**High pollinator population connectivity in heavily disturbed landscapes: substantial gene flow despite large urbanized areas in two hoverflies**

Julian Wittische 1,2,\*, Ximo Mengual 3, Alain Frantz 1,2

1: Musée National d’Histoire Naturelle, 25, rue Muenster, L-2160, Luxembourg, Luxembourg

2: Fondation Faune-Flore, 24, rue Muenster, L-2160, Luxembourg, Luxembourg

3: Zoologisches Forschungsmuseum Alexander Koenig, Leibniz‐Institut zur Analyse des Biodiversitätswandels, Adenauerallee127, D‐53113 Bonn, Germany

\*: Corresponding author (julian.wittische@mnhn.lu)

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**ABSTRACT**

Hoverflies (Syrphidae) are essential pollinators and their severe decline jeopardizes their enormous contribution to plant diversity and agricultural production. However, we know little about the dispersal abilities of hoverflies in urbanized landscapes, limiting our understanding of the spatiotemporal dynamics of plant–pollinator systems, and reducing our ability to preserve biodiversity in the context of global changes. Previous work has failed to address how urbanization affects the functional connectivity of hoverflies, and whether dispersal is a limiting factor in their population dynamics. In this study, we investigate the spatial genetic structure and spatial variation in genetic diversity of two species of hoverflies in two urban areas. Using specimens collected by hand-netting from two urbanized study areas of 490 km2 (Cologne, Germany) and 460 km2 (southwest Luxembourg) in 2021, we identified 11 and 24 microsatellite SNP loci for *Syritta pipiens* (831 and 1226 individuals) and *Myathropa florea* (559 and 394 individuals), respectively. Using STRUCTURE, DAPC and IBD analyses, we found evidence for high genetic connectivity for both species, suggesting similar effective dispersal at scales larger than metropoles, despite urbanization. Although anthropogenic land cover changes generally have dramatic consequences on biodiversity, some hoverfly species retain high connectivity, which suggests that colonization is not a limiting factor in their metapopulational dynamics.

**KEYWORDS**

Landscape genetics; Spatial ecology; Diptera; Urbanization; Machine learning

# INTRODUCTION

**Pollinators provide a key ecosystem service to agricultural crops and wild plants, and their importance for food security is widely acknowledged (Potts et al., 2015).** It has been estimated that, globally, the economic value of pollination is worth a total of €153 billion (Gallai et al., 2009). Crop production is often limited by a lack of pollinators (Reilly et al., 2020). The vast majority of European crops and of temperate wildflowers benefit from insect pollination by, in particular, bees (Anthophila) and hoverflies (Syrphidae) (Potts et al., 2015). Besides being essential to the maintenance of plant diversity, pollinators also provide enormous added-value by indirectly supporting an immense range of other organisms, from microbes and parasites, to specialist predators, herbivores, fruit- and seed-eating animals, among others (Ollerton, 2017). The maintenance of pollinator abundance and diversity is therefore of critical importance for both ecosystems and agricultural services. However, evidence of the loss of pollinators is clear-cut: wild pollinators are declining at local, regional and global scales, in both diversity and abundance. Numerous species are threatened with extinction, primarily as consequence of human activities (Gill et al., 2016; Ollerton, 2017; Potts et al., 2016). This is a serious cause for concern because pollinators are an integral part of ecosystems and their precipitous decline presents a crisis for food security and human wellbeing.

**Multiple interacting causes are responsible for pollinator declines.** The main underlying drivers are the intensification of land-use, climate change, and the spread of invasive species and parasites/pathogens (Dicks et al., 2021; Gill et al., 2016; Vanbergen et al., 2013). Especially land-use change and the resulting habitat loss and homogenization are often seen as major individual factors causing the problem (Vanbergen et al., 2013). The spread of urban areas and the intensification of agriculture have resulted in the destruction and fragmentation of many of the natural habitats that pollinators depend on for feeding and nesting resources (Potts et al., 2010; Vanbergen et al., 2013). While it appears that the rapid man-made landscape alterations of recent decades were associated with declines in the species richness of insect pollinators (Senapathi et al., 2015), there is a considerable lack of knowledge on the mechanisms underlying the responses of invertebrate pollinators to land-use change (Winfree et al., 2011). This makes it difficult to reliable quantify the interactive effects with other drivers of decline and to develop effective approaches to conserve pollinator populations and the associated ecosystem services (Gill et al., 2016).

**Dispersal capability is a key life-history trait affecting an organism’s ability to deal with habitat fragmentation.** It is required to maintain connectivity between distant habitat patches, to colonize new habitats and to allow re-colonization after local extinction. It thus impacts species distribution, community structure, (meta-)population dynamics, gene flow and extinction risk (Bowler and Benton, 2005). Species with high dispersal ability generally are better able to move efficiently between suitable habitat patches and may exploit fragmented resources more efficiently (Öckinger et al., 2010). Beyond a species’ intrinsic dispersal ability, however, dispersal between remnant habitat patches will be influenced by the functional connectivity of the landscape, which refers to how the behavior of an organism is affected by the distance between patches and the composition of the intervening habitat matrix (Baguette and Van Dyck, 2007; Jauker et al., 2009).

**We only have a limited understanding of the dispersal ability of most insect pollinators and about their functional connectivity in fragmented habitats (Dicks et al., 2013; Vanbergen et al., 2013)**. Specifically, further insights are needed into distances moved in different landscapes as well as the features and environmental factors that hinder or facilitate movement through the habitat matrix (Dicks et al., 2013; Gill et al., 2016; Vanbergen et al., 2013). A particular difficulty with evaluating the impact of land-use change relates to the fact that flying ability differs significantly between different insect pollinator species (Greenleaf et al. 2007). Even closely related species can respond differently to habitat fragmentation (Jauker et al., 2009; Steffan-Dewenter et al., 2002). Further studies on the impact of fragmentation on different pollinator groups/species in contrasting landscapes are thus needed. These would be of key importance for answering questions relative to the landscape structure and composition necessary to support insect pollinators, as well as the geographic scale at which maintenance measures should be implemented.

**One important group of plant pollinators are hoverflies (Syrphidae), a biologically diverse family of flower-visiting flies (Bickel et al., 2009; Speight, 2017; Wardhaugh, 2015).** Adults feed on nectar to gain energy and adult females on pollen to gain nutrients for egg production (van Rijn and Wäckers, 2016; Wäckers and van Rijn, 2012). Species do not display strict selectivity for specific flower species (Branquart and Hemptinne, 2000; Lucas et al., 2018). However, preferences do exist (Cowgill et al., 1993), and these preferences have an effect on hoverfly fitness (Amorós-Jiménez et al., 2014; Laubertie et al., 2012; van Rijn and Wäckers, 2016). Their dependence on floral resources makes hoverflies the most important pollinators besides bees, providing a major contribution to plant diversity and agricultural production (Hodgkiss et al., 2018; Jauker et al., 2009; Pekas et al., 2020; Rader et al., 2016; Ssymank et al., 2008). Hoverfly larvae use a diverse array of habitats and feeding modes, including fungal fruiting bodies, nests of social Hymenoptera, decaying wood, dung and different water bodies. Many larvae also feed on aphids and are very effective biocontrol agents, especially in agricultural landscapes (Speight, 2017). Given the ecological and economic importance of hoverflies, it would thus be important to gain a more thorough understanding of their movement ecology in fragmented landscapes.

**Little is known about dispersal of hoverflies in general and the effects of landscape fragmentation on their dispersal in particular.** In Europe, some 30 species migrate southwards in the autumn, some covering long distances and crossing mountain ranges in the process (Aubert and Goeldlin de Tiefenau, 1981; Gatter and Schmid, 1990; Lack and Lack, 1951; Odermatt et al., 2017; Wotton et al., 2019) likely using the sun as a compass (Massy et al., 2021). The majority of hoverfly species, however, are non-migratory (Keil et al., 2008; Schweiger et al., 2007; Speight, 2017) and not much is known about their intrinsic dispersal ability. Schweiger et al. (2007) assumed that hoverflies with large body sizes had high dispersal abilities. In a mark-recapture study on the aspen hoverfly (Hammerschmidtia ferruginea, Fallén 1817), Rotheray et al. (2014) found wing length to be positively correlated with dispersal, but only in males. There is also little knowledge about dispersal distances. While Rotheray et al. (2014) recovered some H. ferruginea individuals at up to 5 km from the release site, during their normal foraging activity, hoverflies move a few hundred meters at most and tall vegetation, bare soil (dirt tracks, asphalt roads or ploughed fields) can act as barriers (Lövei et al., 1998; Wratten et al., 2003). Studies investigating hoverfly richness in relation to habitat patch isolation suggest that hoverflies are significantly impacted by habitat fragmentation (Jauker et al., 2019; Moquet et al., 2018; Ouin et al., 2006).

**Molecular genetic methods are powerful tools to investigate the effect of fragmentation on target species where dispersal capability cannot be studied directly, or only with great difficulty.** In particular, investigating the spatial organization of genetic variation can help to clarify the degree of isolation of different habitat patches and identify landscape elements that hinder or facilitate gene flow (Holderegger and Wagner, 2006; Manel et al., 2003; Manel and Holderegger, 2013; Peterman, 2018). Frequently, abrupt genetic discontinuities are linked with elements in the landscape that may disrupt dispersal in a species of interest. For example, motorways and large water bodies can act as gene flow barriers for different vertebrate (Frantz et al., 2012, 2010) and insect species (Pérez-Espona et al., 2012; Vandergast et al., 2009). However, methods that detect abrupt genetic discontinuities can provide only limited information on how animals move through a landscape. By statistically relating the genetic distance, or relatedness, to landscape characteristics, it is possible to relate gene-flow patterns to landscape structure and develop rigorous empirical models of the functional connectivity of a landscape (Peterman, 2018).

**There are only very few studies that use genetic methods to investigate the effect of habitat fragmentation on dispersal of insect pollinators, particularly at the landscape scale.** Studies on hoverflies either looked at large spatial scales and/or did not statistically evaluate the effect of environmental features on dispersal (Raymond et al., 2013; Schauer et al., 2018). Nevertheless, the results from work on Apiformes suggest that even good dispersers can be impacted by habitat fragmentation. Bumblebee (Bombus) species normally exhibit very little genetic structure at smaller spatial scales (Dreier et al., 2014; Lozier et al., 2011), and sometimes even at very large scales . However, impervious cover associated with built-up areas significantly limited gene flow in a North American bumblebee (Jha and Kremen, 2013). Even at larger spatial scales, urban areas can be a substantial gene flow barrier for rare pollinators (Davis et al., 2010).

**Because of demographic growth, land use change for new infrastructure and urban development is expected to be considerable.** This, in turn, will lead to further loss and fragmentation of natural and semi-natural habitats (Jaeger & Madrinan 2011). Luxembourg has recognised that habitat loss and fragmentation are threatening its biodiversity in general and insect pollinators in particular. Key strategies to counteract the negative effects of habitat fragmentation include the design of a network of ecological corridors as well as land set-a-side to support pollinators within the agricultural landscape (Ministère du Développement durable et des Infrastructures 2017). In order for these mitigating measures to be successful, however, it is important to understand the functional connectivity of the landscape from the viewpoint of the pollinator (Dreier et al., 2014; Rands, 2014).

**In this study, we investigate the genetic structure of two species of hoverflies as well as how landscape features affect their genetic connectivity in urbanized landscapes.** First, we describe the genetic clustering and patterns of isolation-by-distance (IBD) of *S. pipiens* and *M. florea*, based onthousands of individuals in two Western Europe urban centers. We expect some genetic structure and IBD at the landscape scale due to the large extent and the anthropogenic nature of the study areas. If connectivity is enabled by unexpectedly large population sizes or unforeseen facilitation of dispersal by anthropogenic features, both genetic structure and IBD are expected to be weak. Second, we identify which landscape features are key in determining connectivity in each species, in each focal urban area, based on a machine-learning optimization algorithm, given the large gaps in expert knowledge regarding dipteran pollinator connectivity. We predict that parts of the landscape with large impervious surfaces would constitute a stronger barrier for *S. pipiens*, due to its much smaller size and XXXdispersal capacity. Similarly, we predict that although it could promote connectivity in both species, higher forest cover could facilitate gene flow in *M. florea* more than in *S. pipiens* due to higher habitat preference. Finally, to understand how general the relationships between gene flow and structural connectivity are across hoverfly species and parts of their ranges, we evaluated model transferability between species (same study area) and between study areas (same species). We predict lower model transferability between study areas, relative to between species, due to the generalist nature of the two species but the homogenization of biodiversity due to disturbances associated with urbanization and peri-urban intensive agriculture could enhance overall model transferability.

# METHODS

## | Study areas, study organisms, and sampling

To ensure successful We chose two hoverfly species likely to occur across the whole study areas based on preliminary field experience and previous inventories. Syritta pipiens (Linnaeus, 1758) is a widespread

Occurrence: Widespread and abundant. MNHNL: 14th most common species; the species has been trapped in different suburban areas of Cologne; Flight time NL/B: April to October, with peaks in abundance in June to September. Identification: Unmistakable, greatly enlarged hind femora, thorax dusted ash-grey. Wing length: 4.25-7 mm; Preferred habitat: wetland, most farmland, suburban gardens and urban parks. Larvae: live in moist, decaying, vegetable matter, including cow dung and garden compost heaps.

## | Laboratory procedures

## | Genetic diversity

We conducted all analyses in this manuscript in R (R Core Team, 2022) using RStudio (RStudio Team, 2022) except for the STRUCTURE analysis.

We conducted basic analyses of our genetic datasets using the *adegenet* v. 2.1.7 (Jombart, 2008; Jombart and Ahmed, 2011) ,the *hierfstat* v.0.5.11 (Goudet, 2005), the *pegas* v. 1.1 (Paradis, 2010), the *PopGenReport* v. 3.0.7 (Adamack and Gruber, 2014) and the *poppr* v. 2.9.3 (Kamvar et al., 2014) R packages. We evaluated allelic richness, heterozygote deficiency, overall fixation indices with bootstrap confidence interval, fixations indices per locus, and the pairwise genetic distance between our study areas. To explore linkage disequilibrium in our dataset, we also calculated standardized indices of association over all loci with a one-sided permutation test, as well as pairwise indices among all loci (Agapow and Burt, 2001; Kamvar et al., 2014). We also evaluated whether null alleles were likely using two resampling-based tests (Brookfield, 1996; Chakraborty et al., 1994). Prior to running genetic structure analyses, we decided to remove only loci which presented both linkage disequilibrium and extreme heterozygote deficiency, as well as a frequency of null alleles at a locus significantly different from zero. Therefore, we remove one locus from the *S. pipiens* dataset (Spp141).

## | Clustering and isolation-by-distance

We used two different approaches to estimate the most likely number of distinct genetic clusters (K). First, we considered a Bayesian model-based approach and used STRUCTURE v. 2.3.4 (Pritchard et al., 2000), and chose the admixture model and correlated allele frequencies. An important parameter to set it α, the Dirichlet prior parameter for the degree of admixture (Hubisz et al., 2009) which conceptually represents the number of ancestral populations from which each individual’s alleles originate. We allowed unequal representation of source populations in the sample (alternative ancestry prior) and set starting values of α it to 1/K because this parametrization led to lower average assignment errors in a simulation study (Wang, 2017). We conducted ten independent runs with 200 000 Markov Chain Monte Carlo burn-in iterations followed by 1 000 000 iterations for one to five clusters. We ruled out higher numbers of cluster based on preliminary analyses. To determine the most likely number of clusters, we directly compared log-likelihoods for all K values across the ten runs, and we used the ΔK statistic which is based on the rate of change in the log probability of data given K (Evanno et al., 2005). We also surveyed the variation in STRUCTURE outputs and matched clusters across runs to avoid issues with label change and multimodality. DISPLAY AVERAGE OR BEST RUN?

Secondly, we considered a model-free approach which is less reliant on assumptions and used discriminant analysis of principal components (DAPC; Jombart et al., 2010, 2009). We considered both a grouping prior based on study areas (2 study areas = 2 potential clusters) and *de novo* grouping because several studies have highlighted that those two alternatives may produce different clustering outcomes (Glück et al., 2022; Miller et al., 2020). When no grouping is input (*de novo*), DAPC uses sequential k-means to find potential clusters prior to the estimation of the best number of genetic clusters. We followed the up-to-date recommendations from the development team regarding the appropriate steps to conduct DAPC (Jombart and Collins, 2022). When using the *de* novo method, we first conducted a principal components analysis which transforms the genotype data to a new coordinate system and generates linear combinations of genetic information. Each of those combinations, also called components or eigenvectors, aligns with the direction of maximum variance in the rotated data while being orthogonal to the previous component. Using all the principal components, we then ran k-means with 1000000 iterations and used Bayesian Information Criterion (BIC) to evaluate the performance of K values from 1 to 20. Similar to the moment interpretation of likelihood values for STRUCTURE, we chose the K represented by a BIC presenting an elbow in the curve of BIC values as a function of k. Regardless of the method we used to describe potential clusters, we chose the best number of components to retain for the DAPC based on both cross-validation and *a*-score optimization. This is a necessary step because the first few components represent most of the genetic variation, we want to find a balance to preserve discrimination power while avoiding overfitting. We also conducted 1000 *de novo* runs with different seeds and 1000000 k-means iterations to evaluate whether they converged on the same number of clusters, and when they converged whether they produced similar clusters. We systematically used all discriminant functions for the assignment of individuals into clusters and used cross-validation to evaluate the general performance of the DAPC and compared it with a random classifier.

To explore whether isolation-by-distance (IBD) is responsible for genetic differentiation in our study landscapes, we first evaluated the linear relationship between the natural logarithms of geographic distance and Loiselle’s kinship values (Loiselle et al., 1995) which measure the genetic relatedness between pairs of individuals. The usual increasing pattern of IBD is, of course, expected to be decreasing one given that kinship is a similarity metric rather than a distance/dissimilarity metric. We chose this genetic distance because it is considered a less biased estimator with low sampling variance (Vekemans and Hardy, 2004). We also computed Mantel’s permutation test for similarity of our two distance matrices (1-Loiselle’s kinship and geographic distance). Finally, to understand the scale at which genetic structure is shaped by dispersal we created a Mantel correlogram using Sturge’s rule to define distance classes and used a Monte Carlo procedure to test whether correlation values are significant.

Because IBD was so low for both species – slopes were not significantly different from 0 within study areas – we could not investigate isolation-by-resistance and the landscape genetics of those two species as was originally planned (Peterman, comm. pers 2022).

# RESULTS

## | Genotyping and filtering

## | Genetic diversity

High Fis, low Fst. Allelic richness increase with sample size. Slight differentiation between study areas.

## | Clustering and isolation-by-distance

K=2 but very messy, so really K=1?

No IBD within study areas.

# DISCUSSION

## | High large-scale population connectivity

Our study showed that two species of hoverflies present high genetic connectivity across tens of kilometers of urbanized landscapes bearing natural and artificial barriers.

Other studies.  
  
The high effective dispersal ability of *M. florea* suggested in our study suggests that this species can live in and move through disturbed habitats in Europe. *M. florea* has been introduced on the west coast of North America pre-2005, likely through the timber trade, and have already spread (BugGuide, 2022; GBIF.org, 2022; Miranda et al., 2013). Hoverflies have been introduced in other parts of the world, notably in a biodiversity hotspot (Hawai) and they could potentially outcompete native species due to their generalism (REF) and high mobility, as suggested by our study and others (REF). The lack of knowledge about those introductions and their potential consequences on biodiversity is dire and further highlight why it is crucial to understand hoverfly dispersal and their community dynamics.

## | Implications for hoverfly biodiversity and pollination services

Although we did not find Constraints on gene flow within urbanized landscapes, they are likely to exist in other systems.

Reminder of threats and how dispersal and connectivity could be used to help understand and mitigate declines.

Highlighting that, given proper habitats, hoverfly could quickly colonize the landscape and that habitat quality and quantity are likely more limiting that isolation between habitat patches. Wildflower strips distributed homogenously in an agricultural or urban landscapes could support some hoverfly species and would foster their pollinator services and their large contribution to aphid control. For some species, urban centers could act as a refuge when the surrounding landscape is unfavorable due to heavy pesticide use or lack of floral resources. Some cities may carry … (car net papers, Cologne hoverfly inventory paper).

## | Methodological limits and future directions

Although STRUCTURE may perform better than DAPC in some scenarios because DAPC may be sensitive to IBD, DAPC performs well for scenarios with low IBD (Blair et al., 2012) which was the case in our study.

We have started investigating this this with other non-honey pollinators, a bee fly and a wild bee. Microsatellite vs. SNPs for genetic structure/IBD/IBR. Mention IBE.

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# SUPPLEMENTARY MATERIAL