

Flower-strip agri-environment schemes provide diverse and valuable summer flower resources for pollinating insects

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Abstract The diversity and abundance of insect pollinators are declining. This decline reduces the potential ecosystem services of pollination for wild and cultivated plants. Specific agri-environment schemes (AES) are subsidised to support and conserve biodiversity in farmlands. In Belgium, the pollinator flower-strips AES, strips of flower-rich hay meadows, has been promoted as a potential scheme to increase pollinator abundance and diversity, even if their effectiveness has not been locally evaluated. The main objective of this research is to assess the capacity of pollinator-strip AES to provide flower-resources to diverse pollinators. During 2 years, we monthly measured the availability of flower resources (pollen and nectar) produced on four flower-strips surrounded by intensive farming in Belgium. We counted and identified insects that visited these flowers, and we constructed the plant–insect interactions networks. The pollinator-strip AES presented a mix of both sown and spontaneous plant species. The ten sown plant species were all present, even after 8 years of strip settings. Three of them, *Centaurea jacea*, *Lotus corniculatus*, and *Daucus carota* were mainly visited for nectar collection, and a spontaneous non-sown species, *Trifolium repens*, had a key role in providing high-quality pollen to insects. Most of the observed flower-visiting insects belonged to common species of Hymenoptera and Diptera. All are considered highly efficient pollinators. The Belgian pollinator flower-strips are effective AES that provide flower resources to pollinators, mainly during summer and support pollination services. Nevertheless, spring and autumn flower resources remain poor and could reduce the strips’ effectiveness for supporting long-term insect diversity.

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Introduction

Pollinator decline and the resulting pollination crisis endanger the sexual reproduction of numerous plant species, wild and cultivated (Allen-Wardell et al. 1998; Cane and Tepedino 2001; Ghazoul 2005; Biesmeijer et al. 2006; Potts et al. 2010). Approximately 78% of temperate plants depend on insects for pollination (Ollerton et al. 2011). Several agricultural practices, mainly linked to agricultural intensification, are considered as the major causes of this crisis. These practices include pesticide use (Godfray et al. 2015; Goulson et al. 2015) and landscape modifications like land consolidation and hedgerows destruction leading to insect habitat and resources loss (Kennedy et al. 2013; Deguines et al. 2014; Goulson et al. 2015). In the European Union, since 1992, incentive measures to environment-friendly farmland management are promoted by the Common Agricultural Policy (CAP). These measures, named agri-environment schemes (AES), are subsidised by the CAP to compensate farmers that implement AES to compensate for landscape homogeneity, excessive intensive farming and by encouraging biodiversity in farmlands (Goulson et al. 2015; Wood et al. 2017). Several regional pollinator initiatives propose specific pollinator-friendly managements. But lot of them are devoted to honeybee and not to the pollinator diversity (Decourtye et al. 2010). In 2005, the Walloon government introduced 11 AES, among which the AES ‘managed-strips’. In 2013, 1275 km of these managed-strips were implemented (Natagriwal 2016). The aim of one of these managed-strip AES, the pollinator flower-strip AES, is to support wild pollinating insects (Le Roi et al. 2010; Natagriwal 2014). The Belgian pollinator flower-strips are within-field strips of flower-rich hay meadows. They are sown with a mix of four native grasses and ten entomophilous wild-flowers, mainly belonging to Asteraceae (e.g. *Leucanthemum vulgare*) and Fabaceae (e.g. *Medicago lupulina*, *Medicago sativa*, *Lotus corniculatus*, and *Trifolium pratense*). Pollinating insects forage on flowers to collect sugars, proteins, and lipids from nectar and pollen (Müller et al. 2006; Michener 2007). Insect development and population growth depend on the quality and diversity of the available flower resources (Pernal and Currie 2001; Tasei and Aupinel 2008; Eckhardt et al. 2014; Vanderplanck et al. 2014). Some insects, especially *Bombus*, can develop flower fidelity based on the resources quality (Leonhardt and Blüthgen 2012; Ruedenauer et al. 2016). Studying this fidelity can help to understand which plants are the best pollen providers. Natural regeneration of plants and spontaneous species settlement are unpredictable but can strongly modify the composition of the sown flower-strips, changing their interest for insects (Carvell et al. 2004; Pywell et al. 2005). Evaluating the biological effectiveness of such flower-strips under local constraints (e.g. landscape, seed bank, insect diversity, farming practices) is essential to assess pertinence and identify improvements to composition and management (Dicks et al. 2013; Batáry et al. 2015). AES optimisation has been identified as a key policy-relevant question (Merckx et al. 2009), but such evaluation has never been performed in old (6 to 8 years old) farmer-implemented pollinator flower-strip AES. Moreover, most of the previous studies on flower-strips focussed on one or few insect groups such as *Bombus* (Carvell et al. 2007; Pywell et al. 2011), other wild bees (Scheper 2015; Wood et al. 2017), butterflies (Haaland and Gyllin 2010; Haaland and Bersier 2010; Pywell et al. 2011) or moths (Merckx et al. 2009) but rarely on the entire guild of flower-visiting insects.

The objective of this paper is to answer the following questions:

- 1) What is the entomophilous plant diversity, the flower resources (pollen and nectar) they provide and the relative importance of sown and spontaneous plant species?
- 2) What are the diversity and abundance of insects foraging on flower-strips?
- 3) What are the plant species visited for their pollen and do insects use pollen sources from outside of the flower-strips?
- 4) Is the flower resources provision by flower-strips adapted to insect phenology?

Materials and methods

Studied sites

Monthly, from April to September, in 2014 and 2015, we studied four eight-year-old pollinator flower-strips located in Condroz, South Belgium (50°22'N, 5°13'E, 250 to 300 m a.s.l., Table 1). The Condroz is characterised by an east–west succession of calcareous sandstone ridges and fertile wind loess soils (Castiau et al. 2011). Meadows (47%), cereal (37%), oilseed rape (5%), sugar beet (4%) and potato (4%) crops dominate the Condroz agricultural landscape (Castiau et al. 2011).

Sites with neighbouring apiaries, orchards, forests, hedges, or villages were omitted to avoid high competition by honeybees, *Apis mellifera* hives or influence from non-agricultural habitats. Honeybees can be very competitive for flower resources, reducing the availability of flower resources for wild bee population in a radius up to one km around the apiary (Pyke and Balzer 1985; Paine 2004; Goulson and Sparrow 2009; Herbertsson et al. 2016). Sites were at least 3 km from apiaries during the flowering period. All the strips were at least 3 km apart to avoid pseudo-replication.

The four studied strips were 12 to 21 m wide, and 560 to 1000 m long (Table 1). They were sown in 2008 with a seed mix (30 kg/ha) of perennial native grasses (85% Poaceae: *Agrostis capillaris*, *Festuca rubra*, *Poa* spp.), and wildflowers (4% Fabaceae: *Medicago lupulina*, *Medicago sativa*, *Lotus corniculatus*, and *Trifolium pratense*, and 11% other entomophilous species: *Achillea millefolium*, *Centaurea jacea*, *Daucus carota*, *Leucanthemum vulgare*, *Malva moschata*, and *Silene x hampeana*, Le Roi et al. 2010). We studied three transects of 100 × 1 m per strip.

It is known that insects abundances, diversity and the plant they use vary among years (Bascompte and Jordano 2014). Therefore, to have a global overview of the flower-insect interactions occurring on the perennial pollinator flower-strip AES we pooled together sites and years.

Table 1 Location of the four studied pollinator flowered strips (all sown in 2008) in Belgian agricultural landscapes in 2014 and 2015

	Locality	Location latitude, longitude	Length (m)	Width (m)
Strip 1	Ciney	50°18'25"N, 5°08'43"E	1000	12
Strip 2	Ciney	50°16'54"N, 5°07'54"E	560	12
Strip 3	Havelange	50°21'42"N, 5°17'20"E	773	21
Strip 4	Ciney	50°17'38"N, 5°00'13"E	1000	20

Observations

Flower observations

To assess the flower resources, we recorded the diversity, the density and the resource productions of the flowering entomophilous species.

For all species, we recorded flower unit densities every 5 m along each transect using 1–m² quadrats. We conducted counting once a month (around the 15th, according to weather conditions) from April to September. For Asteraceae, a flower unit corresponds to a capitulum while for all the other species the flower unit corresponds to a single flower.

For the flower resources already evaluated, we used values provided by Hicks et al. (2016), or Baude et al. (2016). For not still evaluated species, we sampled pollen volumes (μL) and 24 h nectar sugar secretion (μg) per flower unit, according to Hicks et al. (2016) and Baude et al. (2016). Supplemental Table S1 presents data of the 12 species we measured.

We standardised all continuous variables to 1 m² ((sum of data)/(sum of observed areas)) or to 100 m² ((sum of data)/(sum of observed areas) × 100).

Insect observations

We recorded the insect diversity foraging on the strips and the flowers they visited.

From April to September 2014 and 2015, we monthly recorded insect-flower interactions along two consecutive walks (100 m, 10–15 min) at least 10 min apart, in the same way, along each transect. We recorded only insects visiting an open flower unit. We conducted observations from 9:00 to 6:00 pm on sunny and warm days (Willmer and Stone 2004; Baldock et al. 2015). Order and time of observation varied among sampling runs to avoid confounding of time and transects. We performed a total of 11 field sessions (two walks each time) per strip.

We focused on insects considered to be effective pollinators, *i.e.* bees (Hymenoptera), butterflies (Lepidoptera), and hoverflies (Syrphidae, Diptera) (Biesmeijer et al. 2006; Potts et al. 2010). When practicable, we identified insects to species level in the field (*i.e.* *Apis mellifera*, *Eristalis tenax*, etc.). Due to morphological similarities, we identified bumblebees in the field up to their Operational Taxonomic Unit (OTU, Terzo & Rasmont 2007). To estimate the within-*Bombus* OTU diversity we collected one of every 30 bumblebees for lab identification. We individually caught other insects for lab identification. *Bombus* (Terzo and Rasmont 2010), Coleoptera (Auber 1960; Unwin 1984), Lepidoptera (Skinner and Wilson 2009; Tolman and Lewington 2009), and Syrphidae flies (Verlinden 1994; Stubbs and Falk 2002; Speight and Sarthou 2016) were identified up to the species by the authors. The non-Apidae wild bees were identified by a taxonomist of the Royal Institute of Natural Sciences of Brussels. The non-Syrphidae Diptera were identified to family level (Stubbs and Falk 2002; Oosterbroek 2006), and the number of morphotypes was recorded. For the current paper, we grouped parasitoid Hymenoptera and non-Syrphidae Diptera all together (one type of insects each) as they are considered poor efficient pollinators. For the other insects, a ‘type’ corresponds to a single species or an OTU for *Bombus*.

To appreciate the attractiveness of flower species according to the flower unit density, we calculated flower unit visitation rates as the total number of visits on a given

species divided by the total number of available flower units of this species in the sampled transects.

Pollen load observations

To identify which flower species were visited by insects for pollen collection, and to assess the proportion of pollen collected from outside the managed strips, pollen loads were sampled all along the sampling walks. We focused pollen load observations on bumblebees as other bees were infrequent.

We removed (with a toothpick) one corbicular pollen load on every *Bombus* individual observed with pollen loads during the insect observations in 2014 and 2015. We analysed a total of 49 pollen loads, from *Bombus lapidarius* OTU (34), *Bombus terrestris* OTU (8), and *Bombus pascuorum* OTU (7). Pollen loads were acetolysed (Erdtman 1954, 1960; Hesse and Waha 1989) for identification under light microscopy (Leitz Wetzlar). Approximately 500 pollen grains per pollen load were identified using the lab collection of reference pollen slides and Reille's published pollen collections (Reille 1992, 1995). Species making up less than 2.0% of a pollen load content were not included in the quantitative analyses and were classified as 'Undetermined' since they could have arisen from contamination (Free 1970; Westrich and Schmidt 1986).

Statistical analyses

We performed all statistical analyses using the software R (version 3.2.4 GUI 1.67). Insect–flower interaction networks were visualised with the 'bipartite' R-package. We considered insect species as higher trophic level and plant species as lower trophic level.

To compare the correlation among insect diversity and density, flower resources quantities and flower unit densities, we calculated Pearson (when no 'na' values) or Spearman (when some 'na' value) correlation factors using the 'rcorr' function of the 'Hmisc' R-package.

To visualise distribution of insect–flower interactions and flower-resources through the season, we generated grey-coloured heat maps using the 'heatmap.2' function of the 'gplot' R- package.

Results

Flowers

We identified 54 flower species and counted a total of 227,081 flower units. The observed flowers were distributed among ten sown, and 44 spontaneous species belonging to 18 different families (Fig. 1). The sown species were all observed in both years. All the spontaneous species were observed in 2015, but only 25 were recorded in 2014. The mean flower diversity (the number of flowering species per strip) reached 28.8 ± 9.5 species per strip over the two field seasons. Sown species represented 68.4% of the flower units. The Fabaceae provided the highest number of flower units (60.4%) with ten species, followed by Apiaceae (17.2%) with two species and Asteraceae (16.6%) with 18 species (Figs. 1, 2).

Four species, *Lotus corniculatus*, *Silene x hampeana*, *Centaurea jacea*, and *Trifolium repens* had the best continuity in flower resources provision as they flowered during

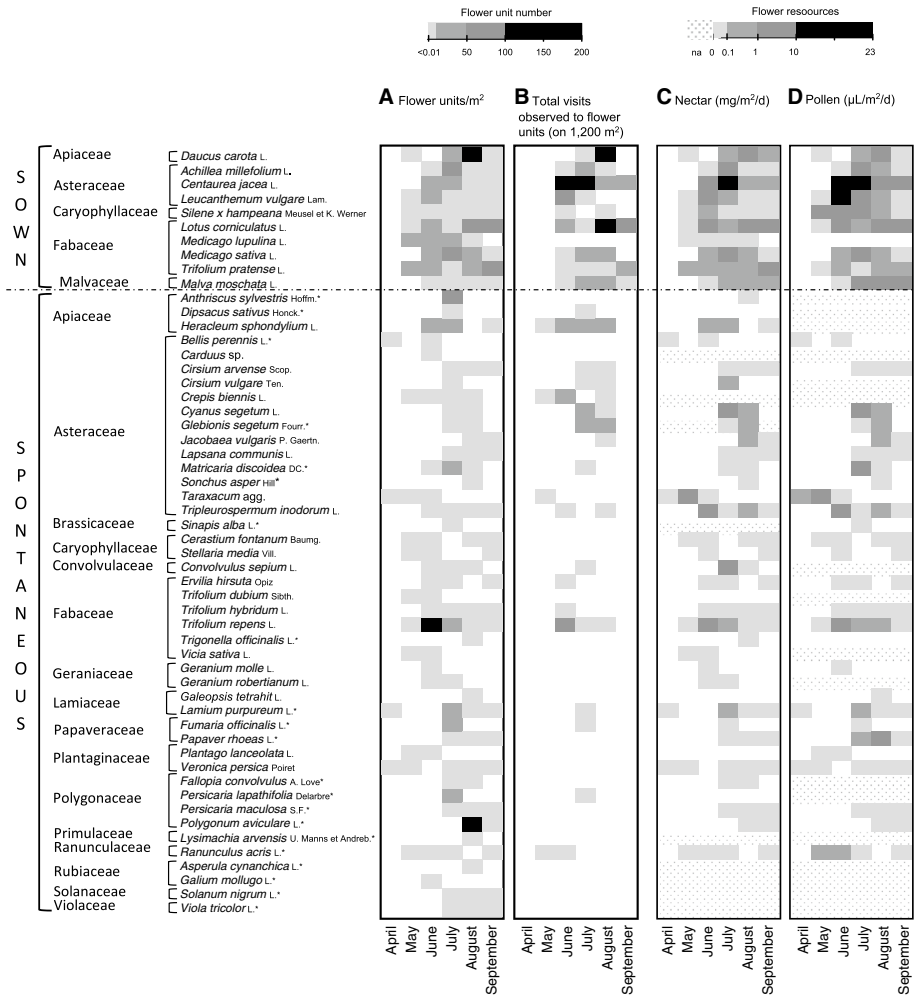


Fig. 1 Flower unit density, flower unit visits numbers and flower resources densities across seasons in the four pollinator flowered strips in both 2014 and 2015. Species are named according to the APG III classification (Tison and de Foucault 2014). **a** Mean number of flower units observed per m². **b** Total number of flower unit visited per species ($n = 3097$, observed area = 1200 m²). **c** Nectar sugar production per species, mg per m² per 24 h. **d** Pollen production per species, μL per m² per 24 h. * indicates species that flowered in 2015 only

eight to nine months over the 11 months of observation. Spontaneous species were the only blooming species in April (Fig. 1, Table 2). The main flowering peaks occurred from June to August: 27.5% of the total flower units were observed in June, 23.2% in July and 27.5% in August (Figs. 1, 2).

The global flower unit density over the two years was 81.6 ± 130.7 flower units/m². Most flower species (57%) showed a very low flower unit density (< 1 flower unit/m²) (Fig. 1). However, the highest floral densities were reached during summer months with

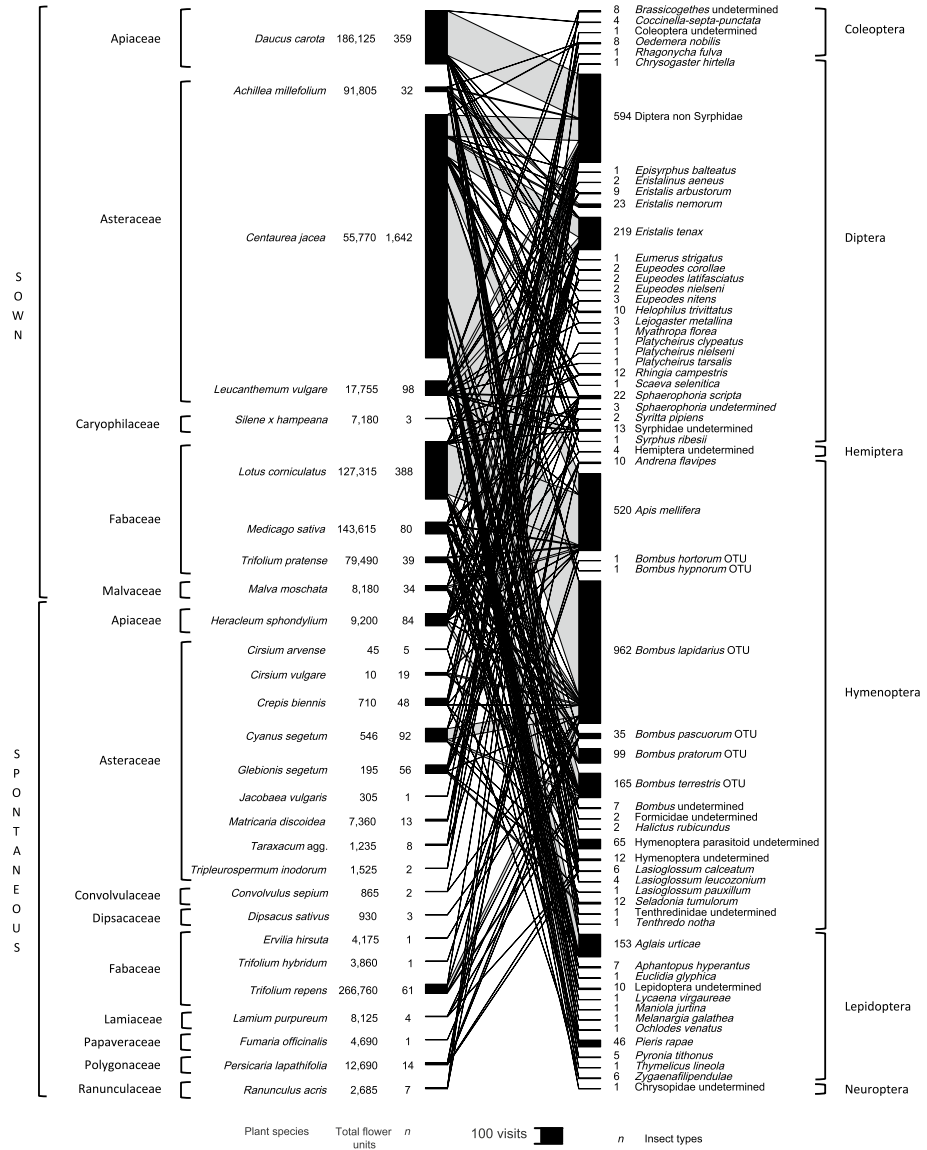


Fig. 2 Global interaction network among flowers and insects over the four pollinator flowered strips studied in 2014 and 2015 (n = 3097). Size of boxes are proportional to ‘n’ the number of insect visits. ‘Total flower units’ refers to the total number of flower units observed

Table 2 Monthly pollen and nectar production per m² per 24 h and contribution of sown species in the observed pollinator flowered strips in both 2014 and 2015.

	April	May	June	July	August	September	Total
Sown species							
Number of flowering species	0	6	9	10	10	9	10
Mean flower unit density (/m ²)	0.00 ± 0.00	13.76 ± 30.77	34.81 ± 42.07	110.76 ± 192.03	103.12 ± 59.96	27.66 ± 55.31	48.35 ± 93.63
Spontaneous species							
Number of flowering species	4	9	17	26	26	18	43
Mean flower unit density (/m ²)	0.00 ± 0.03	2.34 ± 1.99	100.31 ± 201.19	23.57 ± 43.01	12.36 ± 25.26	2.00 ± 3.16	23.43 ± 87.61
Total flower unit visited	0	15	836	1106	805	121	3097
Contribution of sown species (%)	–	0	87	84	90	100	86
Pollen							
μL/m ² /day	0.40	8.64	400.77	203.68	70.45	20.33	
global %	0.06	1.23	56.90	28.92	10.00	2.89	100.00
Monthly contribution of sown species (%)	0.00	39.53	93.33	84.92	38.82	92.32	84.70
Nectar							
mg sugar/m ² /day	0.30	2.81	50.74	90.74	29.22	9.63	
Global %	0.16	1.53	27.66	49.47	15.93	5.25	100.00
Monthly contribution of sown species (%)	0.00	35.37	63.31	23.36	35.00	84.39	39.62

Flower unit density are mean ± SD, resources values are calculation over the four strips altogether

Trifolium repens up to 192 flower units/m² in June, *Achillea millefolium* up to 187 flower units/m² in July and *Lotus corniculatus* up to 162 flower units/m² in August.

Flower resources

Flower resources were mainly available during June and July with 401 and 204 $\mu\text{L}/\text{day}/\text{m}^2$ of pollen and 51 and 91 $\text{mg}/\text{day}/\text{m}^2$ of nectar sugar. The sown species provided 84.7% of the pollen and 39.6% of the nectar resources (Table 2). Four families provided most of the pollen resources: Asteraceae (82.0%), Malvaceae (7.1%), Fabaceae (5.5%), and Papaveraceae (3.2%). Asteraceae flowers were the major nectar resources, providing 38.3% of all the nectar sugar in the strips, followed by Convolvulaceae (36.3%), Fabaceae (13.5%), and Malvaceae (4.4%) (Table 3). *Leucanthemum vulgare* and *Papaver rhoeas* were the primary pollen producers, supplying 15.9 and 13.3 μL of pollen per flower unit per day. *Cirsium vulgare* and *Taraxacum* agg. produced the most nectar, providing 2.6 and 2.4 mg of sugars per flower unit per day.

Insect visitors

We identified a total of 3097 visitors, distributed among more than 110 morphotypes belonging to 5 orders and grouped into 64 visitor types (Figs. 4–5). More than a third (37.7%) of the observed species were recorded only once. Hymenoptera represented 61.7% of all the insect visitors, followed by Diptera (30.0% including Syrphidae, 10.7%) and Lepidoptera (7.5%) (Figs. 2, 3). Visits of Coleoptera, Hemiptera, and Neuroptera were negligible (< 0.9% altogether). *Apis mellifera* and the *Bombus* OTUs were the major Hymenoptera visitors, representing 28.5% and 69.4% of the interactions. The most commonly observed bumblebee OTU was *Bombus lapidarius*, constituting 74.8% of all *Bombus* visitors. Among the collected *Bombus* individuals, we identified eight species (*Bombus hypnorum*, *Bombus lapidarius*, *Bombus pascuorum*, *Bombus pratorum*, *Bombus ruderalis*, *Bombus ruderatus*, *Bombus rupestris*, *Bombus terrestris*) belonging to six OTUs. The 35 non-Apidae bee visitors caught belonged to four genera (*Andrena*, *Halictus* and *Lasioglossum*) and six species (*Andrena flavipes*, *Halictus rubicundus*, *Halictus (Seladonia) tumulorum*, *Lasioglossum calceatum*, *Lasioglossum leucozonium*, and *Lasioglossum pauxillum* Figs. 2, 3) and represented 1.1% of total recorded interactions. The common *Eristalis tenax* (Diptera) was the most recorded Syrphidae visitor species (67.6% of all Syrphidae observed).

Flower visitors were mainly observed during summer months: 29.6% in June, 37.1% in July and 28.5% in August. Visitors first appeared in May (0.6% of all the visitors), while the first bee (Hymenoptera) visitors were recorded in June and the last ones in September (Fig. 3). The global flower visit abundances were 0.0 in April, 0.4 visits/100 m²/25 min in May, 23.4 visits/100 m²/25 min in June, 54.9 visits/100 m²/25 min in July, 33.5 visits/100 m²/25 min in August and 5.0 visits/100 m²/25 min in September.

Insect–flower interactions

Insects visited 28 of the 54 flowering species, primarily Asteraceae (65.1% of the total number of interactions), Fabaceae (18.4%) and Apiaceae (14.4%, Table 3). The sown species represented 86.6% of the insect visits (Table 2). *Medicago lupulina* was the unique sown species with no recorded visits (Table 3). The main visited species were among the most

Table 3 Plant species contribution (%) to global flower unit number, insect visits, flower resources (pollen and nectar) production and for each species, the number of visits observed for 100 flower units, over both 2014 and 2015 and the four studied strips. Plants are named according to the APG III classification (Tison and de Foucault 2014). The total number of insect types observed was 64. 'na' indicates the absence of flower resource production data

Family	Species	Flowerunits % (n = 227,081)	Visits % (n = 3097)	Contribution to pol- len production (%)	Contribution to nec- tar production (%)	Number of insect types hosted	Number of visits for 100 flower units
Apiaceae	<i>Daucus carota</i>	16.71	11.59	0.60	4.19	19	0.19
	<i>Achillea millefolium</i>	8.33	1.03	0.90	2.17	9	0.03
Asteraceae	<i>Centaurea jacea</i>	4.60	53.02	61.71	54.39	39	3.14
	<i>Leucanthemum vulgare</i>	1.62	3.16	17.36	4.30	16	0.53
Caryophyllaceae	<i>Silene x hampeana</i>	0.61	0.10	0.99	0.37	3	0.04
	<i>Lotus corniculatus</i>	11.67	12.53	3.20	7.17	15	0.29
	<i>Medicago lupulina</i>	4.59	0.00	na	0.08	0	0.00
Fabaceae	<i>Medicago sativa</i>	11.36	2.58	1.44	4.79	14	0.06
	<i>Trifolium pratense</i>	7.26	1.26	0.27	3.18	7	0.05
Malvaceae	<i>Malva moschata</i>	0.73	1.10	7.18	5.58	7	0.41
	<i>Antriscus sylvestris</i>	0.82	0.00	na	0.08	0	0.00
Apiaceae	<i>Dipsacus sativus</i>	0.09	0.10	na	na	1	0.31
	<i>Heracleum sphon- dylium</i>	0.73	2.71	na	0.75	13	1.02
	<i>Bellis perennis</i>	< 0.01	0.00	0.00	0.00	0	0.00
	<i>Carduus</i> sp.	< 0.01	0.00	na	na	0	0.00
	<i>Cirsium arvense</i>	< 0.01	0.16	0.00	0.10	3	10.66
	<i>Cirsium vulgare</i>	< 0.01	0.61	na	0.19	4	182.20
	<i>Crepis biennis</i>	0.07	1.55	na	na	7	6.48
	<i>Cyanus segetum</i>	0.23	2.97	1.62	3.34	6	3.59
	<i>Glebionus segetum</i>	0.02	1.81	0.17	0.15	8	27.54

Table 3 (continued)

Family	Species	Flowerunits % (n = 227,081)	Visits % (n = 3097)	Contribution to pollen production (%)	Contribution to nectar production (%)	Number of insect types hosted	Number of visits for 100 flower units
Asteraceae	<i>Jacobaea vulgaris</i>	0.03	0.03	0.05	0.28	1	0.31
	<i>Lapsana communis</i>	0.03	0.00	0.02	0.03	0	0.00
	<i>Matricaria discoidea</i>	0.68	0.42	0.55	0.00	3	0.17
	<i>Sonchus asper</i>	< 0.01	0.00	0.00	0.00	0	0.00
	<i>Taraxacum</i> agg.	0.10	0.26	0.60	2.19	3	0.69
	<i>Tripleurospermum inodorum</i>	0.14	0.06	0.78	1.78	2	0.13
Brassicaceae	<i>Sinapis alba</i>	< 0.01	0.00	0.00	na	0	0.00
	<i>Cerastium fontanum</i>	0.05	0.00	0.00	0.01	0	0.00
Caryophyllaceae	<i>Stellaria media</i>	< 0.01	0.00	0.00	0.00	0	0.00
Convolvulaceae	<i>Convolvulus sepium</i>	0.01	0.06	na	1.10	2	1.60
	<i>Ervilia hirsuta</i>	0.38	0.03	na	0.09	1	0.02
	<i>Trifolium dubium</i>	0.08	0.00	na	0.00	0	0.00
Fabaceae	<i>Trifolium hybridum</i>	0.35	0.03	0.04	0.00	1	0.02
	<i>Trifolium repens</i>	24.46	1.97	1.31	2.68	5	0.02
	<i>Trigonella officinalis</i>	< 0.01	0.00	na	0.00	0	0.00
	<i>Vicia sativa</i>	0.02	0.00	na	0.05	0	0.00
	<i>Geranium molle</i>	0.01	0.00	0.00	0.00	0	0.00
Geraniaceae	<i>Geranium robertianum</i>	< 0.01	0.00	na	0.00	0	0.00
	<i>Galeopsis tetrahit</i>	< 0.01	0.00	0.00	na	0	0.00
Lamiaceae	<i>Lamium purpureum</i>	0.75	0.13	0.03	0.72	3	0.05
Papaveraceae	<i>Fumaria officinalis</i>	0.43	0.03	0.01	0.09	1	0.02
	<i>Papaver rhoeas</i>	0.02	0.00	0.48	0.00	0	0.00
	<i>Plantago lanceolata</i>	0.22	0.00	0.00	na	0	0.00

Table 3 (continued)

Family	Species	Flowerunits % (n = 227,081)	Visits % (n = 3097)	Contribution to pol- len production (%)	Contribution to nec- tar production (%)	Number of insect types hosted	Number of visits for 100 flower units
Plantaginaceae	<i>Veronica persica</i>	0.07	0.00	0.00	0.00	0	0.00
	<i>Fallopia convolvulus</i>	0.07	0.00	na	na	6	0.11
	<i>Persicaria lapathi- folia</i>	1.17	0.45	na	na	0	0.00
Polygonaceae	<i>Persicaria maculosa</i>	0.06	0.00	0.00	0.02	0	0.00
	<i>Polygonum aviculare</i>	1.09	0.00	0.01	0.03	0	0.00
Primulaceae	<i>Lysimachia arvensis</i>	0.02	0.00	na	na	0	0.00
Ranunculaceae	<i>Ranunculus acris</i>	0.15	0.23	0.65	0.05	3	0.40
Rubiaceae	<i>Asperul cynanchica</i>	< 0.01	0.00	na	na	0	0.00
	<i>Galium mollugo</i>	0.02	0.00	na	na	0	0.00
Solanaceae	<i>Solanum nigrum</i>	0.12	0.00	na	na	0	0.00
Violaceae	<i>Viola tricolor</i>	0.05	0.00	na	na	0	0.00

abundant sown flowering species: *Centaurea jacea* ($53.3 \pm 18.8\%$ of total visits), *Daucus carota* ($12.4 \pm 16.5\%$), and *Lotus corniculatus* ($10.7 \pm 21.1\%$, Table 3). These three species combined represented 33% of all flower units, 65% of the pollen, 66% of the nectar sugar production and hosted 80% of all insect visits (Table 3). All together, the three most-visited spontaneous species (*Cyanus segetum*, *Crepis biennis*, and *Glebionis segetum*) received 6.3% of all insect visits (Table 3). Pearson correlation factor between the number of insect visits and the number of open flower units per species was $r = 0.28$, $p = 0.0419$. Combining pollen or nectar quantities per flower unit and the flower unit density, we obtain the flower resource densities. These values had high Spearman correlation factor with insect visits for both pollen ($r = 0.93$, $p < 0001$) and nectar sugar ($r = 0.98$, $p < 0001$).

Six Asteraceae species had a high number of insect visits per flower unit: *Cirsium vulgare* (1.58 visits per flower unit), *Glebionis segetum* (0.29), *Cirsium arvense* (0.11), *Crepis biennis* (0.07), *Centaurea jacea* (0.03), and *Cyanus segetum* (0.03).

We recorded a total of 3097 insect-flower interactions, summarised by a global bipartite network (Fig. 2). Of the 64 observed insect types, 60 were observed on sown species and 29 on spontaneous plant species. The sown *Centaurea jacea* attracted the largest diversity of insects (60.9% of observed insect diversity). Three other sown species were visited by a large proportion of the observed insect diversity: *Daucus carota* (27.5% of insect diversity), *Leucanthemum vulgare* (24.6%) and *Lotus corniculatus* (21.7%, Table 3).

We recorded a total of 65.7% of non-Apidae wild bees on spontaneous species: 5.7% on *Cyanus segetum*, 51.4% on *Glebionis segetum*, 2.9% on *Lamium purpureum* and 5.7% on *Persicaria lapathifolia*. Non-Apidae wild bee species visited four sown species: *Achillea millefolium* (2.9% of the non-Apidae wild bee visits), *Centaurea jacea* (25.7%), *Daucus carota* (2.9%) and *Malva moschata* (2.9%) (Fig. 2). Oppositely, we observed 88.2% of the Apidae (*Apis mellifera* and *Bombus*) on sown species.

We observed the non-Syrphidae Diptera (41 morphotypes), in 60.7% of visited plant species, *Bombus lapidarius* OTU in 57.1% of visited plant species and *Eristalis tenax* in 46.4%. We observed *Apis mellifera*, *Bombus terrestris* OTU, and *Sphaerophoria scripta* each in 35.7% of visited plant species (Fig. 2).

Insect fidelity

We identified a total of 18 plant species from the 49 collected pollen loads. The plant species present in the strips accounted for 97.5% of the collected pollen with 53.8% for the sown species. Most of the collected pollen loads contained a spontaneous species, *Trifolium repens* (80%), and two sown species, *Centaurea jacea* (59%) and *Lotus corniculatus* (55%, Table 4). The Fabaceae family was the predominant pollen supplier representing 77.1% of collected pollen grains, especially *Trifolium repens* (39.3%). The Asteraceae family was the second-most-common pollen supplier with 18.2% of collected pollen grains.

On average, each pollen load included pollen from 3.5 different plant species (e.g. 3.1 ± 1.1 for *Bombus lapidarius* OTU, 4.6 ± 1.0 for *Bombus pascuorum* OTU and 4.1 ± 1.9 for *Bombus terrestris* OTU). Two pollen loads coming from *Bombus lapidarius* OTU individuals caught on *Lotus corniculatus* contained only pollen of this plant species.

Fig. 3 Insect visitor diversity and abundance across seasons over the four pollinator flower-strips in 2014 and 2015. (total number of observed insect–flower interactions (N=3097)). Within each order, species are in alphabetical order

Discussion

During our two years of observations, we mostly recorded *Bombus* (41% of the visits) and Diptera (30%) visitors in (Belgian) flower-strips, dominated by *Centaurea jacea* (53% of the visited flower units). The spontaneous plant species, despite their contribution to the nectar sugar production (60%) were poorly visited (14% of the visits) and by only 50% of the observed insect types. We observed six non-Apidae wild bee species in very few number (1.1% of the visits). In the collected *Bombus* pollen loads, *Trifolium repens* (spontaneous) was the most collected species, even if sown species provided more than 50% of the *Bombus* pollen diet.

Asteraceae provided most of the flower resources

Asteraceae were the most visited family with 65% of visits. Notably, *Centaurea jacea* was the most-visited species for nectar collection, as also recorded in a previous study on flower-strips in Sweden and Switzerland (Haaland and Gyllin 2010; Hennig and Ghazoul 2011; Sutter et al. 2017). This species attracted the largest insect diversity in the present study. Asteraceae pollen represented 82% of the available pollen in the pollinator flower-strips whereas it constituted 18% of the *Bombus* pollen diet (loads). Species of the Asteraceae family are known to be good nectar suppliers, both in quality and quantity (Pywell et al. 2004, 2011; Hicks et al. 2016). However, this family provides poor-quality and low-attractive pollen, that does not provide all the requisite essential amino acids, leading to poor larvae development for numerous insect species (Goulson et al. 2005; Hanley et al. 2008; Forcone et al. 2011; Nicolson and Human 2013; Somme et al. 2015; Spear et al. 2016; Vanderplanck et al. 2016).

The majority of the pollen collected by the *Bombus* visitors came from species present on the strips (97.5%), mainly sown species (53.8%). The other collected plant species could be used to improve the seed mixes. Fabaceae was the most abundant family, *i.e.* the best pollen supplier, in the *Bombus* pollen loads (77% of pollen grains collected). This family provides good quality pollen for insects (Forcone et al. 2011; Moerman et al. 2017). Bumblebee individuals largely collected pollen of *Trifolium repens*. This pollen has a high content of proteins and essential amino acids (Hanley et al. 2008), with a high degree of digestibility by bees (Liolios et al. 2016). The sown plant mix does not include this species, and its presence depends on the seed bank of each site or spontaneous seed dispersal. Despite the predominance of the Asteraceae flower resources, we found only one Asteraceae species in *Bombus* pollen loads. *Bombus* essentially used strips species (14 of the 18 species found in pollen loads). The spontaneous species were of particular interest, representing 46% of the *Bombus* pollen diet. Thus, the various flower species of the pollinator flower-strips provided opportunities for mixing different pollen sources, which is particularly interesting for nutrition and health of some bee species (Di Pasquale et al. 2013). In summer, the pollinator flower-strips can provide sufficient pollen resources for insects. Nevertheless, to increase the quality of pollinator flower-strips, independently of the spontaneous species, we recommend including

Table 4 Pollen species presented in the pollen loads of the three-main bumblebee OTU observed on four pollinator flower-strips in 2014 and 2015

Bombus OTU	Plant species	Plant family	Number of pollen loads containing the species	% in pollen load	% in OTU diet
<i>Bombus lapidarius</i> n = 34	<i>Brassicaceae</i> sp.	Brassicaceae	1	39.0	1.2
	<i>Centaurea jacea</i>	Asteraceae	21	35.2 ± 41.8	19.9
	<i>Lotus corniculatus</i>	Fabaceae	20	54.4 ± 45.7	32.8
	<i>Morus alba</i> L.*	Moraceae	1	8.7	0.2
	<i>Trifolium repens</i>	Fabaceae	25	59.3 ± 43.4	44.6
<i>Bombus pascuorum</i> n = 7	<i>Lotus corniculatus</i>	Fabaceae	6	45.2 ± 36.3	38.6
	<i>Medicago lupulina</i>	Fabaceae	1	57.9	8.7
	<i>Medicago sativa</i>	Fabaceae	1	78.9	10.9
	<i>Trifolium hybridum</i>	Fabaceae	2	26.8 ± 17.9	7.5
	<i>Trifolium pratense</i>	Fabaceae	5	12.9 ± 11.6	9.2
	<i>Trifolium repens</i>	Fabaceae	5	29.9 ± 27.6	21.7
	<i>Trifolium repens</i>	Fabaceae	4	74.2 ± 49.1	33.4
<i>Bombus terrestris</i> n = 8	<i>Centaurea jacea</i>	Asteraceae	3	73.0 ± 10.3	26.8
	<i>Chenopodium quinoa</i> Willd*	Chenopodiaceae	1	91.8	15.7
	<i>Daucus carota</i>	Apiaceae	2	5.4 ± 6.9	1.2
	<i>Medicago lupulina</i>	Fabaceae	3	15.7 ± 19.1	6.2
	<i>Medicago sativa</i>	Fabaceae	1	6.2	1.1
	<i>Raphanus sativus</i> L.*	Brassicaceae	1	19.7	1.7
	<i>Tilia</i> sp.*	Tiliaceae	1	10.4	1.6
	<i>Trifolium dubium</i>	Fabaceae	1	6.5	0.8
	<i>Trifolium pratense</i>	Fabaceae	2	44.3 ± 61.9	10.4
	<i>Trifolium repens</i>	Fabaceae	4	74.2 ± 49.1	33.4

Percentage in pollen load and in OTU diet refers to the pollen grain numbers. Only species representing more than 2% of pollen load composition were considered. Values are mean ± SD. Sown species are in bold

* Indicates species from outside of the flower-strips. N = 49

Even surprising for the area, *Chenopodium quinoa* (a 5 ha field) and *Morus alba* were identified in the vicinity of a strip

Trifolium repens in the seed mix, even if this species has to be used at a low density to preserve the plant mix balance (Warren 2000).

We found positive correlation among the number of insect interactions with a plant species and the density of flower resources it provided. The quantity and the nutritional value of the flower resources are first clues to assess the value of a plant species for insects. Nevertheless, several other parameters like resources accessibility, colour, odours, and flower shape (Giurfa et al. 1994; Dafni et al. 1997; Campbell et al. 2010) are known to influence insect flower choices strongly. The plant spatial organisation of the strips could explain the prevalence of visits to some species. The two most-visited species for nectar collection, *Centaurea jacea* and *Daucus carota*, have long flowering periods and provided densely grouped flowers (capitulum and umbels respectively) on the top of long rigid stems (> 80 cm) that constituted the highest stratum of the strips. These species were locally the most visible and accessible, present in the upper layer of the strip. To optimise the flower-strip, plant mixes have to provide flowers visited by insects. Thus, the number of visits per flower unit could help to select the sown species. Nevertheless, the most interesting species regarding these criteria are weed pest (*Cirsium* species, Pauly and Coppée 2017) or corn-field annuals (*Cyanus segetum*, *Glebionis segetum*) not adapted to perennial strip management. The next species, *Crepis biennis*, *Convolvulus sepium* or *Heracleum sphondylium* could nevertheless be interesting to be added or favoured in the plant mixes. In the same way, the density of sown species with a low flower unit visit rate (e.g. *Achillea millefolium* or *Medicago lupulina*) could be reduced in the seed mix. Nevertheless, more research should be conducted to determine an optimal flower unit visit rate per plant species.

Floral visitor abundance and diversity

The observed visitor diversity, more than 110 insect morphotypes, was within the top range of other observations in European farmland flowered areas as 34 to 131 pollinator species in Germany (Fründ et al. 2010; Ebeling et al. 2011) and 25 in England (Campbell et al. 2017). The wild bee diversity included six non-*Bombus* wild bee species and eight *Bombus* species. These species, all polylectic, represent a small fraction of the Walloon Hymenoptera diversity of 300 non-*Bombus* wild bee species (Rasmont et al. 2005) and 30 *Bombus* species (Pauly and Rasmont 2010). The number of Hymenoptera species observed was similar to other studies on European sown strips (Carreck and Williams 2002; Carvell et al. 2004; Aviron et al. 2009; Ebeling et al. 2011; Wood et al. 2017) and in European fields near semi-natural habitat (Le Féon et al. 2010). Nevertheless, this low wild bee diversity observed on pollinator strip AES could reflect the lack of habitat elements on strips (lack of floral resource diversity or nesting areas) or insufficient area at the landscape scale. A more complex landscape, with a higher density of connected semi-natural elements, could help filling this gap (Mitchell et al. 2013; Defra 2014; Carvell et al. 2016).

The visitor abundance we observed (29.2 visits/100 m²/25 min from June to September), was comparable to those in other pollinator favourable areas in summer. Blaauw and Isaacs (2014) recorded 32.6 visits/100 m²/25 min in sown wild-flowers plots (even if they recorded only bees and Syrphidae) and Forup and Memmott (2005) observed 28.6 visits/100 m²/25 min in meadows. Oppositely, the insect abundance we observed was higher than in areas without specific pollinator-friendly management studied by Baldock et al. (2015) in the UK (6.7, 11.1 and 13.0 visits/100 m²/25 min respectively in urban areas, farmlands, and nature reserves).

The scarcity of non-*Bombus* wild bees (1.1% of the visits) was characteristic of intensively cropped farmland area with a low proportion of semi-natural habitats (Holzschuh

et al. 2008; Le Féon et al. 2010; Wood et al. 2017). But Apidae species, especially *Bombus* species (41% of visits), chiefly *Bombus lapidarius* OTU, and *Apis mellifera* (17%), were the foremost visitors on the pollinator flower-strips. Such predominance of polylectic bee visitors may support pollination services at the landscape scale as demonstrated in other studies (Kleijn et al. 2015; M'Gonigle et al. 2015; Wood et al. 2017). The presence of *Apis mellifera*, despite the distance from apiaries (3 km), emphasises the attractiveness of the pollinator flower-strips for insects on a landscape scale.

Syrphidae (Diptera) represented 11% of observed visitors on our studied strips with 25 different species. These species represent 8% of the 310 Walloon Syrphidae species (Speight et al. 2015). Syrphidae use several habitats during their life cycle and are highly mobile among habitats (Sommaggio 1999), which could explain their higher diversity than bees even in intensively managed landscape. *Eristalis tenax* was the most frequently observed Syrphidae, as in previous studies in farmland areas (Rader et al. 2012). These Syrphidae are complementary pollinators to Hymenoptera and improve overall pollination services (Ssymank et al. 2008; Jauker et al. 2009; Rader et al. 2015). In addition to their importance in pollination services, 50% of observed Syrphidae species have an aphidophagous larval stage (Speight 2016). Therefore, they might offer additional pest management ecosystem service for surrounding crops (Ssymank et al. 2008).

Differences of phenology between insects and flowers

All the observed bee species are early emerging, from March to April (Benton 2006; Falk 2015). But, nearly no flowers were available in April (0.03 flower units/m²) and only a few in May (16.10 flower units/m²). This flower scarcity probably explained the absence of Hymenoptera individuals during spring and the small number of *Bombus* species observed (Scheper 2015). Also, as flower density and diversity decreased from August to September (from 115.48 to 29.65 flower units/m² and from 15.8 ± 9.5 to 9.5 ± 5.5 species per strip), available resources for late insect individuals were also reduced. In the current study, most of the observed *Bombus* species were early-nesting ones (March to April, (Benton 2006; Falk 2015). Nevertheless, we observed the first bumblebees in June. Spring flower resources are critical for insect population growth (Osborne et al. 2008; O'Rourke et al. 2014; Moquet et al. 2015, 2017) and autumn resources are essential for their overwintering success. Providing flower resources during summer months helps to support insects, while continuity in resource provision is necessary to sustain populations (Roulston and Goodell 2011; Schellhorn et al. 2015; Scheper et al. 2015). Adding early- and late-blooming flower resources could, therefore, bolster insect abundance and diversity (Haaland and Gyllin 2010; Garbuzov and Ratnieks 2014; Schellhorn et al. 2015; Wood et al. 2017). We recommend introducing local spring or autumn blooming species, both attractive for insects and producing abundant flower resources, like *Lamium purpureum*, *Ranunculus acris* or *Taraxacum* agg. (Baude et al. 2016; Hicks et al. 2016), in strip seed mixes. As threes can also provide valuable spring resources (Aupinel et al. 2001), we also recommend coupling flower strips with semi-natural landscape elements as hedges or with other AES favouring threes to increase the duration of flower resource availability.

Durability and diversity of flower-strips

On the observed pollinator flower-strips, all ten entomophilous sown species were still dominant 8 years after sowing (70% of flower units). Most of the previously studied

flower-strips of Europe contained more sown species (about 20 species) and up to 52 spontaneous species (Engels et al. 1994; Bokenstrand et al. 2004; Carvell et al. 2006; Haaland et al. 2011; Hicks et al. 2016; Campbell et al. 2017). However, the diversity of sown species was better conserved in our strips (100%) than in other studies after the same period (Bokenstrand, Lagerlöf and Torstensson, 2004; 69% of the sown species present after 10 years). Consequently, the current Walloon species mix and management are suitable for a mid to long-term period of at least 8 years.

Conclusion

Our study revealed that the Walloon pollinator flower-strips provided flower resources mainly during summer to insect species. Observed insects were mostly common polylectic Hymenoptera (honeybees and bumblebees) and hoverflies which are good candidates for supplying pollination services. But the support for insect diversity was moderate. The sown plant species provided most of the nectar sugar, but only half of the pollen collected by insects. The spring flower resources were scattered, and some sown species were not or poorly used by insects. Thus flower-strips could be improved. The most visited and highly accessible sown species *Centaurea jacea*, *Daucus carota* and *Lotus corniculatus* have to be kept in the seed mix. Species like *Trifolium repens*, whose pollen is largely collected by *Bombus*, *Lamium purpureum*, *Ranunculus acris* or *Taraxacum* agg. with early and extended flowering period, could be sown instead of poorly visited sown species as *Achillea millefolium* or *Medicago lupulina*. Moreover, we recommend combining this AES, along with other measures as AES supporting hedgerows that provide complementary resources in the early and late seasons and increase landscape connections. Studying the insect dispersal from the strips to the countryside could elucidate the potential for ecosystem services in the surrounding area and exchanges among habitats that could help to set up strips in the best location according to landscape elements.

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Authors' contributions PO and ALJ conceived the ideas and designed the methodology; PO and JT collected and analysed the data; PO and ALJ led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Data access Raw data will be archived and freely accessible on a Figshare folder (<https://figshare.com/s/5487a55f74f109e04542>).

Compliance with ethical standards

Conflict of interest The authors declare having no conflicts of interest.

References

- Allen-Wardell G, Bernhardt P, Bitner R et al (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv Biol* 12:8–17
- Auber L (1960) Atlas des coléoptères de France Belgique, Suisse Tome II. N. Boubée & Cie, Paris
- Aupinel P, Genissel A, Gomond S et al (2001) Collection of spring pollens by *Bombus terrestris* queens. Assessment of attractiveness and nutritive value of pollen diets. *Acta Hort* 561:101–105. <https://doi.org/10.17660/ActaHortic.2001.561.15>
- Aviron S, Nitsch H, Jeanneret P et al (2009) Ecological cross compliance promotes farmland biodiversity in Switzerland. *Front Ecol Environ* 7:247–252. <https://doi.org/10.1890/070197>
- Baldock KCR, Goddard MA, Hicks DM et al (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proc R Soc* 282:20142849. <https://doi.org/10.1098/rspb.2014.2849>
- Bascompte J, Jordano P (2014) Mutualistic Networks, Monographs. Princeton University Press, Princeton
- Batáry P, Dicks LV, Kleijn D, Sutherland WJ (2015) The role of agri-environment schemes in conservation and environmental management. *Conserv Biol* 29:1006–1016. <https://doi.org/10.1111/cobi.12536>
- Baude M, Kunin WE, Boatman ND et al (2016) Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature* 530:85–88. <https://doi.org/10.1038/nature16532>
- Benton T (2006) Bumblebees. HarperCollins, London
- Biesmeijer JC, Roberts SPM, Reemer M et al (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313:351–354. <https://doi.org/10.1126/science.1127863>
- Blaauw BR, Isaacs R (2014) Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. *Basic Appl Ecol* 15:701–711. <https://doi.org/10.1016/j.baee.2014.10.001>
- Bokenstrand A, Lagerlöf J, Torstensson PR (2004) Establishment of vegetation in broadened field boundaries in agricultural landscapes. *Agric Ecosyst Environ* 101:21–29. [https://doi.org/10.1016/S0167-8809\(03\)00275-5](https://doi.org/10.1016/S0167-8809(03)00275-5)
- Campbell DR, Bischoff M, Lord JM, Robertson AW (2010) Flower color influences insect visitation in alpine New Zealand. *Ecology* 91:2638–2649
- Campbell AJ, Wilby A, Sutton P, Wäckers FL (2017) Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. *Agric Ecosyst Environ* 239:20–29. <https://doi.org/10.1016/j.agee.2017.01.005>
- Cane JH, Tepedino VJ (2001) Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conserv Ecol* 5:1–8
- Carreck NL, Williams IH (2002) Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *J Insect Conserv* 6:13–23. <https://doi.org/10.1023/A:1015764925536>
- Carvell C, Meek WR, Pywell RF, Nowakowski M (2004) The response of foraging bumblebees to successional change in newly created arable field margins. *Biol Conserv* 118:327–339. <https://doi.org/10.1016/j.biocon.2003.09.012>
- Carvell C, Westrich P, Meek WR et al (2006) Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. *Apidologie* 37:326–340. <https://doi.org/10.1051/apido2006002>
- Carvell C, Meek WR, Pywell RF et al (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J Appl Ecol* 44:29–40. <https://doi.org/10.1111/j.1365-2664.2006.01249.x>
- Carvell C, Heard M, Vanbergen A, et al (2016) Managing farmed landscapes for pollinating insects. Increasing floral resources and improving habitat conditions can benefit pollinating insect species, wildflowers and crop production. *Living with Environment Changing Policy Practical Notes* 4
- Castiau E, Neuray C, Nielsen M, et al (2011) Atlas des Paysages de Wallonie 3: Le plateau condruzien, Isatz D. CPDT, Namur
- Dafni A, Lehrer M, Kevan PG (1997) Spatial flower parameters and insect spatial vision. *Biol Rev Camb Philos Soc* 72:239–282. <https://doi.org/10.1017/S0006323196005002>
- Decourtye A, Mader E, Desneux N (2010) Landscape enhancement of floral resources for honey bees in agro-ecosystems. *Apidologie* 41:264–277. <https://doi.org/10.1051/apido/2010024>
- Defra (2014) The National Pollinator Strategy: for bees and other pollinators in England. Bristol
- Deguines N, Jono C, Baude M et al (2014) Large-scale trade-off between agricultural intensification and crop pollination services. *Front Ecol Environ* 12:212–217. <https://doi.org/10.1890/130054>
- Di Pasquale G, Salignon M, Le Conte Y et al (2013) Influence of pollen nutrition on honey bee health: do pollen quality and diversity matter? *PLoS ONE* 8:e72016. <https://doi.org/10.1371/journal.pone.0072016>

- Dicks LV, Abrahams A, Atkinson J et al (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>
- Ebeling A, Klein A-M, Tscharrntke T (2011) Plant–flower visitor interaction webs: temporal stability and pollinator specialization increases along an experimental plant diversity gradient. *Basic Appl Ecol* 12:300–309. <https://doi.org/10.1016/j.baae.2011.04.005>
- Eckhardt M, Haider M, Dorn S, Müller A (2014) Pollen mixing in pollen generalist solitary bees: a possible strategy to complement or mitigate unfavourable pollen properties? *J Anim Ecol* 83:588–597. <https://doi.org/10.1111/1365-2656.12168>
- Engels W, Schulz U, Rädle M (1994) Use of Tübingen mix for bee pasture in Germany. In: Matheso A (ed) *Forage for bees in an agricultural landscape*. International Bee Research Association, Cardiff, pp 57–65
- Erdtman G (1954) *An introduction to pollen analysis*. Almquist and Wiksell, Stockholm
- Erdtman G (1960) The acetolysis method. A revised description. *Sven Bot Tidskr* 54:561–564
- Falk S (2015) *Field guide to the bees of Great Britain and Ireland*. British Wildlife, London
- Forcone A, Aloisi PV, Ruppel S, Munoz M (2011) Botanical composition and protein content of pollen collected by *Apis mellifera* L. in the north-west of Santa Cruz (Argentinean Patagonia). *Grana* 50:30–39. <https://doi.org/10.1080/00173134.2011.552191>
- Forup ML, Memmott J (2005) The restoration of plant-pollinator interactions in hay meadows. *Restor Ecol* 13:265–274
- Free JB (1970) The flower constancy of bumblebees. *J Anim Ecol* 39:395–402
- Fründ J, Linsenmair KE, Blüthgen N (2010) Pollinator diversity and specialization in relation to flower diversity. *Oikos* 119:1581–1590. <https://doi.org/10.1111/j.1600-0706.2010.18450.x>
- Garbuzov M, Ratnieks FLW (2014) Ivy: an underappreciated key resource to flower-visiting insects in autumn. *Insect Conserv Divers* 7:91–102. <https://doi.org/10.1111/icad.12033>
- Ghazoul J (2005) Buzziness as usual? Questioning the global pollination crisis. *Trends Ecol Evol* 20:367–373. <https://doi.org/10.1016/j.tree.2005.04.026>
- Giurfa M, Núñez JA, Backhaus W (1994) Odour and colour information in the foraging choice behaviour of the honeybee. *J Comp Physiol A* 175:773–779. <https://doi.org/10.1007/BF00191849>
- Godfray HCJ, Blacquière T, Field LM et al (2015) A restatement of the natural science evidence base concerning neonicotinoid insecticides and insect pollinators. *Proc R Soc Biol Sci* 282:20151821. <https://doi.org/10.1098/rspb.2015.1821>
- Goulson D, Sparrow KR (2009) Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *J Insect Conserv* 13:177–181. <https://doi.org/10.1007/s10841-008-9140-y>
- Goulson D, Hanley ME, Darvill B et al (2005) Causes of rarity in bumblebees. *Biol Conserv* 122:1–8. <https://doi.org/10.1016/j.biocon.2004.06.017>
- Goulson D, Nicholls E, Botías C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*. <https://doi.org/10.1126/science.1255957>
- Haaland C, Bersier L-F (2010) What can sown wildflower strips contribute to butterfly conservation? An example from a Swiss lowland agricultural landscape. *J Insect Conserv* 15:301–309. <https://doi.org/10.1007/s10841-010-9353-8>
- Haaland C, Gyllin M (2010) Butterflies and bumblebees in greenways and sown wildflower strips in southern Sweden. *J Insect Conserv* 14:125–132. <https://doi.org/10.1007/s10841-009-9232-3>
- Haaland C, Naisbit RE, Bersier L-F (2011) Sown wildflower strips for insect conservation: a review. *Insect Conserv Divers* 4:60–80. <https://doi.org/10.1111/j.1752-4598.2010.00098.x>
- Hanley ME, Franco M, Pichon S et al (2008) Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Funct Ecol* 22:592–598. <https://doi.org/10.1111/j.1365-2435.2008.01415.x>
- Hennig EI, Ghazoul J (2011) Plant–pollinator interactions within the urban environment. *Perspect Plant Ecol Evol Syst* 13:137–150. <https://doi.org/10.1016/j.ppees.2011.03.003>
- Herbertsson L, Lindström SAM, Rundlöf M et al (2016) Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic Appl Ecol*. <https://doi.org/10.1016/j.baae.2016.05.001>
- Hesse M, Waha M (1989) A new look at the acetolysis method. *Plant Syst Evol* 163:147–152
- Hicks DM, Ouvrard P, Baldock KCR et al (2016) Food for pollinators: quantification of the nectar and pollen resources of urban flower meadows. *PLoS ONE* 11:e0158117. <https://doi.org/10.1371/journal.pone.0158117>
- Holzschuh A, Steffan-Dewenter I, Tscharrntke T (2008) Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* 117:354–361. <https://doi.org/10.1111/j.2007.0030-1299.16303.x>

- 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>
- Kennedy CM, Lonsdorf E, Neel MC et al (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol Lett* 16:584–599. <https://doi.org/10.1111/ele.12082>
- Kleijn D, Winfree R, Bartomeus I et al (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat Commun* 6:7414. <https://doi.org/10.1038/ncomms8414>
- Le Féon V, Schermann-Legionnet A, Delettre Y et al (2010) Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. *Agric Ecosyst Environ* 137:143–150. <https://doi.org/10.1016/j.agee.2010.01.015>
- Le Roi A, Walot T, Thirion M, et al. (2010) Programme Agro-environnemental en Région Wallonne: MAE9—Bande de parcelles aménagées
- Leonhardt SD, Blüthgen N (2012) The same, but different: pollen foraging in honeybee and bumblebee colonies. *Apidologie* 43:449–464. <https://doi.org/10.1007/s13592-011-0112-y>
- Liolios V, Tananaki C, Dimou M et al (2016) Ranking pollen from bee plants according to their protein contribution to honey bees. *J Apic Res*. <https://doi.org/10.1080/00218839.2016.1173353>
- M’Gonigle LK, Ponisio LC, Cutler K, Kremen C (2015) Habitat restoration promotes pollinator persistence and colonization in intensively managed agriculture. *Ecol Appl* 25:1557–1565. <https://doi.org/10.1890/14-1863.1>
- Merckx T, Feber RE, Riordan P et al (2009) Optimizing the biodiversity gain from agri-environment schemes. *Agric Ecosyst Environ* 130:177–182. <https://doi.org/10.1016/j.agee.2009.01.006>
- Michener CD (2007) *The Bees of the world*, 2nd edn. Johns Hopkins, Baltimore
- Mitchell MGE, Bennett EM, Gonzalez A (2013) Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps. *Ecosystems* 16:894–908. <https://doi.org/10.1007/s10021-013-9647-2>
- Moerman R, Vanderplanck M, Fournier D et al (2017) Pollen nutrients better explain bumblebee colony development than pollen diversity. *Insect Conserv Divers*. <https://doi.org/10.1111/icad.12213>
- Moquet L, Mayer C, Michez D et al (2015) Early spring floral foraging resources for pollinators in wet heathlands in Belgium. *J Insect Conserv* 19:837–848. <https://doi.org/10.1007/s10841-015-9802-5>
- Moquet L, Vanderplanck M, Moerman R et al (2017) Bumblebees depend on ericaceous species to survive in temperate heathlands. *Insect Conserv Divers* 10:78–93. <https://doi.org/10.1111/icad.12201>
- Müller A, Diener S, Schnyder S et al (2006) Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee-flower relationships. *Biol Conserv* 130:604–615. <https://doi.org/10.1016/j.biocon.2006.01.023>
- Natagriwal (2014) Liste des MAEC. <https://www.natagriwal.be/fr/mesures-agro-environnementales/liste-des-mae/fiches>. Accessed 2 Feb 2017
- Natagriwal (2016) Les methodes agroenvironnementales et climatiques du PwDR (2014–2020)
- Nicolson SW, Human H (2013) Chemical composition of the “low quality” pollen of sunflower (*Helianthus annuus*, Asteraceae). *Apidologie* 44:144–152. <https://doi.org/10.1007/s13592-012-0166-5>
- O’Rourke AT, Fitzpatrick Ú, Stout JC (2014) Spring foraging resources and the behaviour of pollinating insects in fixed dune ecosystems. *J Pollinat Ecol* 13:161–173
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Oosterbroek P (2006) *The European families of the diptera*. KNNV Publishing, Utrecht
- Osborne JL, Martin AP, Shortall CR et al (2008) Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *J Appl Ecol* 45:784–792. <https://doi.org/10.1111/j.1365-2664.2007.01359.x>
- Paini DR (2004) Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: a review. *Austral Ecol* 29:399–407. <https://doi.org/10.1111/j.1442-9993.2004.01376.x>
- Pauly A, Coppée I (2017) Abeilles et chardons. *Bull la Soc R belge d’entomologie* 153:155–159
- Pauly A, Rasmont P (2010) Les bourdons de la Belgique. In: Atlas Hymenopt. <http://www.atlashymenopter.a.net/page.asp?id=160>
- Pernal SF, Currie RW (2001) The influence of pollen quality on foraging behavior in honeybees (*Apis mellifera* L.). *Behav Ecol Sociobiol* 51:53–68. <https://doi.org/10.1007/s002650100412>
- Potts SG, Biesmeijer JC, Kremen C et al (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol* 25:345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Pyke GH, Balzer L (1985) Honey-bees: effects of the introduced honey-bee on Australian native bees: a report prepared for NSW National Parks & Wildlife Service. National Parks & Wildlife Service, Sydney

- Pywell RF, Warman EA, Sparks TH et al (2004) Assessing habitat quality for butterflies on intensively managed arable farmland. *Biol Conserv* 118:313–325. <https://doi.org/10.1016/j.biocon.2003.09.011>
- Pywell RF, Warman EA, Carvell C et al (2005) Providing foraging resources for bumblebees in intensively farmed landscapes. *Biol Conserv* 121:479–494. <https://doi.org/10.1016/j.biocon.2004.05.020>
- Pywell RF, Meek WR, Hulmes L et al (2011) Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes. *J Insect Conserv* 15:853–864. <https://doi.org/10.1007/s10841-011-9383-x>
- Rader R, Howlett BG, Cunningham SA et al (2012) Spatial and temporal variation in pollinator effectiveness: do unmanaged insects provide consistent pollination services to mass flowering crops? *J Appl Ecol* 49:126–134. <https://doi.org/10.1111/j.1365-2664.2011.02066.x>
- Rader R, Batomeus I, Garibaldi L et al (2015) Non-bee insects are important contributors to global crop pollination. *Proc Natl Acad Sci*. <https://doi.org/10.1073/pnas.1517092112>
- Rasmont P, Pauly A, Terzo M et al (2005) The survey of wild bees (Hymenoptera Apoidea) in Belgium and France. FAO, Roma
- Reille M (1992) Pollen et spores d'Europe et d'Afrique du nord. Laboratoire de botanique historique et palynologie, Marseille
- Reille M (1995) Pollen et spores d'Europe et d'Afrique du nord, supplément 1. Laboratoire de botanique historique et palynologie, Marseille
- Roulston TH, Goodell K (2011) The role of resources and risks in regulating wild bee populations. *Annu Rev Entomol* 56:293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>
- Ruedenauer FA, Spaethe J, Leonhardt SD (2016) Hungry for quality—individual bumblebees forage flexibly to collect high-quality pollen. *Behav Ecol Sociobiol* 70:1209–1217. <https://doi.org/10.1007/s00265-016-2129-8>
- Schellhorn NA, Gagic V, Bommarco R (2015) Time will tell: resource continuity bolsters ecosystem services. *Trends Ecol Evol* 30:524–530. <https://doi.org/10.1016/j.tree.2015.06.007>
- Scheper JA (2015) Promoting wild bees in European agricultural landscapes. Wageningen University, Alterra
- Scheper J, Bommarco R, Holzschuh A et al (2015) Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *J Appl Ecol* 52:1165–1175. <https://doi.org/10.1111/1365-2664.12479>
- Skinner B, Wilson D (2009) Colour identification guide to the moths of the British Isles: Macrolepidoptera, 3rd edn. Harley Books, Melbourne
- Sommaggio D (1999) Syrphidae: can they be used as environmental bioindicators? *Agric Ecosyst Environ* 74:343–356. [https://doi.org/10.1016/S0167-8809\(99\)00042-0](https://doi.org/10.1016/S0167-8809(99)00042-0)
- Somme L, Vanderplanck M, Michez D et al (2015) Pollen and nectar quality drive the major and minor floral choices of bumble bees. *Apidologie* 46:92–106. <https://doi.org/10.1007/s13592-014-0307-0>
- Spear DM, Silverman S, Forrester JRK (2016) Asteraceae pollen provisions protect *Osmia* mason bees (Hymenoptera: Megachilidae) from brood parasitism. *Am Nat* 187:797–803. <https://doi.org/10.1086/686241>
- Speight MCD (2016) Species accounts of European Syrphidae 2016. *Eur Syrphidae* 93:288
- Speight MCD, Sarthou J-P (2016) StN keys for the identification of the European species of various genera of Syrphidae (Diptera) 2016. *Eur Syrphidae* 92:129
- Speight MCD, Castella E, Sarthou JP, Vanappelghem C (2015) StN 2015. In: Vanappelghem C (eds) *Syrph the Net on CD*. Syrph the Net Publications, Dublin
- Ssymank A, Kearns CA, Pape T, Thompson FC (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>
- Stubbs A, Falk SJ (2002) British hoverflies: an illustrated identification guide. British Entomological and Natural History Society, Dorchester
- Sutter L, Jeanneret P, Bartual AM et al (2017) Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. *J Appl Ecol*. <https://doi.org/10.1111/1365-2664.12907>
- Tasei J-N, Aupinel P (2008) Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (*Bombus terrestris*, Hymenoptera: Apidae). *Apidologie* 39:397–409. <https://doi.org/10.1051/apido>
- Terzo M, Rasmont P (2007) MALVAS (Méthodes Agroenvironnementales Liées à la Valorisation des Abeilles Sauvages) Suivi, étude et vulgarisation sur l'interaction entre les MAE et les abeilles sauvages. Mons
- Terzo M, Rasmont P (2010) Catalogue et clé des sous-genres et espèces du genre *Bombus* de Belgique et du nord de la France (Hymenoptera, Apoidea).
- Tison J-M, de Foucault B (2014) Flora gallica. Biotope, Mèze

- Tolman T, Lewington R (2009) Collins butterfly guide: the most complete guide to the butterflies of Britain and Europe (collins guides). HarperCollins, London
- Unwin DM (1984) A key to the families of British beetles (reprint). *F Stud* 6:149–197
- Vanderplanck M, Moerman R, Rasmont P et al (2014) How does pollen chemistry impact development and feeding behaviour of polylectic bees? *PLoS ONE* 9:1–9. <https://doi.org/10.1371/journal.pone.0086209>
- Vanderplanck M, Declèves S, Roger N et al (2016) Is non-host pollen suitable for generalist bumblebees? *Insect Sci.* <https://doi.org/10.1111/1744-7917.12410>
- Verlinden L (1994) Faune de Belgique: Syrphides. Institut royal des Sciences naturelles de Belgique, Bruxelles
- Warren JM (2000) The role of white clover in the loss of diversity in grassland habitat restoration. *Restor Ecol* 8:318–323. <https://doi.org/10.1046/j.1526-100X.2000.80044.x>
- Westrich P, Schmidt K (1986) Methoden und anwendungsgebiete der pollenanalyse bei wildbienen (hymenoptera, Apoidea). *Linzer Biol Beitr* 18:341–360
- Willmer PG, Stone GN (2004) Behavioral, ecological, and physiological determinants of the activity patterns of bees. *Adv Study Behav* 34:347–466
- Wood TJ, Holland JM, Goulson D (2017) Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species. *J Appl Ecol* 54:323–333. <https://doi.org/10.1111/1365-2664.12718>