**High population connectivity across large urbanized landscapes for two pollinators**

**ABSTRACT**

**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). 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.

Pollinator declines are frequently attributed to multiple interacting causes, with the intensification of land-use, climate change, the spread of invasive species and parasites/pathogens usually considered as the main underlying drivers (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).

Until now, we only have a limited understanding of the dispersal ability of most insect pollinators and about the functional connectivity of 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 utilise 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, covering long distances and crossing mountain ranges in the process (Gatter & Schmid 1990). The majority of hoverfly species, however, are non-migratory (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 (Ouin et al. 2006, Moquet et al. 2018).

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 (Guillot et al. 2005; Peterman 2018). Frequently, abrupt genetic discontinuities are linked with elements in the landscape that may disrupt dispersal in a species of interest. For example, during my research I have shown that motorways and large water bodies can act as gene flow barriers for different vertebrate species (Frantz et al. 2010b, Frantz et al. 2012). However, methods that detect abrupt genetic discontinuities can provide only limited information on how animals move through a landscape. By statistically relating the distribution of genetic similarities among individuals 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). Recently, I have applied this genetics-based resistance modelling to show that urban foxes in Berlin used railways and motorways as main dispersal corridors within the cityscape, while avoiding densely built-up areas. Based on these results, it was possible to model landscape resistance to fox dispersal (Kimmig et al. 2020). I have also applied resistance modelling to assess the effects of landscape features on large ungulates in Belgium and Germany (Renner et al. 2015, Dellicour et al. 2019). Finally, by comparing the characteristics of spatial genetic structure it is possible to infer difference in dispersal patterns of populations or sexes, as I have shown for badgers in the UK and Switzerland (Frantz et al. 2010a).

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 little genetic structure at smaller spatial scales (10s of km; Lozier et al. 2011, Dreier et al. 2014). Jha & Kremen (2013) nevertheless showed that impervious cover associated with built-up areas significantly limited gene flow in a North American Bombus species. Even though working at a larger spatial scale, Davis et al. (2010) similarly showed that urban areas were a substantial gene flow barrier for a rare solitary bee.

As a consequence 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).

**METHODS**

**RESULTS**

**DISCUSSION**

**REFERENCES**

Amorós-Jiménez, R., Pineda, A., Fereres, A., Marcos-García, M.Á., 2014. Feeding preferences of the aphidophagous hoverfly Sphaerophoria rueppellii affect the performance of its offspring. BioControl 59, 427–435. https://doi.org/10.1007/s10526-014-9577-8

Baguette, M., Van Dyck, H., 2007. Landscape connectivity and animal behavior: Functional grain as a key determinant for dispersal. Landsc. Ecol. 22, 1117–1129. https://doi.org/10.1007/s10980-007-9108-4

Bickel, D., Pape, T., Meier, R. (Eds.), 2009. Diptera Diversity: Status, Challenges and Tools. Brill.

Bowler, D.E., Benton, T.G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol. Rev. 80, 205–225. https://doi.org/10.1017/S1464793104006645

Branquart, E., Hemptinne, J.-L., 2000. Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). Ecography 23, 732–742. https://doi.org/10.1111/j.1600-0587.2000.tb00316.x

Cowgill, S.E., Sotherton, N.W., Wratten, S.D., 1993. The selective use of floral resources by the hoverfly Episyrphus balteatus (Diptera: Syrphidae) on farmland. Ann. Appl. Biol. 122, 223–231. https://doi.org/10.1111/j.1744-7348.1993.tb04029.x

Dicks, L.V., Abrahams, A., Atkinson, J., Biesmeijer, J., Bourn, N., Brown, C., Brown, M.J.F., Carvell, C., Connolly, C., Cresswell, J.E., Croft, P., Darvill, B., De Zylva, P., Effingham, P., Fountain, M., Goggin, A., Harding, D., Harding, T., Hartfield, C., Heard, M.S., Heathcote, R., Heaver, D., Holland, J., Howe, M., Hughes, B., Huxley, T., Kunin, W.E., Little, J., Mason, C., Memmott, J., Osborne, J., Pankhurst, T., Paxton, R.J., Pocock, M.J.O., Potts, S.G., Power, E.F., Raine, N.E., Ranelagh, E., Roberts, S., Saunders, R., Smith, K., Smith, R.M., Sutton, P., Tilley, L.A.N., Tinsley, A., Tonhasca, A., Vanbergen, A.J., Webster, S., Wilson, A., Sutherland, W.J., 2013. Identifying key knowledge needs for evidence-based conservation of wild insect pollinators: a collaborative cross-sectoral exercise. Insect Conserv. Divers. 6, 435–446. https://doi.org/10.1111/j.1752-4598.2012.00221.x

Gallai, N., Salles, J.-M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol. Econ. 68, 810–821. https://doi.org/10.1016/j.ecolecon.2008.06.014

Gill, R.J., Baldock, K.C.R., Brown, M.J.F., Cresswell, J.E., Dicks, L.V., Fountain, M.T., Garratt, M.P.D., Gough, L.A., Heard, M.S., Holland, J.M., Ollerton, J., Stone, G.N., Tang, C.Q., Vanbergen, A.J., Vogler, A.P., Woodward, G., Arce, A.N., Boatman, N.D., Brand-Hardy, R., Breeze, T.D., Green, M., Hartfield, C.M., O’Connor, R.S., Osborne, J.L., Phillips, J., Sutton, P.B., Potts, S.G., 2016. Chapter Four - Protecting an Ecosystem Service: Approaches to Understanding and Mitigating Threats to Wild Insect Pollinators, in: Woodward, G., Bohan, D.A. (Eds.), Advances in Ecological Research, Ecosystem Services: From Biodiversity to Society, Part 2. Academic Press, pp. 135–206. https://doi.org/10.1016/bs.aecr.2015.10.007

Hodgkiss, D., Brown, M.J.F., Fountain, M.T., 2018. Syrphine hoverflies are effective pollinators of commercial strawberry. J. Pollinat. Ecol. 22, 55–66. https://doi.org/10.26786/1920-7603(2018)five

Jauker, F., Diekötter, T., Schwarzbach, F., Wolters, V., 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landsc. Ecol. 24, 547–555. https://doi.org/10.1007/s10980-009-9331-2

Laubertie, E.A., Wratten, S.D., Hemptinne, J.-L., 2012. The contribution of potential beneficial insectary plant species to adult hoverfly (Diptera: Syrphidae) fitness. Biol. Control 61, 1–6. https://doi.org/10.1016/j.biocontrol.2011.12.010

Lucas, A., Bodger, O., Brosi, B.J., Ford, C.R., Forman, D.W., Greig, C., Hegarty, M., Jones, L., Neyland, P.J., de Vere, N., 2018. Floral resource partitioning by individuals within generalised hoverfly pollination networks revealed by DNA metabarcoding. Sci. Rep. 8, 5133. https://doi.org/10.1038/s41598-018-23103-0

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S., Bommarco, R., 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol. Lett. 13, 969–979. https://doi.org/10.1111/j.1461-0248.2010.01487.x

Ollerton, J., 2017. Pollinator Diversity: Distribution, Ecological Function, and Conservation. Annu. Rev. Ecol. Evol. Syst. 48, 353–376. https://doi.org/10.1146/annurev-ecolsys-110316-022919

Pekas, A., De Craecker, I., Boonen, S., Wäckers, F.L., Moerkens, R., 2020. One stone; two birds: concurrent pest control and pollination services provided by aphidophagous hoverflies. Biol. Control 149, 104328. https://doi.org/10.1016/j.biocontrol.2020.104328

Potts, S., K., B., Bommarco, R., Breeze, T., Carvalheiro, L., Franzén, M., González-Varo, J.P., A., H., Kleijn, D., Klein, A., Kunin, Lecocq, T., Lundin, O., Michez, D., Neumann, P., A., N., Penev, L., Rasmont, P., Ratamäki, O., Schweiger, O., 2015. Status and trends of European pollinators. Key findings of the STEP project. Pensoft Publishers, Sofia, Bulgaria.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. Nature 540, 220–229. https://doi.org/10.1038/nature20588

Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jaggar, S., Jauker, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattemore, D.E., de O. Pereira, N., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. Proc. Natl. Acad. Sci. 113, 146–151. https://doi.org/10.1073/pnas.1517092112

Senapathi, D., Carvalheiro, L.G., Biesmeijer, J.C., Dodson, C.-A., Evans, R.L., McKerchar, M., Morton, R.D., Moss, E.D., Roberts, S.P.M., Kunin, W.E., Potts, S.G., 2015. The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. Proc. R. Soc. B Biol. Sci. 282, 20150294. https://doi.org/10.1098/rspb.2015.0294

Speight, M.C.D., 2017. Species account of European Syrphidae, Syrph the Net, the database of European Syrphidae (Diptera). Syrph the Net publications, Dublin, Ireland.

Ssymank, A., Kearns, C.A., Pape, T., Thompson, F.C., 2008. Pollinating Flies (Diptera): A major contribution to plant diversity and agricultural production. Biodiversity 9, 86–89. https://doi.org/10.1080/14888386.2008.9712892

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T., 2002. Scale-Dependent Effects of Landscape Context on Three Pollinator Guilds. Ecology 83, 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

van Rijn, P.C.J., Wäckers, F.L., 2016. Nectar accessibility determines fitness, flower choice and abundance of hoverflies that provide natural pest control. J. Appl. Ecol. 53, 925–933. https://doi.org/10.1111/1365-2664.12605

Vanbergen, A.J., 1, 2, 3, 4, 2013. Threats to an ecosystem service: pressures on pollinators. Front. Ecol. Environ. 11, 251–259. https://doi.org/10.1890/120126

Wäckers, F.L., van Rijn, P.C.J., 2012. Pick and Mix: Selecting Flowering Plants to Meet the Requirements of Target Biological Control Insects, in: Gurr, G.M., Wratten, S.D., Snyder, W.E., Read, D.M.Y. (Eds.), Biodiversity and Insect Pests. Wiley, pp. 139–165. https://doi.org/10.1002/9781118231838.ch9

Wardhaugh, C.W., 2015. How many species of arthropods visit flowers? Arthropod-Plant Interact. 9, 547–565. https://doi.org/10.1007/s11829-015-9398-4

Winfree, R., Bartomeus, I., Cariveau, D.P., 2011. Native Pollinators in Anthropogenic Habitats. Annu. Rev. Ecol. Evol. Syst. 42, 1–22. https://doi.org/10.1146/annurev-ecolsys-102710-145042