Conservation of hoverflies (Diptera, Syrphidae) requires complementary resources at the landscape and local scales

LAURA MOQUET, ESTELLE LAURENT,* ROSSANA BACCHETTA[†] and
ANNE-LAURE JACQUEMART   Research Group Genetics, Reproduction, Populations, Earth and
Life Institute – Université catholique de Louvain, Louvain-la-Neuve, Belgium

Abstract. 1. Accumulating evidence shows that landscape fragmentation drives the observed worldwide decline in populations of pollinators, particularly in species of Lepidoptera and Hymenoptera. However, Little is known about the effects of landscape fragmentation on hoverfly (Diptera, Syrphidae) communities. Hoverflies provide varied ecosystem services: larvae contribute to waste decomposition (saprophagous species) and pest control (aphidophagous species), and adults pollinate a wide range of flowers.

2. To determine how the diversity and quantity of resources for larvae and adults affect hoverfly abundance and species richness at three spatial scales, we recorded insect visitors of five target plant species in Belgian heathlands, habitats that have decreased considerably due to human activities.

3. Hoverflies represented the most abundant visitors on two plant species, and the second most abundant visitors (after bumblebees) on the other target plant species. A large proportion of hoverflies observed were aphidophagous species associated with coniferous and deciduous forests. Resources for the larvae and floral resources for the adults influenced interactions among hoverflies and plants, but acted at different scales: larval habitat availability (distance to larval habitat) was relevant at the landscape scale, whereas adult resource availability (floral density) was relevant at the plot scale.

4. Hoverfly abundance and species richness decreased with distance to larval habitat but increased with floral density. Moreover, landscape structure and composition had different effects according to hoverfly ecological traits. Landscape composition influenced aphidophagous but not saprophagous hoverflies, in that their abundance and species richness decreased with distance to forests. Maintenance of the interactions between plants and their hoverfly visitors requires complementary resources at both landscape and local scales.

Key words. Aphidophagous, ericaceous species, forest, heathlands, pollinators.

Correspondence: Laura Moquet, Research Group Genetics, Reproduction, Populations, Earth and Life Institute – Université catholique de Louvain, Croix du Sud 2, Box L7.05.14, B-1348, Louvain-la-Neuve, Belgium. E-mail: laura.moquet@uclouvain.be

*Present address: Research group Quantitative Conservation Biology, Earth and Life Institute – Universite catholique de Louvain, Louvain-la-Neuve, Belgium

†Present address: Centre Wallon de Recherches Agronomiques, Rue du Bordia 4, 5030, Gembloux, Belgium

Introduction

As an ecosystem service, pollination was estimated to be worth €153 billion in 2005 (Gallai *et al.*, 2009). Bees (Hymenoptera), hoverflies and other anthophilous flies (Diptera), butterflies (Lepidoptera) and beetles (Coleoptera) are the main pollinators in temperate regions (Kevan & Baker, 1983; Vanbergen & The Insect Pollinators Initiative, 2013; Rader *et al.*, 2016). Many studies have shown

that the abundance and species richness of pollinators has decreased over the past 50 years, and that the ecological homogenisation of bee and butterfly communities has increased (Biesmeijer *et al.*, 2006; Carvalheiro *et al.*, 2013). These studies have highlighted land-use changes that destroy, fragment and degrade habitats as one of the main causes of this decline in pollinators (Goulson *et al.*, 2005; Stokstad, 2006; Potts *et al.*, 2010). Although many studies have examined the effects of fragmentation on bees and butterflies (Cane, 2001; Maes & Van Dyck, 2001; Van Dyck *et al.*, 2009; Winfree *et al.*, 2009; Hadley & Betts, 2011), few studies have examined the effects on hoverfly communities, and these studies have produced limited, often contradictory, results (Biesmeijer *et al.*, 2006; Keil *et al.*, 2011; Carvalheiro *et al.*, 2013).

Adult hoverflies (Diptera, Syrphidae) depend on floral resources, that is, pollen and nectar. Pollen is consumed mainly by females to provide nutrients (proteins, sterols) for egg production, and nectar is mainly consumed by males and females to provide energy (sugars) for flight while searching for partners (Haslett, 1989; Woodcock *et al.*, 2014). Hoverflies are pollinators or co-pollinators of many plant species (Larson *et al.*, 2001; Inouye *et al.*, 2015). Although there appears to be little specialisation at the species level, individuals can be highly flower constant over short time scales (Branquart & Hemptinne, 2000). Their degree of specialisation is linked to distinct morphological traits. For example, large-body species with a short proboscis are limited to flowers that produce unconcealed nectar, such as several species of the Rosaceae or Apiaceae family. By contrast, ubiquitous hoverfly species generally have a small body with a long proboscis (Gilbert, 1981, 1986; Branquart & Hemptinne, 2000).

Hoverfly larvae have extremely diverse diets. Some species are saprophagous, feeding on decaying plant or animal matter and thereby helping to decompose waste. Other species are insectivorous (aphids, thrips, etc.) and provide biological pest control, especially in agricultural landscapes. A number of these species are migrants that exploit local fluctuations in aphid abundance (Stubbs & Falk, 1983). Some species are phytophagous or mycophagous (Ball & Morris, 2015; Speight *et al.*, 2015). Their diets, therefore, restrict each species to specific microhabitats (identifiable structural features used by hoverfly larvae such as plant debris, foliage or cow dung) during larval development. Their restricted microhabitats allow hoverflies to be used as biological indicators to evaluate the state of conservation of a specific ecosystem (Sommaggio, 1999; Speight *et al.*, 2000; Burgio & Sommaggio, 2007).

Ecological and morphological traits of hoverflies could influence their responses to landscape composition and resource availability. For example, several studies have shown that fragmentation affects species differently depending on their level of specialisation and ability to disperse (Schweiger *et al.*, 2007). Nevertheless, community analyses supported by ecological and morphological data

are infrequent in animal ecology, mainly due to a lack of information at the community level. The *Syrph the Net* database (Speight *et al.*, 2015), which contains data on the ecological traits of hoverfly species, has facilitated community-level analyses for hoverflies. To analyse the responses of hoverfly communities to environmental conditions, studies group species with similar ecological traits (Branquart & Hemptinne, 2000; Ouin *et al.*, 2006; Schweiger *et al.*, 2007). Most studies separate hoverfly groups by ecological traits such as larval diet, larval microhabitat or adult body size (Dziock, 2006; Schweiger *et al.*, 2007; Keil *et al.*, 2008), or a combination of larval and adult traits (Ouin *et al.*, 2006).

Because hoverflies require different resources at the larval and adult stages, the persistence of hoverfly communities requires a set of varied resources. For example, larvae of *Scaeva selenitica* grow under closed-canopy conditions, whereas adults need open biotopes rich in floral resources (Gittings *et al.*, 2006). Thus, the composition of the landscape matrix matters at the landscape scale (Kleijn & Van Langevelde, 2006; Meyer *et al.*, 2009; Öckinger *et al.*, 2012). Furthermore, dispersal capability influences the spatial scale at which individuals perceive their environment. Species of hoverflies vary in their dispersal capability from a few metres to 2 km per day (Schönrogge *et al.*, 2006; Schweiger *et al.*, 2007). In general, hoverflies are affected by the landscape matrix in a radius of 500–1000 m (Kleijn & Van Langevelde, 2006; Meyer *et al.*, 2009).

In addition to landscape scale resources, the resources available at smaller scales also affect the spatial distribution of adult hoverflies. At the patch scale (habitat fragments), the probability of finding suitable microhabitats and floral resources increases with patch size. Thus, the abundance and species richness of hoverflies are predicted to be higher in large patches than in small patches (Sarthou *et al.*, 2005; Ouin *et al.*, 2006; Herrault *et al.*, 2016). At the local scale, optimal foraging theory suggests that hoverflies should preferentially visit plots with high floral density because such plots provide a high quantity of resources at a low foraging cost (Meyer *et al.*, 2009).

The literature provides increasing information about the effects of landscape changes on hoverfly populations and hoverfly–plant interactions in forests (Gittings *et al.*, 2006; Ouin *et al.*, 2006; Meyer *et al.*, 2009) and agricultural landscapes, but these studies have mainly focused on aphidophagous species (Sutherland *et al.*, 2001; Haenke *et al.*, 2014; Raymond *et al.*, 2015). Semi-natural open habitats such as heathlands remain poorly studied, although they constitute habitats for many hoverfly species (77 species according to Speight *et al.*, 2015; and see also Stubbs & Falk, 1983; Jacquemart, 1993; Mahy *et al.*, 1998; Meyer *et al.*, 2009; Descamps *et al.*, 2015). Heathlands were extensively destroyed and fragmented in Europe during the last two centuries (Gimingham, 1972; Webb, 1998) and have been largely converted into agricultural or afforested areas (e.g. spruce plantations in

Belgium, Clicheroux, 1957). Compared to forests and wetlands, heathlands do not offer many microhabitats for larvae (Speight & Castella, 2015), but they do offer floral resources for adult hoverflies during the entire flight period (Moquet *et al.*, 2017b). The main floral resources in heathlands are ericaceous species, which provide pollen and nectar. Ericaceous species have poricidal anthers (which require vibrations to release pollen) and are therefore considered bee pollinated because their pollen is not easily accessible; nevertheless, these species are visited by hoverflies. Moreover, the presence of *Salix* spp. in wet heathlands in early spring provides floral resources for early emerging species (Moquet *et al.*, 2015).

Here, we analysed the effects of the landscape at different spatial scales on hoverfly–plant interactions in Belgian heathlands. We examined the following aspects of these interactions:

1 We hypothesised that the dominant hoverfly species observed on ericaceous flowers are species associated with heathlands, according to the Syrph the Net database (Speight & Castella, 2015).

2 Larval and adult requirements differ substantially among hoverfly species. We supposed that resources for adults and larvae vary across different spatial scales and influence communities of hoverfly visitors. For adults, crucial resources include floral density at the local plot scale, floral cover at the habitat patch scale and availability of floral-rich habitats at the landscape scale. For larvae, crucial resources include availability of larval microhabitats at both patch and landscape scales.

3 Hoverflies have diverse ecological and morphological traits. We hypothesised that each ecological hoverfly group is influenced differently by landscape composition and resource availability.

Methods

Studied heathland patches

The study was carried out in 10 heathland patches in the Plateau des Tailles, Upper Ardenne, Belgium (50°10′N; 5°43′E). Eight patches were an assemblage of wet and dry heathlands and the two others, Fange aux Mochettes and Grand Passage, were ombrotrophic mires (raised bogs that receive all water from direct precipitation). Heathland patch elevation ranged from 550 to 630 m and heathland patch size ranged from 0.3 to 40.7 ha (Table 1).

The landscape matrix consisted mainly of forests: spruce plantations of *Picea abies* (48%) and deciduous forests (8%) of beech (*Fagus sylvatica*) or oaks (*Quercus robur* and *Q. petraea*). These closed habitats were interspersed with open habitats such as pastures and hay meadows (31%) and wetlands and heathlands (8%).

Urbanisation and population density were very low (<50 inhabitants per km^2, Grimmeau *et al.*, 2013).

Target plant species

Over three successive years (2013–2015), we observed the visitors to the four most abundant ericaceous species, *Vaccinium myrtillus* L., *V. vitis-idaea* L., *Erica tetralix* L. and *Calluna vulgaris* (L.) Hull. These ericaceous species are dwarf evergreen shrubs (except *V. myrtillus*, which is deciduous). Floral morphology differs among species: *E. tetralix* and *V. myrtillus* have a deep and urceolate corolla (5–7 mm), *V. vitis-idaea* has a campanulate corolla and *C. vulgaris* has an open corolla (Ritchie, 1955, 1956; Gimingham, 1960; Bannister, 1966). Flowers are tetra- or pentameric and secrete nectar at the base of the style. Except for *C. vulgaris*, pollen grains are contained in poricidal anthers only accessible to species able to generate vibrations (some bee species, Buchmann, 1983). In addition, in 2014, we observed visitors to *Salix* x *multinervis* Döll, the main floral resource in early spring in the studied heathlands (Moquet *et al.*, 2015). We observed *Salix* x *multinervis* in April, *V. myrtillus* between April and June, *V. vitis-idaea* between May and July, *E. tetralix* between July and August and *C. vulgaris* in August.

Hoverfly observations

Insect visitors were surveyed between 9:00 am and 6:20 pm during one to four full days per heathland patch (depending on the weather conditions), per target plant species, and per year. For each target plant species, we performed observations in at least six of the 10 heathland patches using a standardised method (Mayer *et al.*, 2012; Descamps *et al.*, 2015; Moquet *et al.*, 2015). Observations took place when the weather conditions were appropriate (i.e. sunny days and wind speed <5 on the Beaufort scale), by one observer, in a plot of 10 m^2 of ericaceous target plant species during 20 min. We conducted a total of 1190 sessions (396 h) over the 3 years. For *S. x multinervis*, observations were performed on a section of one grove with approximately 500 catkins of male individuals. When plant populations were sufficiently large, the position of the plot was changed each day of observation. Insects were considered visitors when they collected floral resources (pollen or nectar). The observer collected all insects visiting target plant species with an insect net. Hoverflies were identified in the field, to the species level when no confusion was possible (*Episyrphus balteatus* De Geer, *Myathropa florea* L., *Rhingia campestris* Meigen, *Scaeva pyrastri* L., *S. selenitica* Meigen, *Sericomyia silentis* Harris, *S. lappona* L., *Syritta pipiens* L., *Volucella bombylans* L.) or to morphotype, grouping morphologically similar species for the following genera: *Chelosia*, *Chrysotoxum*, *Eristalis*, *Eupeodes*, *Helophilus*, *Platycheirus*, *Sphaerophoria*, *Syrphus*. Insects were released on the plot immediately

Table 1. Characteristics of the studied heathland patches located in the Upper Ardenne, Belgium.

Heathland patches	Coordinates		Localities	Heathland area (ha)	Patch perimeter (m)	Altitude (m)	Spruce plantation cover	Deciduous forest cover	Meadow cover	Wetland cover	Number of macrohabitats (100 m)	Distance to spruce plantations (m)	Distance to deciduous forests (m)	Distance to meadows (m)
Grande fange	50°14′40″N	5°46′45″E	Vielsalm	0.3	308	560	8.2	35.6	5.9	50.3	15	195 ± 130	15 ± 20	400 ± 60
Wé des pourceaux	50°14′42″N	5°44′57	Vielsalm	1.1	447	630	57.9	2.5	24.5	1.5	4	35 ± 5	240 ± 20	250 ± 10
Pisserotte	50°13′13″N	5°47′54″E	Gouvy	1.6	698	594	42.3	36.5	7.3	10.7	7	85 ± 60	20 ± 15	235 ± 55
Crépale	50°16′40″N	5°44′07″E	Lierneux	7.6	1800	557	79.6	0.0	0.3	20.1	7	30 ± 15	585 ± 0	390 ± 20
Fange aux mochettes	50°13′21″N	5°40′55″E	La Roche-en-Ardenne	9.6	1225	602	9.8	35.6	8.0	45.8	15	195 ± 85	15 ± 30	150 ± 30
Grand Passage	50°13′44″N	5°45′46″E	Houffalize	10.9	1800	611	3.9	5.1	7.6	79.6	13	445 ± 140	230 ± 150	300 ± 150
Pouhon	50°14′32″N	5°41′51″E	Manhay	18.6	1937	580	23.2	9.0	0.0	64.1	8	180 ± 20	215 ± 20	590 ± 10
Robiefa	50°15′27″N	5°42′10″E	Manhay	25.4	2216	565	32.9	25.4	6.2	31.8	13	180 ± 35	55 ± 20	180 ± 45
Nazieufa	50°15′05″N	5°43′09″E	Manhay	35.9	2605	625	20.4	0.0	0.0	53.6	8	5 ± 0	480 ± 0	1000 ± 0
Sacrawé	50°14′33″N	5°45′46″E	Vielsalm	40.7	3678	600	35.6	15.9	0.0	44.9	9	70 ± 50 m	55 ± 50	360 ± 50

Heathland patch area is the surface dominated by ericaceous species. Percentage of each type of land cover was analysed in 2013 within a radius of 500 m from the centre of heathland patches. Number of macrohabitats is the habitat diversity according to Speight and Castella (2015). The minimal distances between the studied plot of 10 m² of heathland and other types of land cover are indicated (mean ± SD). Heathland patches are arranged by increasing heathland patch size.

after the 20-min session, except several individuals per morphotype (a total of 215 individuals) that were killed to determine the precise species diversity within each morphotype. Then, precise identification in the laboratory was conducted, using identification keys (Verlinden, 1994; Van Veen, 2004) and the reference collection of the Royal Belgian Institute of Natural Sciences. Abundance was calculated as the number of individuals and species richness was estimated as the number of morphotypes observed during 1 day (10 sessions of 20 min, Table 2).

Hoverfly ecological traits

We used the *Syrph the Net* database (a list of 926 European species including ecological traits, geographical repartition, and preferred environment, Speight *et al.*, 2015) to establish a list of expected hoverfly species. We applied three selection filters: (i) Belgian species (321 species); (ii) species visiting shrub flowers for pollen or nectar (148 species); and (iii) species living in recorded macrohabitats (94 species). Macrohabitat categories were equivalent to categories used in the CORINE *habitat* classification system, and supplementary macrohabitats were small habitat features that occurred in association with macrohabitats (e.g. a temporary pool in open ground, Appendix S1). We divided the total species observed and precisely identified into three categories: *predicted and observed*, *predicted but missing* and *non-predicted but observed*.

Each ecological group (clustering species with the same ecological traits) has a species richness and abundance determined by different factors (Schweiger *et al.*, 2007; Keil *et al.*, 2008). This suggests that an ecological group approach provides a better base for conservation research than a global community approach. Hoverfly species were ranked according to six ecological traits: (i) larval microhabitat (aquatic or terrestrial); (ii) larval diet (aphidophagous, bumblebee larval predator, mycophagous, phytophagous or saprophagous); (iii) migratory status (not migratory, occasionally migratory or strongly migratory); (iv) preferred environment (coniferous and deciduous forests, grasslands and heathlands, urbanised areas, wet forests such as *Betula* swamps or fen carr or wetlands); (v) body size of the adults; (vi) length of proboscis (Gilbert, 1985; Ssymank, 1991; Speight *et al.*, 2015). Continuous variables were categorised: species with mean proboscis length <3 mm were considered as *small proboscis* species, from 3 to 5 mm as *medium proboscis* species and more than 5 mm as *long proboscis* species. In the same way, three body size categories were created: *small species* when mean body size was <6 mm, *medium species* between 7 and 10 mm and *large species* when mean body size was more than 10 mm.

Spatial characteristics

Immediately before performing hoverfly observations, the floral density of the target plant species was estimated

Table 2. Abundance and species richness by observation day (10 × 20 min, mean ± SD) according to heathland patches and plant species.

	Abundance					Species richness				
	S. x multinervis	V. myrtillus	V. vitis-idaea	E. tetralix	C. vulgaris	S. x multinervis	V. myrtillus	V. vitis-idaea	E. tetralix	C. vulgaris
Grande fange	45.0 ± 11.3 (2)	4.0 ± 0.0 (1)	6.0 ± 5.4 (4)		56.4 ± 32.3 (5)	2.0 ± 0.0 (2)	2.0 ± 0.0 (1)	3.0 ± 1.1 (4)		8.0 ± 2.1 (5)
Wé des pourceaux			12.7 ± 9.2 (4)					5.0 ± 3.6 (4)		
Pisserotte	17.0 ± 2.8 (2)	9.5 ± 0.7 (2)	2.5 ± 2.5 (6)		68.8 ± 35.5 (5)	3.5 ± 3.5 (2)	5.0 ± 1.4 (2)	1.8 ± 1.3 (6)		8.2 ± 3.4 (5)
Crépale				15.5 ± 9.7 (4)					4.2 ± 1.5 (4)	
Fange aux mochettes	72.0 ± 60.8 (2)	2.0 ± 2.5 (5)		10.2 ± 8.5 (7)	54.0 ± 31.4 (4)	1.5 ± 0.7 (2)	1.2 ± 1.3 (5)		4.1 ± 3.5 (7)	8.2 ± 2.3 (4)
Grand passage	32.5 ± 34.6 (2)	0.6 ± 1.1 (3)	1.7 ± 1.7 (4)	6.0 ± 8.1 (7)	39.6 ± 35.3 (3)	2.0 ± 0.0 (2)	0.3 ± 0.5 (3)	1.2 ± 0.9 (4)	2.2 ± 2.2 (7)	5.0 ± 3.4 (3)
Pouhon				14.1 ± 8.3 (6)	55.3 ± 27.0 (3)				3.8 ± 1.1 (6)	8.0 ± 3.6 (3)
Robiefa	4.5 ± 2.3 (4)	1.2 ± 1.7 (5)		8.2 ± 10.5 (9)	82.6 ± 53.0 (3)	1.0 ± 0.0 (4)	0.8 ± 1.3 (5)		2.0 ± 1.6 (9)	10.3 ± 2.0 (3)
Nazieufà			9.5 ± 8.5 (4)					3.2 ± 2.2 (4)		
Sacrawé	44.0 ± 32.6 (3)	1.3 ± 2.3 (6)	1.5 ± 1.5 (8)	2.1 ± 3.2 (7)	64.1 ± 37.9 (7)	3.3 ± 3.2 (3)	1.0 ± 1.5 (6)	0.7 ± 0.7 (8)	1.4 ± 2.1 (7)	6.4 ± 2.9 (7)

Heathland patches are arranged by increasing heathland patch size. *N* values are indicated between brackets.

on the studied plots. This was done by counting the number of open flowers on four randomly selected quadrats of 1 m². For *C. vulgaris*, due to its high flower density, flower numbers were assessed on five quadrats of 0.25 m².

Plot, heathland patch and landscape spatial characteristics were recorded (Table 1) with GPS (GPSMAPS 62; Garmin Olathe, KS, USA) and georeferenced images (cartopro1.wallonie.be) and were mapped with QGIS (version 2.2.0). The following characteristics related to resource diversity for the larval stage were calculated: (i) at the heathland patch scale: the number of macrohabitats and supplementary macrohabitats in the studied heathland patches and 50 m around it was recorded according to Speight *et al.*, 2015 and (ii) at the landscape scale: minimal distances between studied plots of 10 m² of heathland and other types of land cover.

Moreover, parameters related to floral availability for adult hoverflies at different scales were measured: (i) at the plot scale: floral density; (ii) at the heathland patch scale: heathland patch size defined by the surface dominated by ericaceous species; (iii) at the landscape scale: we described the proportion of each type of land cover within 500 m from the centre of the heathland patches. Proportions were adjusted each year according to restoration projects (LIFE10 NAT/BE/000706) and to spruce cuts.

Statistical analyses

Statistical analyses were performed with R (R Development Core Team, 2013). Unless indicated otherwise, data are presented as a mean ± standard deviation.

We tested for correlations between the different spatial characteristics (Table 1) with Spearman's rank tests. The proportion of spruce plantations was negatively correlated with the proportion of wetlands around the studied heathland patches ($P = 0.05$, $r_s = -0.85$) and the number of macrohabitat ($P = 0.04$, $r_s = -0.85$). We therefore chose to analyse three parameters that directly and indirectly affect larvae: number of macrohabitats (heathland patch scale), distance to deciduous forests and distance to spruce plantations (landscape scale), as well as three parameters related to floral availability: floral density (plot scale), heathland patch size (heathland patch scale) and dominant type of land cover (landscape scale).

We used multiple correspondence analysis (*MCA* command, R-package FactoMineR) to describe the relationships between total hoverfly species and the six selected ecological traits. We used hierarchical clustering on principal components (*HCPC* command, R-package FactoMineR) to identify hoverfly main ecological groups. Canonical correspondence analysis (*CCA* command, R-package vegan) was performed to link hoverfly abundance in each ecological group to the environmental spatial characteristics. All species identified in each morphotype were included in MCA, HCPC and CCA.

We used generalised linear mixed models (GLMM, *glmer* command, R-package lme4, Bates *et al.*, 2014)

and information-theoretic approaches to assess to what extent the explanatory variables were related to the abundance and species richness (to morphotype) of hoverfly communities. GLMMs are an excellent tool for analysing non-normal data that involve random effects. GLMMs make it possible to analyse hierarchically structured and unbalanced data sets such as ours and effectively eliminate the statistical problem of pseudoreplication due to statistically non-independent data points (i.e. repeated observations, Bolker *et al.*, 2009; Zuur *et al.*, 2009). We pooled our observations by day (10 × 20 min sessions) resulting in 137 data points. The global model consisted of the six parameters as fixed effects and heathland patches, target plant species and year as random effects. These three factors were included as random effects because their levels were sampled from a larger sample (patches and years) and because we are interested in variation among levels rather than the specific effects of each level (target plant species, Bolker *et al.*, 2009). We used a Poisson distribution, and ranked all possible models according to their Akaike's information criterion corrected for small sample size (AICc) and selected the model with the smallest AICc (*dredge* command, R-package MuMIn). When necessary, factors were rescaled with the *standardised* or *rescale* command of the R-package arm. The significance of each of the fixed effects specified in the model was tested with *Type III Tests of Fixed Effects*.

Results

Abundance and species richness

During the 395 h of observation, we observed a total of 6887 visitors, including 2476 individuals belonging to 49 hoverfly species. Other visitors belonged to the Apidae (*Apis* 3% and *Bombus* 45%, see Moquet *et al.*, 2017a,b), other Diptera families (Bibionidae, Calliphoridae, Conopidae, Empididae, Muscidae, Sarcophagidae, Sepsidae, Tachinidae, 7%), solitary bees (Andrenidae, Halictidae, 4%) and butterflies (Hesperiidae, Noctuidae, Nymphalidae, 2%). Hoverflies represented the most abundant visitors on *S. x multinervis* (67%) and *C. vulgaris* (43%) and the second most abundant visitors on our other target plant species (between 12% and 20%). Visitor species richness varied among target plant species from 11 species on *V. myrtillus* to 32 species on *C. vulgaris* (Appendix S2), and for all studied plant species, hoverflies represented the most diverse family.

Most hoverfly species observed in the heathland patches (56%) had forests (wet, coniferous or deciduous forests) listed as their preferred habitat. Other species preferred wetlands and open habitats like grasslands and heathlands (Table 3). Based on the *Syrph the Net* database, 88 hoverfly species were expected. Missing species were mainly non-migrant forest and wetland species. More species were observed on the target plant species flowering late in

Table 3. Numbers of species predicted according to the database *Syrph the Net*, observed in heathlands on studied target plant species, predicted and observed, predicted but missing, and observed but non-predicted according to the preferred habitats.

Preferred habitat	Predicted	Observed	Predicted and observed	Missing	Not predicted
Urbanised areas	3	5	3	0	2
Coniferous and deciduous forests	42	18	12	30	7
Wet forests	14	10	6	8	4
Wetlands	15	11	7	8	4
Grasslands and heathlands	15	5	5	10	0
Total	88	49	33	55	17

the season (*C. vulgaris*) than in early spring plant species (*S. x multinervis*).

The five target plant species were visited by hoverflies with different ecological traits (Fig. 1). The main visitors to *S. x multinervis* belonged to large and saprophagous species with a long proboscis (*Eristalis pertinax*). The number of wetland and saprophagous individuals decreased from approximately 80% on *V. myrtillus* and *V. vitis-idaea* in the spring to approximately 40% on *E. tetralix* and *C. vulgaris* in the summer. Furthermore, there were more individuals with a long proboscis on *V. myrtillus* (60%) than on other ericaceous species (between 25% and 30%). The number of migrant hoverflies varied between 2% (*S. x multinervis*) and 80% (*V. vitis-idaea*).

The abundance of hoverfly individuals per day varied from 0 to 125 depending on the target plant species. Per day of observations (200 min) on the 10 m^2 plot of the target plant species, the number of hoverflies was higher on *C. vulgaris* (60.8 ± 34.2 individuals) than on *S. x multinervis* (32.2 ± 32.3), *V. myrtillus* (2.2 ± 3.1), *V. vitis-idaea* (4.9 ± 6.2), and *E. tetralix* (8.8 ± 9.0).

Hoverfly groups

Hoverfly species were separated into two groups according to larval diet ($P < 0.001$), larval habitat ($P < 0.001$), proboscis length ($P < 0.001$) and preferred habitats ($P = 0.007$; Fig. 2; Appendix S3). The first group (group 1) was mainly composed of aphidophagous species (93% of individuals, $P < 0.001$), with terrestrial larvae (100%, $P < 0.001$), adults having a short or medium proboscis (100%, $P < 0.001$), and a preference for forests (coniferous and deciduous, 50%, $P = 0.030$) or grasslands and heathlands (17%). This group was mainly represented by the Syrphini tribe (*Chrysotoxum*, *Didea*, *Epistrophe*, *Episyrphus*, *Eupeodes*, *Meliscaeva*, *Leucozona*, *Parasyrphus*, *Scaeva*, *Sphaerophoria*, *Syrphus*). The second group (group 2) was composed of species with saprophagous (95%, $P < 0.001$), aquatic larvae (90%, $P < 0.001$), having a long proboscis (71%, $P < 0.001$) and a preference for wetlands (29%) or wet forests (38%, $P = 0.030$). This group was mainly represented by the Eristalini tribe (*Eristalis*, *Helophilus*, *Myathropa*).

Parameters influencing hoverfly abundance

Model averaging across our set of candidates revealed that distances from the observation plots to spruce plantations and deciduous forests were the two most important factors associated with hoverfly abundance. Abundance significantly decreased with the distance to forests (GLMM, *z*-value = 3.79, $P < 0.001$).

The abundance of *group 1* hoverflies (aphidophagous and terrestrial) was significantly positively influenced by floral density (plot scale, GLMM, *z*-value = −4.46, $P = <0.005$; Table 4; Fig. 4a). Moreover, abundance of hoverflies in this group significantly decreased with distance to spruce plantations (landscape scale, GLMM, *z*-value = −2.59, $P = 0.010$; Fig. 4c) and to deciduous forests (landscape scale, GLMM, *z*-value = 2.06, $P = 0.040$). The CCA plot (Fig. 3) shows the relationships between the abundance of *group 1* hoverflies and the spatial characteristics of the landscape. The eigenvalues of axis 1 (CCA1) and axis 2 (CCA2) were 0.79 and 0.32 respectively. We observed a distinct distribution of species according to spatial characteristics. Hoverflies were ordered in relation to the proportions of forest (spruce plantations and deciduous forest) and distances in the landscape. For example, *Meliscaeva cinctella* and *Platycheirus albimanus* were found in landscapes dominated by forests, at close proximity to the forest edges, but *Parasyrphus lineolus*, *Epistrophe grossulariae* and *Episyrphus balteatus* were mainly observed in landscapes dominated by wetlands, distant from forest edges. No tested factor had a significant effect on the abundance of *group 2* hoverflies (saprophagous and aquatic hoverflies, Fig. 4b, see Appendix S4 for CCA illustrating the relationships between the abundance of *group 2* hoverflies and spatial characteristics).

Parameters influencing hoverfly species richness

The best model to explain differences in hoverfly species richness included the distances between observation plots and spruce plantations and heathland land cover. Species richness significantly decreased with distance to spruce plantations (landscape scale, GLMM, *z*-value = −2.11, $P = 0.035$) and with heathland patch area (heathland
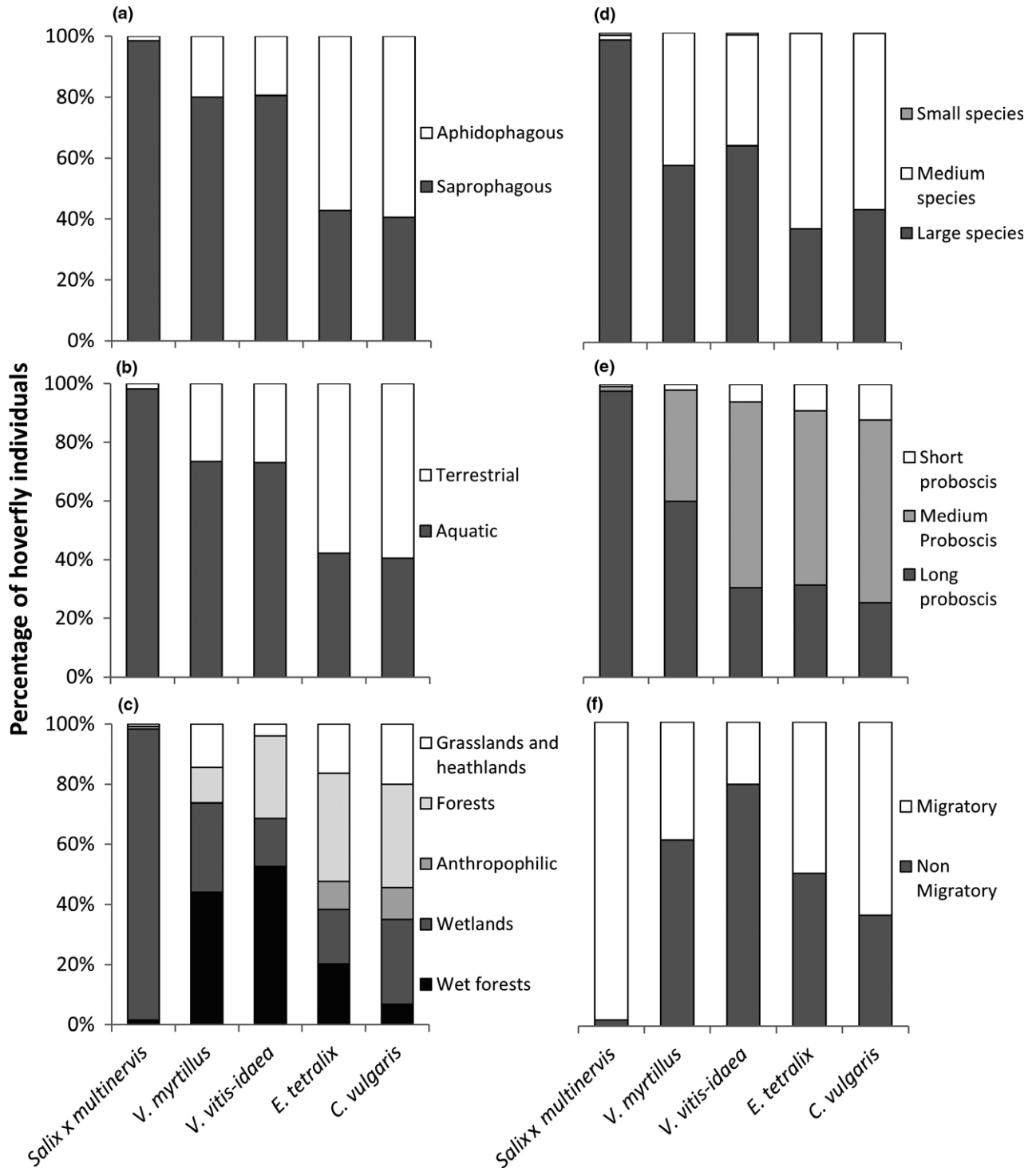
Fig. 1. Ecological traits of hoverfly individuals visiting the five target plant species, ordered according to their flowering period: larval diet (a), larval habitat (b), adult preferred habitat (c), adult size (d), proboscis length (e) and migratory status (f). Small species < 6 mm; 7 mm < medium species < 10 mm; large species > 10 mm. Short proboscis, length < 3 mm; medium proboscis, between 3 and 5 mm; long proboscis, > 5 mm.
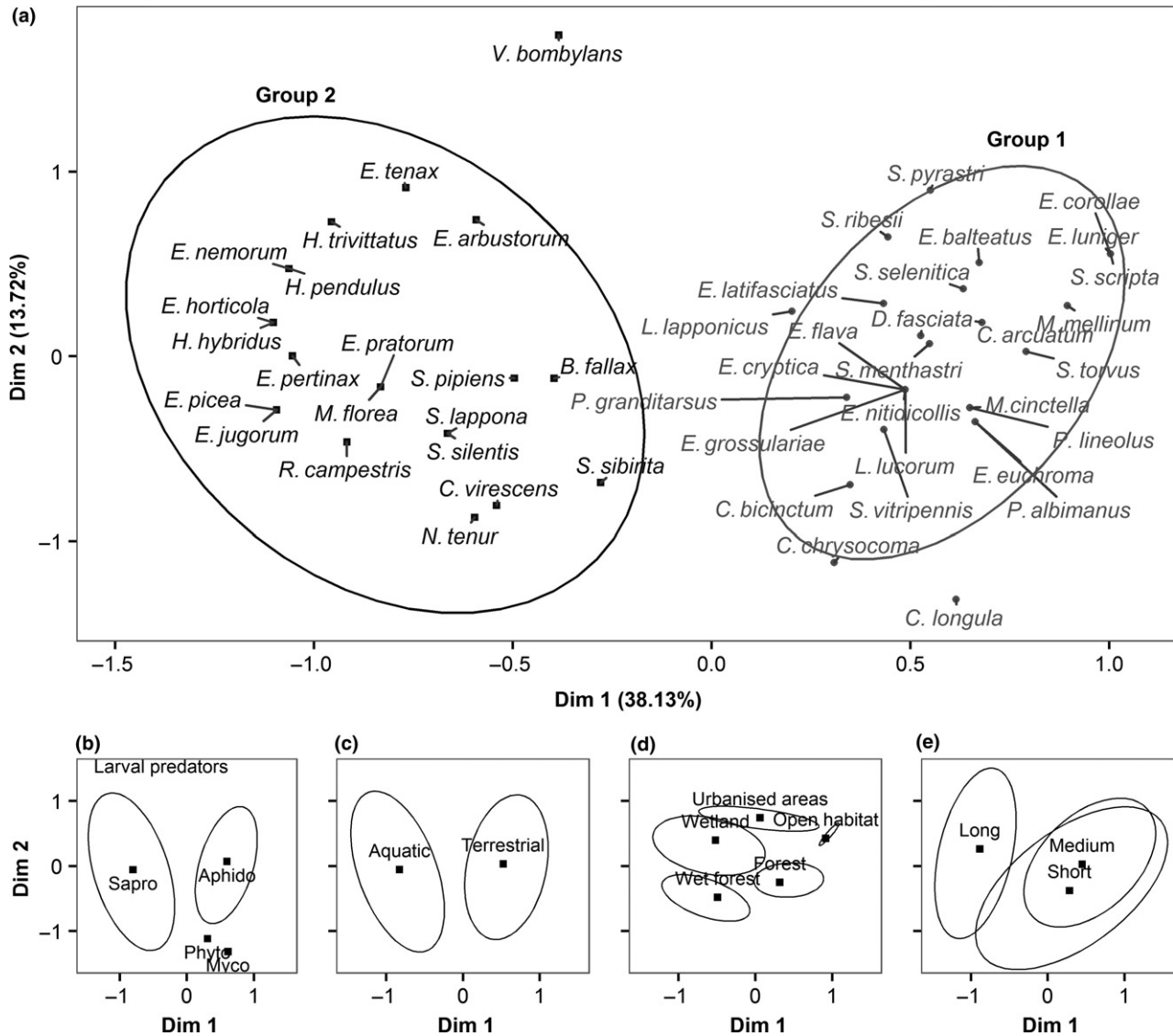
Fig. 2. Multiple correspondence analysis (MCA) plot showing hoverfly species according to the six life-history traits. (a) 95% confidence ellipses around groups of hoverfly species according to hierarchical clustering on principal components. (b–e) 95% confidence ellipses around significant ecological traits: (b) larval diet, (c) larval habitat, (d) preferred habitat, (e) proboscis length. Adult body size and migratory status were not significant factors in MCA (not shown). Aphido = Aphidophagous, Sapro = Saprophagous, Myco = Mycophagous, Phyto = Phytophagous in (b). Open habitats included heathlands and grasslands in (d). Short proboscis, length < 3 mm; medium proboscis, between 3 and 5 mm; long proboscis, > 5 mm.

patch scale, GLMM, z-value = −1,88 P = 0.051). Similarly, the species richness of *group 1* decreased with the distance to spruce plantations (landscape scale, GLMM, z-value = −1.76, P = 0.011; Fig. 5c) and heathland area (heathland patch scale, GLMM, z-value = −1.85, P = 0.015; Fig. 5e.). In contrast, for *group 2*, species richness was significantly negatively influenced by heathland patch area (heathland patch scale, GLMM, z-value = −2.18, P = 0.029; Fig. 5b) and positively influenced by floral density (plot scale, GLMM, z-value = 3.07, P < 0.002; Table 4; Fig. 5f).

Discussion

Hoverfly species associated with forests were major visitors to ericaceous plants

Hoverflies were abundant visitors to flowers in the heathlands and represented more than one third of all recorded visitors. For the 49 hoverfly species recorded in this study, species richness was comparable to that observed in other studies in heathlands (Dupont & Nielsen, 2006; Descamps *et al.*, 2015). For *C. vulgaris* alone,

Table 4. Model selection and results for candidate models explaining hoverfly abundance and species richness for the two functional groups.

Response variables	Models	Intercept	Dominant cover land	Floral density	Distance to deciduous forest	Distance to spruce plantation	Number of macrohabitat	Heathland area	AICc	d.f.	ΔAICc	ω_m
Abundance *group 1*	**Model 1**	**0.09242**		**−0.3987***	**0.7202***	**−0.8454****			**704.7**	7	0	0.2
	Model 2	0.1841		−0.4048	0.6396	−0.6307			706.5	6	1.8	0.081
	Model 3	0.09065		−0.3966	0.746	−0.7663	−0.2325		706.7	8	2.02	0.073
	Model 4	0.09291	−0.2236	−0.3988		−0.89			706.7	8	2.04	0.072
	Model 5	0.07525		−0.3991	0.7238	−0.8547		−0.1351	706.9	8	2.18	0.067
Abundance *group 2*	**Model 1**	**2.048**		**−0.131**	**−0.2169**	**0.1402**			**1444**	6	0	0.087
	Model 2	2.044		−0.1377	−0.2598	0.2005	−0.07182		1445	7	1.14	0.049
	Model 3	2.054	−0.09135	−0.1283	−0.1477			−0.08886	1445	7	1.39	0.043
	Model 4	2.048	−0.04873	−0.128	−0.2157	0.1236			1445	7	1.53	0.04
	Model 5	2.057		−0.1216	−0.1344				1445	5	1.61	0.039
Species richness *group 1*	**Model 1**	**−0.1318**				**−0.3491***		**−0.3466.**	**398.9**	6	0	0.061
	Model 2	−0.1339			0.2374	−0.402		−0.3353	399	7	0.12	0.057
	Model 3	−0.1223					−0.2976	−0.3462	399.2	6	0.34	0.051
	Model 4	−0.07546							399.6	4	0.67	0.044
	Model 5	−0.1092						−0.2885	399.8	5	0.88	0.039
Species richness *group 2*	**Model 1**	**0.4247**		**0.3804****		**−0.3007**		**−0.4239***	**423.6**	7	0	0.111
	Model 2	0.4398		0.3955				−0.3623	424.2	6	0.62	0.081
	Model 3	0.4297		0.3988			−0.2144	−0.3898	424.9	7	1.29	0.058
	Model 4	0.4767		0.3717					424.9	5	1.3	0.058
	Model 5	0.4223		0.3852		−0.2502	−0.1144	−0.4284	425.5	8	1.87	0.044

Group 1 mainly consisted of aphidophagous, terrestrial hoverflies and *group 2* mainly consisted of saprophagous, aquatic hoverflies. Candidate models are ranked in order of increasing corrected Akaike's information criterion (Δ AICc). Explanatory variables were standardised. In bold, the selected model with the degree of factor significance (***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$).

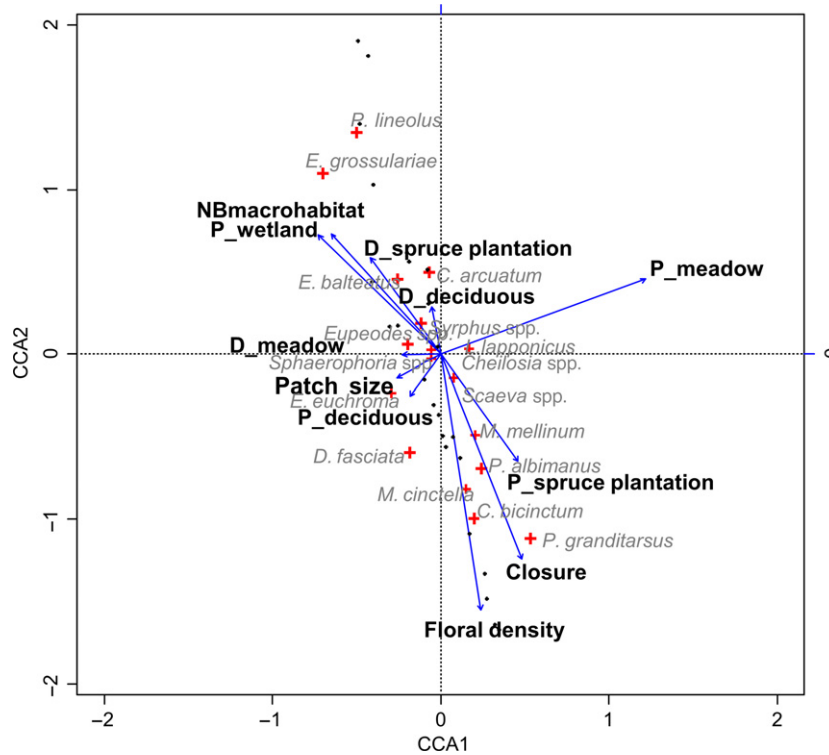**Fig. 3.** Canonical correspondence analysis (CCA) ordination plots of hoverfly abundance (+), site (•) and environmental data (→) for *group 1* hoverfly species. The length and angle of the arrows shows the contribution of a particular environmental variable to the CCA axes. The eigenvalues of axis 1 (CCA1) and axis 2 (CCA2) are 0.79 and 0.32 respectively. *P_land cover* is the percentage of each type of land cover (spruce plantations, deciduous forests, meadows, and wetlands). *D_land cover* is the minimal distance between the studied plot of 10 m² of heathland and other types of land cover. Number of macrohabitats is the habitat diversity according to Speight and Castella (2015). *Closure* is the proportion of the heathland patch edge that consisted of woody elements. *Patch size* is heathland patch area. *Floral density* is mean number of open target flowers per m² (see Appendix S2 for hoverfly species name). [Colour figure can be viewed at wileyonlinelibrary.com]

Descamps *et al*. (2015) observed 25 species at Mont Lozère (Languedoc-Roussillon, France) compared with our 39 species, with 19 species in common. The presence of rare or threatened species such as *Blera fallax* and *Epistrophe flava* on *Vaccinium* species further emphasises the value of heathlands for hoverfly conservation.

Most of the observed hoverfly species were associated with coniferous forests, wet forests and wetlands; only five of the observed species were associated with heathlands. These results are consistent with previous studies indicating that most of the hoverfly species in northwest Europe have larval stages in flower-poor forests and the adults disperse to open habitats, such as heathlands, to acquire floral resources, that is, pollen and nectar (Humphrey *et al*., 1999; Branquart & Hemptinne, 2000; Speight *et al*., 2015). Within forest hoverfly species, the predicted but missing species were non-migratory, suggesting that they have a limited capacity for large-scale dispersal and probably a greater susceptibility to ongoing heathland degradation.

Our results showed that the relevant hoverfly traits for the separation of ecological groups were larval diet, larval habitat and proboscis size. Other studies using similar approaches have also highlighted the importance of these two larval traits (Dziock, 2006; Schweiger *et al*., 2007; Keil *et al*., 2008), which Thompson and Rotheray (1998) considered to be the most significant characteristics of the Syrphidae. Moreover, because we focused on flower visitors mainly on ericaceous species, it is not surprising that proboscis size explains a large amount of the variation in our study. In consequence, hoverfly species on heathlands can be separated into two groups: one composed of species with aphidophagous and terrestrial larvae, adults with a short or medium proboscis and having a preference for forests (coniferous and deciduous) or grasslands and heathlands; and the other composed of species with saprophagous and aquatic larvae, a long proboscis and a preference for wetlands and wet forests.

Species richness and abundance driven by the availability of resources for both larvae and adults

Factors associated with the availability of resources for larvae (distance to larval habitat, macrohabitat diversity)
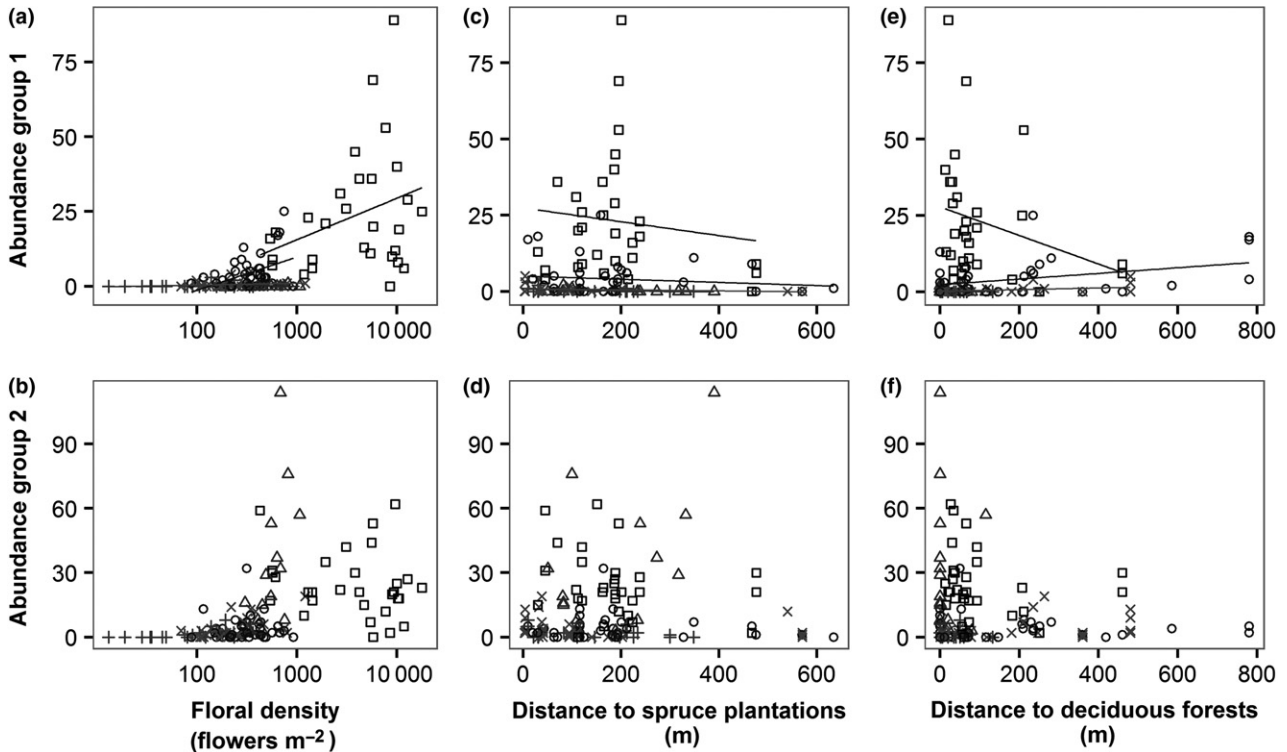
Fig. 4. Abundance of *group 1* (a, c, e) and *group 2* hoverfly individuals (b, d, f) per day of observation (10 sessions × 20 min on 10 m^2) according to floral density (a, b), distances to spruce plantations (c, d) and distances to deciduous forests (e, f). Observations were carried out on *S. x multinervis* (△), *V. vitis-idaea* (✗), *V. myrtillus* (+), *E. tetralix* (○) and *C. vulgaris* (□). *Group 1* mainly consisted of aphidophagous, terrestrial larvae species and *group 2* contained principally saprophagous, aquatic larvae species (see Fig. 2). Lines are linear regression lines for each target plant species (only shown when the factor was significant).

as well as floral resources for adults (floral density) influenced hoverfly abundance and species richness. Studies in agricultural landscapes have also suggested that both adult and larval habitat requirements have to be considered when analysing hoverfly communities (Kleijn & Van Langevelde, 2006; Meyer *et al.*, 2009). Hoverfly abundance and species richness depend on factors related to floral resources for adults, such as the quantity and quality of pollen and nectar, as well as factors associated with larval development, such as microhabitat diversity (Meyer *et al.*, 2009). Different scales were relevant depending on whether factors were related to larval or to adult resources. For example, larval habitat availability influenced hoverfly community composition at the landscape scale (distance to larval habitat), whereas floral resource availability for adults influenced community composition at the plot scale (floral density).

Our study showed that the distance to larval habitat, especially forests, was the main factor related to larval habitats that influenced hoverfly visitor composition. These results are consistent with other studies (Dupont & Nielsen, 2006; Meyer *et al.*, 2009; Bortolotto *et al.*, 2016) in which adult hoverflies were highly influenced by the types of larval macrohabitats, especially forest fragments, in the surrounding landscape. For an insect species to persist in a heathland fragment, larval and adult resources have to be available within the flight distance of the specific insect species. When most flower visitors could fly only a short distance, communities were strongly influenced by the surrounding vegetation (Dupont & Nielsen, 2006).

For factors associated with adult resources, floral density (plot scale) positively influenced the abundance of hoverfly individuals at the plot level, whereas heathland patch area (patch scale) and landscape composition (landscape scale) had no effect. A previous study found the opposite results for bumblebees in the same heathland patches and on the same target plant species, showing that bumblebee abundance was influenced by floral availability at the landscape scale (Moquet *et al.*, 2017a). Differences in the spatial scale affecting Diptera and Hymenoptera imply that their perception of the landscape, foraging ranges and resource requirements differ (Kleijn & Van Langevelde, 2006; Jauker *et al.*, 2009; Öckinger *et al.*, 2012). Hoverflies disperse over very short distances (except during migration events), compared with bumblebees (200 m vs. up to 3000 m, Lövei *et al.*, 1998; Wratten *et al.*, 2003; Westphal *et al.*, 2006). Therefore, only floral resources at a small scale influenced hoverfly abundance. Hoverfly abundance increased with floral density, which is consistent with other studies of hoverflies in agricultural landscapes (Meyer *et al.*, 2009) and even other pollinators such as bumblebees and solitary bees
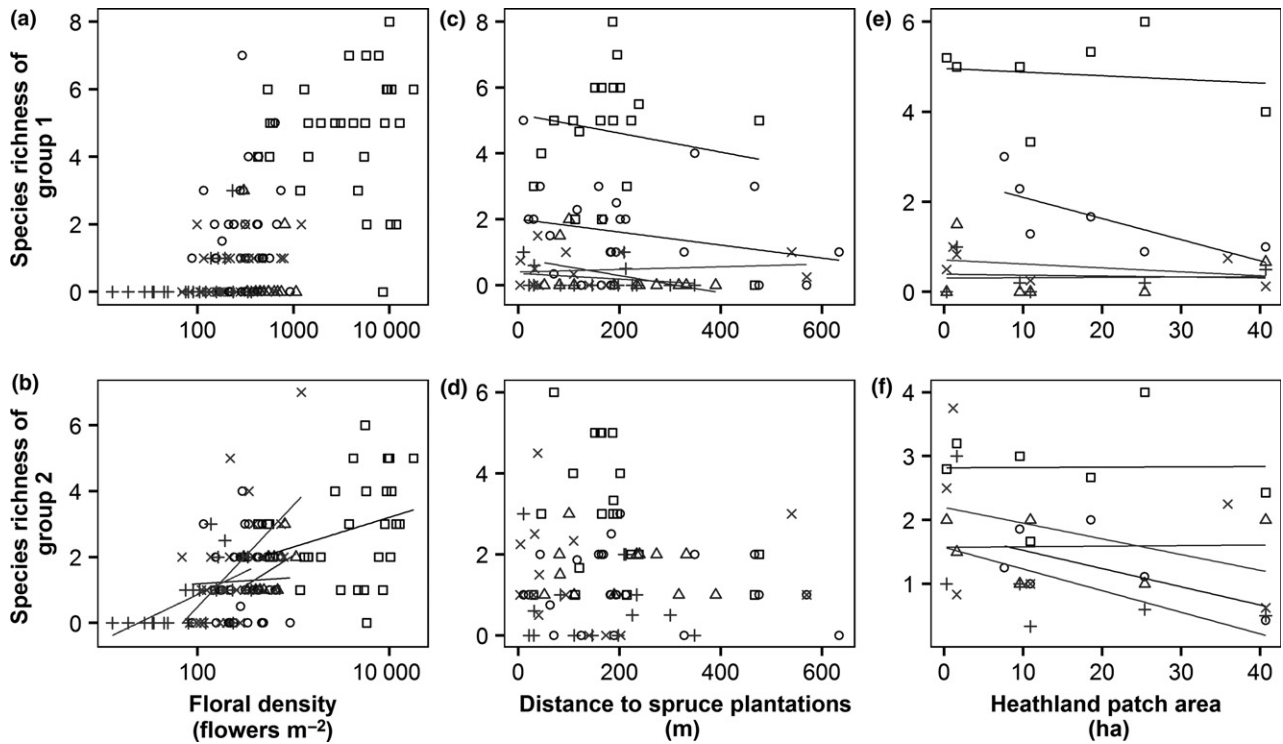
Fig. 5. Species richness of *group 1* (a, c, e) and *group 2* hoverflies (b, d, f) per day of observation (10 sessions × 20 min on 10 m²) according to floral density (a, b), distances to spruce plantations (c, d) and heathland patch area (e, f). Observations were carried out on *S. x multinervis* (△), *V. vitis-idaea* (✕), *V. myrtillus* (+), *E. tetralix* (○) and *C. vulgaris* (□). *Group 1* mainly consisted of aphidophagous, terrestrial hoverfly larvae species. *Group 2* mainly consisted of saprophagous and aquatic hoverfly larvae species (see Fig. 2). Lines are linear regression lines for each target plant species (only shown when the factor was significant).

(Sih & Baltus, 1987; Ohashi & Yahara, 2002; Somme et al., 2014). All these results are consistent with optimal foraging theory, which predicts higher abundance of pollinators in dense patches of flowers (Pyke et al., 1977). Indeed, high floral density provides a greater quantity of resources at lower foraging costs for all anthophilous insects (Hegland & Boeke, 2006).

Contrasting responses according to ecological group

Factors that affected the abundance and species richness of hoverfly visitors of our target plant species differed according to ecological group. Species richness and abundance of saprophagous hoverflies were not affected, in the context of our study, by parameters related to larval wetland macrohabitats, but the abundance and species richness of aphidophagous hoverflies decreased with distance to forests. One other study has shown that landscape context affects differently according to hoverfly ecological traits (Schweiger et al., 2007); in this study, the main traits influencing response to landscape structure were degree of specialisation in habitat or in feeding. Aphidophagous species were probably more affected by landscape structure than saprophagous wetland species, because they need

different resource patches for larval and adult stages. Such species require different landscape elements at different life stages (Dunning et al., 1992) and thus are particularly dependent on landscape heterogeneity (Fahrig & Nuttle, 2005). This sensitivity will depend on the interaction between heterogeneity and dispersal capability. Because we observed no aphidophagous species farther than 500 m from spruce plantations, we suppose that distance limited adult dispersal to heathlands. Some studies have found a low dispersal capability for aphidophagous forest species (Wratten et al., 2003; Herrault et al., 2016). Our results showed that, in this range, adult dispersal varied according to species, as some forest species were mainly found in forest-dominated landscapes at close proximity to forest edges (*M. cinctella* and *P. albimanus*), while others were abundant in wetland-dominated landscapes at larger distances from forest edges (*Parasyrphus lineolus*, *Epistrophe grossulariae* and *Episyrphus balteatus*).

Conclusion

We showed that Belgian heathlands are habitats where diverse hoverfly species, especially species from forests, can feed on flower resources. These resources are rare

under coniferous canopies, but abundant in heathlands. Forest hoverfly species were mainly aphidophagous species, more affected by landscape structure than saprophagous wetland species, probably because they need two different resource patches for larval and adult stages, yet have limited dispersal capability. Landscape complementation (patches for larval development and patches for adult requirements) is therefore needed to preserve the species pool of hoverflies and the ecosystem services they provide.

Acknowledgements

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12245:

Appendix S1. Macrohabitats observed on each studied sites in the Upper Ardenne (Belgium).

Appendix S2. Abundance of hoverfly species observed on the five target plant species during 3 years in 10 heathland patches located in the Upper Ardenne, Belgium.

Appendix S3. Life-history traits of hoverfly species observed on the five target plant species in the Upper Ardenne (Belgium), according to Speight *et al.* (2015), Gilbert (1985) and Ssymank (1991).

Appendix S4. Canonical correspondence analysis (CCA) ordination plots of hoverfly abundance (cross), site (black points) and environmental data (arrows) for *group 2* hoverfly species.

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