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**INFLUENCE OF AGRICULTURAL INTENSIFICATION ON PREY AVAILABILITY
AND NESTLING DIET IN TREE SWALLOWS (*TACHYGINETA BICOLOR*)**

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ABSTRACT

Influence of agricultural intensification on prey availability and nestling diet in Tree Swallows (*Tachycineta bicolor*)

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Over the last decades, aerial insectivorous birds have been declining in both North America and Europe. Those declines have been hypothetically attributed to a decrease in prey availability caused by agricultural intensification but empirical evidence remains scarce. Here, we quantify the effect of landscape composition on the abundance and diversity of potential prey of Tree Swallows (*Tachycineta bicolor* Vieillot, 1808) and on nestling diet in southern Québec, Canada. We collected food boluses from nestlings and compared their composition with spatio-temporally corresponding samples from traps on farms distributed along a gradient of agricultural intensification. The diet of nestlings was mostly composed of Diptera, both in biomass and abundance, but by mid-June, these decreased with increasing proportions of intensively cultivated crops within 500 m from nests. Trap catches for Diptera and all arthropods combined followed the same trends. Yet, the associations between Diptera subgroups (Nematocera, non-schizophoran Brachycera, Schizophora (Calyptratae), and Schizophora (Acalyptratae)) and landscape composition differed between traps and boluses, suggesting that prey selection was altered by agricultural intensification. Our results suggest that agriculture can alter the availability of preferred prey for aerial insectivores and further studies should evaluate the impact of prey availability to explain the decline of aerial insectivores.

Key words: Aerial insectivorous bird, Arthropods, Agricultural intensification, Diptera, Redundancy analysis (RDA), Tree Swallow, *Tachycineta bicolor*.

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INTRODUCTION

Anthropogenic environmental changes are affecting a large number of species worldwide and in many cases result in their decline (Fuller et al. 1995; Wittmer et al. 2007; Cahill et al. 2012). Insectivorous bird populations, for instance, have been declining steadily in several parts of North America and Europe over the last decades (Donald et al. 2001; Nebel et al. 2010; Hallmann et al. 2014; but see Michel et al. 2016). Various causes have been suggested to explain these negative population trends, including a mismatch effect for long-distance migrants caused by a shift in the peak of insect prey availability due to climate change (Both et al. 2006; Cormont et al. 2011), the deterioration of non-breeding habitats (Fuller et al. 1995; Norris et al. 2004), and an increase in predation pressures (Bayne and Hobson, 1997; Bohning-Gaese et al., 1999; Johnson et al. 2006). The latter two also lead to a reduction of parental activity and provisioning (Dunn et al. 2010). In addition, many studies have suggested a link between agricultural intensification and the decline of insectivorous farmland bird populations (e.g., Donald et al. 2001; Benton et al. 2002; Askins et al. 2007; Hallmann et al. 2014).

Changes in agricultural practices due to the ever-increasing food demands over the years have taken many forms in order to improve crop yields, including an increased use of mechanization and drainage as well as greater inputs of fertilizers and pesticides (Tilman et al. 2002; Tscharntke et al. 2005; Meehan et al. 2011). Agricultural intensification has also contributed to large-scale habitat homogenization through the implantation of a low diversity of monocultures which alternate according to simplified spatio-temporal rotation schemes, as well as through the destruction of forest and other natural habitats found along field margins (Benton et al. 2003; Tscharntke et al. 2005; Gibbons et al. 2008; Brown and Schulte 2011). Besides the increased

mortality (and nest destruction) caused by tilling, seeding and mowing/harvesting (Tews et al. 2013) or poisoning via pesticide exposure (Mineau and Palmer 2013), agricultural intensification has been reported to have several negative effects on important life history traits of insectivorous farmland birds. Those include, among others, a disruption of breeding phenology, through delay of clutch initiation date in intensively managed farms, potentially attributed to lower arthropod availability in those habitats (Bradbury et al. 2000). Intensive agricultural habitats also have negative effects on other life history traits such as a reduction of clutch and brood sizes as well as of fledging rate (Boatman et al. 2004; Ghilain and Bélisle 2008; Poulin et al. 2010). Recently, Stanton et al. (2016) also reported that male Tree Swallows spent more time away from the nest, hence reducing parental care, in agricultural sites as well. The hypotheses suggested to explain those effects generally refer to a decrease in arthropod prey availability and diversity in intensively managed farmlands, particularly as a result of landscape simplification and pesticide use. Indeed, many studies have reported that both arthropod richness and abundance decrease with increasing agricultural intensity (Schweiger et al. 2005; Attwood et al. 2008; Gruebler et al. 2008). The effect of agricultural intensification on insect biomass was however shown to be both positive and negative in previous studies (Rioux Paquette et al. 2013; Michelson 2016). Yet, while agricultural intensification appears to reduce arthropod abundance and diversity, very few studies have clearly assessed its impact on the diet of insectivorous birds. Of those that did, most reported a change in diet among habitats or periods differing in management intensity (e.g., Britschgi et al. 2006; Poulin et al. 2010; Nocera et al. 2012). Such changes are worrying as diet composition can be more important than food abundance for nestling growth and health (Twining et al. 2016) with lasting effects up to adulthood (Wilson et al. 2017).

Tree Swallows (*Tachycineta bicolor* Vieillot, 1808) are semi-colonial passerines breeding in

Canada and USA and overwintering in the southern USA, Mexico and Central America (Winkler et al. 2011). They are secondary cavity nesters that breed in open fields like meadows and grassland near sources of water and readily use man-made nest boxes, which facilitates population studies (Jones 2003; Winkler et al. 2011). Tree Swallows predominately eat flying insects that have aquatic or terrestrial larval stages (McCarty 2002). Previous studies conducted on different Tree Swallow populations reported that the nestlings' diet was mainly composed of Diptera, with proportions ranging between 60% and 80% of food items (e.g., Blancher and McNicol 1990; McCarty and Winkler 1991, 1999; Johnson and Lombardo 2000; Beck et al. 2013). Like several other aerial insectivores, Tree Swallows have been declining in the northeastern part of North America since 1995 (Shutler et al. 2012; Michel et al. 2016). In Québec, populations have also been declining steadily over the last three decades (Rioux Paquette et al. 2014). The objective of the present work was to assess the effects of agricultural intensification on the diet of Tree Swallow nestlings in southern Québec, Canada. Studies conducted in this study system have suggested negative impacts of intensive agriculture on several aspects of the breeding success of Tree Swallows. For example, Ghilain and Bélisle (2008) have shown that individuals breeding in areas with a high proportion of extensive cultures (i.e., hayfields and pastures) fledge twice as many young than those breeding in areas mainly composed of intensive cultures (i.e., corn and soybean). Rioux Paquette et al. (2013) reported that Diptera abundance was negatively correlated with the proportion of intensively managed cultures in this study system, especially late in the breeding season, a critical period for nestlings (Martin, 1987). Here we first assess the effects of agricultural intensification on the abundance, biomass and diversity of arthropods in our study system and more specifically in the diet of Tree Swallows. We then describe the associations between various components of the agricultural landscape, the nestling's diet and the availability of insect prey.

METHODS

Study area

Field work was conducted from June 1st to July 10th in 2011 and 2012. The study area covered 10,200 km² and included 40 farms distributed along a gradient of agricultural intensification ranging from extensive cultures (hayfields, pastures, and fallows, as well as small amounts of various nectar flowering cultures, such as peas, canola, and buckwheat) in the east to more intensively managed cultures (corn, soybean, and other cereals) in the west (Figure 1). The agricultural intensification gradient also paralleled a gradient of forest loss and fragmentation (Bélanger and Grenier 2002). Ten nest boxes per farm, installed in 2004 and spaced by 50 m, were distributed along a 500-m transect following field edges (see Ghilain and Bélisle 2008 for further details). Two insect traps were installed on each farm to assess arthropod availability (see details below).

Landscape characterization

We characterized habitat composition within a 500-m radius around each nest box from which at least one food bolus was collected. This radius conservatively includes foraging radii that have been found in previous studies (Quinney and Ankney 1985; McCarty and Winkler 1999; Mengelkoch et al. 2004) and allows comparisons with previous studies conducted in our system (Rioux Paquette et al. 2013). We delimited each field using aerial photographs (1:40 000 Ministère des Ressources Naturelles et de la Faune 2000) and visually determined in situ the

crop/land use associated to each of those fields. Agricultural landscapes consisted of anthropogenic structures (buildings and roads), natural habitats (water and forest), extensive cultures (hayfields, pastures, and fallows), and a suite of more intensively cultivated crops. This last category included corn, soybean, and other cereals (oat, wheat, millet, barley, and rye), as well as vegetables and some nectar flowering plants (peas, canola, flax, buckwheat, and sunflower). We consider the relative cover occupied by this last category as a proxy of agricultural intensification since most of these crops involve significant mechanical treatments and applications of fertilizers and pesticides. Moreover, the amount of cultivated areas (henceforth CA) characterized by these crops is negatively correlated with natural habitats and crop diversity in our study area (see Supplementary Materials Figure S1)¹. We determined the relative cover of each structure, habitat, or culture listed above using ArcGIS 9.3 (ESRI 2008).

Arthropod sampling

Nestling diet

We determined the diet of Tree Swallow nestlings based on the food that adults provided to their young in the form of boluses. Boluses were collected using a ligature method that consisted in installing a collar around the neck of each nestling of a brood to prevent them from swallowing food beyond the crop. The collar was made of a folded elastic band, which passed through a 5-mm long piece of feeding tube #8 (Smits et al. 2005). The collar was adjusted by sliding the piece of feeding tube along the loop formed by the elastic band (similar to a bolo tie). This method is frequently used to assess the diet of insectivorous birds because arthropods in boluses are not yet

¹ Supplementary Figure S1 is available with the article through the journal Web site.

digested, therefore making their identification easier and less biased (McCarty and Winkler 1991; Johnson and Lombardo 2000; Smits et al. 2005). We fitted collars to nestlings for a first 30-min period, after which we checked for boluses, we then waited for another 30 min. period before collecting additional boluses (if present) and removing the collars. Boluses were individually stored in 75% ethanol. For each sampling period, we recorded the start time as well as the temperature (± 0.1 °C) and wind speed (± 0.1 km/h; using a Kestrel 2000 Pocket Weather Meter, Nielsen-Kellerman, USA) until the data stabilized (~ 2 min). We sampled boluses from 4 randomly selected broods per farm whenever possible (4 broods per farm = 93.7% of data, 3 broods = 1.7% and 2 broods = 4.6%). Two of the four broods were sampled when nestlings were 6 and 10 days old and the other two when nestlings were 8 and 12 days old, covering the period of highest growth rate (McCarty 2001). A total of 242 broods were sampled. We found no differences in fledging probabilities between manipulated nestlings and those that were not (mixed logistic regression correcting for nestling sex and body mass at day 6, brood size, and including farm and year as random effects: estimate \pm SE, -0.024 ± 0.23 , $P = 0.91$, $n = 1507$ nestlings).

Prey availability

We estimated arthropod availability on each farm from the content of two passive traps that consisted of 4-L yellow buckets with a 21-cm diameter and containing about 2 L of saturated-salt water with detergent to reduce surface tension and slow down bacterial and fungal growth. Above the bucket, two perpendicular transparent plastic plates (20 cm wide x 30 cm high) were attached at their center to intercept flying insects from all directions. Passive open trap contents might not reflect the exact composition of aerial arthropods found in the surrounding environment, but

provide a good proxy of the relative abundance of aerial arthropods available to swallows as they reflect prey density and activity (Høye and Forchhammer 2008). Traps were installed 1.5 m above ground at the first and second third of the 500-m nest box transects. We collected the content of each trap every second day when monitoring the breeding activities of Tree Swallows. Each trap sample thus represented the prey availability of the two previous days, including the actual prey availability at the time when boluses were obtained. We subsequently randomly selected one trap out of two for each sampling occasion to assess arthropod availability on farms where a minimum of one bolus was collected from nestlings, for a total of 151 trap samples.

Arthropod identification

We counted and identified arthropods from traps and boluses to taxonomic order following Marshall (2006). Because of the extensive diversity in morphology and flying capacity of Diptera, as well as their preponderance in the diet of Tree Swallows, we refined the identification resolution for this group. Following McAlpine et al. (1981) and Pape et al. (2011) we assigned all Diptera specimens to one of four mutually exclusive groups sharing similar traits: 1) Nematocera; 2) non-schizophoran Brachycera; 3) Schizophora (Acalyptratae); and 4) Schizophora (Calypttratae). A detailed overview of the composition and general biology of these groups is presented in the Supplementary material section. After identification, all arthropods were dried at 50°C for 24 h and then weighed (± 0.0001 g). We excluded two large species of Lepidoptera, the monarch butterfly (*Danaus plexippus*) and the Canadian tiger swallowtail (*Papilio canadensis*), as well as cockchafer (*Phyllophaga* spp.: Coleoptera) and bumblebees (*Bombus* spp.: Hymenoptera), from trap sample counts and weights. These insects were also not considered in all further analyses because they were never found in bolus samples (see Supplementary

Materials Table S1)², nor have they ever been reported to be eaten by Tree Swallows, likely due to their large size and/or unpalatability.

Statistical analyses

All statistical analyses were performed using the R statistical software (R Development Core team 2013, version 3.0). Significance of inferential tests was determined using an alpha level of 0.05.

Nestling diet and prey availability

We performed two different statistical tests to compare the proportions of arthropod abundance from different taxa collected in traps and boluses. These groups included Nematocera, non-schizophoran Brachycera, Schizophora (Acalyptratae), Schizophora (Calypttratae), Lepidoptera, Coleoptera, Hemiptera, Hymenoptera, Neuroptera, Mecoptera, Ephemeroptera, Plecoptera, Odonata, Trichoptera, Psocoptera, Thysanoptera, Collembola, Araneae, and Acari. We first assessed if the overall proportions of arthropods collected in boluses differed from proportions collected in traps using a Pearson's chi-square test. Due to their low abundances, we merged some taxa according to their biology: i) Neuroptera and Mecoptera (terrestrial predaceous larvae and long-winged adults); ii) aerial plankton (Psocoptera, Thysanoptera, Collembola, Araneae and Acari). We also excluded from this first analysis some orders with an aquatic larval stage (Ephemeroptera, Plecoptera, Odonata, and Trichoptera), as they form emergence swarms that may be easily eaten by Tree Swallows but are rarely collected by the traps we used. Then, in a

² Supplementary Table S1 is available with the article through the journal Web site.

second analysis, we performed generalized linear mixed models (with a logit link function and binomial error) using the *glmer* function of the *lme4* package (Bates et al. 2015) for each order mentioned above (no merging or exclusions) to compare their average proportion between traps and boluses, while controlling for the farm identity (random effect). We applied a Dunn-Sidak correction to keep the familywise Type I error rate at 0.05 when performing the above multiple comparisons.

Effects of agricultural intensification and time on arthropod abundance, biomass and diversity

We first modeled the total abundance and biomass (log-transformed) of all arthropod groups found in traps and assessed if they varied during the sampling period and as a function of CA proportion (see Landscape characterization for details) using linear mixed models. Fixed effects included Julian day and its second order term, mean proportion of CA within 500-m of all nest boxes within a farm, and the two-way interactions between date variables and CA. Farm identity was included as a random effect.

The same explanatory variables were then used to model the diversity of arthropods found in traps. We used Simpson's diversity index (expressed as $1-D$) to estimate arthropods diversity. It was calculated for each trap and included each group of arthropods used when comparing the diet of Tree Swallows to prey availability (see above). We then further assessed the effects of sampling time and CA on the abundance and biomass of the main groups of arthropods found in traps and boluses. To do so, we used two sets of linear mixed models in which the abundance and biomass of Diptera (not subdivided into 4 groups), Coleoptera, Hemiptera and Ephemeroptera were modeled. These four orders were used because they represented most of the items found in

the Tree Swallows' diet (95.2%). Since only a few Ephemeroptera specimens were collected in traps, we only modeled their abundance and biomass in boluses. Explanatory variables included the Julian day and its second order term, the proportion of CA in a 500-m radius around nest boxes for boluses, the mean proportion of CA in 500-m around all nest boxes within a farm for traps, and finally the two-way interactions between date variables and CA. Farm identity was included as a random effect in all models. Model selection was performed using a backward variable selection procedure, sequentially removing the least significant term from the model, starting with interactions.

Agricultural landscape and insect composition in traps and in boluses

We described the association between the composition of agricultural landscapes of our study area and that of groups of insects (including the four Diptera subgroups) found in traps and in boluses, respectively, using redundancy analyses (RDA; computed with the *rda* function of the *vegan* package, version 2.4; Oksanen et al.2013). For both RDAs, response variables consisted in the proportions of Nematocera (N: Diptera), non-schizophoran Brachycera (NS: Diptera), Schizophora (Calyptratae (Ca: Diptera)), Schizophora (Acalyptratae (Ac: Diptera)), Coleoptera (Co), Hemiptera (He), Lepidoptera (Le), and Hymenoptera (Hym). Proportions of Trichoptera (Tr) and Ephemeroptera (Eph) were included in the matrix of response variables for RDA on boluses, but excluded of the RDA on traps (see justification above in *Nestling diet and prey availability* section). Insect groups showing a minimal abundance of 40 individuals in both traps and boluses were included in analyses and a Hellinger transformation was applied to both response matrices (Legendre and Gallagher 2001). Five boluses that did not include insects were removed from this analysis. No trap samples were excluded since all of them contained at least

one of the insect groups. For boluses, explanatory variables included the proportions of corn, soybean, other cereals, vegetables and other nectar flowering cultures (flowers), fallows, pastures, and forest within a 500-m radius around nest boxes. For traps, we used the mean proportions of the habitat categories found within 500-m of all nest boxes of a farm. Finally, we assessed if explanatory variables of each RDA explained a significant proportion of variance using permutation tests ($N = 999$) in the form of an ANOVA using the *anova.cca* function of the *vegan* package (Oksanen et al. 2013). To further assess if the associations between landscape and arthropod composition differed between traps and boluses, we tested for a differential effect of the proportion of CA on the proportion of Diptera detected in boluses and in traps with a generalized linear mixed models (logit link function and binomial error), which fixed effects included the proportion of CA, the sample type (bolus or trap), and the interaction between those two variables. Farm identity was included as a random effect.

RESULTS

Nestling diet and prey availability

A total of 489 boluses were analyzed (including 450 from 2011 and 39 from 2012) together with their corresponding samples obtained from traps ($N = 151$, including 117 from 2011 and 34 from 2012). Overall, 12,338 and 13,702 arthropods of edible size for Tree Swallows were identified from boluses and traps respectively (see Table S1)³. In boluses, their average abundance was 25.2 (SE = 1.6), ranging from 0 to 538 (molluscs was the only prey item in 5 boluses), and the average

³ Supplementary Table S1 is available with the article through the journal Web site.

biomass was 0.034g (SE = 0.001), ranging from < 0.001g to 0.178g. For trap samples, the average abundance of arthropods was 91.8 (SE = 4.9), with a range from 9 to 312, and their average biomass was 0.088g (SE = 0.005), ranging from 0.005g to 0.364g. While the proportions of arthropod groups found in boluses differed from those collected in traps ($\chi^2 = 6183$, $df = 9$, $P < 0.001$; Figure 2a), Diptera represented the most abundant group of arthropods in both (0.671 in boluses and 0.664 in traps). Other important groups included Ephemeroptera (0.193 in boluses and < 0.001 in traps), Hemiptera (0.057 in boluses and 0.053 in traps), and Coleoptera (0.031 in boluses and 0.156 in traps). The mean proportion of Diptera found in boluses and traps, calculated by averaging their proportion across samples (see Figure 2b), were higher in boluses (estimate \pm SE for boluses vs. traps = 0.767 ± 0.030 vs. 0.653 ± 0.018 , $P < 0.001$) and for each of the four Diptera subgroups: Nematocera (boluses vs. traps = 0.118 ± 0.021 vs. 0.285 ± 0.016 , $P < 0.001$), non-schizophoran Brachycera (0.157 ± 0.019 vs. 0.049 ± 0.008 , $P < 0.001$), Schizophora (Calyptratae) (0.131 ± 0.018 vs. 0.064 ± 0.007 , $P < 0.001$), and for Schizophora (Acalyptratae) (0.227 ± 0.021 vs. 0.191 ± 0.005 , $P < 0.001$). Other arthropod groups that showed a significant difference between their proportion in boluses and traps are identified on Figure 2b; detailed results for each group can be found in Table S2⁴.

Effects of agricultural intensification and time on arthropod abundance, biomass and diversity

The temporal pattern in total abundance of arthropods found in traps varied with the mean proportion of CA within 500 m of all nest boxes on a farm (Table 1). Abundance was higher in landscapes entirely covered by cultures early in the season and increased to reach a small peak as

⁴ Supplementary Table S2 is available with the article through the journal Web site.

early as mid-June before decreasing strongly until early July (Figure 3). In contrast, arthropod abundance increased at an increasing rate throughout much of the sampling period in non-cultivated landscapes, leading to the greatest abundance across landscapes by early July (Figure 3). Landscapes with 50% of CA showed only a slight increase in arthropod abundance throughout the sampling season (Figure 3).

Overall, the abundance of arthropods in traps was positively correlated with their biomass ($r = 0.58$, $P < 0.001$). Yet biomass showed no variation during the sampling season or with the mean proportion of CA (all $P > 0.07$; Figure 3). Similarly, arthropod diversity showed no variation over time or with CA (all $P > 0.26$). Nevertheless, the Simpson's diversity index for traps averaged 0.757 (SE = 0.007), meaning that trap contents showed a high arthropod diversity across landscapes. This value was slightly lower for boluses (0.504, SE = 0.013; $N = 484$), and both significantly different (effect size \pm SE = 0.253 ± 0.023 , $P < 0.001$). No variables were found to affect the overall abundance or biomass of arthropods in boluses (all $P > 0.39$).

Diptera abundance varied in time and across landscapes in the same patterns as described for all arthropods (Table 2, Figure 4). However, Diptera biomass increased linearly during the sampling period but was not affected by the mean proportion of CA within 500 m of all nest boxes on a farm (Table 2, Figure 4). Coleoptera abundance showed a decreasing yet marginally non-significant effect of the date (Table 2). In contrast, Hemiptera abundance increased linearly during the sampling period (Table 2). We found no significant effect of time or landscape variables on biomass of Coleoptera (all $P > 0.16$) and Hemiptera (all $P > 0.08$).

The abundance and biomass of Diptera in boluses showed similar temporal trends that varied with the proportion of CA within 500 m of nest boxes (Table 2, Figure 5a, b). In early and late June the abundance and biomass of Diptera was higher in landscapes without cultures and followed concave-up patterns over time (being lowest by mid-June). On the other hand, the abundance and biomass of Diptera peaked in highly cultivated landscapes around mid-June, as illustrated by a concave-down shape of the curves over time.

Ephemeroptera abundance in boluses was stable through time but decreased as landscapes became more cultivated (Table 2, Figure 5c). The biomass of Ephemeroptera showed a pattern opposite to that of Diptera (Table 2, Figure 5d); in heavily cultivated landscapes it was highest in early June with a rapid decrease until mid-June, at which time it peaked in non-cultivated landscapes. Coleoptera abundance increased during the sampling period but was not affected by the amount cultures in landscapes (Table 2). Coleoptera biomass remained constant through time and across landscapes (all $P > 0.07$). Hemiptera abundance (all $P > 0.53$) and biomass (all $P > 0.59$) were also stable through time and landscapes.

Effects of agricultural landscape on insect composition in traps and boluses

The habitat composition of agricultural landscapes explained 16.4% of the variation in arthropod composition in traps ($F_{7,143} = 4.01$, $P = 0.005$). The first RDA axis explained 8.7% of variation and was mainly associated with the proportion of forest and to a lesser extent fallows on one side and with the proportion of corn and soybean on the opposite side of the axis (Table 3, Figure 6a). The first RDA axis thus represented a gradient from natural habitats (negative scores) to intensively managed cultures (positive scores). Groups mostly associated with this gradient

included non-schizophoran Brachycera (associated with forests and fallows) and Schizophora (Acalyptratae) (mostly associated with corn and soybean; Table 3, Figure 6a). The second RDA axis explained 4.2% of variation in insect composition and was strongly driven by the proportion of cereals and flowers on one side and of fallows and pastures on the other side (Table 3, Figure 6a). This second RDA axis thus represented a gradient from intensive cultures to livestock production. Nematocera was the only insect group strongly associated with this gradient and peaked in landscapes with important fallow and pasture covers (Table 3, Figure 6a).

The habitat composition of agricultural landscapes explained 7.6% of the variation in insect composition of boluses ($F_{7,477} = 5.59$, $P = 0.005$). The first RDA axis, which explained 4.1% of the insect composition variance, was driven by the proportion of corn on one side and by the proportion of fallows and forest on the other side (Table 3, Figure 6b). The second RDA axis, which explained 1.8% of the insect composition variance, was driven by the proportion of forest, pastures and fallows on one side and by corn, soybean and other flowering cultures on the other side (Table 3, Figure 6b). The combination of both axes thus described the gradient of agricultural intensification found in our study area, contrasting the cattle and dairy productions (positive scores on both axes) with intensively managed crops (negative scores on both axes). Non-schizophoran Brachycera were strongly associated with both axes (Table 3). This group was positively associated with the proportion of fallows (axis 1) but also with the proportion of soybean (axis 2; Table 3, Figure 6b). The other insects strongly associated with axis 1 included the Schizophora (Acalyptratae) and Schizophora (Calyptratae), which were both associated with intensively managed cultures, especially corn and soybean (Table 3, Figure 6b). Ephemeroptera was the only other group highly associated with axis 2 (Table 3). This group was strongly associated with forests, fallows and pastures (Table 3, Figure 6b). Other groups were not

specifically associated with any component of the landscape as shown by their central position in the triplot and their low scores (Table 3, Figure 6b).

The above analyses showed associations between landscape and arthropod composition that differed between traps and boluses, suggesting a differential prey selectivity by Tree swallows along the gradient of agricultural intensification. Further evidence for such a phenomenon was found for Diptera, as regardless of date, the proportion of Diptera in boluses increased more rapidly with an increasing proportion of cultivated area than in traps (Table S3⁵).

DISCUSSION

In this study, we assessed the diet of Tree Swallow nestlings and the prey availability experienced by their parents along a gradient of agricultural intensification in southern Québec, Canada. As expected, Diptera was by far the most important group in the diet of nestlings and the most available in our system. Our results indicate that while agricultural intensification had a positive influence on Diptera abundance in both traps and boluses early to mid-season, the trend was reversed later in the season, when Diptera abundance decreased with increasing proportion of intensively cultivated areas. Such density-dependent variation in diet composition has been observed several times in swallows (Bryant 1973; Turner 1982; Quinney and Ankney 1985; Orłowsky et al. 2014) and may be compatible, at least qualitatively, with both optimal diet (Sih and Christensen 2001) and prey switching theory (van Leeuwen et al. 2013). We also documented associations between the different habitats (i.e., forest and crop types) found in

⁵ Supplementary Table S3 is available with the article through the journal Web site.

agricultural landscapes and the Diptera composition in traps and boluses. Those associations differed between traps and boluses, suggesting that Tree Swallows select their prey differently across the agricultural intensification gradient. To our knowledge, this study is one of the first to assess the diet of an aerial insectivore and to compare it to prey availability along a gradient of agricultural intensification.

Nestling diet and prey availability

Our findings are consistent with previous assessments of the diet of Tree Swallow nestlings. First, the predominance of Diptera (67.1% of bolus specimens) compares well to the 60% to 80% range found by others (Blancher and McNicol 1990; Johnson and Lombardo 2000, Quinney and Ankney 1985). Second, the prevalence of Ephemeroptera, which accounted for nearly 20% of specimens in boluses, are also similar to those documented in systems where freshwater bodies are abundant (Blancher and McNicol 1990; McCarty 2002; McCarty and Winkler 1991, 1999; Mengelkoch et al. 2004; Johnson and Lombardo 2000; Dods et al. 2005; Beck et al. 2013). Whereas Diptera taken as one group showed similar relative abundances in both traps and boluses, Ephemeroptera were, however, virtually absent from our trap samples. Two parsimonious explanations for this result are (1) that Ephemeroptera were truly absent from the sampled areas and Tree Swallows travelled beyond the 500-m radius around nest boxes to reach habitats where they could feed upon those prey; and (2) that our traps performed poorly for this group. Evidence in favor of the first explanation includes the fact that there were very few water bodies within 500 m from nest boxes (mean (\pm SD) water cover across farms = 1.2 % \pm 5.7 %). Moreover, mayflies go through a short-lived subimago stage with poor flying abilities between the aquatic nymphal and terrestrial adult stages. While the two specimens found in traps were

adults, all mayflies in boluses were subimagoes, suggesting that they were captured near-water, during or soon after their emergence (Edmunds 1988). Despite the fact that window-traps have been used to study Ephemeroptera flight behavior in the past (Lingdell and Müller 1979), it remains that the second explanation cannot be ruled out and warrants further investigation. The possibility that Tree Swallows travelled further in order to have access to Ephemeroptera would not be surprising given the high nutritional quality, swarming behavior, and poor escape capability of these prey when compared to more terrestrial arthropods. Indeed, Twining et al. (2016) found that Tree Swallow nestlings fed on a diet with a fatty acid composition comparable to that of aquatic insects, like Ephemeroptera, grew faster and showed a better body condition and immunocompetence.

Another aspect of prey which may contribute significantly to their value for predators is body size, which can affect both their nutritional value and handling time (Sih and Christensen 2001). In accordance with previous findings on swallows (Turner 1982; Quinney and Ankney 1985; McCarty and Winkler 1999; Orłowski and Karg 2013), our results suggest that Tree Swallows tend to select large prey items such as non-schizophoran Brachycera (e.g., syrphid flies) and *Schizohora calyptratae* (e.g., house flies), as their relative abundance was higher in boluses than in traps. While the nutritional value of prey may be relatively easy to determine based on their size, their handling time and net energy value are much more difficult to estimate, especially for highly mobile prey like flying insects (Sih and Christensen 2001). As escape capability is likely to be positively correlated to body size in flies, future research should address whether it is more profitable for aerial insectivores to prey, for example, upon small, swarming flies (e.g., midges), or large, fast flying flies, a question that will have to take into account both the spatiotemporal distribution and abundance of prey (Bryant 1973; Turner 1982; van Leeuwen et al. 2013), as well

as the fitness currency that the predators are trying to maximize (Kacelnik 1984; Barette et al. 2009). Until then, it will remain difficult to make predictions or interpret results about diet composition.

Effects of agricultural intensification and date on arthropod abundance, biomass and diversity

In less cultivated areas, the abundance of arthropods in traps generally increased throughout the season, whereas in intensively cultivated areas it increased until mid-June before decreasing sharply by early-July. Abundance was thereby moderately higher in intensively cultivated areas in mid-June but extremely low by early-July, with points of equivalence in all environments in early and late-June. The same pattern was observed for Diptera alone, which was expected given the predominance of this group. These findings bring support to those of Rioux Paquette et al. (2013) who found (1) no difference in Diptera abundance throughout the same gradient of agricultural intensification in early June (2006 and 2007), and (2) quadratic increases that peaked earlier in the season and at lower abundances in intensively cultivated areas than in extensive ones. Besides the obvious contribution of vegetation change across intensification levels, such patterns may originate from pesticide use as those chemicals (e.g., neonicotinoid insecticides, which are strongly associated with corn and soybean production in southern Québec; Giroux 2015) can alter the abundance, emergence phenology, and behavior of various insects, including Diptera and Ephemeroptera (Morrissey et al. 2015). Sub-lethal effects of pesticides are certainly a possibility in our system as we found that the prey fed to Tree Swallow nestlings are contaminated by numerous pesticides (Haroune et al. 2015).

The temporal patterns in Diptera biomass we observed in traps showed a linear temporal increase and a lack of landscape composition effect. Altogether our results imply that the size of Diptera specimens in traps changed over time, an effect that was more pronounced in intensively cultivated landscapes where abundance decreased while biomass increased as the season progressed. Such patterns are congruent with the fact that insect sizes in natural habitats have been showed to be smaller than in cultivated areas, an observation mostly attributed to pesticides and dispersal limitations that favor bigger arthropods in cultivated areas (Blake et al. 1996; Schweiger et al. 2005).

We found no changes in arthropod diversity in traps either throughout the season or along the gradient of agricultural intensification. These results are similar to those of Burel et al. (1998) but contrast with other studies that showed negative effects of intensive agricultural practices on insect diversity (Blake et al. 1996; Schweiger et al. 2005; Hendrickx et al. 2007; Attwood et al. 2008). Although our results must be interpreted with caution because our diversity estimate was based on high taxonomic levels (i.e., order instead of family or species) and did not include functional aspects (e.g., body size; Guerold 2000), they still indicate that Tree Swallows had access to a variety of prey from which to select across the gradient of agricultural intensification.

Previous studies have shown that the diet and foraging habitat use of aerial insectivorous birds can be altered by agricultural practices, notably by the availability of grazed pastures (Evans et al. 2003, 2007; Orłowski and Karg 2013), harvesting (Orłowski et al. 2014), and by insecticide use (Poulin et al. 2010; Nocera et al. 2012). Although all of these studies identified reduced, or at least modified, prey availability as the potential cause underlying these shifts, none of them reported concurrent, empirical estimates of prey availability. One important contribution of our

study is that it reports that prey selectivity by Tree swallows vary with agricultural intensification and that the composition of agricultural landscapes can alter both the diet and prey availability of the nestlings, as exemplified with Diptera subgroups that composed nearly 70% of their diet. The relative availability of Schizophora (Calyptratae) and Schizophora (Acalyptratae) was indeed positively associated with corn and soybean (and thus negatively with forest, fallows and pastures), two dominant and intensively managed cultures in southern Québec. These results are consistent with our expectations, since some species of these two groups are well known pests of these crops (Capinera 2001; Soroka et al. 2004). Moreover, only the proportion of Schizophora (Calyptratae) in boluses was positively associated with corn and soybean, as the proportion of Schizophora (Acalyptratae) in boluses was only positively associated with corn. Such a difference may lie in the fact that Schizophora (Calyptratae) are generally larger than Schizophora (Acalyptratae) and may therefore be more valuable and systematically preyed upon by swallows. Unlike the previous taxa, the non-schizophoran Brachycera and the Nematocera were associated with different components of the landscape in traps and boluses. In traps, these two taxa were mostly associated with fallows and pastures while in boluses, the proportion of non-schizophoran Brachycera was associated with both fallows and soybean, and the proportion of Nematocera showed no strong affinities to any of the landscape characteristics investigated. Several non-independent factors may explain these results. Landscapes dominated by fallows and pastures generally comprise more water, forest and hedgerows than more intensively cultivated landscapes in our study area (see Figure 6 and Bélanger and Grenier 2002). Almost all Nematocera and many non-schizophoran Brachycera have aquatic larval stages (McAlpine et al. 1981, 1987; Courtney et al. 2009). Furthermore, many species in those two groups form mating swarms (McAlpine et al. 1981, 1987; Courtney et al. 2009), a phenomenon facilitated by forest edges and hedgerows (Grüebler et al. 2008) and that could make these insect groups especially

susceptible to capture if Tree Swallows target clumped food sources, even if present in low numbers as in intensively cultivated areas (St-Louis et al. 1990; Evans et al. 2003, 2007). The overall under-representation of Nematocera in the diet (based on relative abundance), and this across all habitats, may however be linked to their smaller body size and/or to a potential decoupling between real and estimated abundances due to emergence and swarming events.

Like most field studies attempting to shed light on the causal paths leading to particular diets of insectivores, our interpretations remain hypothetical at best. Several factors are responsible for such weak explanatory capacity. Among them, we note the diversity of life histories showed by arthropod species, if even known, combined to the diversity of prey available and taken by insectivores, as well as the difficulties of estimating reliable spatiotemporal patterns of arthropod abundance at relevant spatiotemporal scales. An illustration of the decoupling between what researchers (can) do and what they may need to do is that arthropod abundance is often estimated at high taxonomic levels (e.g., order) in spite of the wide range of species-specific habitat requirements needed for life cycle completion, an outcome which likely results from the large numbers of specimens to process and the taxonomic challenges they represent. It is thus unsurprising that the habitat composition of agricultural landscapes explained only 16.4% and 7.6% of the variation in arthropod composition of traps and boluses in our study, respectively. Furthermore, arthropod abundance and activity levels in agricultural environments can be influenced by a number of weather variables, such as temperature (Peng et al. 1992; Pearce-Higgins and Yalden 2004; Winkler et al. 2013), wind speed (Peng et al. 1992) and precipitations (Torok and Toth 1988; Pearce-Higgins and Yalden 2004), which sometimes act in interaction with particular habitat features to influence insect availability and vulnerability to predation (Grüebler et al. 2008). Future research will have to address such complexity and may need to

consider alternative or complementary methods like DNA metabarcoding for processing samples more efficiently (Trevelline et al. 2016) or stable isotope analysis to identify the type of agricultural habitat used by prey to develop or forage (Girard et al. 2012).

Conclusion

Our study illustrates that complex spatiotemporal patterns related to agricultural intensification are at play in our study system and affect the food availability and diet of a declining aerial insectivorous bird. Our results indicate that birds facing changes in prey availability in distinct environments can respond by consuming different prey items in different proportions. Yet, interpreting such diet changes is challenging as it minimally requires (1) unbiased and precise estimates of prey availability across habitats at relevant spatiotemporal scales, as well as under different weather conditions; and (2) better estimates of prey value as defined by optimal diet theory (Sih and Christensen 2001). We call for more studies to provide concurrent measures of prey availability and bird responses for a better assessment of the role played by agricultural intensification in the global decline of farmland birds and areal insectivores. In particular, this would improve our inferences of the direct (toxicological) and indirect (trophic) impacts of pesticides on the behavior and fitness of birds (Hallmann et al. 2014).

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Table 1. Final linear mixed models computed on the abundance of all arthropods in traps ($N = 151$, $df = 110$) sampled along the gradient of agricultural intensification, in Southern Québec, Canada, in 2011 and 2012, which represent insect availability for Tree Swallow (*Tachycineta bicolor*). Variables are shown with their respective effect size and standard error (SE).

Variables	Effect size	SE	<i>t</i>	<i>P</i>
Intercept	78.26	9.80	7.99	< 0.001
CultAreaTrap	34.82	18.88	1.84	0.068
JDay	340.77	96.17	3.54	0.006
JDay ²	184.72	94.21	1.96	0.052
CultAreaTrap * JDay	-622.71	188.66	3.30	0.001
CultAreaTrap * JDay ²	-483.63	207.82	2.33	0.022

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Table 2. Final models computed on the abundance and biomass of Diptera, Coleoptera and Hemiptera in traps and Diptera, Coleoptera, Hemiptera and Ephemeroptera in boluses collected on Tree swallow (*Tachycineta bicolor*) nestlings with their respective significant (or marginally significant) variables, effect size, standard error, t-value and P-value. Biomass is measured in milligrams.

Orders (Obs, df)	Variables	Effect size	SE	t	P
ABUNDANCE					
<u>Traps</u>					
Diptera (151, 110)	Intercept	52.07	7.85	6.63	< 0.001
	CultAreaTrap	23.93	15.13	1.58	0.117
	JDay	289.71	75.15	3.85	0.002
	JDay ²	154.87	73.59	2.10	0.038
	CultAreaTrap * JDay	-496.87	147.33	3.37	0.001
	CultAreaTrap * JDay ²	-394.01	162.13	2.43	0.017
Coleoptera (151, 114)	Intercept	76.04	32.03	2.37	0.019
	JDay	-0.36	0.19	1.93	0.055
Hemiptera (151, 114)	Intercept	-23.19	9.82	2.36	0.020
	JDay	0.16	0.06	2.86	0.005
<u>Boluses</u>					
Diptera (489, 448)	Intercept	14.36	2.05	6.97	< 0.001
	CultAreaNest	5.50	3.89	1.41	0.158
	JDay	20.15	35.10	0.57	0.566
	JDay ²	96.46	35.66	2.71	0.007
	CultAreaNest * J Day	-26.10	66.93	0.39	0.70
	CultAreaNest * JDay ²	-139.66	66.80	2.09	0.037
Coleoptera (489, 453)	Intercept	-6.68	2.91	2.30	0.022
	Year2012	0.69	0.29	2.34	0.020
	JDay	0.04	0.02	2.54	0.012
Hemiptera (489, 453)	Intercept	1.52	0.24	6.30	< 0.001
Ephemeroptera (488 [†] , 451)	Intercept	7.02	1.87	3.75	< 0.001
	CultAreaNest	-7.28	3.46	2.10	0.036
BIOMASS					
<u>Traps</u>					

Orders (Obs, df)	Variables	Effect size	SE	<i>t</i>	<i>P</i>
Diptera (151, 114)	Intercept	-114,82	65.99	1.74	0.085
	JDay	0.84	0.39	2.16	0.032
Coleoptera (151, 115)	Intercept	28.35	3.55	7.98	< 0.001
Hemiptera (151, 115)	Intercept	10.37	1.64	6.32	< 0.001
<u>Boluses</u>					
Diptera (488 [‡] , 447)	Intercept	20.21	2.55	7.93	< 0.001
	CultAreaNest	9.58	4.75	2.02	0.044
	JDay	34.78	35.24	0.99	0.324
	JDay ²	71.72	35.31	2.03	0.043
	CultAreaNest * JDay	20.66	68.45	0.30	0.763
	CultAreaNest * JDay ²	-138.64	66.68	2.08	0.038
Coleoptera (489, 453)	Intercept	1.01	0.19	5.44	< 0.001
Hemiptera (488 [‡] , 452)	Intercept	0.99	0.14	7.13	< 0.001
Ephemeroptera (488 [‡] , 451)	Intercept	7.25	1.90	3.82	< 0.001
	CultAreaNest	-7.47	3.50	2.13	0.033
	JDay	19.01	23.35	0.81	0.416
	JDay ²	-67.60	23.31	2.90	0.004
	CultAreaNest * JDay	-78.17	45.64	1.71	0.088
	CultAreaNest * JDay ²	157.30	44.12	3.57	< 0.001

[†] One outlier bolus was removed from analysis (bolus of abundance of 511 Ephemeroptera, the mean abundance of Ephemeroptera in bolus = 3.84)

[‡] Mass missing for one Diptera in a bolus, which was removed.

Table 3. Taxa/groups and constraint variables scores (on the two main axes) for RDAs on the proportion of insects in boluses collected on Tree Swallow (*Tachycineta bicolor*) nestlings and in traps.

	Boluses		Traps	
	Axis1	Axis2	Axis1	Axis2
<u>Taxa/groups</u>				
Nematocera	-0.124	-0.008	0.077	0.286
Non-schizophoran Brachycera	0.500	-0.261	-0.380	0.104
Schizophora (Acalyptratae)	-0.416	0.021	0.393	-0.040
Schizophora (Calyptratae)	-0.363	-0.223	0.211	-0.107
Lepidoptera	0.024	0.022	-0.069	-0.033
Coleoptera	-0.110	0.103	-0.185	-0.213
Hemiptera	-0.018	-0.025	-0.076	-0.190
Hymenoptera	-0.011	0.113	-0.008	0.039
Trichoptera	0.048	-0.042	NA	NA
Ephemeroptera	0.197	0.360	NA	NA
<u>Constraint variables</u>				
Forest	0.299	0.674	-0.896	-0.215
Fallow	0.483	0.259	-0.326	0.579
Pasture	0.202	0.520	-0.089	0.507
Corn	-0.516	-0.527	0.594	-0.145
Soy	0.004	-0.589	0.646	-0.249
Cereals	-0.213	-0.059	0.184	-0.674
Vegetables	0.090	-0.298	-0.113	-0.272

Figure legends

Figure 1. Map of the study area located in Southern Québec in Canada. The gradient of agricultural intensification is represented by light grey areas (intensively managed cultures), increasing from east to west, and forest is represented by dark grey areas. Each farm is represented by a circled number.

Figure 2. Proportions of arthropods found in Tree Swallow (*Tachycineta bicolor*) nestlings' food boluses (dark gray) and in traps (pale gray) collected and analyzed from 2011 and 2012, in southern Québec, Canada (see Table S1 details). a) Proportions were calculated by pooling prey items across all boluses and traps, respectively. b) Proportions were averaged (\pm SE) across boluses and trap samples, respectively, using a mixed logistic regression without fixed effects but with farm identity as random effect to take the hierarchical sampling structure into account averaging the proportions of each prey. Due to their very low abundance and occurrence, Phthiraptera, Neuroptera and Mecoptera are not presented. Groups for which a significant difference between the proportions of individuals in boluses and in traps was found are indicated by asterisks.

Figure 3. Predictions of the abundance of all arthropods in traps throughout the sampling period in 2011 and 2012, Southern Québec, Canada, for different mean proportions of cultivated areas within 500 m of Tree Swallows (*Tachycineta bicolor*) nest boxes. The solid line represents landscapes with 0% cultivated areas, the dashed line and dotted line represent landscapes with 50% and 100% cultivated areas, respectively. Arthropod biomass was not influenced by agricultural intensification and is represented by the opened circle line.

Figure 4. Predictions of Diptera abundance in traps throughout the sampling period in 2011 and 2012, in Southern Québec, Canada, for different mean proportions of cultivated areas within 500 m of Tree Swallows (*Tachycineta bicolor*) nest boxes. The solid line represents landscapes with 0% cultivated areas, the dashed line and dotted line represent landscapes with 50% and 100% cultivated areas, respectively. Diptera biomass was not influenced by agricultural intensification and is represented by the opened circle line.

Figure 5. Predictions of Diptera (a, b) and Ephemeroptera (c, d) abundance (a, c) and biomass (b, d) in boluses sampled along a gradient of agricultural intensification in Southern Québec, Canada, at different proportion of cultivated area in 500-m radius of Tree Swallows (*Tachycineta bicolor*) nest boxes (solid lines = 0% cultivated, dashed lines = 50% cultivated and dotted lines = 100% cultivated).

Figure 6. Correlation triplot (scaling = 2) of redundancy analyses (RDA) on the proportion of different insects in A) traps ($N = 151$) and B) boluses along a gradient of agricultural intensification in Southern Québec, Canada (see Table 3 for species and constraint scores). Arrows represent the mean proportion cover of component of agricultural landscape in a 500-m radius A) around all of Tree Swallows (*Tachycineta bicolor*) nest boxes within a farm (Axis1 = 8.70% of the relative variation in insect composition and Axis2 = 4.20%) and B) around the nest box where the food bolus was collected (Axis1 = 4.14% of the relative variation in insect composition and Axis2 = 1.82%). Taxa/groups are represented by little diamond (◆) and consist of Nematocera (N; Diptera), non-schizophoran Brachycera (NS; Diptera), Schizophora (Calyptratae (Ca; Diptera)), Schizophora

(Acalyptratae (Ac; Diptera)), Coleoptera (Co), Hemiptera (He), Lepidoptera (Le) and Hymenoptera (Hym), Trichoptera (Tr) and Ephemeroptera (Eph).

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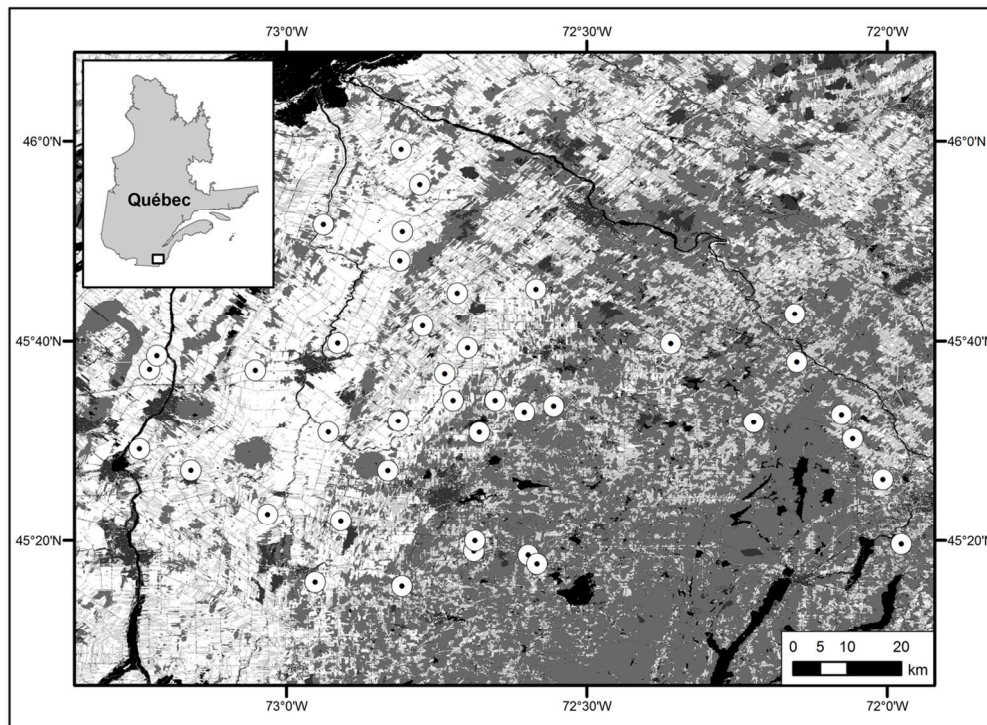


Figure 1. Map of the study area located in Southern Québec in Canada. The gradient of agricultural intensification is represented by light grey areas (intensively managed cultures), increasing from east to west, and forest is represented by dark grey areas. Each farm is represented by a circled number.

119x87mm (300 x 300 DPI)

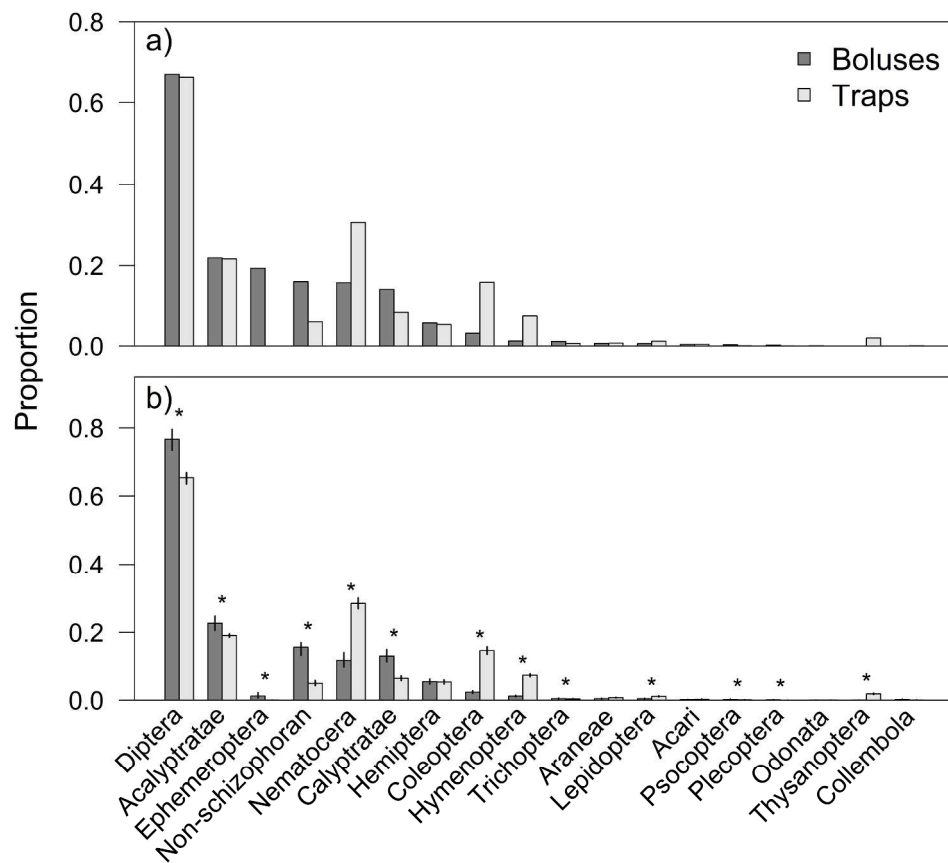


Figure 2. Proportions of arthropods found in Tree Swallow (*Tachycineta bicolor*) nestlings' food boluses (dark gray) and in traps (pale gray) collected and analyzed from 2011 and 2012, in southern Québec, Canada (see Table S1 details). a) Proportions were calculated by pooling prey items across all boluses and traps, respectively. b) Proportions were averaged (\pm SE) across boluses and trap samples, respectively, using a mixed logistic regression without fixed effects but with farm identity as random effect to take the hierarchical sampling structure into account averaging the proportions of each prey. Due to their very low abundance and occurrence, Phthiraptera, Neuroptera and Mecoptera are not presented. Groups for which a significant difference between the proportions of individuals in boluses and in traps was found are indicated by asterisks.

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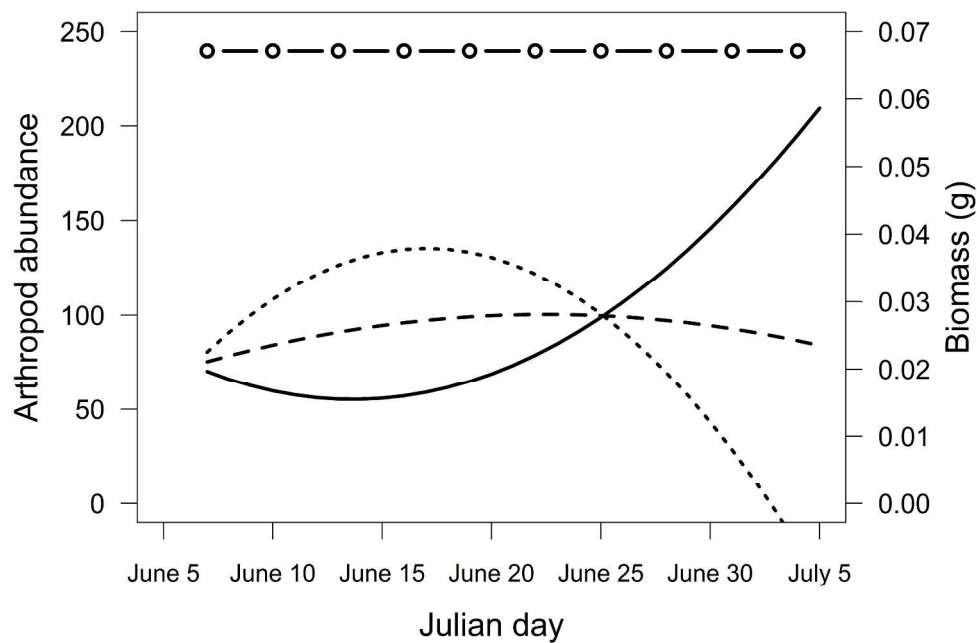


Figure 3. Predictions of the abundance of all arthropods in traps throughout the sampling period in 2011 and 2012, Southern Québec, Canada, for different mean proportions of cultivated areas within 500 m of Tree Swallows (*Tachycineta bicolor*) nest boxes. The solid line represents landscapes with 0% cultivated areas, the dashed line and dotted line represent landscapes with 50% and 100% cultivated areas, respectively. Arthropod biomass was not influenced by agricultural intensification and is represented by the opened circle line.

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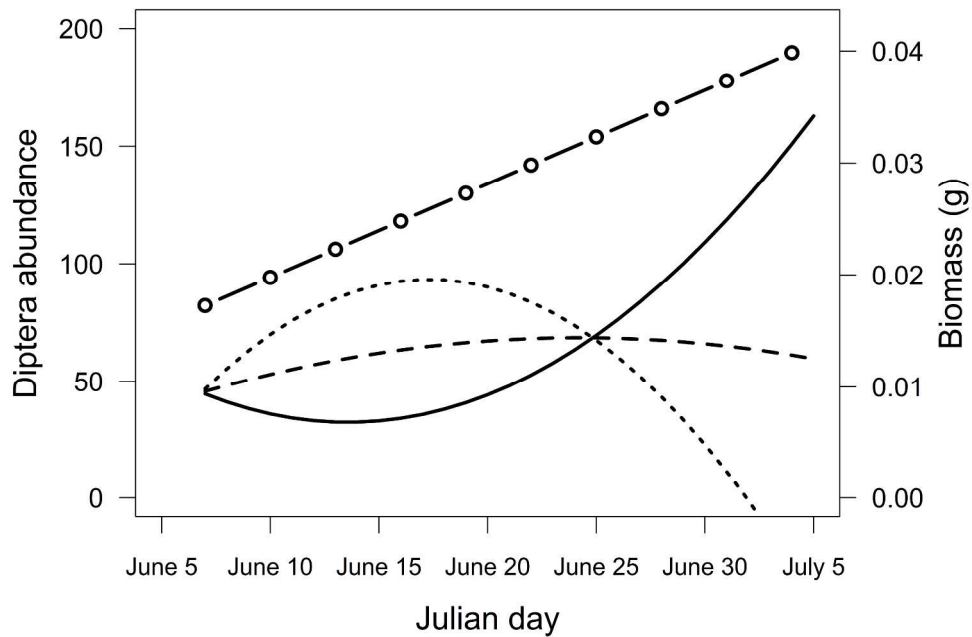


Figure 4. Predictions of Diptera abundance in traps throughout the sampling period in 2011 and 2012, in Southern Québec, Canada, for different mean proportions of cultivated areas within 500 m of Tree Swallows (*Tachycineta bicolor*) nest boxes. The solid line represents landscapes with 0% cultivated areas, the dashed line and dotted line represent landscapes with 50% and 100% cultivated areas, respectively. Diptera biomass was not influenced by agricultural intensification and is represented by the opened circle line.

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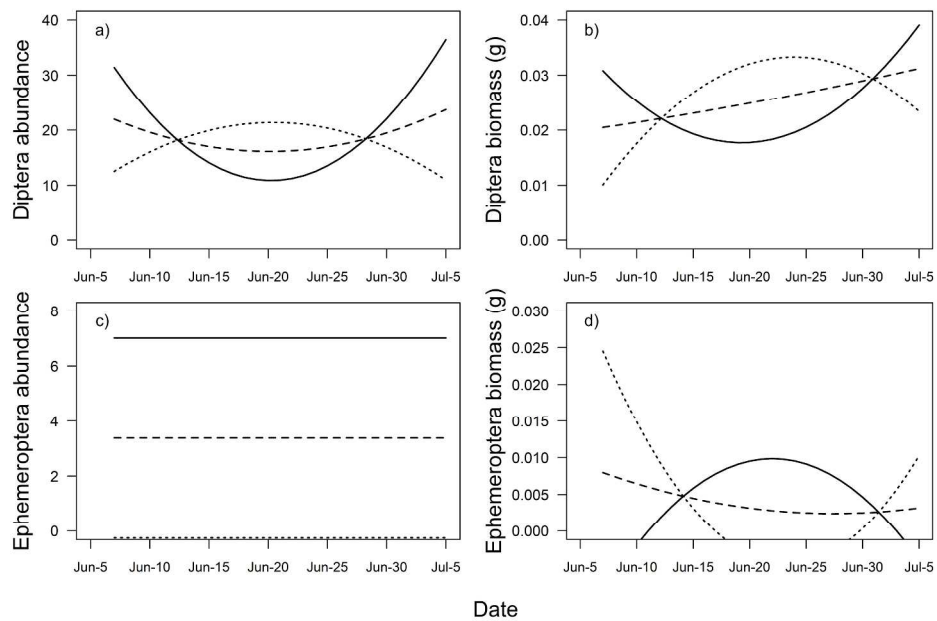


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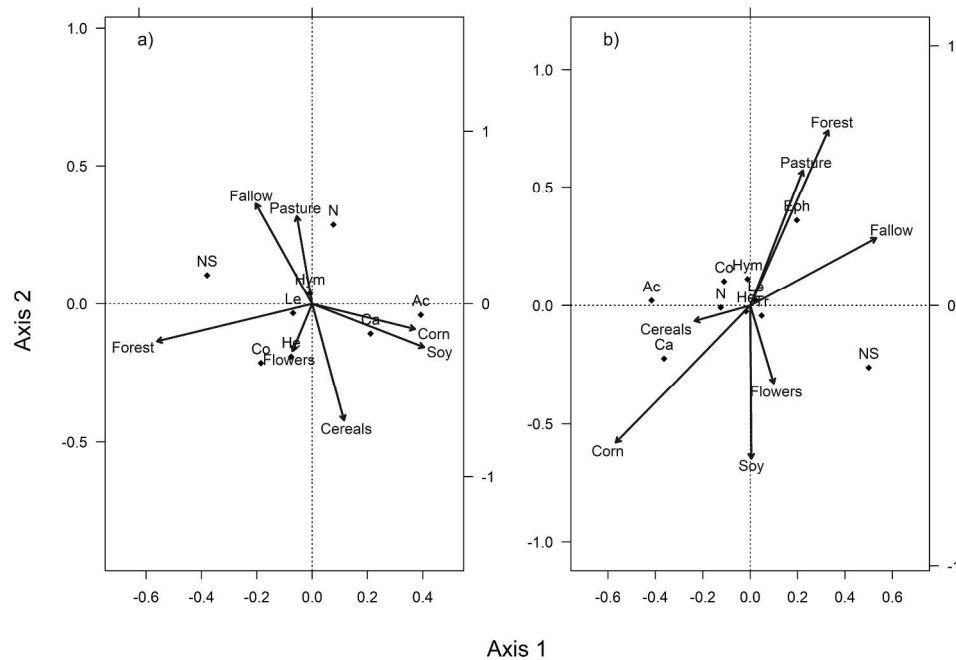


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130x88mm (600 x 600 DPI)