased CR and/or low NR have been reported in urban streams (Eitzmann and Paukert 2010) and streams impacted by acid mine drainage (Hogsden and Harding 2014) and sugarcane cultivation (de Carvalho et al. 2017). Thus, these isotopic measures may be good indicators of anthropogenic degradation of stream food webs.

Fish communities in agricultural streams were more $\delta^{13}C$ enriched and had a lower trophic position compared to forested and buffered streams. $\delta^{13}C$ enrichment is indicative of increased reliance on periphyton-derived carbon sources in agricultural streams. Previous studies have demonstrated that reduction in riparian forest and increase nutrient input due to agriculture (pasture) is associated with an increased dependence on autochthonous production (Hicks 1997; Bunn et al. 1999; England and Rosemond 2004; Hladyz et al. 2011b; de Carvalho et al. 2017). A shift in energy base is significant because terrestrial detritus is often considered the most important nutritional resource in the food webs of temperate forested streams (Hicks 1997; Finlay 2001; England and Rosemond 2004). However, algal production has been shown to be important to consumers, even in shaded reaches with high terrestrial inputs, because periphyton has a higher nutritional value than detritus (Thorp and Delong 2002; March and Pringle 2003; Brett et al. 2017). Our results suggest that some fish species, such as creek chub, follow the periphyton energy pathway in all land use groups, whereas significant $\delta^{13}C$ shifts occurred at the bottom (i.e., central stoneroller) and top (i.e., orangethroat darter, largemouth bass) trophic positions. Although shifts in primary invertebrate consumers are a consistent response to changes in riparian vegetation and canopy cover (i.e., Bunn et al. 1999; England and Rosemond 2004; Hladyz et al. 2011b), few studies have documented significant $\delta^{13}C$ shifts in fishes (but see England and Rosemond 2004; de Carvalho et al. 2017).

Central stoneroller, like primary invertebrate consumers, appears to be tracking the dominant basal energy source in each stream, with little difference in trophic position among land use groups. Circular statistics with arrow diagrams illustrated the community and species level shifts, highlighting the benefits of adding this tool to food web analyses.

The higher relative trophic position of most fish species in forested and buffered streams could be caused by two different mechanisms: 1) variation in $\delta^{15}N$ fractionation rates among streams, or 2) insertion of predatory invertebrates in the food chain. Previous studies question the use of a single $\delta^{15}N$ fractionation value (e.g., 3.4‰) for estimates of trophic position because of known variation among taxa and potential differences among locations (Adams and Sterner 2000; Jardine et al. 2005; Lee et al. 2018). Streams supported by an allochthonous base could have higher fractionation rates because low-quality detritus leads to high rates of nitrogen cycling, resulting in enriched $\delta^{15}N$ consumer values (Adams and Sterner 2000; Jardine et al. 2005). $\delta^{15}N$ of herbivorous invertebrates and fish that consume detritus directly may be more affected (Jardine et al. 2005; Bunn et al. 2013), but it has less influence on invertivore fishes that are feeding on multiple trophic levels with potentially different energy pathways (Vander Zanden and Rasmussen 2001; Bunn et al. 2013). In addition, selecting an appropriate baseline organism is more crucial for trophic position estimates than attempting to account for possible fractionation variability within the entire food web (Vander Zanden and Rasmussen 2001; Anderson and Cabana 2007; Lee et al. 2018). Therefore, our observed differences in fish trophic position among land use groups are more likely due to variation in diet. We suggest that fish trophic position was higher due to more predatory invertebrates in their diet and higher omnivory resulting from a wider resource base (sensu Post and Takimoto 2007). Densities of aquatic invertebrate predators (e.g., odonates) tended to be more abundant in forested and buffered streams than in agricultural streams, although significant differences were not detected (Effert-Fanta et al. 2019). In addition to aquatic predatory invertebrates, fish may also be consuming more terrestrial invertebrates in forested and buffered streams related to a greater canopy cover (Kawaguchi et al. 2003; Inoue et al. 2013). Terrestrial invertebrates are another high-quality food source to stream fishes (Edwards and Huryn 1996; Nakano et al. 1999) and can make up a significant proportion of small fish diets (up to 44%, Sullivan et al. 2012).

Our results highlight the overarching influence of riparian canopy cover to stream ecosystems and the potential benefits of riparian forests to food web structure in streams impacted by cropland agriculture. In the absence of riparian buffer, we found community-wide shifts in basal energy and smaller trophic niche size that suggests substantial alterations to ecosystem function in agricultural streams. Omnivorous species, such as most taxa in our study, can persist in these stressed streams; however, their ecological roles may be significantly altered (Layman et al. 2007b). Homogenization of energy flow pathways and overall simplification of food web structure can create less stable food webs (Post et al. 2000; Rooney et al. 2006). The presence of riparian forests mitigated the impacts of watershed agriculture on food web structure by increasing trophic niche size to a level similar to forested streams, particularly in spring.

There is an emerging need to include measures of integrated ecosystem processes in assessment programs, as many goals of stream management relate directly to the maintenance of natural ecological processes (Lake et al. 2007). Currently, the most common ecosystem measurements (e.g. leaf litter breakdown) focus on primary consumers and their resources, which undervalue potentially important biological drivers of ecosystem function (Power 1990; Woodward et al. 2008; Hladyz et al. 2011b). Food web analysis provides important information about interactions among species and trophic levels, along with an insight into ecological processes linked to energy flow and nutrient cycling (Woodward 2009). We found predictable differences in stream food web structure, as measured with isotopic metrics, related to variation in riparian forest and watershed agricultural land use. Agricultural streams that lacked sufficient forest buffer had food webs with low trophic diversity driven by a higher reliance on autochthonous resources and lower fish trophic position. Streams with riparian forests had a significantly higher range in basal resources used by consumers and greater trophic diversity in buffered streams. Our results suggest that food web structure is an effective indicator of agricultural impacts on stream ecosystem function and highlight the importance of allochthonous energy inputs in headwater streams, which has implications for managing riparian areas in agricultural watersheds.

Author contributions Eden Effert-Fanta conceived of the study idea. All authors contributed to the study design. Field work, lab processing and data analyses were completed by Eden Effert-Fanta. Eden Effert-Fanta wrote the first draft of the manuscript. Robert Fischer and David Wahl provided editorial advice.

Availability of data and material The datasets used and/or analyses during the current study are available from the corresponding author on reasonable request.

Declarations

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