


Complex temporal trends in biomass and abundance of Diptera communities driven by the impact of agricultural intensity

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Abstract

1. Insect biodiversity and abundance declines have been reported widely and are expected to alter ecosystem functions and processes. Land use change has been recognised as a major cause of such declines.
2. However, variation in local environmental drivers and the scale of available monitoring data have left large knowledge gaps in which taxa are declining, where declines are the greatest, and how these declines will impact ecosystems.
3. We used 11 years (2006–2016) of monitoring data on 40 farms distributed over ~10,000 km² in southern Québec, Canada, to quantify the impact of agricultural intensity on temporal trends in abundance and biomass of Diptera (true flies).
4. There was a large difference in temporal trends between farms, which we found to be driven by agricultural landcover.
5. Contrary to expectation, increases in Diptera abundance over time were greater in areas with higher agricultural intensity, especially with an increase in cereal crops. In contrast, declines in biomass were steeper in areas of higher agricultural intensity, although only with greater maize and soy production rather than cereals such as wheat.
6. Variation in forest cover around farms had the least effect on trends.
7. We found steeper declines in biomass per total number of Diptera with increasing agricultural intensive cover, suggesting the presence of community turnover towards smaller bodied flies with lower individual biomass.
8. Our results imply that land use may not only alter abundance and species composition of insect species assemblages but also the distribution of key functional traits such as body size.

KEYWORDS

agricultural intensification, biodiversity change, Canada, insect declines, temporal trends

INTRODUCTION

There has been increased awareness of declines in the abundance and diversity of insects and other invertebrates over recent decades (Didham, Barbero, et al., 2020; Goulson, 2019; Hallmann et al., 2017;

Montgomery et al., 2019). These declines are typically attributed to two main drivers: changes in land use and climate (Raven & Wagner, 2021; Wagner et al., 2021). A principal example of land use change that has impacted insects is the process of agricultural intensification (Leclère et al., 2020; Raven & Wagner, 2021; Sala et al., 2000;

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Wagner et al., 2021). This process led to the historical shift towards agricultural production that focuses on increasing the amount of agricultural intervention or input per unit area over increasing the footprint of agricultural lands. Examples of agricultural intensification include the increased removal of marginal and forested habitats, drainage of water bodies and increasing the amount of area devoted to a small number of crops (Fenoglio et al., 2020; Flick et al., 2012; Habel et al., 2019). Agricultural intensification has resulted in the increased reliance on mechanisation and agro-chemical inputs such as fertilisers and pesticides. These practices therefore increase exposure to toxic contaminants and cause the large-scale homogenisation of farmlands and the important resources they provide for insects (Kovács-Hostyánszki et al., 2017; Schreinemachers & Tipraqsa, 2012).

Insects and other invertebrates contribute important ecosystem functions to terrestrial systems, such as being prey for higher trophic levels and supporting abundant predator populations (Schowalter et al., 2018). Diptera (true flies) provides a substantial food source for aerial insectivores—such as birds—in a wide range of ecosystems including agricultural areas (Holland et al., 2006). Long-term declines in Diptera and other insect abundance and biomass due to agricultural intensification are therefore expected to have negative consequences for the long-term abundance and diversity of their predators (Bowler et al., 2019). Diptera also contributes to crop pollination in agro-ecosystems, alongside other insects (Rader et al., 2016), and some groups such as Tachinidae, Bombyliidae, Syrphidae and Asilidae, act as important controllers of pest populations through parasitisation and predation effects. Diptera also has a larval stage, the larvae occupying different niches to their adult form and carrying out additional ecological functions such as decomposition and nutrient cycling of decaying organic matter in terrestrial and aquatic ecosystems (Graça, 2001). Declines in Diptera could therefore have negative consequences for these functions and services in agro-ecosystems (Klein et al., 2007; Powney et al., 2019; Rader et al., 2016; Stanley et al., 2015).

While global syntheses of insect trends increase our understanding of the general state of biodiversity, further work using robust, long-term quantitative monitoring data is vital to understand how the biodiversity and abundance of insects and other invertebrates are changing across space and time, and for understanding the complex array of environmental drivers that affect biodiversity and, consequentially, ecosystem functioning (Montgomery et al., 2019; Shortall et al., 2009). Here, we quantify long-term temporal trends in Diptera abundance and biomass, using a dataset of Diptera samples taken on 40 farms across a gradient of agricultural intensity in Québec, Canada, between 2006 and 2016. To understand the change in the quantity of Diptera, we calculated trends in (1) the total abundance and (2) the total biomass of Diptera over the 11-year time series, and we asked whether trends in Diptera abundance and biomass are impacted by the transition to more intensive agriculture over space and time. We expected that, given the ongoing pressures of agricultural intensification in this area of Canada and the expected negative impact that this intensification has on agro-ecosystems, we would find an overall decline in both biomass and abundance of

Diptera communities, and that this decline would occur more rapidly in Diptera communities on farms with greater intensity of land use. As well as quantifying total Diptera, we calculated trends in Diptera biomass, but ‘offset’ by total abundance caught in samples, to estimate the change in the biomass per average number of Diptera. This allowed us to explore whether species (of different sizes) may have varied in their response to agricultural pressures over time, signalling a possible change in the evenness or composition of Diptera communities underpinning the community-level biomass and abundance trends.

METHODS

Study area

We monitored Diptera between 2006 and 2016 (11 years) on 40 farms distributed along a ~10,000-km² gradient of agricultural intensity in southern Québec, Canada (Figure 1a). Geological differences across the longitudinal gradient of our study area resulted in the eastern section being primarily covered by pasture and forage crops (e.g., hay, alfalfa [*Medicago sativa*] and clover [*Trifolium* spp.]) embedded within large expanses of forest. In contrast, the west was primarily composed of large-scale monocultures (principally maize [*Zea mays*], soybean [*Glycine max*] and wheat [*Triticum* spp.]), and small, highly interspersed forest patches (Bélanger & Grenier, 2002; Jobin et al., 2005; Ruiz & Domon, 2009). Between 2011 and 2019, about 100% of the maize and 60% of the soybean were sown as neonicotinoid-coated seeds (MDDELCC, 2015). As a result, neonicotinoids, alongside many other pesticides, were regularly detected in water bodies of the western part of the study area at concentrations threatening to aquatic life—including Diptera species with aquatic larval stages—if chronically exposed (Giroux, 2019; Montiel-León et al., 2019).

Diptera monitoring

Diptera was monitored using two flight interception traps placed on field margins of each farm ($N = 80$ per year). Traps were spaced approximately 250 m apart and in a way that avoided blockage from vegetation. The traps consisted of yellow buckets (15 cm deep and 21 cm in diameter), filled with 1 L of saltwater and soap solution and surmounted by two bisecting plexiglass sheets (11.5 × 30 cm), and they were placed 1 m above the ground (Bellavance et al., 2018; Rioux Paquette et al., 2013). Flight interception traps, or ‘window traps’, have previously been shown to be effective for capturing Diptera (Knuff et al., 2019), although there may have been a slight bias towards capturing particular groups, such as flower-visiting flies and maize pests, that may be more attracted to the yellow colour of the bucket compared to other flies that were intercepted more by chance (Allan, 2024; Garcia et al., 2022). The contents of each trap were collected every 2 days by straining insects into a tube filled with 70%

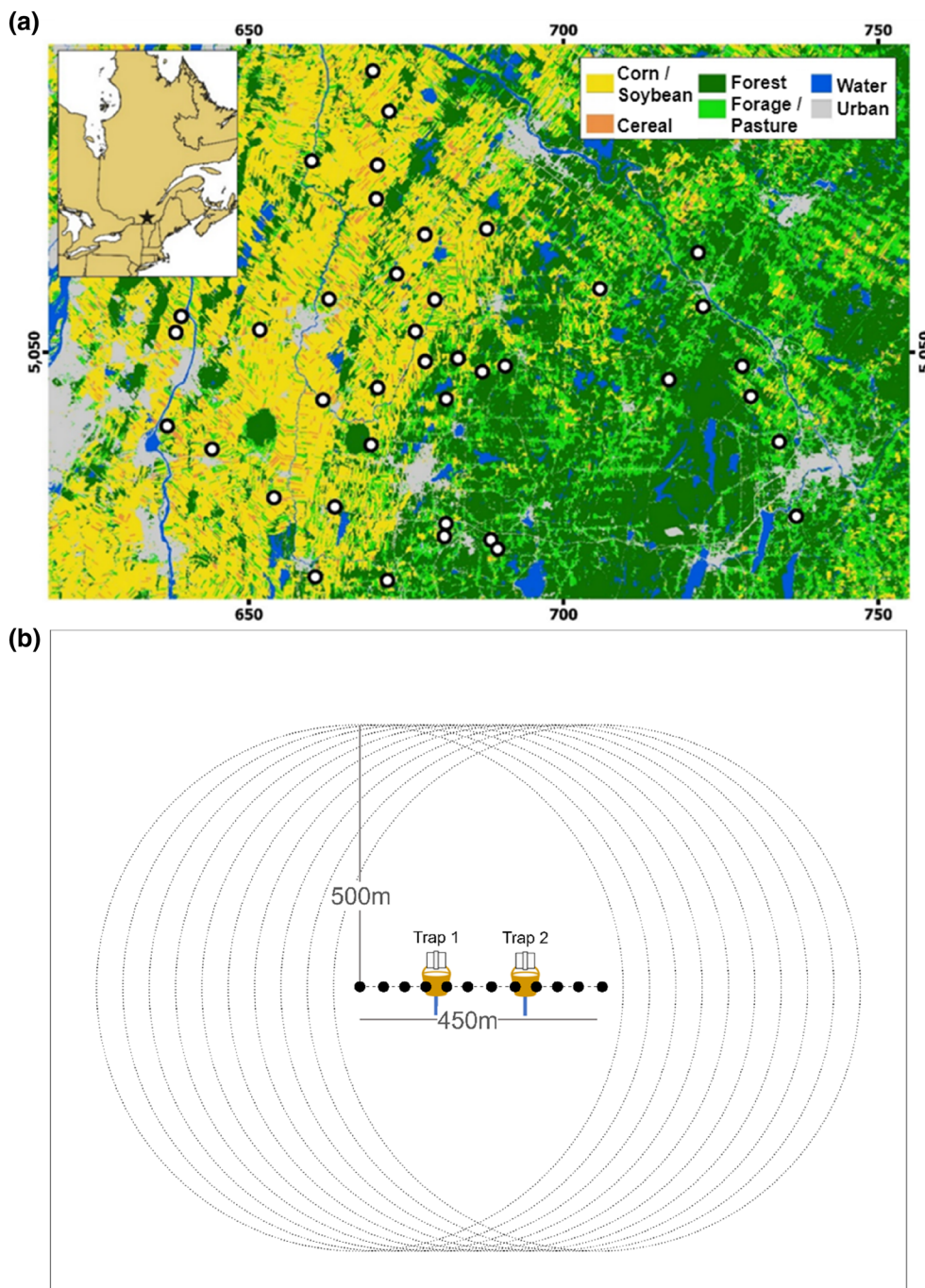


FIGURE 1 (a) The geographical position of the 40 farms sampled during the study, with the gradient of agricultural intensification and landscape context shown. Inset shows the position of the study site—or farm—in Québec, Canada, indicated by the star symbol. Coordinates are given in metres (°m). Figure adapted from Garrett et al. (2022). (b) The typical layout of a sampling transect, with the two Diptera traps placed along the transect. Buffers of 500 m around 10 centroids placed equidistantly along the transect are shown; these buffers were used to calculate the relative habitat cover surrounding farms.

ethanol. Samples were stored in closed boxes at room temperature until processing. We processed samples collected between 1 June and 15 July. This period was chosen as the sampling protocol was originally created for a project studying the impact of Diptera availability on tree swallow (*Tachycineta bicolor*) fitness (Garrett et al., 2022). Tree swallows are aerial insectivorous birds preying primarily upon Diptera

while food provisioning their nestlings during the above 6-week period in our study area. Regardless, the period generally captures the height of the seasonal abundance of Diptera and was therefore judged to be an appropriate time window for our study. Diptera was individually counted and then dried in an oven at 60°C for 24 h. Once dried, samples were weighed without delay (± 0.0001 g). Due to time

constraints and the volume of data, abundance and biomass of insects were recorded at order level (Diptera).

Diptera communities

Two previous studies investigated abundance patterns of Diptera communities in our study area at a finer taxonomic resolution than our study was able to but over a shorter time frame. Garrett et al. (2022) addressed Diptera abundance patterns between 2011 and 2012 for Nematocera, non-Schizophoran Brachycera and two Schizophoran Brachycera groups: Acalyptratae and Calyptratae (Garrett et al., 2022), while Laplante (2013) investigated Diptera abundance at the species level in 2008 (not yet published in a peer-reviewed journal). The latter study collected 5313 specimens, with a mean (\pm SD) of 133 ± 95 specimens per farm. A total of 18 families and 178 species were found, with an average of 10 ± 2 families and 32 ± 12 species per farm, implying a relatively large change in composition (beta diversity) between farms. Two families were very abundant relative to others: Anthomyiidae, with 1280 specimens (24.1%), closely followed by Sphaeroceridae, with 1211 specimens (22.8%). Similarly, two families were very species-rich: Chloropidae, with 57 species (32.0%), followed by Sphaeroceridae, with 32 species (18.0%). *Delia platura*, the dominant representative of the Anthomyiidae in this study, is a phytophagous pest of maize and other cereals. In its larval stage, Chloropidae are predominantly phytophagous, while Sphaeroceridae are predominantly saprophagous. The full list of species captured can be found in Laplante (2013).

Landscape context

We defined the landscape context surrounding each farm on a given year based on its habitat composition relative to other farms and years. Every year on each farm, we calculated the relative cover of habitat within 500 m around 10 points, which were positioned 50 m apart from each other along a 450-m transect on which the Diptera traps were positioned (Figure 1b). We then calculated a mean of these habitat values to give the average relative habitat cover around traps, for each farm–year combination. We determined land cover types within each 500-m buffer in situ between the middle and the end of July, before crop harvesting. We delineated the principal land cover types found within each 500-m buffer using orthophotos (scale 1:40000) in QGIS software (2020). Land covers, including crop varieties, were then classified into one of five higher order categories, namely forest, maize, soybean, forage (hay fields, other grasses, alfalfa, clover, pastures and old fields) and cereals (other than maize and soybean). The relative cover in aquatic habitats in the 500-m buffers was extremely low ($0.66\% \pm 1.07\%$; mean \pm SD) and thus not considered further.

A total of 440 ‘landscape contexts’ (40 farms \times 11 years), were determined using the farm scores of a robust principal components analysis (PCA) for compositional data (Filzmoser et al., 2009) fitted on

the yearly percent cover of all higher order habitats of each farm by year combination (Figure 2a). The robust PCA was performed using the robCompositions package (Templ et al., 2011) in R v. 3.6.2 (R Core Team, 2020). The first two components explained over 95% of variance in landscape composition; we therefore used the scores for each farm–year combination along these two axes to represent the landscape context of each Diptera sample (see below).

Specifically, the first component (Comp.1) explained 80.34% of the variance in landscape habitat composition and was positively correlated with maize and soybean and negatively with forage and forest cover (Figure 2a). The second component (Comp.2) explained 14.69% of the variance in landscape habitat composition and was negatively correlated with forage and positively with forest cover. Landscape contexts characterised by maximal Comp.1 and minimal Comp.2 values, thus comprised of a mixture of maize, soybean and cereals, were stripped of forest cover. Landscape contexts characterised by minimal Comp.1 and negative Comp.2 values were dominated by forage fields and pastures interspersed by remnant forest cover and are thus referred to as forage landscapes.

Biomass and abundance trends

We took a model comparison approach, using maximum likelihood generalised linear mixed effect models (GLMMs), to estimate temporal trends in Diptera abundance and biomass and how these trends varied with landscape context. We first started with an identical candidate set of models for each response variable (biomass and abundance; ‘Model Set 1’ and ‘Model Set 2’, respectively). These models focused on both additive and interactive effects between the main covariates of interest (i.e., year and the scores representing landscape context; Figure 2a, Tables 1 and 2). We included the ordinal date of sample collection (i.e., 1 May = 150) in each model in the candidate set as a second-order polynomial term, due to the quadratic relationship between abundance/biomass and date in seasonally abundant insects, rising to a peak and then falling again during the sampling season (see Figure S3; Garrett et al., 2022). We tested two models in which landcover did not influence Diptera values and thus included a model (‘Model B’) including only the ordinal date of sample collection (i.e., 1 May = 150) and another with both the date and year of sample collection (‘Model C’). Furthermore, various possible confounding variables, such as climatic and geological factors, may influence local abundance, biomass and community composition of Diptera, along with the likelihood of trapping individuals independently of their relative abundance or biomass. Many of these factors vary along the longitudinal spatial gradient in this region of Québec, along with the degree of agricultural intensity (Comp.1 values) at farms, potentially confounding the effect of our landscape context values on temporal trends in Diptera. To control for this, we included the longitude of farms as UTM, WGS-84 coordinate reference values in the models that tested the effect of landscape context. Prior to including longitude as a variable, we checked the variance inflation factors using the `vif()` function in the ‘car’ package in R (Fox &

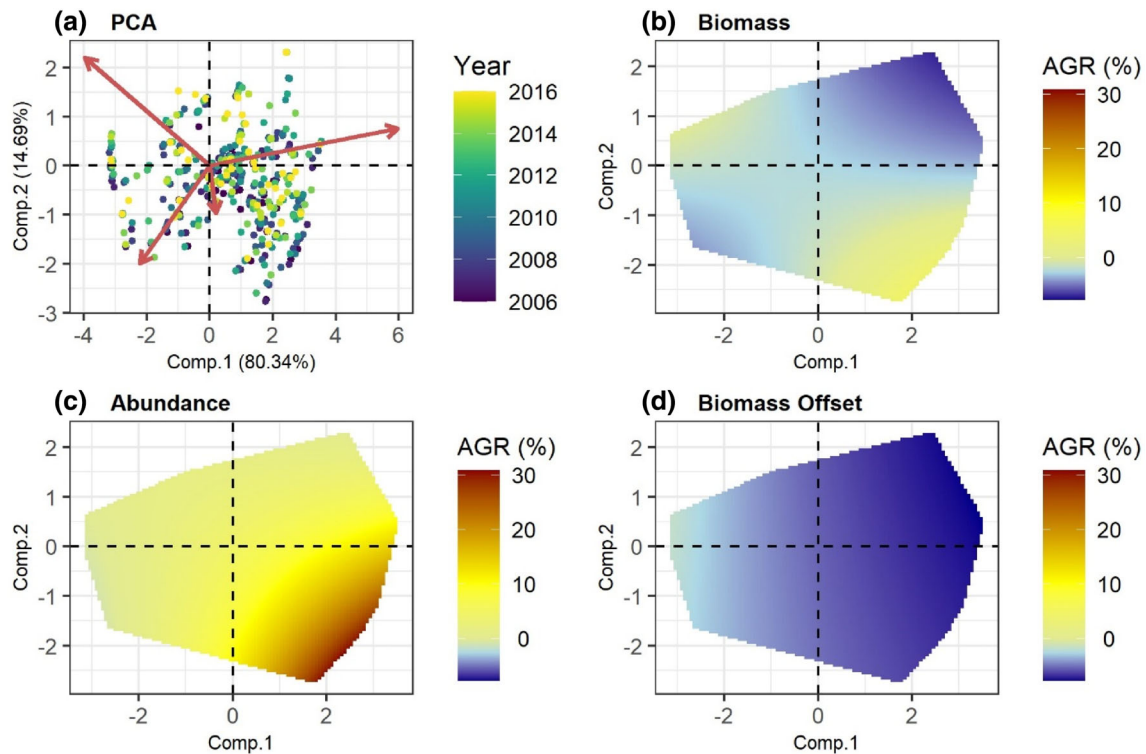


FIGURE 2 (a) Position of each farm–year point ($n = 440$) along the landscape PCA axes (Comp.1 and Comp.2) used in analyses. (b) Predictions of annual growth rate (AGR), calculated as the average annual percentage change in Diptera biomass from 2006 to 2016, across the axes Comp.1 and Comp.2. The surface area represents a convex hull of the space within the two dimensions of the PCA occupied by our 40 farms, inclusively. Model predictions were produced using the top model from Model Set 1 (Table 2, Model H). (c) Predictions of AGR for Diptera abundance, calculated in the same way as described for biomass, using predictions from Model Set 2 (Table 2, ‘Model H’). (d) Predictions of AGR of Diptera biomass offset by abundance, using predictions from the top model from Model Set 3 (Table 2, ‘Model G’).

TABLE 1 Reference table for candidate model set with varying additive and interacting fixed effects structures.

Model name	Fixed effects structure
H	Date + Longitude + Year * Comp.1 * Comp.2
G	Date + Longitude + Year + Comp.1 + Comp.2 + Year: Comp.1 + Year: Comp.2 + Comp.1: Comp.2
F	Date + Longitude + Year + Comp.1 * Comp.2
E	Date + Longitude + Year + Comp.1 + Comp.2 + Year: Comp.1 + Year: Comp.2
D	Date + Longitude + Year + Comp.1 + Comp.2
C	Date + Year
B	Date
A	1 (intercept only, no fixed effects)

Note: The values of landscape PCA axes are represented here as ‘Comp.1’ (farm score on the first axis) and ‘Comp.2’ (farm score on the second axis). See Figure 2 for an understanding of the landscape structure according to Comp.1 and Comp.2.

Weisberg, 2011) and found no evidence of multicollinearity between fixed effects that may have distorted the estimation of effect sizes. In order to check whether we should further include the impact of climatic or weather variables in our models, such as temperature and

precipitation, due to their potential impacts on the availability of capturable insects, we analysed potential model structures leading to inadequate controls (Cinelli et al., 2020) using directed acyclic graphs in DAGgitty software (Textor et al., 2016). Due to the interconnectivity between climatic or weather variables and the variables of interest in our models, DAG analysis showed that controlling directly for climatic or weather variables would bias estimates of the total effect of Year and Comp.1 and Comp.2 on our response variables (insect biomass and abundance) and that longitude alone provides a sufficient adjustment for the models. This allowed us to assess the direct and indirect causal effects of landscape habitat composition on insects while controlling for the confounding effects that regional weather/climate could have (see Figure S1 for further details).

The main models of interest were those hypothesising landcover acts additively or interactively (on a log scale; see Spake et al., 2023), with the year of sample collection. We therefore included a model treating the landscape context terms additively (‘Model D’) and interactively by including two-way interaction terms between year and each of the landscape context terms Comp.1 and Comp.2 (‘Model E’). We finally predicted that there would be an effect of the interaction between landscape variables on biomass and abundance rather than additive alone (‘Model F’, replacing Model D), plus interactions between year and the landscape components (‘Model G’, replacing

TABLE 2 Comparison between candidate biomass models (Model Set 1), abundance models (Model Set 2) and biomass offset by abundance models (Model Set 3) in order from lowest AIC_c and highest AIC_c weight (and therefore the preferred model) first to highest AIC_c and lowest AIC_c weight last.

Model set	Model	K	Delta_AIC _c	AIC _c Wt
1. Biomass	H	24	0.00	0.86
	E	22	4.38	0.10
	G	23	6.27	0.04
	B	16	10.66	0.00
	C	17	11.10	0.00
	D	20	11.99	0.00
	F	21	13.63	0.00
	A	14	52.72	0.00
2. Abundance	H	24	0.00	0.55
	E	22	1.26	0.29
	G	23	2.58	0.15
	D	20	20.47	0.00
	F	21	21.74	0.00
	C	17	25.20	0.00
	B	16	25.55	0.00
	A	14	33.99	0.00
3. Biomass offset	G	23	0.00	0.69
	H	24	1.67	0.30
	E	21	7.59	0.02
	F	21	26.40	0.00
	D	19	32.34	0.00
	B	17	54.44	0.00
	C	16	60.54	0.00
	A	14	92.85	0.00

Note: Log-likelihood values for the top models of Set 1 = 42,594.59; Set 2 = -20,731.31; and Set 3 = 45,495.73. Models were performed on data from 15,916 individual insect samples, from 80 traps across 40 farms, on 493 days in total over 11 years. See Table 1 for model parameters in models A–H and Table S3–S5 for model coefficients.

Model E) and that year itself would influence the effect of the interaction formed by the two landscape context terms, and therefore included a three-way interaction term between year and the two components ('Model H', our most inclusive model). See Table 1 for a breakdown of terms found within each model.

We then recreated the candidate set of models for biomass (Model Set 1) but included abundance as an 'offset' variable in each model, to model the rate of biomass change per number of Diptera across farms ('Model Set 3'). Each model was subject to the same model comparison approach using Akaike information criteria (AIC_c) values. We used Model Set 3 to test our hypothesis that the average biomass of individual Diptera changed over time yet differentially across the gradient of agricultural intensity. We used abundance as an offset variable as this is a more statistically sound method of modelling rates of change in a response

variable than using a ratio (i.e., biomass/abundance) as the response itself, which can lead to spurious correlations between variables (Kronmal, 1993).

Diptera biomass was modelled using a gamma distribution (with a log link function; Model Sets 1 and 3), while Diptera abundance ($\log_e(\text{abundance}+1)$) was modelled via a Gaussian distribution (Model Set 2). Prior to modelling, we rescaled the 'year', 'date' and 'longitude' covariates to give a mean value of 0 and a standard deviation of 1. We compared models using sample-corrected AIC_c (Table 2). All modelling was conducted using the glmmTMB package in R (Brooks et al., 2017). We calculated conditional R² values for the final models (one per model set), using the r.squaredGLMM() function from the 'MuMIn' package in R (Bartoń, 2023). For Model Sets 1 and 3, which used a gamma distribution, the 'lognormal' method was used to estimate the R² value, while the R² for Model Set 2 was calculated using a Gaussian distribution.

Beyond checks of variance inflation factors, other model validation checks included checks on the posterior predictions, residuals versus fitted values, homogeneity of variance and normality of residuals and random effects. All model checks were completed using the 'performance' package in R (Lüdtke, 2021).

Random effect structure

Prior to comparing the fixed effects of different models, we carried out preliminary analyses to establish a random effects structure. The spatial and temporal structure of our sampling regime is such that observations of Diptera abundance and biomass were taken repeatedly at farms, across multiple days within each year. Therefore, we wanted to account for variation in the conditional model caused by the inherent differences in local baseline abundance and biomass of Diptera on different farms, as well as non-directional variation in abundance and biomass within and between years, while also accounting for the fact that this non-directional change in abundance and biomass within and between years may vary depending on the farm. This resulted in the need for both 'crossed' and 'nested' random effects, such that our final models contained 'date' (second-order polynomial) nested within 'year' and 'farm' as random intercepts, as well as the slope of farms varying by 'date' nested within 'year' (i.e., a random slope model). We compared this structure sequentially with less complex random effects structures using restricted maximum likelihood and by examining AIC_c values (Table S2). These less complex structures included those where the slope of farms did not vary by date and year (i.e., removing the 'random slope' element), those where the variation in baseline abundance and biomass was not dependent on the date within years and those where the variation of abundance and biomass between years was completely removed and those where no temporal variation in intercepts were included (i.e., the variation in the intercept was only affected by farms). The resulting random effect structure for our models can be written as such using the glmmTMB package:

$$(1 | \text{Year/Date}) + (\text{Year/Date} | \text{Farm}).$$

Rate of change

For all selected models for biomass, abundance and biomass offset by abundance ($\log_e(\text{abundance} + 1)$), we used the 'ggeffects' package in R (Lüdtke, 2018) to predict biomass and abundance for each year of the time series, the values of which were back-transformed from the log-link to the response scale, to calculate marginal and conditional effects of our predictor variables. We then calculated rates of change across the time series for biomass and abundance across the landscape gradients using the following equations for overall percentage change (ψ) and annual growth rate (AGR) as:

$$\psi = 100 \frac{(y_n - y_1)}{y_1},$$

and

$$\text{AGR} = \frac{\psi}{n - 1},$$

where y_n is the model estimate of the biomass or abundance value for the final year of the time series (2016), y_1 is the estimated biomass or abundance value for the starting year of the time series (2006) and n is the number of years total in the time series.

R version 4.2.2 was used for all data manipulation and analysis outside of QGIS (R Core Team, 2022).

RESULTS

We collected and processed 15,916 insect samples, resulting from 8614 farm visits over 11 years. Overall mean Diptera biomass (\pm SD) was 0.030 ± 0.044 g per trap and per farm for each 2-day sampling period. While it did not vary greatly between years (range of means: 0.019–0.037 g), the variance within each year was high (range of SD: 0.023–0.059 g; Table S1, Figures S2 and S3). Overall mean Diptera abundance (\pm SD) was 59.7 ± 79.8 individuals per trap and per farm for each 2-day sampling period. The abundance of Diptera was highly variable for both between and within years (range of means and SD between years: 24.8–98.8 and 27.9–126.2 individuals, respectively; range of means and SD within years: 35.2–71.9 and 38.1–133.1 individuals, respectively; Table S1, Figures S2 and S3). There was no sudden discernible decline in the mean biomass or abundance of Diptera after the introduction of neonicotinoid insecticides in 2011 (Figure S2), although we did not statistically test for this.

Biomass trends: Model Set 1

The covariate contributing the most to variation in biomass, from Model Set 1, was 'Ordinal date'. We found no main effect of 'Year' on biomass from our temporal models ($\beta = -0.075 \pm 0.058$, $p = 0.2$;

Figure 3a; Table S3: 'Model C'). However, we found an interaction between 'Year', 'Comp.1' and 'Comp.2', with our model selection process suggesting the fixed effect structure containing a three-way interaction was preferred ($\beta = -0.035 \pm 0.012$, $p \leq 0.01$; Table S3: 'Model H'; Table 2, model AIC_c weight = 0.86; conditional $R^2 = 0.43$). Our model suggested that biomass decreased the most over time in locations that were either (a) high in both Comp.1 and Comp.2 scores (e.g., increasing agricultural intensity, dominated by soy and maize cropping) or (b) low in both Comp.1 and 2 scores (e.g., agriculture dominated by pasture and forage landscapes; Figure 2b).

Abundance trends: Model Set 2

Like Model Set 1, 'Ordinal date' was found to have the largest effect on abundance from our covariates. However, our predictions for total Diptera abundance over time in samples showed a slight increase, though the estimate of the main effect of 'Year' again lacked precision ($\beta = 0.19 \pm 0.118$, $p = 0.12$; Figure 3b; Table S4: 'Model C'). There were interactions between 'Year' and 'Comp.1' and 'Comp.2', however, with abundance increasing over time at rates that varied with landscape context ($\beta = -0.024 \pm 0.011$, $p < 0.05$; Table S4: 'Model H' model; Table 2, model AIC_c weight = 0.55; conditional $R^2 = 0.46$). Our model predicted that abundance increased over time most in locations that were high in Comp.1 scores and low in Comp.2 scores (i.e., in intensively cultivated areas dominated by a diversity of cereal cropping; Figure 2c). We estimated abundance increases in areas of intense cereal cropping of up to 32% per year compared to 2006 levels. In general, abundance increased more slowly over time in locations with lower Comp.1 scores, and, at these low scores of Comp.1, abundance increase over time was similar across locations with varying Comp.2 scores (i.e., was similar across forested and pasture–forage landscapes; Figure 2c).

Biomass offset by abundance: Model Set 3

Including the abundance of Diptera within the sample as an offset showed a decline in biomass per individual Diptera over time ($\beta = -0.267 \pm 0.079$, $p \leq 0.001$; Figure 3c, Table S5: 'Model C'). We found that the rate of decline in offset biomass varied over 'Comp.1', with biomass per number of Diptera declining more over time as agricultural intensity increased towards row-crop production landscapes ($\beta = -0.057 \pm 0.01$, $p \leq 0.001$; Figure 2; Table S5: 'Model G'; Table 2, model AIC_c weight = 0.69; conditional $R^2 = 0.43$). We found little variation in the rate of decline in the offset biomass over Comp.2 values (Figure 2d).

DISCUSSION

The temporal trends in abundance and biomass of the Diptera community varied with landscape context within the boundaries of our sampling region of Southern Québec. Although our findings are in

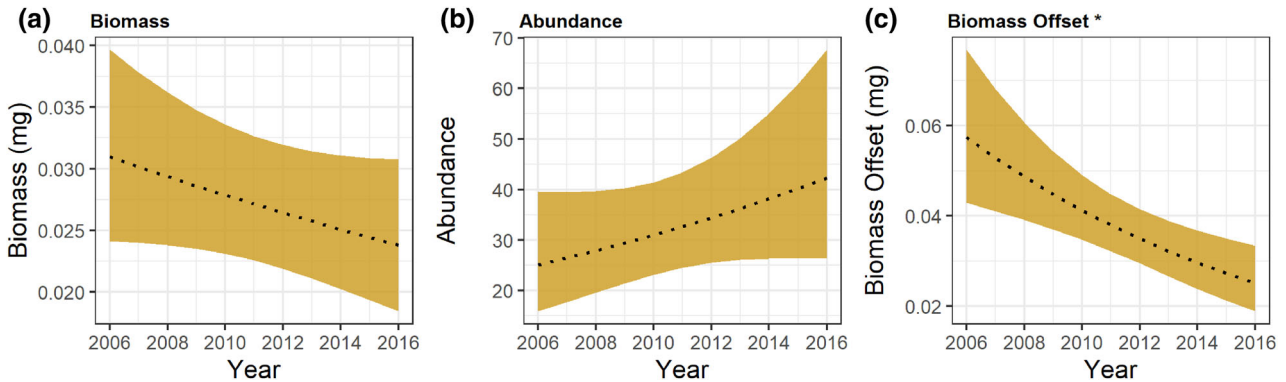


FIGURE 3 Marginal effect of (a) ‘Year’ on Diptera biomass (predictions from Model Set 1, Table 2 ‘Model H’), (b) abundance (predictions from Model Set 2, Table 2, ‘Model H’) and (c) biomass offset by abundance (predictions from Model Set 3, Table 2, ‘Model G’). The marginal effects on the ‘y’ axis depict the predictions for the response variables as the level of each predictor is held constant at their mean values. An asterisk (*) indicates a significant effect of ‘Year’ on the response variable ($p \leq 0.05$). 95% confidence intervals are represented by shaded envelopes.

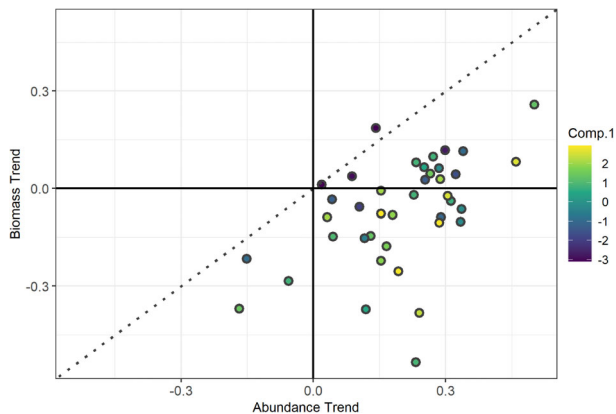


FIGURE 4 The relationship between the temporal trend in abundance and biomass of Diptera, for each of the 40 farms. The ‘trend’ values are the slope of ‘Year’ calculated from adding the random effects of each farm to the main effect of year on abundance and biomass from the ‘Model C’ models of Model Sets 1 and 2 (Table 2, ‘Model C’). The dotted line indicates where the points would be if the relationship between biomass trend and abundance trend on each farm was $y = x$ or 1:1, that is, abundance and biomass change at the same rate. The ‘Comp.1’ values indicated in the plot are the mean landscape context values from the first axis of the PCA performed (Figure 2a) for each farm, averaged over 2006–2016.

partial agreement with our hypotheses that intensively cultivated areas focusing on row cropping result in greater biomass declines over time in comparison to less intensively cultivated areas (dependent on whether there were cereals other than maize and soy growing on farms or not), the abundance trends contradicted our hypotheses, increasing overall and more rapidly so with high-intensity agriculture.

Given that the temporal change in Diptera biomass varied widely from that of abundance, changes in total biomass must have been driven by processes other than changes in the total number of Diptera, and therefore potentially correspond with community and/or trait turnover. Figure 4 shows the relationship between the temporal

trends in Diptera abundance and biomass across the 40 farms in the study; while there is a logical general increase in the temporal slope value of biomass as abundance trends increase, more than half of all farms show a rise in abundance but a drop in biomass over time. Almost all other farms still either show biomass to be decreasing faster than abundance or increasing slower than abundance.

We addressed this phenomenon further through offsetting our biomass trends by abundance in additional models (Figure 3c). The decline in biomass per number of Diptera suggests the possibility that community-level changes—such as a change in the relative abundance of the species that compose the Diptera communities—could be occurring, shifting towards Diptera with lower individual mass on average over time. Furthermore, an increase in agricultural intensity strengthened the declines of biomass per Diptera, indicating that this trend towards lower per capita mass of Diptera is happening more rapidly in areas of more intensive farming practices (Figure 2d). Due to a lack of further taxonomic information, our analyses were unable to distinguish whether this phenomenon is occurring because of an overall decline in large species and an increase in small species, representing a whole community change or by change in abundance of one or two very dominant species over time. Indeed, other mechanisms, such as phenotypic plasticity or adaptation to changing conditions, may mean that intraspecific variation in body size and biomass over time and across the landscape gradient may play a role in the processes leading to our observations (de Bello et al., 2011; Violle et al., 2012).

However, the investigation of the Diptera community in our study system in 2008 found that the community composition, and relative abundance of different groups of Diptera, varied along the spatial gradient of agricultural intensity (Laplante, 2013). While we cannot assume a space-for-time substitution, there were size-level differences across these communities that agree with our notion that the intensity of agriculture may support small species over large ones in our study area, driving community change. For example, the most dominant species that increased in abundance with an increase in maize cover (i.e., agricultural intensity) were *D. platura*. (4.8–6.4 mm

in length; Gesell, 2000), *Spelobia clunipes* (~2.5 mm in length; Lindsey, 2017) and *Spelobia ochripes* (~2.1 mm in length; Ilona, 2019), which are much smaller than the most dominant species that decreased in abundance with maize cover (*Pollenia rudis*, 9.5–12.7 mm in length; Mihályi, 1976). These four species together composed 47% of the total number of specimens that were caught in 2008.

Correlations between traits and population declines of insects in Germany indeed showed that larger insect species, and those that were more abundant and of a higher trophic level, declined the most over time, although this was only investigated in forested systems (Staab et al., 2023). In more intensively managed ecosystems, higher disturbance and resource availability can filter life history traits to favour communities with ‘fast’ traits such as faster reproduction, smaller body size and higher relative abundance compared to lower intensity production systems (Hanson et al., 2016; Neyret et al., 2024). Such traits can enable populations to recover more quickly following ecosystem disturbance, as well as allow competitive exploitation of resources, and are often associated with pest status (Gavina et al., 2018; Körösi et al., 2022).

Regarding intraspecific change in per capita mass, body size has previously been found to vary among individuals of a given species across space in Diptera, according to variables such as local temperature (Atkinson, 1994; Gilbert, 1985). Similar to the way in which environmental variables can ‘filter out’ species traits, such pressures can also operate within species to filter individuals according to their traits, as well as act on the plasticity of traits like body size to determine the adult phenotype of individuals (Atkinson, 1994). For example, Chironomidae (non-biting midges) are predicted to decrease in size over time with future climate warming (Wonglersak et al., 2021). Further investigation into species-level trends in our study area would help untangle possible interspecific and intraspecific trait mechanisms.

A complex array of variables determines the characterisation of a landscape and may affect the trends in Diptera abundance and biomass in our study, including the homogenisation of landscapes around farms and reduction in the abundance and diversity of resources and habitats available to support larger species of Diptera (Forister et al., 2019; Nilsson et al., 2008; Wagner et al., 2021). Agricultural intensification is often accompanied by increased use of pesticides and artificial and organic fertilisers, which can further compound the exposure of coprophagous Diptera species to pesticides through residue in manure sprayed on fields, or more widely to Diptera species through leaching into waterways (Buijs et al., 2022; Ewald et al., 2015; Schreinemachers & Tipraqsa, 2012; Wagner et al., 2021). Such organic and chemical pollution can alter community structure as some species are considerably more sensitive to these inputs than others (Buendia et al., 2013; Hellawell, 1986; Powell et al., 2022; Timm & Haldna, 2019; Vaughan & Ormerod, 2012). Typically, species of Diptera with lower biomass, such as chironomids, are more resilient to pollution effects than larger species (De Haas et al., 2005).

Our findings that total abundance and biomass increase at a greater rate in landscapes containing ‘small’ cereals (other than just soy and maize), despite the more rapid decline in biomass per number of individuals on these farms, suggests other cereals support larger populations within Diptera communities than maize and soy

monocultures do. This suggests the increase in Diptera abundance in these more diverse, mixed-crop cereal landscapes results in compensation of total biomass despite the turnover to lower biomass individuals, resulting in a greater abundance and biomass of flies even relative to the lower intensity farms and forested areas (Figure 2).

Change in climatic or weather patterns is yet another possible driver of Diptera biomass (Boggs, 2016). Maximum temperature as well as precipitation levels in the days leading up to Diptera sampling were found by Garrett et al. (2022) to influence spatial variation in biomass of Diptera in our study area. However, we explored whether there were changes in weather patterns across years, which could have explained the temporal trends we found in Diptera communities but found no trend in the maximum or mean temperature nor in precipitation levels over time across our sampling region (Figure S4a–c). We did, however, find an increase in the proportion of land occupied by intensive agriculture around farms over time, driven by an increase in maize and soy cultivation (Figures S5 and S4d–i). If the agricultural shift to converting more forage and pasture towards intensive maize and soy production in our sampling region continues, we may expect further and more significant declines in biomass of Diptera communities in the future.

Although species-level data are more ideal to retain in monitoring programmes, valuable insights can still be gained from using other metrics such as community abundance and biomass in combination. Many monitoring schemes sample with lower intensity, including citizen science schemes, and may not extract biomass information from samples. Using abundance alone in our study would have shown an incomplete picture of biodiversity change in Diptera communities within our sampling area, perhaps leading to the interpretation that agricultural intensification leads to more resilient Diptera communities with increased abundance and diversity. We, therefore, recommend that, where species information is too time-consuming or not possible to obtain, efforts are made to go beyond abundance metrics, such as using biomass to further understand functional change in insect communities over time.

We recognise that, although we have obtained very high-resolution temporal data, constraints on our ability to sample at this high intensity for longer periods of time restricted the sampling window within years. We are therefore likely to have missed the activity of some species of Diptera, which live out their entire adulthood before 1 June or after 15 July. Further to this, the single colour choice for our traps may further bias our sampling towards particular groups of Diptera that are attracted to—and more likely to fly towards—yellow traps, such as pollinators and maize pests (Allan, 2024; Garcia et al., 2022). It may be that the patterns in biomass and abundance change we detected over space and time in this study are largely driven by these groups of Diptera, rather than changes for species across the Diptera order as a whole. Indeed, as previously mentioned, the higher taxonomic resolution data available for our traps in 2008 showed that *D. platura*—an important crop pest—partially dominated the catch in Diptera samples (24.1% of the 5313 specimens) and increased in abundance relative to other groups along the spatial gradient of agricultural intensity (Laplante, 2013). It is thus possible that another sampling method, such as malaise trapping, would have

shown a different pattern of biomass and abundance given that this other method is likely more efficient and inclusive for trapping flies (Lamarre et al., 2012).

Finally, the length of our time series is relatively short and therefore provides a ‘snapshot’ of trends through time (Didham, Basset, et al., 2020). While we think our analyses deliver valuable insights into changes in Diptera communities under agricultural intensification, the beginning of our sampling period in 2006 is subsequent to much larger agricultural transformations in this region of Québec. Previous land use change consisted of the removal of forest and semi-natural habitat for forage and pasture-dominated agriculture such as dairy farms from the 1950s and then a transformation of dairy farms to intensive maize and soybean farming in the 1990s (Jobin et al., 2003; Ruiz & Domon, 2009). Therefore, it is probable that the baseline abundance and biomass of Diptera were much higher in the decades prior to our sampling period, and that Diptera biomass and abundance have declined much more rapidly prior to our study, possibly representing a shifting baseline (Didham, Basset, et al., 2020; Soga & Gaston, 2018). The collection of long-term data on insect communities becomes even more important in this light.

AUTHOR CONTRIBUTIONS

Kathryn E. Powell: Conceptualization; methodology; investigation; funding acquisition; writing – original draft; visualization; software; formal analysis; project administration. **Daniel Garrett:** Validation; writing – review and editing; data curation. **David B. Roy:** Funding acquisition; writing – review and editing; supervision. **Tom H. Oliver:** Funding acquisition; writing – review and editing. **Maxim Larrivé:** Funding acquisition. **Marc Bélisle:** Conceptualization; investigation; funding acquisition; writing – review and editing; validation; project administration; data curation; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interests regarding the production of this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Dryad at <https://doi.org/10.5061/dryad.xd2547dj8>. The R scripts used to analyse the data and produce our results can be found at <https://github.com/katpow/Diptera-trends>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting information.

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