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Contrasting responses in community structure and phenology of migratory and non-migratory pollinators to urbanization

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Abstract

Aim: Anthropogenic landscape change, such as urbanization, can affect community structure and ecological interactions. Furthermore, changes in ambient temperature and resource availability due to urbanization may affect migratory and non-migratory species differently. However, the response of migratory species to urbanization is poorly investigated, and knowledge for invertebrates in particular is lacking. Our aim was to investigate whether there was a shift in community structure and phenology of hoverflies in urban landscapes, depending on migratory status.

Location: Switzerland.

Methods: Using a paired design, we compared urban and rural landscapes to investigate the impact of urbanization on the abundance, diversity and phenology of hoverflies. Furthermore, we tested whether migratory and non-migratory species responded differently to urbanization.

Results: We observed a difference in the response of migratory and non-migratory hoverfly communities. Although the abundance of hoverflies was higher in the rural ecosystem, driven by a high abundance of migratory species, there was no difference in species richness between the land use types. However, the community structure of non-migratory species was significantly different between urban and rural ecosystems. The phenology of hoverflies differed between the two ecosystems, with an earlier appearance in the year of migratory species in urban landscapes.

Main conclusions: To our knowledge, this is the first study to investigate the response of migratory insect communities to urbanization. We demonstrated that migratory and non-migratory hoverflies respond differently to urbanization. This highlights the importance of differentiating between trait and mobility groups to understand community assemblage patterns in anthropogenic landscapes. The differences in phenology supports the growing evidence that urbanization not only affects the phenology of vegetation, but also affects the higher trophic levels. Changes in the phenology and community composition of species as a result of anthropogenic landscape change may have important implications for the maintenance of key ecosystem functions, such as pollination.

KEYWORDS
beta diversity, ecosystem services, hoverflies, insect migration, phenology, pollinators, syrphids, urban ecology

1 | INTRODUCTION

Anthropogenic landscapes, such as agricultural and urban areas, are expanding globally, and these habitats will increase in area as the human population increases (Gerard et al., 2010; Seto, Güneralp, & Hutyra, 2012), along with the proportion of the population living in urban areas (Cohen, 2003; UNFPA, 2007). While the negative effects of agricultural intensification on biodiversity are well known (e.g., Kleijn et al., 2009; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005), the nature of the impact of urbanization remains relatively unclear (Faeth, Bang, & Saari, 2011; Mckinney, 2008). Previous research comparing urbanized areas to rural areas has found contrasting effects of urbanization on species richness and diversity across taxa (e.g., Baldock et al., 2015; Faeth et al., 2011; Magura, Lövei, & Tóthmérész, 2010; Mckinney, 2008; Turrini & Knop, 2015). On a large scale, urbanization may lead to changes in the structure of biological communities through ecological filtering, leading to species extinctions and an increased prevalence of generalist species (e.g., Deguines, Julliard, de Flores, & Fontaine, 2016; Knop, 2016). However, beyond this, little is known regarding which traits allow species to persist in urban compared to rural landscapes, and the effect of this interaction on species phenology in urban landscapes.

Changes in abiotic conditions within cities (i.e., temperature, light and water availability) can lead to the alteration of biotic conditions, such as primary productivity and overall resource availability. Compared to rural and natural habitats, there are more heat-absorbing surfaces, such as concrete, in urban habitats, which can lead to relatively warm environments, termed the urban heat island effect (e.g., Hart & Sailor, 2009; Oke, 1973). Changes in ambient temperature can lead to a shift in species phenology, such as the flowering times of plants. For example, plants have been shown to flower earlier, leading to a higher primary productivity and a longer growing season (see Jochner & Menzel, 2015; Mimet et al., 2009). Furthermore, the maintenance of parks and gardens within urban landscapes and the presence of many exotic plant species can result in a longer flowering period and more consistent resources (Comba et al., 1999; Harrison & Winfree, 2015), compared to intensive agricultural landscapes, which provide abundant, but seasonal resources (e.g., Rundlöf, Persson, Smith, & Bommarco, 2014). The change in the relative availability of resources within urban landscapes, compared to agricultural or natural landscapes, could result in shifts in the phenology and behaviour of organisms. However, little is known about how this change in the availability of resources affects organisms reliant on them, aside from bees (Harrison & Winfree, 2015). In the United Kingdom, *Bombus terrestris* remained active in cities during winter, indicating the presence of adequate resources, even during typically resource-limited times (Stelzer, Chittka, Carlton, & Ings, 2010). Furthermore, Leong, Ponisio, Kremen, Thorp, and Roderick (2016) showed a significant shift in the phenology of wild bees, with abundance in natural landscapes already declining by the time it was just reaching its peak in agricultural and urban landscapes.

For species that move across large areas, such as migratory species, changes in ambient temperature and resource availability due to urbanization may alter life history traits, such as arrival time or overwintering tendency, which may in turn influence key ecosystem processes. However, there have been relatively few studies investigating the response of migratory species to urbanization, and these few have primarily focused on birds (Evans et al., 2012; Møller, Jokimäki, Skorka, & Tryjanowski, 2014). For example, Tryjanowski, Sparks, Kuźniak, Czechowski, and Jerzak (2013) demonstrated an advance in the arrival date of migratory birds in urban compared to rural areas in Poland, whereas Plummer, Siriwardena, Conway, Risely, and Toms (2015) showed a change in the overwintering tendency of blackcap (*Sylvia atricapilla*) in the United Kingdom, due to urbanization. To date, studies investigating the response of migratory and non-migratory insect communities to urbanization are lacking. Insects are the most diverse, abundant and economically important group of terrestrial migrants, and have significant impacts on terrestrial ecosystems through the provision of nutrients, to ecosystem functions such as herbivory and pollination (Bauer & Hoye, 2014; Chapman, Reynolds, & Wilson, 2015).

Hoverflies (Diptera, Syrphidae) are one of the most biologically diverse fly families, and inhabit numerous terrestrial, but also many aquatic ecosystems (Rotheray & Gilbert, 1999). Many species are migratory in Europe, and move southwards towards the Mediterranean in autumn in large numbers (Aubert, Aubert, & Goeldlin, 1976; Gatter & Schmid, 1990; Odermatt, Frommen, & Menz, 2017). The adults visit flowers to feed on pollen and nectar, and are one of the most important pollinator groups besides bees (Jauker, Bondarenko, Becker, & Steffan-Dewenter, 2012; Rader et al., 2009, 2016). Furthermore, the larvae show a diverse range of life histories covering a wide spectrum of resource use, for example plants (phytophagous), aphids and other insects (zoophagous) and decaying organic material (saprophagous) (Rotheray & Gilbert, 1999). Zoophagous species such as the common and widespread *Episyrphus balteatus* are also important biological control agents for crop aphids (Hondelmann & Poehling, 2007; Tenhumberg & Poehling, 1995). Most hoverfly species overwinter as larvae (Keil, Dziock, & Storch, 2008). However, in some cases, individuals of migratory species may also overwinter as adults (Hondelmann & Poehling, 2007; Raymond et al., 2014). As migratory species are highly mobile, they may react differently to landscape change, such as urbanization, compared to local non-migratory species.

Using a paired design, we investigated the following questions: (1) Is there a difference in the abundance and species richness of hoverfly communities in urban and nearby intensively managed agricultural landscapes? (2) Is there a significant dissimilarity between the urban and rural communities? (3) Does phenology of the hoverfly communities differ between urban and rural landscapes? Finally, we ask (4) if the observed patterns in the communities differ for migratory or non-migratory species guilds. Due to the heat island effect of urban landscapes and the early and stable resources available in the urban ecosystem, we predicted an earlier appearance and a later disappearance of species in the urban landscape than in the agricultural landscape. Furthermore, we predicted that this would be more pronounced in non-migratory species. Higher temperature shortens development time and therefore insects may emerge earlier in the year. One could also predict that the first migratory hoverflies arriving invade the cities first, because of the relatively higher temperature and the earlier availability of food resources, with a shift towards a higher abundance of migratory hoverflies in the rural landscape in late spring.

2 | METHODS

2.1 | Study sites and sampling methods

Our study was conducted using a paired design in eight Swiss cities (urban) and nearby intensively managed agricultural (rural) areas (Figure 1). Cities were selected based on population size, with a minimum of 30,000 inhabitants (range 37,000–405,000; Table S1). The distance between the paired sites varied between 4.2 km and 7.3 km (Table S1). Sites within cities were selected within "green" areas, outside of the core city centre. The main vegetation in the city sites was ruderal vegetation, road verges and some private gardens.

Hoverflies were sampled by sweep-netting, at all eight urban–rural pairs (16 sites total) once each month from March until September 2015. From a central point, the sampling took place along four 500 m transects, by following the closest road to the four cardinal directions and walking back to the centre point. Therefore, the total length of the transect sampled at each site was 4 km (Figure S1). Each 500 m transect was sampled for 30 min (15 min up and 15 min down), leading to 2 hr per sampling session per site. All hoverflies observed along the transect (including a 10 m buffer either side) were collected with a sweep net and taken to the laboratory for identification. Private gardens were included in the sampling where possible, depending on accessibility. Additionally, to collect species that may be dwelling in the vegetation, the vegetation along the transect was also systematically sweep-netted for 5 min, once per sampling session. Sampling was always performed by the same collector. The data of all four 500 m transects were pooled per sampling session.

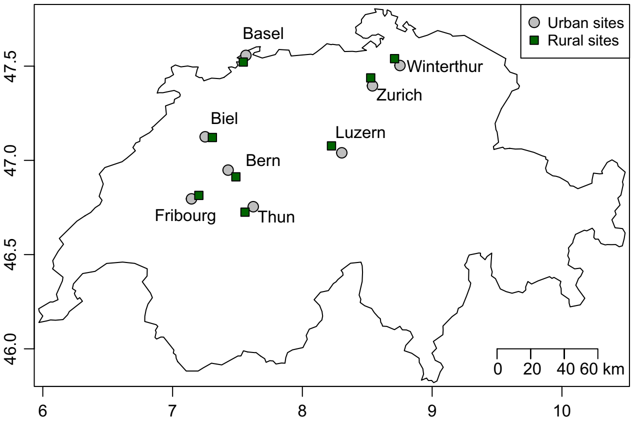

FIGURE 1 Map of Switzerland showing the location of the eight study regions, each with a paired urban and rural site. [Colour figure can be viewed at wileyonlinelibrary.com]

Sampling was conducted on warm, sunny days without wind, with nightly temperatures above 0°C and a minimum daytime temperature of 10°C. The sampling of each urban–rural pair took place between 10:00 and 16:00 hr on the same day. Due to the extraordinary heat period in July–early August 2015, sampling began earlier in the day to avoid sampling at ambient temperatures above 30°C. To avoid the effects of diurnal variation in species activity, the sampling order of the urban–rural pair was changed each month.

Hoverfly specimens were identified to species where possible, or morphospecies, in the laboratory. Hoverflies that were observed but could not be caught were recorded and identified to the lowest possible taxonomic level. All species were assigned as either migratory or non-migratory groups based on the available literature, including long-term studies of hoverfly migration in Europe (Aubert et al., 1976; Gatter & Schmid, 1990; Maibach, Goeldlin de Tiefenau, & Dirickx, 1992; Speight, 2014). For species where no information was available, they were assigned as non-migratory if they had not been previously reported in the long-term studies of hoverfly migration in Europe, mentioned above (Aubert et al., 1976; Gatter & Schmid, 1990; Table S2).

2.2 | Statistical analysis

To investigate differences in the abundance and species richness of hoverfly communities in urban and agricultural landscapes (question one), we first used linear mixed-effects models (LMM), with the abundance of hoverflies and species richness, as the response variables, and land use (two levels, urban vs. rural) and migratory status (two levels, migratory vs. non-migratory) as the explanatory factors. We also included the interaction between land use and migratory status. Region was included as a random factor in the models. Models assumed a Gaussian error distribution. Secondly, we repeated the analysis for the migratory and non-migratory hoverfly guilds separately, using land use as a predictor, which allowed us to interpret patterns in the abundance and species richness of the two migratory guilds between the different land use types.

To investigate the community differences between urban and rural landscapes (question two), pairwise dissimilarities were calculated for each urban–rural pair, using the Bray–Curtis index of dissimilarity (d_{BC}). The Bray–Curtis dissimilarity was calculated using the packages *vegan* (Oksanen, 2014) and *betapart* (Baselga, Orme, Villeger, De Bartoli, & Leprieur, 2013) in R (R Core Team, 2015). Baselga (2013) proposed a framework that allows for the separation of the two additive components of abundance-based Bray–Curtis dissimilarity (d_{BC}), the balanced variation in abundance ($d_{BC\text{-}bal}$) and the abundance gradient ($d_{BC\text{-}gra}$), which are analogous to turnover and nestedness, respectively, as derived from incidence-based frameworks. This partitioning allows for the underlying patterns in beta diversity to be disentangled (Baselga, 2013; Knop, 2016). To determine whether the observed Bray–Curtis dissimilarities were significantly different than would be expected by chance, we performed a permutation procedure, whereby species sampled within one urban–rural pair were randomly assigned to the urban or rural ecosystem (i.e., Knop, 2016). The dissimilarities between the urban and rural pairs were then recalculated, and this procedure was repeated 1,000 times. Significance values were calculated as the number of times the observed dissimilarity was larger than that of the randomized communities, divided by 8,000 (1,000 permutations for each of the eight regions). This procedure was conducted for all species and the migratory and non-migratory species separately.

To test for differences in hoverfly community phenology between urban and rural landscapes (question three), we tested whether abundance varied across the course of the season. We initially fitted a LMM with hoverfly abundance as the response variable and day of the year (day; expressed as the Julian day) and day squared as the explanatory variables. We also included the interaction between landscape and day. We assumed a Gaussian error distribution for the model. Day squared was included in the model as we expected there may be a quadratic relationship with abundance. The variable day was standardized so that the start of the sampling period (day 70) was represented as day 0. Sampling region was included as a random factor in the model. Following the initial full model, we then investigated whether there was a difference between the landscapes in the phenology of the migratory and non-migratory guilds, by modelling these separately. Abundance was square-root transformed.

All models were visually checked for conformity to model assumptions. The significance of the focal explanatory variable, land use type, migratory status and the interactions was tested by comparing the full model to a model without the variable in question, using a likelihood-ratio test (LRT; Elman & Hill, 2009). Models were run using the R package *lme4* (Bates, Maechler, Bolker, & Walker, 2015).

3 | RESULTS

We collected 3,404 hoverflies, belonging to 65 species (Table S2). The most abundant species was *Melanostoma mellinum* with a total of 1,050 specimens (31% of total individuals), followed by *Eristalis tenax* with 641 individuals (19%, Table S2). Sixty-seven per cent (*n* = 2,293) of individuals were recorded in rural sites, whereas 33% (*n* = 1,111) of individuals were found in the urban sites. Twenty-one specimens could not be identified and were excluded from further analysis. In total, eight species were exclusively recorded in the rural ecosystem, but these species were only represented by a small number of individuals (*n* = 21, 1% of the total rural abundance; Table S2). In comparison, 20 species were exclusively found in the urban ecosystem (*n* = 36, 3% of the total urban abundance; Table S2). We recorded 2,710 individuals from 22 migratory species, and 673 individuals from 43 non-migratory species (Table S2).

The interaction between landscape and migratory status was significant (*p* = .027, Table S3), and the overall abundance of hoverflies was significantly higher in rural (mean ± *SE*, 41.47 ± 6.04) compared to urban sites (20.04 ± 2.53, *p* = .017; Figure 2a, Table S3). The abundance of migratory species was also significantly higher in rural sites (34.87 ± 5.59) than urban sites (14.40 ± 2.07, *p* = .010; Figure 2a, Table S4). In contrast, there was no significant difference in the abundance of non-migratory species between urban (5.64 ± 0.79) and rural sites (6.60 ± 1.07; Figure 2a, Table S4). There was no significant difference in overall species richness between the two landscapes (Table S3), nor for either of the migratory species guilds (Figure 2b, Table S4).

For the overall hoverfly community and the migratory species, there was a trend towards higher observed Bray–Curtis dissimilarities between the urban and rural sites, compared to the randomly assigned communities (*p* = .066 and *p* = .079, respectively). For non-migratory species, Bray–Curtis dissimilarity for the observed communities was significantly higher compared to the randomly assigned communities (*p* < .001; Figure 3a). Similarly, balanced variation in the Bray–Curtis dissimilarity was also significantly higher for the observed non-migratory hoverfly community, compared to the randomly assigned community (*p* = .008; Figure 3b). There were no significant differences in the abundance gradient of the Bray–Curtis dissimilarity between the observed and randomly assigned communities, for any of the groups (Figure 3c).

Seasonal abundance differed significantly between the urban and rural areas. When considering all species, hoverflies were present earlier in the year in urban compared to rural landscapes (Intercepts of Equations (1) and (2), $\chi^2 = 4.032$, *df* = 1, *p* = .045, Table 1, Figure 4a). The curve of the relationship was also significantly steeper in rural landscapes (coefficients of Day, Equations (1) and (2), $\chi^2 = 10.903$, *df* = 1, *p* = .001), but broader in urban landscapes (coefficients of Day^2, Equations (1) and (2), $\chi^2 = 8.888$, *df* = 1, *p* = .003, Table 1, Figure 4a). This pattern was reflected by both the migratory and non-migratory species guilds, with the curves of the relationship being steeper and broader for rural sites compared to urban sites (migratory: Equations (3) and (4), Day: $\chi^2 = 12.588$, *df* = 1, *p* = <.001, Day^2: $\chi^2 = 9.032$, *df* = 1, *p* = .003, Table 1, Figure 4b; non-migratory: Equations (5) and (6), Day: $\chi^2 = 5.345$, *df* = 1, *p* = .021, Day^2: $\chi^2 = 6.322$, *df* = 1, *p* = .012, Table 1, Figure 4c). Migratory species appeared earlier in the year in urban compared to rural sites (Intercept of Equations (3) and (4), $\chi^2 = 4.939$, *df* = 1, *p* = .026, Table 1, Figure 4b), but this pattern was not reflected in non-migratory species. The plotted relationship between abundance and day of the year shows that abundance appears to peak higher and earlier in rural areas compared to urban areas for migratory species (Figure 4b).

4 | DISCUSSION

This is the first study to our knowledge to specifically investigate the impact of urbanization on migratory insect communities. Our results show that migratory and non-migratory hoverfly communities respond differently to urbanization. While the abundance of migratory species was higher in the rural compared to the urban ecosystem, there were no differences in species richness for either migratory or non-migratory species. However, the composition of the communities differed, with significant dissimilarity between urban and rural

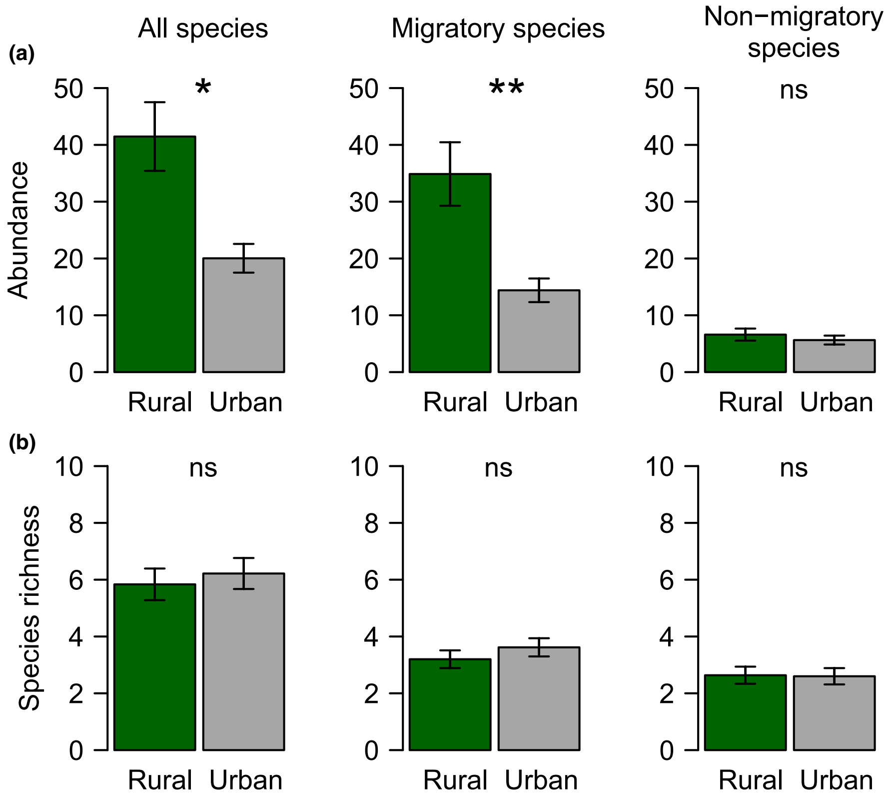

FIGURE 2 Mean (±*SE*) abundance (a) and species richness (b) of hoverflies in urban and rural landscapes. Stars represent significant differences determined by linear mixed-effects models: $^{*}p < .05$, $^{**}p < .01$. Linear mixed-effects model results are given in Tables S3 and S4. Results are based on 16 sites (eight urban, eight rural) each visited seven times. One location was visited only six times ($n = 110$). We recorded a total of 3,404 hoverflies (2,710 migratory, 673 non-migratory and 21 unidentified individuals). [Colour figure can be viewed at wileyonlinelibrary.com]

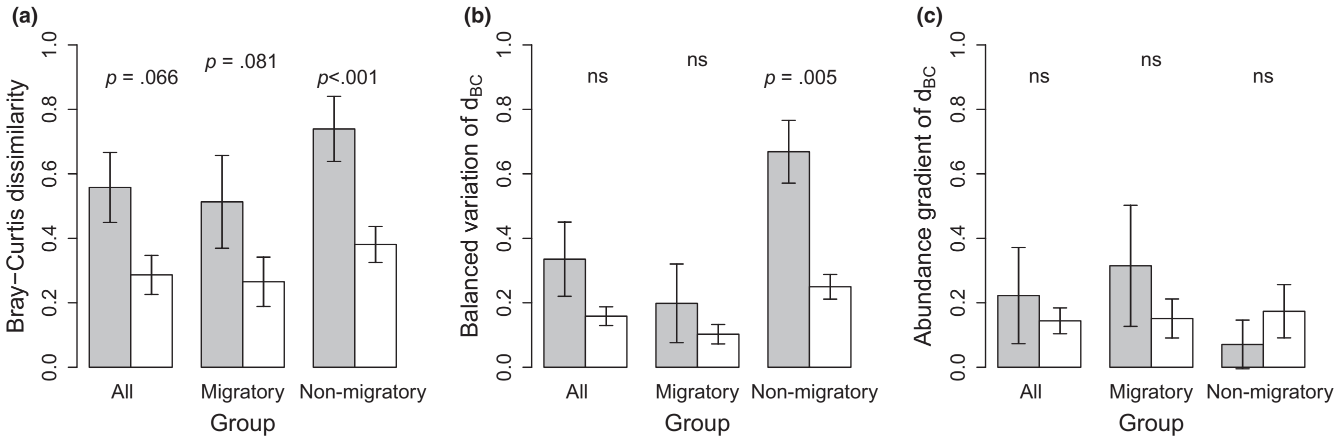

FIGURE 3 Mean (±*SE*) of observed (grey) and randomized (white) Bray–Curtis dissimilarities (d_{BC}) (a) between urban and rural pairs within each region, and the components of d_{BC}, the balanced variation (b) and the abundance gradient (c). *p*-Values were calculated using a permutation procedure and represent the probability of the observed dissimilarities being larger than those of the randomized communities. Results are based on 16 sites (eight urban, eight rural) each visited seven times. One location was visited only six times ($n = 110$). We recorded a total of 3,404 hoverflies (2,710 migratory, 673 non-migratory and 21 unidentified individuals)

communities of non-migratory hoverfly species. This is in contrast to the migratory species, which showed no difference in community composition between land use types. Furthermore, we recorded differences in the phenology of hoverflies between urban and rural ecosystems, with an earlier start in urban compared to rural sites for migratory species and a broader curve for both migratory and non-migratory species, indicating a relatively longer season.

The lack of a significant difference in overall species richness is in agreement with previous studies comparing arthropod communities between urban and rural landscapes (Baldock et al., 2015; Jones

TABLE 1 Linear mixed-effects models of abundance of migratory and non-migratory hoverflies across the season (represented here by Julian Date). Coefficients are presented along with standard errors in parentheses. Models are based on eight paired urban and rural sites, sampled monthly from March to September in the same year. Terms that are significantly different from rural landscapes (*p* < .05), based on likelihood-ratio tests (chi-square, χ^2), are highlighted in bold

	Landscape	Equation
All species		
Equation 1	Rural	y^2 ~ −1.015 (0.493) + −0.098 (0.012) Day + −0.0004 (0.0001) Day^2
Equation 2	Urban	y^2 ~ **0.364 (0.493) + −0.004 (0.012) Day + −0.0001 (0.0001) Day^2**
Migratory species		
Equation 3	Rural	y^2 ~ −1.201 (0.690) + 0.120 (0.017) Day + −0.0004 (0.0001) Day^2
Equation 4	Urban	y^2 ~ **0.930 (0.690) + 0.036 (0.017) Day + −0.0001 (0.0001) Day^2**
Non-migratory species		
Equation 5	Rural	y^2 ~ −0.832 (0.362) + 0.075 (0.008) Day + −0.0003 (0.0000) Day^2
Equation 6	Urban	y^2 ~ −0.204 (0.362) + **0.048 (0.008) Day + −0.0002 (0.0000) Day^2**

The variable "day" was standardized such that the first sampling day of the study is treated as day 0. Abundance was square-root transformed for all groups.

& Leather, 2012; Knop, 2016; Magura et al., 2010; Turrini & Knop, 2015). In contrast, these results are in disagreement with the studies of Bates et al. (2011) and Verboven, Uyttenbroeck, Brys, and Hermy (2014) who reported a significant difference and a trend for a difference in hoverfly species richness between urban and rural landscapes. However, these two studies sampled only one city, whereas this study and that of Baldock et al. (2015) systematically compared replicate urban and rural landscapes. Both urban and rural landscapes are likely to differ between regions and climates, and community composition can vary between regions, due to local heterogeneity. Therefore, by sampling in different regions, the effect of local heterogeneity can be accounted for and a more representative pattern over the broader landscape scale can be achieved (Baldock et al., 2015).

Several hoverfly species can be abundant in agro-ecosystems (Burgio & Sommaggio, 2007; Jauker, Diekötter, Schwarzbach, & Wolters, 2009). This was observed in our study, with the overall abundance of hoverflies being significantly higher in rural areas compared to cities. This pattern was found to be driven by the migratory species, as there was no significant difference in the abundance of non-migratory species between the two ecosystems. The overall higher abundance of hoverflies in the agricultural landscape might be explained by a seasonally higher availability food resources, in particular flowers. Even though seasonal fluctuation is high, intensive agricultural landscapes can provide abundant nectar and pollen resources (Bates et al., 2011; Rundlöf et al., 2014), along with a high abundance of prey species for zoophagous hoverflies, such as aphids. In comparison, urban landscapes provide relatively low resource abundance, but typically display high small-scale heterogeneity in resources and more constant resource availability throughout the season (Alberti, 2005; Cane, Minckley, Kervin, Roulston, & Neal, 2006; Öckinger, Dannestam, & Smith, 2009). Thus, the reason why the overall higher abundance of hoverflies in rural areas was driven by migratory species might be

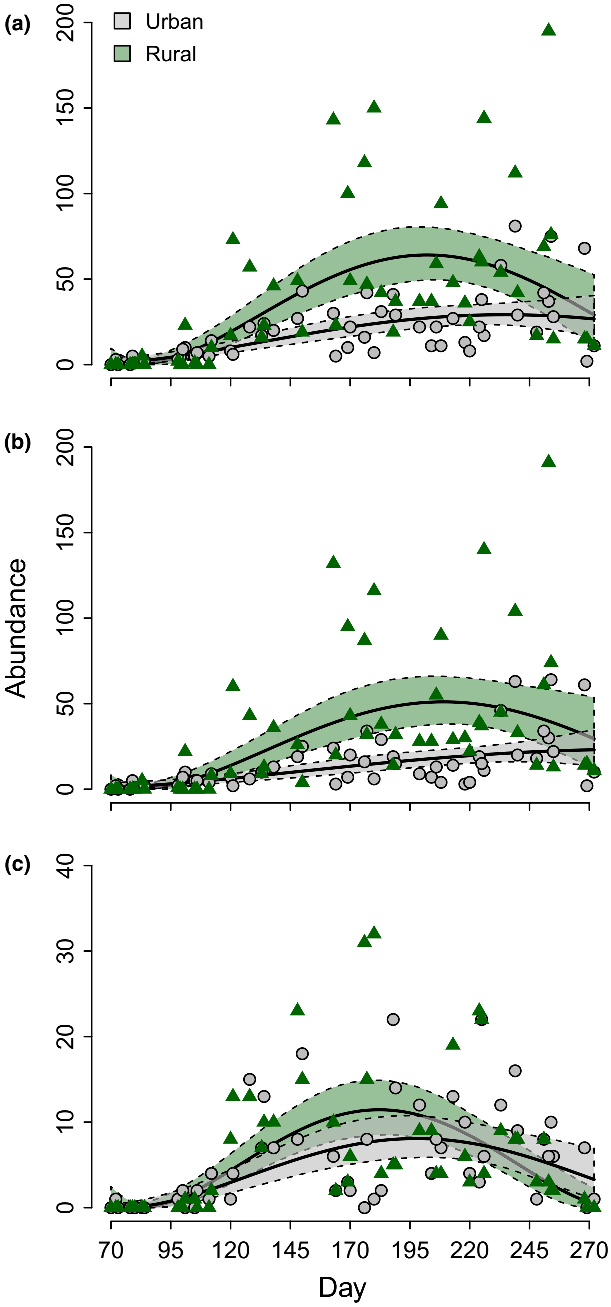

FIGURE 4 Predicted seasonal changes in abundance of the whole hoverfly community (a), migratory (b) and non-migratory species (c) in urban and rural landscapes. Grey circles and green triangles represent observed values in the urban and rural landscapes, respectively. Curves were fitted using linear mixed-effects models. Day of the year is presented as the Julian Date. Solid lines represent the mean and shaded areas represent the 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com]

because they are highly mobile and able to exploit floral and larval food resources distributed over a large area, which is probably often the case in rural systems. Thus, it seems that resource availability may be limiting hoverfly densities, mediated through mobility traits, which may be more limiting than resource access.

We observed no difference in the composition of the overall community, or the migratory species, between the cities and the rural areas. However, community composition of non-migratory species was significantly dissimilar between the two landscapes. This dissimilarity was also driven by a significant balanced variation, indicative of an abundance-based turnover of species between cities and rural areas, a pattern which has observed in other invertebrate groups, such as beetles, bugs and leafhoppers (Knop, 2016). The high mobility of migratory hoverfly species, along with a general tendency towards migrants being relatively generalist with regard to larval life history (e.g., *Eristalis tenax*, *Melanostoma mellinum*), may explain why we observed no differences in overall species composition of the communities between the cities and rural areas. Furthermore, migratory species may recolonize urban landscapes each year. In contrast, the non-migratory community included many species with relatively specialized larval life history strategies (e.g., *Cheilosia* spp., Speight, 2014), which may limit their distribution in the landscape, due to resource availability.

As predicted, we demonstrated an earlier appearance of hoverflies in the cities compared to the rural landscapes. Furthermore, abundance appeared to peak earlier in the season in rural areas, compared to the cities. The earlier appearance of migratory hoverflies in cities might be due to the fact that they offer earlier favourable conditions for them, that is higher temperatures and earlier availability of food resources in cities. Alternatively, some individuals of migratory species, such as *Episyrphus balteatus*, may also overwinter as adults in the summer quarters (Gilbert, 1985; Graham-Taylor, Stubbs, & Brooke, 2009; Hondelmann & Poehling, 2007). Urban areas may provide additional refugia for overwintering (i.e., greenhouses, crevices in walls and buildings), along with availability of some floral resources in the winter months (Hondelmann & Poehling, 2007). Similarly, the delayed decline in abundance in cities may be due to the prolonged resource constancy, with habitats such as managed gardens providing floral resources longer than would naturally occur (Harrison & Winfree, 2015; Jochner & Menzel, 2015; Mimet et al., 2009; Satterfield, Maerz, & Altizer, 2015). A similar pattern was shown by Leong et al. (2016) for bees, with an earlier decline in abundance in natural areas compared to agricultural and urban landscapes. Interestingly, there was also a significant difference between the landscapes in the predicted phenology for non-migratory species. However, in contrast to the migratory species, there was no difference in date of first appearance. Intensive management practices in agricultural areas, such as mowing and harvesting of crops, could explain the decline in the rural populations at the end of the season. Such practices can lead to a significant limitation of resources, particularly for insects that are reliant on standing vegetation and not very mobile. Hoverflies are highly mobile and unlike bees, are not constrained by the requirement to provision their young (Jauker et al., 2009). This may confer some level of resilience to certain species that may be able to move widely in the landscape to exploit new resources as they become available.

We demonstrated a clear difference in the response of migratory and non-migratory hoverfly communities to urbanization. Although the abundance of hoverflies was generally higher in the rural ecosystem, the urban ecosystem harboured a different community of non-migratory species. Alternatively, the community composition of migratory species did not differ between the landscapes. Therefore, to understand differences in species diversity (abundance and richness) between urban and rural areas, it is important to differentiate between different trait and mobility groups. This indicates that not only alien and generalist species reduce dissimilarity between cities and the agro-ecosystem (Deguines et al., 2016; Knop, 2016), but also migratory behaviour. Furthermore, there was a significant difference in the seasonal abundance of both migratory and non-migratory species between urban and rural areas. This supports the growing evidence that urbanization not only affects the phenology of vegetation (Jochner & Menzel, 2015; Mimet et al., 2009), but also affects the higher trophic levels, such as pollinators (Harrison, Gibbs, & Winfree, 2018; Leong et al., 2016; Stelzer et al., 2010).

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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