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Quality versus quantity: response of riparian bird communities to aquatic insect emergence in agro-ecosystems

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In many agricultural landscapes where field drainage is required to enhance crop production, agricultural drainage ditches, and their associated banks and hedgerows can support riparian biodiversity, including bird communities. Against a global background of farmland bird and terrestrial insect decline due to agricultural intensification and extensification, emerging aquatic insects in these aquatic corridors can provide a pulse of energy-rich, nutritionally-important food for birds and other wildlife. In this paper, we quantify the value of drainage ditch habitats in terms of aquatic insect production as a potential food source for riparian foraging birds in a river basin in eastern Canada. Despite being highly managed, agricultural drainage ditches remained extremely productive in terms of emerging biomass of aquatic insects (high quantity), but large-bodied aquatic insects such as mayflies, stoneflies and caddisflies, which are rich in fatty acids, were more common in natural, forested streams and less common in agricultural streams and ditches. The proportion of riparian insectivorous birds was lowest along straight ditches running through agricultural fields and highest among meandering (sinuous) streams in more forested areas, suggesting that agricultural drainage systems may not be able to fully support resource use for foraging predators that rely on emerging aquatic insects. Agricultural producers can improve habitat provisioning for birds on their farms by supporting mosaicked farmscapes through careful conservation and management of ditches and ditch bank vegetation. Establishing larger forest blocks with natural or unmanaged streams between areas of more intense land use can ensure the provisioning of more high quality prey to riparian insectivorous birds, helping to find the balance between agricultural productivity and protection of declining bird populations.

KEYWORDS

secondary production, agricultural streams, agricultural drainage ditches, insectivorous birds, emerging aquatic insects, ecosystem services, agriculture intensification

1 Introduction

Bird population declines have been correlated with agricultural intensification and extensification in both Europe and North America (Rigal et al., 2023; Betini et al., 2023; de Zwaan et al., 2022; Benton et al., 2002; Johnson et al., 2011; Endenburg et al., 2019; Bowler et al., 2019), corresponding with loss of physical habitat, increased fertiliser and pesticide use, and the move toward larger field sizes with less edge habitat (i.e., hedgerows). Some habitat losses are accelerated following farmers' perceptions that these edge habitats can harbor crop damaging pests (Deschênes et al., 2003), reduce crop yields via shading and reduce the amount of arable land (e.g., Graves et al., 2017; Blanco et al., 2020). It has been proposed that declines in insect populations represent a major driver in declines in agricultural bird populations (Benton et al., 2002), particularly aerial insectivores—birds that capture insects on the wing (Spiller and Dettmers, 2019; Nebel et al., 2010). In fact, emerging aquatic insects provide multiple ecosystem services on agro-landscapes (Raitif et al., 2019), and are an essential aspect of habitat provisioning as a source of nutritionally-important omega-3 highly unsaturated fatty acids (ω-3 HUFA; Twining et al., 2021; Shipley et al., 2022; Parmar et al., 2022). Moreover, these essential fatty acids in aquatic insects can be up to ten-times greater than terrestrial insects (Twining et al., 2016), underscoring the importance of maintaining healthy riparian and ditch habitats for wildlife conservation in areas where (semi) natural habitat is limited by agricultural use. Most studies in Canada examining agricultural avian populations have focused on the effect of on-farm habitat and landscape composition, such as hedgerow and woody feature complexity, crop heterogeneity and type (e.g., de Zwaan et al., 2024; Wilson et al., 2017; Jobin et al., 2001; Jobin et al., 2004).

Although ditches and ponds remain prominent features in many agro-ecosystems throughout the world, their importance to avian populations has been disputed and may differ across taxonomic groups or niches. For example, in their study of bird habitat use in southern Quebec's agricultural fields, Jobin et al. (2001) found that the presence of a ditch, standing water or aquatic vegetation did not influence use of marginal habitat like hedgerows, but rather that the structural complexity of the woody features themselves influenced bird habitat use and diversity. Conversely, work done in England found that aquatic insect emergence from farmland ponds was strongly linked to bird community richness and abundance, and that the management of these ponds enhanced both the emergent aquatic insect community and the riparian bird community (Lewis-Philips et al., 2020). Tree swallows in agricultural areas have been found to travel further to preferentially forage for Ephemeroptera that emerged from other water bodies (Bellavance et al., 2018) as they are highly nutritious prey for their growing offspring due to their large size and high levels of ω-3 HUFAs (Shipley et al., 2022). In fact, there is evidence that the presence of wetlands may be able to buffer changes related to agricultural intensification and extensification impacts on tree swallow diets and support successful breeding, as these aerial insectivores predominantly feed on aquatic prey rich in HUFAs (Michelson et al., 2018; Berzins et al., 2021; Berzins et al., 2022). There may be nutritional and population-wise consequences for some species if there is a lack of aquatic insect prey in their diets; for example, bank swallows (*Riparia riparia*), another aerial insectivore that relies on emerging aquatic insects have been shown to have significantly lower levels of HUFAs in their plasma when they breed away from aquatic habitats (e.g., at inland mining pits) (Génier et al., 2021).

The phenology of emergence and dispersal of aquatic insects results in a pulsed resource from aquatic to riparian habitats (Nash et al., 2023). This resource can be influenced by external factors arising from agricultural management such as ambient temperature, agricultural run-off, deposited fine sediment and low flows, through direct and indirect impacts on aquatic insect composition, drift (a stress response to find more suitable environments), body size and emergence patterns (Piggott et al., 2015; Woods et al., 2021). Under mesocosm experiments simulating conditions in agricultural streams and ditches, increased fine sediment and elevated temperatures have been found to result in communities of smaller organisms, and cause increased variability in drift and emergence (Piggott et al., 2015). Aquatic insect communities can also be influenced by water toxicity, such as pesticides, which can both change communities and lower emergence rates (Cavallaro et al., 2019; Kraus et al., 2021). In some agricultural aquatic systems experiencing pesticide run-off, declines in emerging aquatic insect biomass of up to 73% were observed compared to less impacted wetlands in grassland ecosystems (Kraus et al., 2021). Vegetation removal along banks and channels—a common practice in agricultural drainage ditch management to improve flow efficiency (Kavanagh et al., 2017; Damphousse et al., 2024; Guo et al., 2024)— can increase insect emergence, as disturbance-tolerant taxa, such as mass-emerging Chironomidae, become dominant (e.g., Cavallaro et al., 2019).

How far species are able to disperse, and subsequently become food for foraging predators can be dependent upon the structure of the landscape, including the presence, density and geometry of woody features like hedgerows along field edges and drainage ditches (Raitif et al., 2018, 2022), which can influence wind strength and direction. For example, agricultural systems can have much higher rates of insect emergence (measured in dry mass) than natural systems, particularly for small-bodied taxa like Chironomidae (Raitif et al., 2022). In general, Chironomidae were also found to disperse further into the broader landscape, whereas the immediate riparian zone had higher deposition rates (more individuals) but were composed mostly of Ephemeroptera (mayflies) and Trichoptera (caddisflies) (Raitif et al., 2022). The timing of these ecosystem fluxes is particularly important as the emergence patterns of many aquatic insect taxa are driven by temperature cues and any change to temperature—which can be influenced by shading by field crops and vegetation along field margins and climate change—can result in ecological mismatches with riparian consumers (e.g., between food availability and breeding cycles; Larson et al., 2016; Shipley et al., 2022; Twining et al., 2022).

Our objective is to examine secondary productivity of emerging aquatic insects as an aspect of the ecosystem service 'habitat provisioning' and determine the linkage between aquatic insect emergence and riparian avian communities in an agriculturally-dominated watershed in eastern Ontario, Canada. We quantify the value of agricultural ditch habitats in terms of aquatic insect production as a potential food source for riparian foraging birds across a dense network of agricultural drainage ditches and streams in the region, experiencing a gradient of agricultural intensity. Working at sites in forested and agricultural streams, and drainage ditches, we took a multi-level approach by examining how a suite of in-stream (water quality) and landscape variables, aquatic insect emergence, and riparian bird and aquatic insect communities change across a gradient of agricultural intensity. In particular, we ask: [1] How do in-stream and landscape variables change across a gradient of agricultural intensity? [2] How does the flux of aquatic emerging biomass change across this gradient? [3] Do insectivorous birds positively respond to aquatic insect emergence in these agricultural landscapes? [4] Does agricultural intensity alter riparian bird and aquatic insect community composition and do the communities co-vary?

2 Methods

2.1 Study system

This study was conducted in the South Nation River watershed (catchment area ≈ 3,900 km^2), a subbasin of the Ottawa River, located in close proximity to Ottawa, Ontario, Canada. Agriculture dominates over 60% of the watershed, typically with corn, soybean and forage-based livestock cropping systems (Crabbé et al., 2012). A dense network of agricultural drainage ditches occurs in the agricultural areas to help improve field drainage for crop production (Sunohara et al., 2016). Depending on the degree of organic matter and sediment accrual, these drainage ditches may be dredged and bank-brushed (i.e., the riparian vegetation removed) to improve flow efficiency. Management cycles can vary, ranging from 5 to 30 years (Kavanagh et al., 2017).

We sampled 31 sites across the South Nation River watershed (Figure 1A). Sites were an average of 24.65 ± 12.40 km from each other (straight line distance), with the minimum and maximum distance between sites being 0.53 km and 62.13 km, respectively. Sites represented different degrees of forest cover, mean field size, crop diversity and vegetation height along the watercourses (including streams and agricultural drainage ditches; see Supplementary material S1). Each site was defined as aquatic habitat, with a riparian area and/or vegetated bank. All sites were located within 1 km of a road to logistically facilitate sampling, and were located on a combination of public and private lands (landowner agreements were established for sampling on private lands).

We visually estimated watercourse sinuosity from Google Earth Pro (version 7.3.6; Google, 2024) for 200 m upstream and downstream of the site as a proxy for "naturalness," with higher sinuosity indicating more natural, meandering forested streams ("sinuous" = 8 sites, "low" = 9 sites, "straight" = 7 sites; Figure 2). Sinuous watercourses were natural streams that had many turns as they traversed the landscape. Straight (linear) watercourses were human-made agricultural drainage ditches that were designed to receive drainage water from fields. Low sinuosity watercourses could be natural or dredged to facilitate drainage from adjacent farmlands.

2.2 In-stream and landscape variables

Single shot grab samples for surface water chemistry to match the benthic samples were collected in September 2023 following protocols outlined by the Canadian Aquatic Biomonitoring Network (CABIN; ECCC, 2011) and analyzed at the City of Ottawa Laboratory for a standard suite of metals, nutrients and ions (Supplementary material S2). The number of analytes assessed were reduced to ease interpretation based on Pearson correlations ($r \geq 0.70$), keeping, among correlated pairs, analytes that were more ecologically relevant or that had the highest between-site variance (Supplementary material S2).

The following geospatial variables describing the agricultural impact on the landscape and site-level characteristics were calculated using ArcGIS Pro [version 3.2, ESRI (2023)] from data extracted from the Agriculture and Agri-food Canada Annual Crop Inventory 2022 (AAFC, 2022): percent forest, land cover Shannon-Wiener diversity, crop Shannon-Wiener diversity and mean field size calculated for 14 buffers: every 100 m up to 500 m, then every 500 m up to 5,000 m. The extracted buffers were highly correlated ($r \geq 0.70$; Supplementary material S2) and so were reduced to a near (<500 m buffer, representing all smaller buffers) and far (>1,000 m buffer, representing all larger buffers) metric for each variable, selecting the buffer size that best represented all others (Supplementary material S2). Percent forest was highly correlated across all buffers and so was reduced to a single measure per site (1,000 m buffer). Hedge height, hedge width—calculated using the Digital Raster Acquisition Project of Eastern Ontario (DRAPE) 2019–2020 (Land Information Ontario, 2019) and multiplied together to form "hedge area" to reduce variables in later models—and distance to nearest forest patch (AAFC, 2022) were extracted for a single point per site.

2.3 Emerging insect biomass

We measured aquatic insect emergence using floating emergence traps, following a modified design by Cadmus et al. (2016) (Supplemrntary file S3). Three emergence traps were deployed at each site in early May 2022 and collected every two weeks through July 2022 (n = 5 collections per site). Any samples from submerged or flipped traps were discarded to ensure consistency in the time between collections. Samples were stored in propylene glycol and kept in a cold room before transportation back to the laboratory for analysis. In the laboratory, samples were sieved with a 250 µm sieve, non-insect orders discarded, dried for 48 h and weighed to 0.001 g. Any remaining missing data were replaced with the collection average, corrected based on the average site magnitude. We further calculated two metrics for each site: [1] the total emerged aquatic biomass as a sum of all included collections, and [2] the coefficient of variation among samples as the 'emergence seasonality' (CV) of a site after Nash et al. (2023).

2.4 Aquatic insect and riparian bird communities

Biotic sampling of the aquatic invertebrate and riparian bird communities was completed at a subset of 24 sites.

The aquatic invertebrate community was sampled with a sterilized 400 µm benthic net in June 2022 following a modified CABIN wetland and stream protocols (ECCC, 2019; ECCC, 2011) for sample collection; notably we used either kick or sweep methods depending on the substrate type for 2 min to dislodge aquatic invertebrates from substrate and macrophytes, ensuring the net was positioned to face upstream of any flow. Samples were rinsed in the field to remove excess sediment and stored in propylene glycol at −20°C until transfer to the University of Guelph Centre for Biodiversity Genomics. Following the standard pipeline outlined in Hajibabaei et al. (2019), DNA was extracted from samples for metabarcoding of the

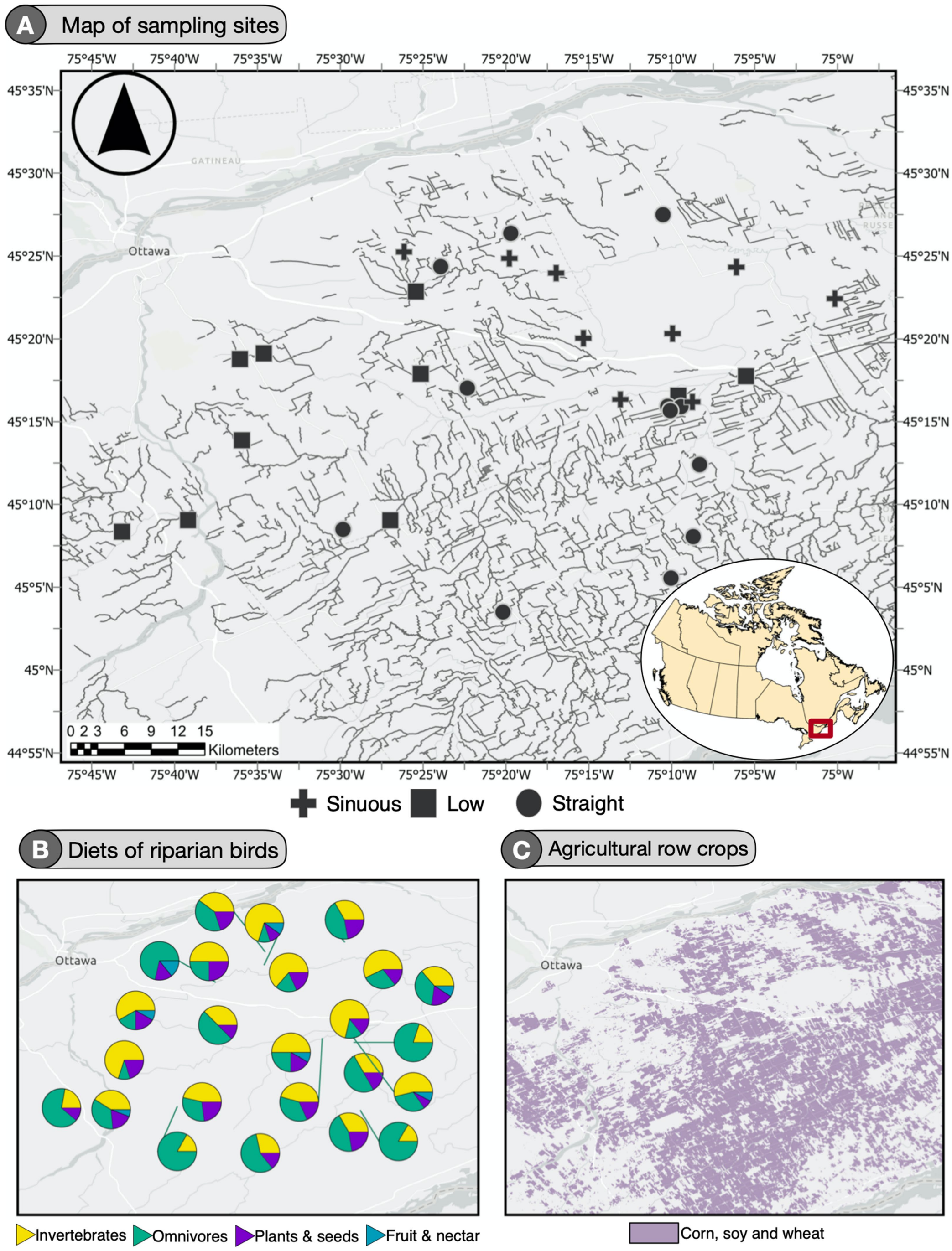

FIGURE 1
(A) Map of sites across the South Nation watershed, with shapes designating watercourse sinuosity. Constructed drainage systems [which "include ditches, buried tile systems, or natural watercourses that have been modified to improve drainage"; OMAFRA (2024)] are shown in grey. **(B)** Map of avian diets across the study area with pie charts denoting the proportion of foraging guilds at each site, with green lines indicating the site location for any jittered plots. Species' diets were assigned using the EltonTraits 1.0 database (Wilman et al., 2014). **(C)** Agricultural row crops in South Nation, comprising corn, soy and wheat, sourced from the AAFC Annual Crop Inventory (AAFC, 2022).

cytochrome c oxidase subunit 1 (CO1) barcoding region with BR5 and F230R amplicons. All taxonomic classifications were processed with MetaWorks (version 1.11.3; Porter and Hajibabaei, 2022) using the Ribosomal Database Project (RDP) classifier (version 4; Wang et al., 2007), which were subsequently filtered for a minimum bootstrap cutoff above 0.3. This results in greater than 99% confidence in correct assignment at the genus level. Data generated from DNA-metabarcoding are best interpreted as presence/absence information (Elbrecht and Leese, 2015). Taxa were filtered to Class Insecta for the purposes of analysis. We further focused on the proportion of Ephemeroptera, Plecoptera and Trichoptera (EPT), and the proportion of Diptera as these groups can be bioindicators of good water quality and disturbance, respectively. Full taxa list for aquatic insects can be found in Supplementary material S4.

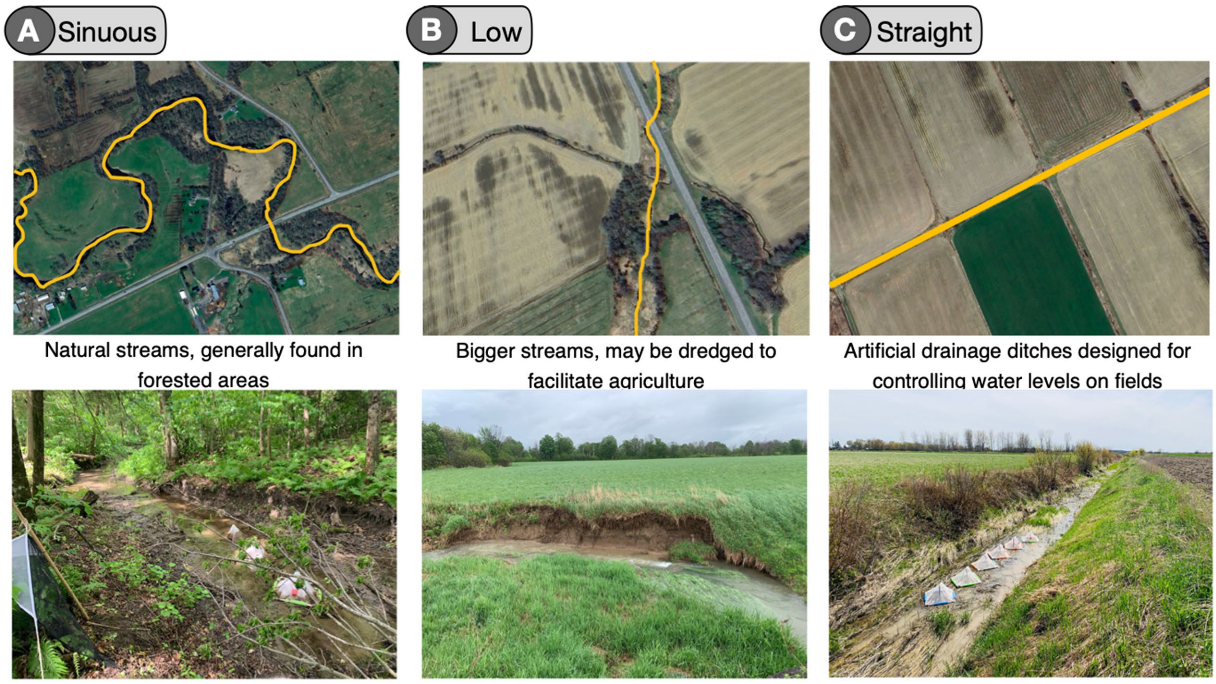

FIGURE 2
Sinuosity types and examples across the study region for sites designated as **(A)** sinuous, **(B)**, low and **(C)** straight across the study region, the South Nation River watershed, ON.

We carried out bird surveys in riparian habitats in June 2022 using standard point count methods where two observers conducted three stationary 5-min point counts, each located 100 m apart along the length of the watercourse, to count and identify all birds seen and heard within 50 m. Surveys were completed from half an hour past sunrise until 10:00 am, when most breeding birds are active, on good weather days with low wind and no rain. All three point counts were combined for each site, resulting in an abundance matrix of total species per site (taxa list in Supplementary material S4). For further details on the riparian bird sampling within the South Nation River watershed study, see Warren (2024). We assigned diets for each species using the EltonTraits 1.0 database (Wilman et al., 2014), summarising each taxa into one of 5 diet categories: invertebrate, plants and seeds, omnivore, fruit and nectar, and vertebrate, fish or scavenger. We calculated the proportion of birds classified as invertebrate-reliant (hereafter "insectivorous birds") for each site as we reasoned that these species would be most affected by any change to insect emergence patterns.

2.5 Statistical analysis

2.5.1 Landscape and in-stream variables across sites

Prior to analyses, variables were reduced based on Pearson correlation coefficients ($r \geq |0.70|$; Supplementary material S2), $\log_{10}$ transformed (variables expressed as percent were logit transformed) and *z*-score standardised. Next, a Principal Components Analysis (PCA) using the *prcomp* function in the *stats* package (version 3.6.2; R Core Team, 2022) was conducted to examine how landscape and in-stream (water chemistry) variables, and thus agricultural intensity, differed across the sites. A table with summary statistics for the variables across the site types can be found in Supplementary material S5. Sinuosity was used as a categorical variable in further analysis due to the clear gradient in agricultural intensity along the first PC axes to facilitate interpretation and make comparisons across different physical site types on the landscape. We also ran the full model, without reducing variables for high correlations and found that patterns remained the same (Supplementary material S7); we report the reduced model in the text for clearer interpretation.

2.5.2 Insect emergence patterns and bioindicator taxa

Aquatic insect emergence was examined in two ways. First, a repeated measures analysis of variance (ANOVA) was performed using the *glmmTMD* package (version 1.1.10; Brooks et al., 2017) to test if emerging biomass ($\log_{10}$ transfomed) differed across the season (week) and among sinuosity type, while accounting for repeated site visits. Second, two one-way ANOVAs were used to test if total emerging biomass ($\log_{10}$ transformed) or emergence seasonality varied among sinuosity types. We examined if the proportion of EPT and Diptera taxa differed across the sinuosity types using binomial GLMMS in the *stats* package (version 3.6.2; R Core Team, 2022), using straight sites as the baseline for comparisons. Post-hoc testing was completed using Tukey Honestly Significant Different tests in the *stats* package (version 3.6.2; R Core Team, 2022).

2.5.3 Response of birds to emergence and agriculture

Next, we examined how bird richness and reliance on invertebrates differs across the sites. Specifically, two regressions were fitted on the data to test the importance of watercourse sinuosity, total emerged aquatic biomass and hedge area (both scaled) on either the proportion of insectivorous birds (binomial GLMM) or bird species richness (multiple linear regression). All model assumptions were tested and met. Model fit was improved through AIC-based stepwise selection to avoid statistical overfitting (Supplementary material S6). We also tested for the effect of detection on bird summary metrics, namely observer, time of survey and noise, but found no significant effects (Supplementary material S6).

2.5.4 Community responses in aquatic insects and riparian birds

The bird and aquatic insect communities were compared using Procrustes analysis to examine congruence of diversity patterns across sites. This multivariate analysis tests the significance (non-randomness) between two dissimilarity matrices (Peres-Neto and Jackon, 2001). First, dissimilarity matrices were calculated for each community using Bray-Curtis distance for the riparian bird community (abundance data, $\log_{10}$-transformed) and Sørenson distance for the aquatic insect community (presence-absence data). Next, a non-metric multidimensional scaling (NMDS) ordination was performed on each community ($k = 3$, permutations = 999). The two ordinations were finally compared using the *protest* function in *vegan* (version 2.6.4; Oksanen et al., 2022) based on Procrustean matrix rotation. As birds are the beneficiaries (i.e., 'function receivers') of secondary production through aquatic insect emergence and thus more likely to have their distribution impacted by differences in community assemblages, they were used as the target community, while the aquatic insects were designated the rotating matrix in the analysis. To examine if communities differed across sinuosity groupings, we first used a multivariate homogeneity of groups dispersions ($p > 0.05$) which determines how compositions vary across groups in multivariate space (Anderson, 2006). Next, we ran a permutational multivariate analysis of variance (permutational MANOVA) within *vegan* package (Oksanen et al., 2022) separately for aquatic insects and riparian birds based on their respective dissimilarity matrices (permutations = 999) to test if community compositions differed significantly across the grouping factor (sinuosity). Multilevel pairwise comparisons were completed as *post hoc* analyses using the *pairwiseAdonis* function in *vegan* (version 2.6.4; Oksanen et al., 2022).

All data visualizations were completed with *ggplot2* (version 3.4.4; Wickham, 2016), using the *viridis* (version 0.6.3; Garnier et al., 2023) color scheme. Unless otherwise stated, all functions were performed with base R (R Core Team, 2022). We tested the effect of geographic distance among sites and found there was no statistically significant effect on environmental or biotic matrices ($p > 0.05$).

3 Results

3.1 How do in-stream and landscape variables change across the habitat types?

The landscape of the South Nation watershed is dominated by agriculture, with the mean percent forest cover (calculated for a 1,000 m buffer) at our sites being 16.2% ± 19.7%. Forest patches remain on the landscape, however, with the average distance from sites to a forest patch at 422.9 ± 608.9 m. More sinuous watercourse sites were located predominantly in the northeastern part of the study area, while low sinuosity watercourse sites were generally found in western areas; straight drainage ditches were located predominantly in the centre and southern part of the study area (Figure 1A).

Principal Components Analysis explained 72.1% of the variation of landscape and environmental variables among sites across the South Nation watershed with the first five axes retained after examination of the scree plot; we focus on the first two axes for reporting (Figure 3). PC1 accounted for 22.5% of the variation and represented a gradient of agricultural intensity on the landscape, with higher scores associated with higher percent forest around sites, taller and wider hedges (or tree blocks), and increased landscape diversity near the sites, while lower scores associated with greater distance to forested areas, bigger field sizes and crop diversity. PC2, explaining 14.6% of the variation, showed a gradient of agricultural intensity at the site level, with higher scores associated with increased levels of water nutrients and metals, including nitrogen, phosphorus, strontium [can be associated with both natural limestone deposits and agricultural lime; Anderson and Thomsen (2021)] and dissolved organic carbon. Sites separated along PC1 by sinuosity, with more sinuous watercourses generally aligning with higher scores and generally associated with higher percent forest and near land diversity, straight watercourses aligning with lower scores and associated with greater distance to forest, greater near field sizes, and lower hedge width and hedge height, while sites with low sinuosity fell mostly in the middle of the other groups (Figure 3). The general separation of sites by sinuosity continued with lower axes (e.g., PC3). Site scores for the sinuosity categories were significantly different along PC1 ($F_{2,26} = 14.43$, $p = 0.0050$); straight sites were significantly different than low ($p = 0.026$) and sinuous sites ($p = 0.0057$).

3.2 How does aquatic secondary productivity change with agricultural intensity?

We detected 130 aquatic insect genera in benthic samples, with 27 EPT taxa. The taxon richness per site ranged from 4 to 31 (mean 15.21 ± 6.03); richness did not differ across the sinuosity types ($F_{2,21} = 0.54$, $p = 0.59$; Figure 4A). Genera were present at an average of 2.81 ± 2.95 sites each, with 66 genera only present at a single site. The proportion of aquatic insect richness attributed to EPT taxa was lower in straight watercourses than sinuous ($p = 0.0017$), with straight vs. low not showing significant differences ($p = 0.064$) (Figure 4B). The proportion of Diptera taxa did not differ between straight and low ($p = 0.68$) or straight and sinuous ($p = 0.54$) (Figure 4C).

Looking across the season, emerging biomass differed across the weeks ($p < 0.001$), while accounting for repeat site visits, and was highest in June (week of June 6: $p = 0.0339$; week of June 13: $p = 0.0438$, both compared to the first week, May 16); all other weeks were not significantly different from the first sampling week (all $p > 0.05$) (Figure 5). Sinuosity did not explain variation in emergence seasonally ($p = 0.098$); however, the comparison between seasonal emerging biomass at straight and sinuous sites approached significance ($t = -1.930$, $p = 0.054$), with straight sites showing marginally more emergence. When examining total emergence, biomass differed significantly across the sinuosity types ($F_{2,278} = 4.44$, $p = 0.013$), with pairwise comparisons showing that sinuous streams had significantly lower emerging biomass than low streams ($p = 0.041$) and straight ($p = 0.016$); low and straight streams were not significantly different

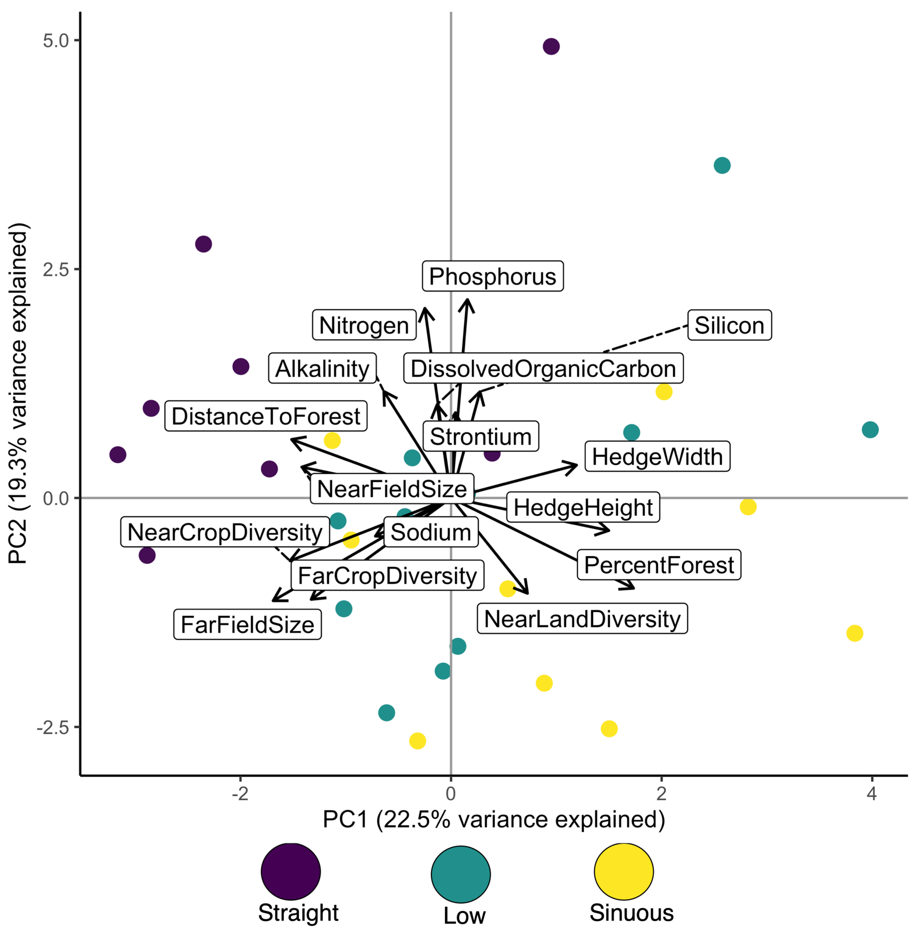

FIGURE 3
Principal components (PC) biplot projecting PC1 and PC2 for landscape and environmental variables across the South Nation Watershed. All variables were $\log_{10}$-transformed and *z*-score standardized before analyses. Sites are colored according to watercourse sinuosity. Eigenvalues for all variables can be found in S7.

($p = 0.94$) (Figure 6A). Emergence seasonality did not differ significantly across the site types ($F_{2,26} = 1.06$, $p = 0.36$; Figure 6B).

3.3 Do insectivorous birds positively respond to aquatic insect emergence?

A total of 50 avian species were detected during the surveys conducted along the riparian and bank edges of the study sites. The most reported species were song sparrow and American goldfinch, which were detected at 100 and 75% of sites, respectively. Within the avian community, 15 species were only present at a single site, and overall species were present at an average of 4.44 ± 4.66 sites each. There were significant differences in avian species richness between straight and low, as well as straight and sinuous watercourses (Table 1), with the average number of species per site higher in sinuous and low sinuosity watercourses, compared to straight agricultural drainage ditches ($R^2_{adj.} = 0.36$, $F_{2,21} = 5.98$, $p = 0.087$; Figure 4D).

Avian foraging guilds shifted across the sampling sites, with more proportionally insectivorous birds at sinuous sites as shown by binomial GLMM analysis which found that the proportion of insectivorous birds was higher near sinuous streams compared to the straight ditches (Table 1; Figure 4E). Total emerging aquatic biomass was selected in the final model (Supplementary material S6) but the effect on the proportion of insectivorous birds was not significant (Table 1). On the landscape level this translated to more insectivorous birds in the northeastern forested region and more omnivorous species in areas of intensive agriculture where there is a higher density of drainage ditches (Figure 1B).

3.4 How do riparian bird and aquatic insect communities co-vary in their response to agricultural intensity?

Aquatic insect communities (stress = 0.126) and riparian birds (stress = 0.148) both showed a separation of biotic communities among sinuosity types (Figures 7A,B, respectively). The composition of the bird community was significantly different among sinuosity categories ($R^2_{adj.} = 0.30$, $F_{2,21} = 4.49$, $p = 0.01$) and there were significant differences between community composition in straight and low watercourses (Table 2). Aquatic insects in low streams demonstrated less uniqueness with NMDS, while straight and sinuous watercourses remained distinct. These results were supported by the permutational MANOVA,

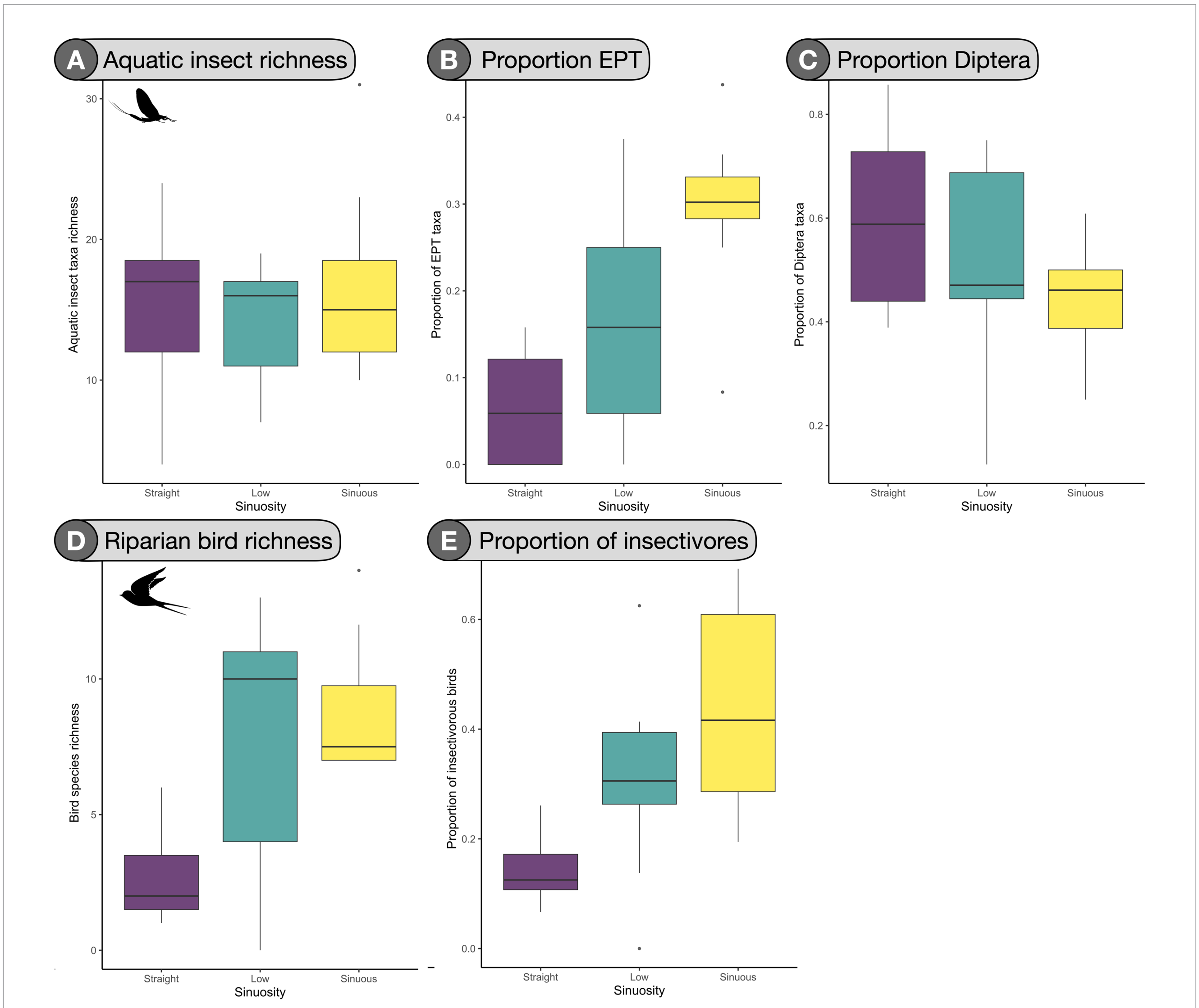

FIGURE 4
Boxplots of biotic communities across the site types (sinuosity), denoting the mean, upper and lower quartiles and outliers for **(A)** the richness of insect genera, **(B)** proportion of EPT taxa, **(C)** proportion of Diptera taxa, **(D)** the richness of bird species, and **(E)** proportion of insectivorous birds.

which showed that sinuosity was a significant factor shaping communities ($R^2_{adj.} = 0.14$, $F = 1.67$, $p = 0.03$) and pairwise comparisons found that straight and sinuous watercourses had significantly different community compositions (Table 2). The Procrustes analysis suggested that the bird and insect communities were more similar to each other than expected by chance, indicating that subsets of the communities covary with each other (permutations = 999, $M_{12}^2 = 0.80$, correlation = 0.44, $p = 0.023$; Figure 7C).

4 Discussion

In this paper, we examined secondary productivity through aquatic insect emergence in agricultural streams and ditches as a critical habitat provisioning service supporting riparian insectivorous birds in agro-ecosystems. By employing watercourse sinuosity as a proxy for a gradient of agricultural intensity, we showed that despite being highly managed, agricultural drainage ditches and streams remained extremely productive in terms of total emerging biomass of aquatic insects, but that higher quality insects (EPT taxa, generally large-bodied and nutrient-rich) were found more frequently in natural, forested streams and rare in agricultural streams and ditches. The proportion of insectivorous birds was lowest along straight drainage ditches running through agricultural fields and highest among meandering (i.e., sinuous) streams in forested areas, corresponding with the availability of higher quality aquatic emergent insects.

4.1 Agricultural land use practices and habitat provisioning in riparian landscapes

The South Nation watershed is dominated by agriculture (typically livestock cropping production systems consisting of corn, soy and hay/ alfalfa forage) and this is reflected in the aquatic habitats that remain on the landscape. Straight ditches—often high-banked features that receive tile drainage from adjacent fields—run through much of the agricultural crop land. Additionally, some streams, particularly those in the western region of the study area, have been transformed

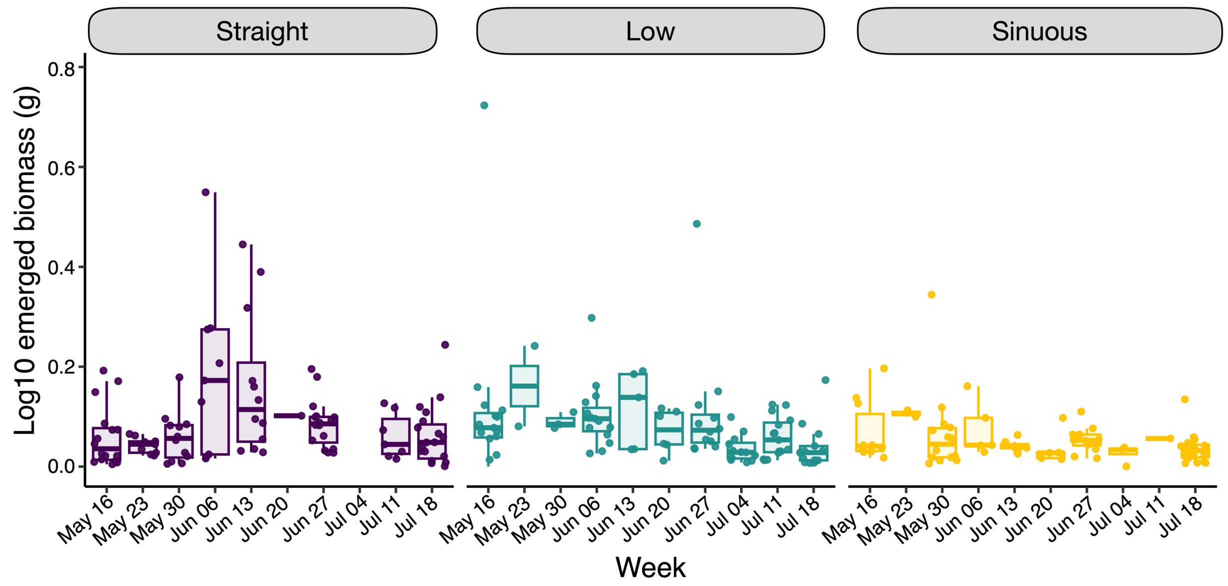

FIGURE 5
Emergence patterns throughout the sampling season, as shown by boxplots (showing mean, upper and lower quartiles) and jittered data for each week of sampling across the sinuosity types. Samples were collected at each site every 14 days on a set 2-week rotation.

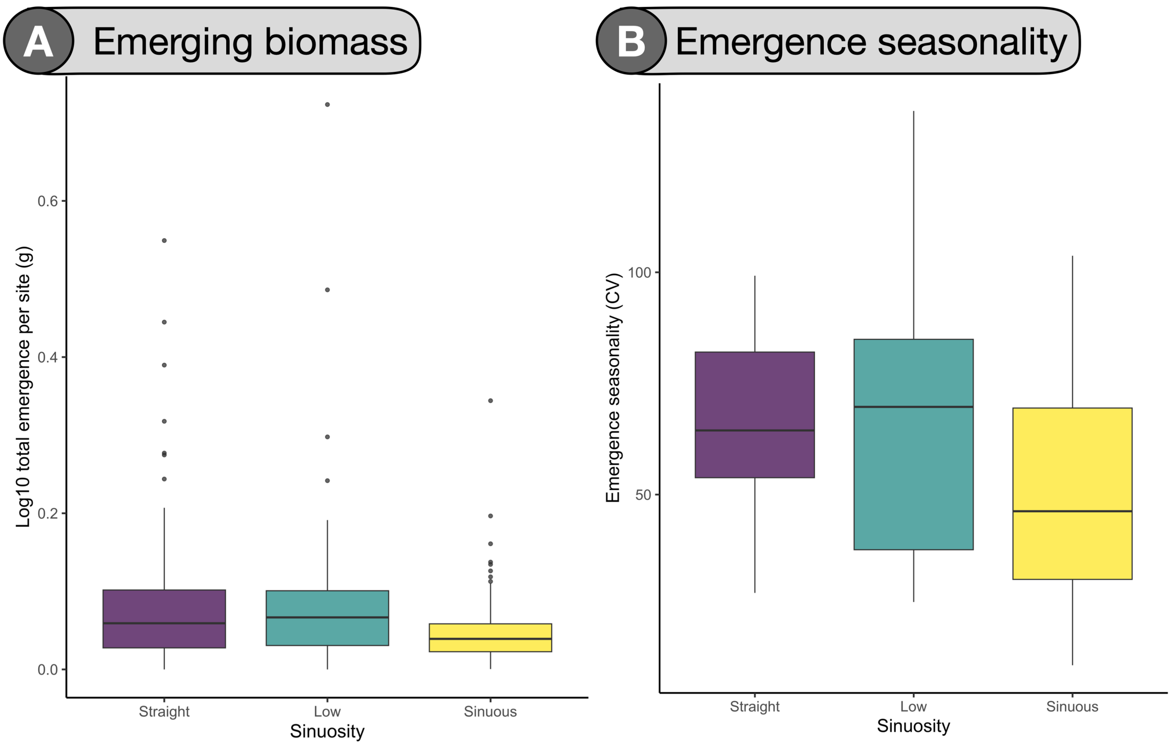

FIGURE 6
Boxplots showing mean, upper and lower quartiles and outliers for **(A)** total aquatic insect emerging biomass and **(B)** emergence seasonality (coefficient of variation) across site types, represented by sinuosity.

into drainage features through regular dredging and riparian vegetation removal. Together, these human altered watercourses are especially dominant across the landscape, with natural, sinuous streams limited to the northeastern region of the study area, where forest cover is more prevalent. Principal components analysis showed that forested regions and treed blocks (i.e., hedgerows) were generally associated with more sinuous, natural streams. Water quality, driven by phosphorus, nitrogen and strontium concentrations, did not follow

TABLE 1 Regression results explaining the proportion of insectivorous birds (binomial GLMM) and species richness (multiple linear regression) in surveys across the South Nation watershed.

Model	Term	Estimate	Standard error	*t*-value	*p*
Proportion of insectivores ~ sinuosity + total emerged biomass	Intercept	−1.86	0.35	−5.27	<0.001*
	Sinuosity- low	0.90	0.42	2.14	0.045*
	Sinuosity- sinuous	1.80	0.44	4.06	0.00062*
	Total emerged biomass	0.34	0.17	1.94	0.066*
Species richness ~ sinuosity	Intercept	6.29	1.04	6.06	<0.001*
	Sinuosity- low	4.60	1.38	3.33	0.0032*
	Sinuosity- sinuous	3.71	1.42	2.61	0.0162*

Results that are statistically significant at $p > 0.05$ are marked with *. For sinuosity, straight watercourses represent the intercept term with low and sinuous representing the effect size difference for each type.

the same separation of sites between sinuosity types. Instead, it was separated from indicators of remnant forests on the landscape, showing a gradient of agricultural intensity at the site level. While even natural, forested sites may be located downstream of farmlands, the impact of runoff is likely reduced, with drainage ditches often performing water purification ecosystem services in the absence of natural wetlands on the landscape (Needelman et al., 2007). We only sampled water quality once, which limits our interpretations; however, there are multiple studies in the South Nation River watershed that have more thoroughly explored the impact of agricultural management—notably dredging and bank brushing—on water quality indicators and further impacts to ecosystem functioning (Guo et al., 2024; Dyck et al., 2021).

The proportion of EPT taxa (ranging from 0 to 15% of the taxa richness) was highest in natural forested streams, with stoneflies (Plecoptera) especially rare. Previous research has shown that agricultural intensity can result in reduced community size structure (i.e., fewer large-bodied EPT and more small-bodied Diptera with increased agricultural influence; Stenroth et al., 2015). EPT taxa are often used as bioindicators due to their low tolerance to disturbance and requirement for clean, highly oxygenated environments and, indeed, ditches can host a variety of disturbances that can shape macroinvertebrate communities. For example, they can have flashy hydrographs at certain times of the year, especially following storms, while at other times of the year, they can experience low flows and become low oxygen environments (Rideout et al., 2021). Sediment, especially from field runoff, can also be a significant stressor for sensitive taxa, reducing habitat availability by clogging interstitial spaces (Burdon et al., 2013), along with influencing macroinvertebrates to drift (Piggott et al., 2015). Even in natural streams, there may be influence from agro-chemicals like pesticides and fertilisers from upstream sources. Collins et al. (2019) found that aquatic macroinvertebrate richness in the South Nation watershed was strongly impacted by fertiliser use and can be used as an indicator of water quality. In our study, aquatic insect richness did not vary across the site types, which could indicate that even natural streams were influenced by upstream farms, although likely to a lesser degree.

Straight ditches and agricultural streams on farmland had the highest rates of aquatic insect emergence, notably producing higher total biomass than natural, forested streams. These results are in agreement with studies in Europe that found that agricultural streams had significantly higher emerging biomass than forested streams (Raitif et al., 2022; Ohler et al., 2023). While we did not find a difference in the proportion of Diptera richness in the benthic community across the site types (although they did comprise up to 85% of the richness in some ditches), it is likely that dipterans contributed a significant portion of the emergent insect community in agricultural systems, driving the increase in biomass, as was found by Raitif et al. (2022). Indeed, Chironomidae (Diptera) have been shown to make up 60–67% of the total emergence in agricultural streams, with dipteran families overall totalling 80–95% (Cavallaro et al., 2019). In these disturbance dominated ecosystems, the shorter generation times of many dipteran taxa are advantageous (Ohler et al., 2023). In fact, vegetation removal—a necessary part of drainage ditch maintenance to improve flow—has been shown to increase emergence in agricultural streams as the community shifts toward more 'tolerant' taxa (Cavallaro et al., 2019). This does highlight one limitation of DNA-metabarcoding in that our data were best interpreted as presence-absence, meaning we lacked any details on how abundance of taxa may shift across sites, even if the species richness stayed the same.

Interestingly, emergence seasonality did not differ across the landscape, meaning the resource of emerging aquatic insects was no less pulsed or extended across the watercourse types. With shorter generation times, and the potential for multiple emerging generations per year, dipterans have lower seasonality than other aquatic insect orders (Nash et al., 2023). Due to their fast development, dipterans and other small-bodied organisms can respond quickly to increasing temperatures to advance their emergence period (Nash et al., 2023), as may be seen in agricultural streams and ditches that lack full canopy coverage (Ohler et al., 2023). In contrast to our study, Ohler et al. (2023) found that there was a shift in both emergence phenology for biomass and abundance, with earlier and higher peaks in agricultural than forested streams. We lost some temporal complexity by sampling every two weeks, which could have masked differences in seasonality among site types, compared to the twice weekly collections reported in Ohler et al. (2023). In our system, emergence seasonality could also fail to differ between site types if the emergence peaks of different orders (including EPT taxa) are offset in natural streams such that they mimic the phenology of more abundant and continually emerging dipteran taxa (Nash et al., 2023; Ohler et al., 2023). We measured total emerging biomass using dry mass, but having abundance information from individual traps would better help elucidate these complex emergence patterns and discern any community shifts along the agricultural gradient.

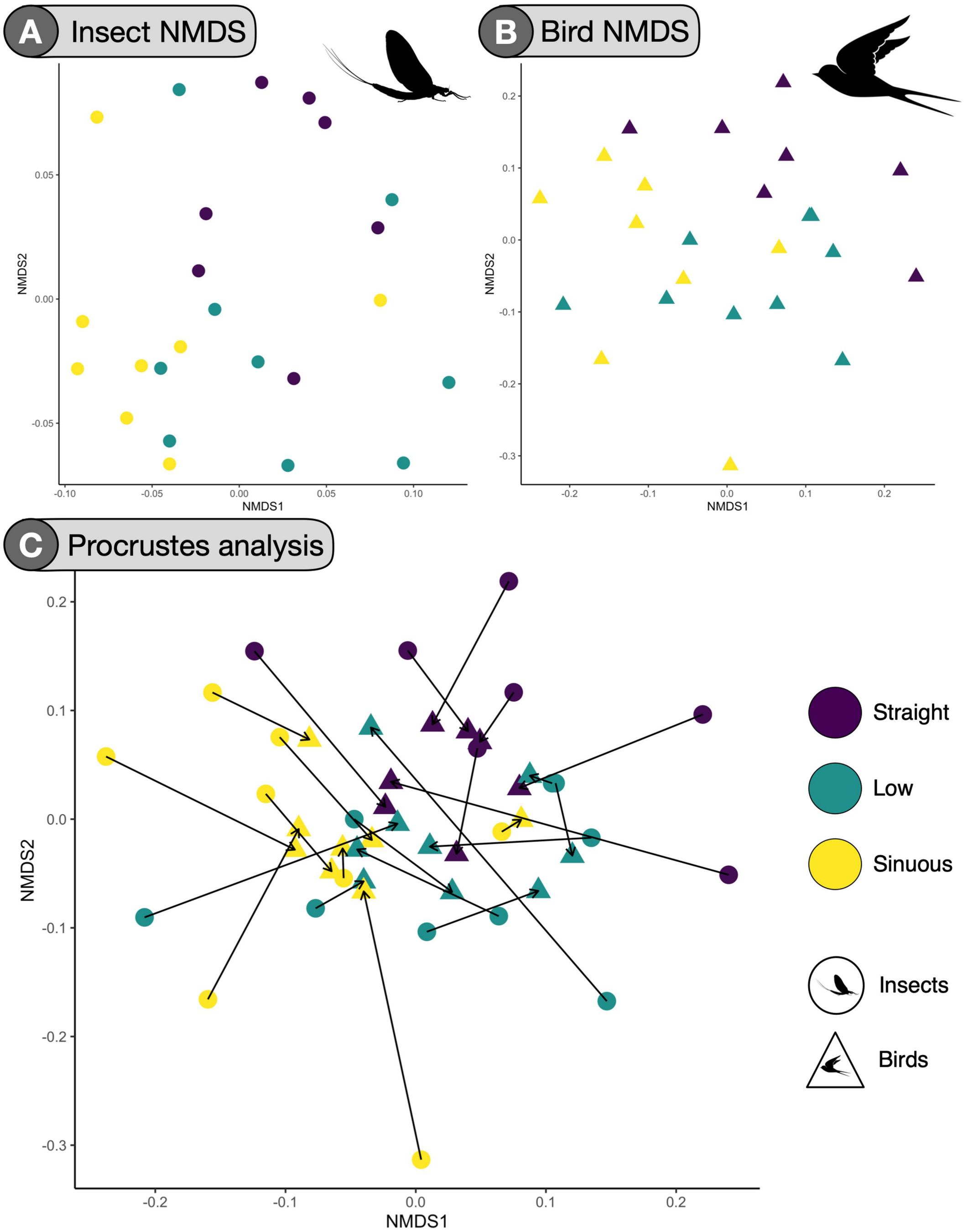

FIGURE 7
Ordination biplots showing NMDS results for **(A)** the aquatic insect community and **(B)** the riparian bird community, as well as **(C)** the Procrustes analysis results. Sites are denoted by colors for watercourse sinuosity, with the biotic community denoted by symbology. Circles show the position of the sites in the first ordination (insects) and arrows point to their positions in the target ordination (birds; triangles).

4.2 Are riparian bird communities in agricultural landscapes responding to in-channel changes in insect community structure?

Aquatic insect and riparian bird communities had distinct communities across the site types, and the two communities were also linked, meaning that we could expect to find specific subsets of the avian community to be present if certain aquatic insect taxa were present. Birds may be responding to insect taxa based on dietary preferences; for example, adult EPT are large-bodied insects that are particularly rich in nutritionally-important HUFAs (Shipley et al., 2022; Parmar et al., 2022), while also being easier to handle (e.g., for tree swallows; Bellavance et al., 2018). This linkage was observed across a forest-agriculture gradient in Sweden, where birds were associated with forested sites that were found to have much higher rates of EPT emergence (Stenroth et al., 2015). Despite increased productivity at agricultural sites, insectivores did not significantly

TABLE 2 Post-hoc pairwise comparisons for permutational MANOVA models for riparian bird and aquatic insect communities.

Model	Comparison	R^2	F	p
Riparian birds	Straight vs. sinuous	0.23	3.81	0.06
	Straight vs. low	0.35	7.69	0.003*
	Sinuous vs. low	0.018	0.27	0.935
Aquatic insects	Straight vs. sinuous	0.17	2.60	0.004*
	Straight vs. low	0.074	1.12	0.34
	Sinuous vs. low	0.087	1.44	0.127

Results that are statistically significant at $p > 0.05$ are marked with *.

respond to increasing insect emergence. Instead, the proportion of insectivores was significantly lower at ditch sites, in concurrence with Endenburg et al. (2019) who found that increasing agriculture resulted in the loss of insectivores from the avian community.

Avian and insect communities could be responding to other unmeasured factors that differentiate sites along the agricultural gradient, such as habitat complexity, availability of nest sites or agro-chemicals. Pesticides can not only influence aquatic insect communities (Cavallaro et al., 2019) but have been shown to be retained through metamorphosis (Kraus et al., 2021) and impact farmland bird communities (Hallman et al., 2014). For example, Twining et al. (2021) found that emerging insects contained higher methylmercury (MeHg) levels than terrestrial insects and that MeHg levels in eastern phoebe (*Syornis phoebe*) chicks were positively associated with agricultural intensity, indicating a possible trade-off between toxic exposure risk and food supply. Additionally, agricultural ditches and riparian hedgerows can be harsh environments as they provide inadequate habitat either due to lack of space, availability of appropriate nest sites (e.g., less riparian edges along ditches than more forested sinuous streams) or increased disturbance, especially following management in the form of riparian tree removal and dredging. Omnivores were more common along agricultural drainage ditches, where their flexible diets may be advantageous in a changing or otherwise resource-depressed ecosystem (Ausprey et al., 2023; Sekercioglu, 2012), including using terrestrial and emerging aquatic insects when availability is high. Indeed, there is evidence that some species, including habitat generalist insectivores, can synthesize critical ω-3 HUFAs from terrestrially-sourced precursors (e.g., barn swallows (*Hirundo rustico*): Génier et al., 2022; and blue tits (*Cyanistes caeruleus*): Twining et al., 2021), allowing more flexibility in prey selection. For the same reasons that sensitive aquatic insect taxa are uncommon in drainage ditches, bird species that require larger, more pristine habitats may be exchanged for those that can tolerate smaller patch sizes with reduced complexity (e.g., scrubs and smaller hedges instead of forests), as was shown across southern and eastern Ontario by Endenburg et al. (2019). Avian species richness in our study was higher in natural streams than drainage ditches, likely partly reflecting habitat complexity of the riparian ecosystem, along with availability of adequate nest sites. Interestingly, however, the proportion of insectivorous birds did not respond to our measure of hedge size; larger hedges are generally correlated with greater habitat complexity (e.g., Gelling et al., 2007), further emphasising the likely role of higher quality insect prey.

The point count data we used in our study provides an index of avian community composition across sites and not absolute measures of species' presence and/or abundance. In this way, our sampling methodology is similar to other surveys of songbirds, such as the Breeding Bird Survey (Sauer et al., 2017). To estimate absolute species richness and individual abundances per site, we would need to perfectly control for species availability and perceptibility (Johnson, 2008). Availability depends largely on the behavior of the species (home-range size, singing at specific times of day, etc.), while perceptibility is driven largely by factors affecting the actual survey, e.g., observer skill and habitat features [reviewed in Johnson (2008)]. While we controlled for potential biases attributed by environmental conditions and noise by sampling on fair weather days (perceptibility), observer skill (perceptibility) and time of day (availability) in our analysis, for logistical reasons we were unable to visit sites for point counts more than one time, which would have allowed for us to better detect species that were not available at the time of the survey. In other words, it is likely that we underestimated species richness and the abundance of individual species. We also acknowledge that we are unable to estimate the potential confounding effects of habitat at the survey site on species detectability. However, we argue that our results are still valid, despite these limitations. First, any bias in avian community composition from single visit point-counts should be similar across sites. Second, if perceptibility of individual species by observers in our study is driven by habitat, e.g., more open drainages versus more vegetated drainages, then we would expect richness to be lower along more vegetated sinusoidal drainages as opposed to more straight and open drainages as we might expect vegetation to interfere with our ability to observe certain species. This is opposite to the pattern we found, where species richness (and proportion) of insectivores was higher in more vegetatively dense habitats. If anything, we suggest that the effect we found regarding higher community richness and the proportion of insectivores being higher along more vegetated sinusoidal streams are likely underestimates. We recommend that future studies along drainages do conduct multiple site visits to better capture species presence to improve the accuracy of parameter estimates.

4.3 Does increased ditch productivity translate to improved habitat quality for insectivorous birds?

Although productive in terms of total biomass, ditches on agricultural fields may provide poorer quality food sources for riparian foraging predators that rely on emerging aquatic insects. For example, windbreaks consisting of tree stands or hedgerows can impact the wind strength, speed and direction, all impacting aquatic insect dispersion (Raitif et al., 2022; Raitif et al., 2018; Gerber et al., 2023). Many aquatic insect orders are not strong flyers as adults, instead using wind as a primary dispersal mechanism (May, 2019). Work done examining aquatic insect deposition following emergence from agricultural streams in France has shown that Chironomidae (dipterans) disperse much farther (50% travel over 25 m inland), while Ephemeroptera and Trichoptera taxa tend to stay nearer to aquatic and riparian habitat, making up the majority of deposition within 10 m of the stream (Raitif et al., 2022; also shown more generally in the meta-analysis by Muehlbauer et al., 2014).

These dispersal patterns in agro-landscapes have important implications for foraging riparian birds. If prey are less clumped and more dispersed across the agricultural landscape, both because of dispersal differences in the dominant insect orders and due to an open landscape with few windbreaks, this may have consequences in terms of energy demand for foraging riparian insectivorous birds. In experiments examining vertical and lateral dispersal of aquatic insects in fragmented landscapes, Ephemeroptera and Trichoptera in particular were captured most frequently in the forest canopy (Didham et al., 2012). The reduction in riparian hedgerows or forest stands can thus also change prey availability for birds that forage for insects through other strategies, such as foliage gleaning (picking insects off of trees or leaves, e.g., warblers) or sallying (darting out from perch to capture flying insects, e.g., flycatchers; Remsen and Robinson, 1990). Indeed, Endenburg et al. (2019) found a loss of foliage gleaning insectivores across southern and eastern Ontario with increasing agricultural intensity. Other taxa, like aerial insectivores, are attracted to mixed swarms of "aerial plankton" (Dreelin et al., 2019; Kusack et al., 2022), which can be constituted in part by the high emerging biomass provided by ditches. These aquatic insects can still contribute nutritionally-important HUFAs, and dipteran taxa have been shown to make up the majority of the diet in tree swallows (Bellavance et al., 2018; Paquette et al., 2013), showing that secondary productivity provided by ditches can still be an important ecological resource.

There may be a consequence if ditches completely lack management in the form of riparian tree removal and dredging, as these ecosystems can quickly become overgrown, acting more like wetlands than streams (Chester and Robson, 2013). Open ponds on intensive agricultural lands in Europe have been shown to have as much as 18 times emerging insect abundance than overgrown ponds, having a positive effect on farmland bird communities (Lewis-Philips et al., 2020). Those open ponds also had higher rates of Ephemeroptera and Trichoptera, attracting swallow species to the HUFA-rich taxa (Lewis-Philips et al., 2020). Those results suggest that heterogeneity and maintenance of natural capital across the agro-landscape is key to balancing anthropogenic water needs with the provisioning of ecosystem functions such as secondary productivity.

4.4 Conclusions and implications for future agro-landscapes

We found that drainage ditches and agricultural streams can be highly productive in terms of emerging aquatic insect biomass, but that their riparian areas do not appear to support a rich community of foraging insectivorous birds. In the South Nation River watershed, the habitat types were clustered together on the landscape rather than as a mosaic, limiting beneficial exchange of organisms between more natural sites and those located adjacent to intensive agriculture. Farmers can improve habitat provisioning to riparian birds by promoting a mosaicked landscape (Haslem and Bennett, 2008) through careful rotational management of native vegetation, including riparian trees, and dredging of ditches and on-farm streams. By establishing larger forest blocks with natural or unmanaged streams between areas of more intense land use, it can ensure the provisioning of more high quality prey to riparian insectivorous birds. Protecting and ensuring the continuation of ecosystem services, such as habitat provisioning and secondary productivity of emerging aquatic insects, is important on working landscapes as they are a pillar of environmental health, as viewed through the One Health lens (Sleeman et al., 2019). Not only are there inherent risks to ignoring the value of wildlife or environmental health (Sleeman et al., 2019), but finding the balance with food production is vital to protect already declining bird populations.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Dryad (doi: 10.5061/dryad.sbcc2frfk).

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

NR: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. NA: Investigation, Writing – review & editing. DL: Funding acquisition, Project administration, Writing – review & editing. MH: Resources, Writing – review & editing. GM: Investigation, Writing – review & editing. WM: Formal analysis, Resources, Writing – review & editing. MaW: Investigation, Writing – review & editing. SW: Investigation, Writing – review & editing. MiW: Investigation, Writing – review & editing. DB: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2024.1484377/full#supplementary-material

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