GfÖ Ecological Society of Germany, Austria and Switzerland

Basic and Applied Ecology 43 (2020) 52–63

Basic and Applied Ecology

www.elsevier.com/locate/baae

Grassland management for meadow birds in the Netherlands is unfavourable to pollinators

M.F. (Marco) Tanis[a], Leon Marshall[a,b], J.C. (Koos) Biesmeijer[a,c], Lisette van Kolfschoten[a,d,*]

[a]*Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands*
[b]*Agroecology and Pollination Group, Landscape Ecology & Plant Production Systems (LEPPS/EIB), Université Libre de Bruxelles (ULB), Avenue Franklin Roosevelt 50, 1050 Brussels, Belgium*
[c]*Institute of Environmental Sciences (CML), Leiden University, Einsteinweg 2, 2333 CC Leiden, The Netherlands*
[d]*Department of Plant Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, Uppsala SE-752 36, Sweden*

Received 6 March 2019; accepted 6 December 2019
Available online 16 December 2019

Abstract

Agricultural intensification and loss of semi-natural grassland have contributed to biodiversity decline, including pollinator species, in pastures around the world. To reverse the decline, agri-environmental schemes have been implemented, varying widely in effectiveness. In addition, many countries, including the Netherlands, have established nature reserves in which semi-natural grasslands are restored and are often managed for specific groups of species, e.g. meadow birds or plants. The effects of such measures on insect biodiversity are not well known but recent reports on the dramatic decline of insect biomass in nature reserves have put even more attention to the impact of land use and management on biodiversity. This study compares pollinator abundance and species richness in three common semi-natural grassland management types in the Netherlands: (1) hay meadows, (2) herb-rich grasslands and (3) meadow bird grasslands. Pollinator abundance and species richness were assessed in eleven study areas, each with all three management types present. Standardized transects, insect sampling within a standard 20 min time frame and plot-based flower surveys were used in spring and summer to assess the relationships between management regime, floral abundance and diversity and pollinator communities. The results show that meadow bird grasslands have lower pollinator abundance and diversity and a less unique pollinator assemblage than both other types. Moreover, flower abundance has a positive effect on pollinator abundance and flower diversity has a positive effect on pollinator species richness. These results indicate that meadow-bird grasslands are a comparatively unfavourable habitat for bees, hoverflies and butterflies, which may be explained by a lack of flowers as well as unsuitable mowing practices. Measures benefitting both insectivorous birds and flower-visiting insects, such as rotational mowing, could remediate this imbalance.

Keywords: Agricultural intensification; Insect decline; Meadow bird conservation; Mowing; Pollinators; Semi-natural grasslands

*Corresponding author.
E-mail addresses: marco_tanis@hotmail.com (M.F. Tanis), leon.marshall@naturalis.nl (L. Marshall), koos.biesmeijer@naturalis.nl (J.C. Biesmeijer), lisette.vankolfschoten@ebc.uu.se (L. van Kolfschoten).

https://doi.org/10.1016/j.baae.2019.12.002
1439-1791/

Introduction

Over the past decades, agriculture in Europe has rapidly intensified to increase productivity, causing widespread losses in farmland biodiversity (Matson, Parton, Power, & Swift, 1997; Krebs, Wilson, Bradbury, & Siriwardena, 1999; Benton, Vickery, & Wilson, 2003). Intensification has been linked to dramatic declines in the populations of farmland birds (Chamberlain, Fuller, Bunce, Duckworth, & Shrubb, 2000; Donald, Green, & Heath, 2001; Benton, Bryant, Cole, & Crick, 2002) and insects (Benton et al., 2002), as well as homogenization of communities (Gossner et al., 2016). Intensive agriculture is most likely responsible for insect declines in nature reserves embedded within the agricultural matrix, with a 75% decline in insect biomass over three decades in German nature reserves, (Hallmann et al., 2017) as a prime example. Agricultural intensification is therefore considered to be the main driver of biodiversity decline in Europe (Benton et al., 2003; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005; Potts et al., 2016).

Pollinators are one example of a declining group of insects (Thomas et al., 2004; Biesmeijer et al., 2006; Kosior et al., 2007; Goulson, Lye, & Darvill, 2008; Potts et al., 2010, 2016; Van Swaay et al., 2015). Pollinators, in particular bees, perform important ecosystem services. At least 75% of food crop species depend to some degree on animal pollination (Klein et al., 2007), while large and diverse pollinator communities have been shown to improve fruit set (Garibaldi et al., 2013; Winfree et al., 2018). Moreover, around 88% of all wild plant species depend on animal pollination (Ollerton, Winfree, & Tarrant, 2011), making pollinators crucial for ecosystem functioning.

A main driver of pollinator decline is land-use intensification, in particular the loss of semi-natural, extensively managed and nectar-rich grasslands (Osborne, Williams, & Corbet, 1991; Goulson, Hanley, Darvill, Ellis, & Knight, 2005; Goulson, Nicholls, Botías, & Rotheray, 2015; Van Swaay et al., 2015). These grasslands are a main habitat for pollinating insects, providing food and resources for reproduction, such as nesting sites for bees and host plants for butterfly larvae (Osborne et al., 1991; Van Swaay et al., 2015). The replacement of semi-natural habitat by monocultures of intensively managed grasslands has led to widespread habitat loss and fragmentation for pollinators, contributing to their declines (Potts et al., 2010).

To counter biodiversity decline in agricultural landscapes, agri-environment schemes (AES) have been implemented in many European countries. These schemes support farmers who adapt the management of their land to increase biodiversity, e.g. through extensification. The effectiveness of AES has been mixed (Kleijn et al., 2006; Batáry, Dicks, Kleijn, & Sutherland, 2015) and local increases in species diversity and abundance (Batáry et al., 2010) seem dependent on the structure and management of the surrounding landscape (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011; Batáry et al., 2015). Another approach often taken for the preservation of farmland biodiversity is to convert agricultural land into nature reserves. These subsidized reserves are typically managed to promote certain aspects of biodiversity, for instance focused on increasing breeding success of meadow birds (Ausden & Hirons, 2002). In the Netherlands, this approach has been successful for meadow birds. They show a positive trend in protected areas while they are declining on farmlands with specific AES targeted at increasing the number of meadow birds (van Egmond & de Koeijer, 2006). However, the effect of protected areas on insect abundance and diversity is not monitored and therefore largely unknown, except for butterflies and grasshoppers (Inter Provinciaal Overleg, 2018: see Appendix A). Given the importance of semi-natural grasslands for insects (Öckinger & Smith, 2007), as well as the functional role of insects as pollinators of wild flowers (Ollerton et al., 2011) and food source for birds (Beintema, Thissen, Tensen, & Visser, 1991), more knowledge on the effect of the different management types on the insect community is needed.

To fill part of this knowledge gap, we assessed abundance and species richness of pollinators and flowering plants in three different management types of protected areas in the Western part of the Netherlands: (1) hay meadows, (2) herb rich grasslands and (3) meadow bird grasslands, to determine the impact of semi-natural grassland management on pollinators. Specifically, we assessed the effect of grassland management on pollinator species richness, abundance and assemblage composition. We expected hay meadows to have the highest pollinator species richness and abundance, as well as the most diverse species composition. These grasslands are typically nutrient-poor, floristically rich and diverse and are mown late in the year (see Appendix B). Meadow bird grasslands, on the other hand, tend to be richer in nutrients, are often mown in June and were thus expected to be floristically poorer, have fewer flowers and consequently the lowest pollinator abundance and diversity of the three management types.

Material and methods

Study areas

“For this study, we selected 11 study areas each with three sites, one for each of the three management types. Areas were chosen from two adjacent regions called Het Groene Hart and Midden-Delfland, situated in west of the Netherlands (provinces of South-Holland and Utrecht; Fig.1). Both regions comprise wet grasslands on peat and clay intersected by ditches. The main activity is agriculture, particularly dairy farming. Both regions are also key breeding areas for meadow birds, which is why there are many nature reserves targeting meadow birds situated there. These reserves are managed as semi-natural grasslands with the goal of promoting species threatened by intensive farming. They are characterized by

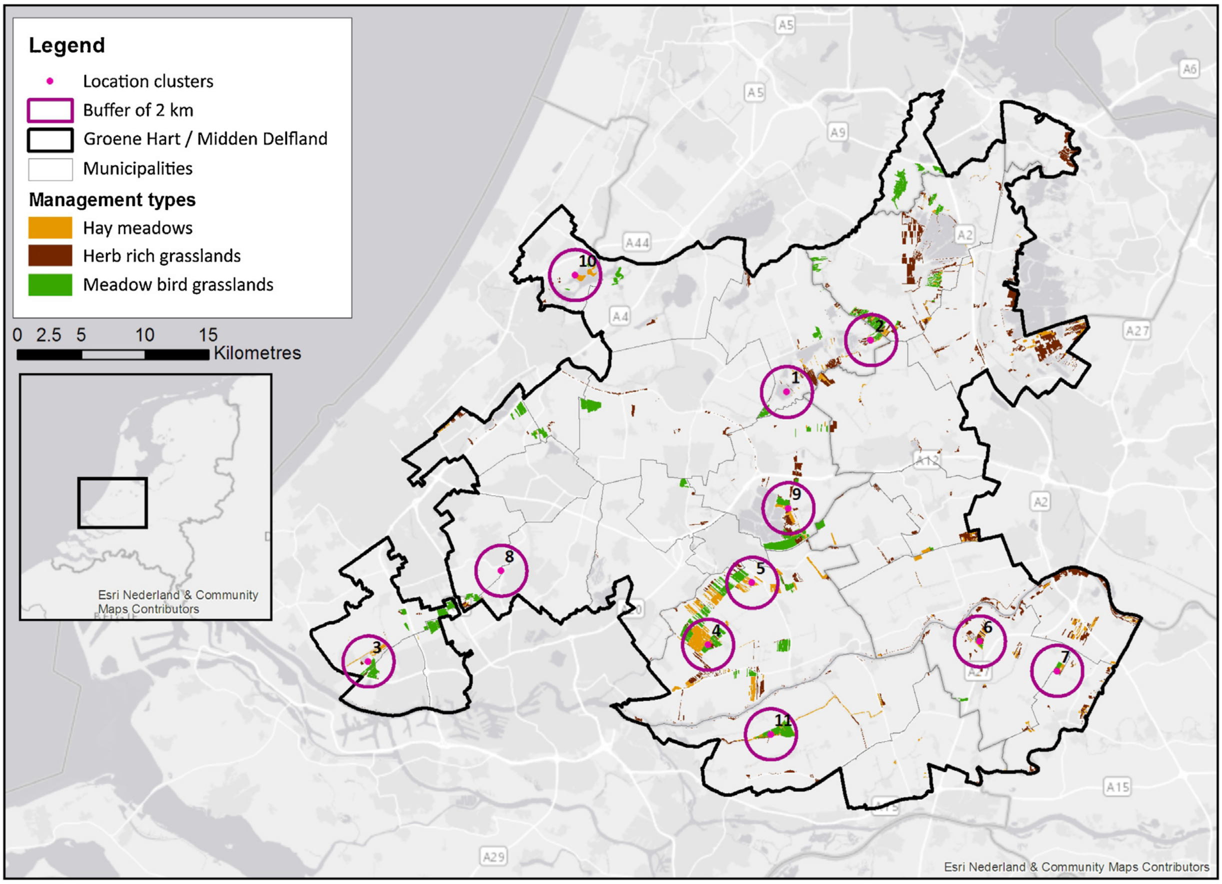

Fig. 1. Locations of the study areas within Het Groene Hart and Midden-Delfland regions of the Netherlands. Grasslands of all three management types were also present in study areas 1 and 8 but are not visible on the map due to their absence in the most recent version of the spatial dataset (Inter Provinciaal Overleg, 2018), as these were either relatively recent conversions from agriculture or unsubsidized grasslands.

high groundwater tables, periodical inundation, less intensive grazing and extended mowing dates. The reserves are owned by NGOs and the government, who decide on how the reserves are managed. Farmers who lease the land from these organisations carry out the management. Often, parcels, i.e. plots of land delineated by ditches, within these reserves are managed according to one of three types: hay meadows, which are botanically rich mesotrophic grasslands used for hay; meadow bird grasslands, which are grasslands rich in meadow birds where mowing is delayed until after the breeding season; and herb-rich grasslands, which are eutrophic grasslands often rich in herbs and thistles which do not meet the criteria for the other two types (see Appendix A; Appendix. B; Inter Provinciaal Overleg, 2018). The three management types often occur in close proximity to each other and are embedded in intensive agriculture. This creates an opportunity to study the effects of the three management types on insect pollinators, as we account for the spatial dependency of the study area, which is treated as a random effect in the analyses.

To select the study areas, the following was done: first, all parcels managed as hay meadows, herb-rich grasslands and meadow bird grasslands were mapped (Fig. 1; Appendix C). Study areas where all three management types were present within a 2-km radius were selected. Highly fragmented areas, defined as areas where at least one of the three management type was represented only by single parcels surrounded by different management, were excluded to prevent edge effects. Thirteen possible study areas met these criteria. From these thirteen areas, eleven were chosen, as we excluded two study areas from a cluster of four overlapping study areas. Finally, within each study area, three representative sites, one for each management type, were chosen randomly (see Appendix D).

Field sampling

Fieldwork was carried out in two periods in 2018, one in late spring, from 8 May to 11 June, and one in summer, from 29 June to 18 July. The three sites within a study area were always sampled within a timespan of three days and most often sampled on the same day. Pollinators were defined as member of Anthophila (bees), Rhopalocera (butterflies), Stratiomyidae (soldier flies) Syrphidae (hoverflies), and Zygaenidae (burnet moths).

At each site, transects of 200 m were set out to measure pollinator abundance. These transects consisted of four parallel sections of 50 m running lengthwise at 50–100 m distance from the field edge. Distance between the sections and the outer ditches were kept equal, dependent on the width of the parcel, with the sections being wider apart with increasing width. The minimum distance between sections was 5 m and the maximum 20 m (see Appendix E). For this reason, parcels narrower than 25 m and wider than 80 m were excluded.

Along these transects, every bee, butterfly, hoverfly and soldier fly easily identifiable to genus or species level in the field (see Appendix F) and seen in a virtual 5-m cage around the observer was identified and counted (this method is known as 'Pollard walk' and follows Van Swaay et al., 2018). After walking the transect, a timed search of twenty minutes was conducted within the area of the parcel enclosed between 50 and 100 m from the edge to obtain an estimate of species richness. During these 20 min, as many species as possible were identified or collected when not directly identifiable to species. To ensure sufficient activity, sampling of pollinators was only done between 10 a.m. and 5:30 p.m. Furthermore, weather conditions were recorded and always met the following criteria: no rain, wind speed below 6 Bft and either a temperature between 13 and 17 °C with less than 50% cloud cover, or a temperature above 17 °C (Van Swaay et al., 2018).

Collected specimens were identified using guides (bees: Falk & Lewington, 2017; hoverflies: Van Veen, 2004 and Schulten, 2018; soldier flies: Reemer, 2014) and online photo albums (Falk, 2018). All identifications were checked by John Smit of EIS-NL (European Invertebrate Survey – the Netherlands).

Besides recording pollinators, all flowering plants were identified to species in 1-m^2 plots set out every 10 m along the transect. All inflorescences were counted per species (Batáry et al., 2010; Appendix G) to estimate flower diversity and abundance. Flower and pollinator surveys were always done on the same day. The three grassland sites within a study area were normally sampled on the same day, but in cases of bad weather, up to five days apart.

Subsequently, pollinator species richness was determined by combining the species lists of the transect and the timed search per site and removing double observations (see Appendix H). Pollinator and flower abundance were determined as the total number of observations along the transects. Lastly, flower diversity was calculated with the Shannon diversity index (Shannon, 1948).

Data analysis

Three generalized linear mixed effects models (GLMM) were constructed, one for species richness, and two for abundance. For species richness response we pooled all species records across all sampling dates per site. For species abundance we analysed spring and summer samples separately because abundance is strongly influenced by season.

For pollinator species richness, a dataset was constructed containing the number of species found per parcel, the management type of each parcel and the averages of flower abundance, flower diversity, cloud cover, wind speed and temperature over the two sampling rounds as explanatory variables. We tested for collinearity between variables using variance inflation factors (VIFs) and removed all variables with VIFs > 1.4 (see Appendix I). Flower abundance was not included in the models of pollinator species richness, due to its correlation with management type. We fitted a poisson distributed model with management type, flower diversity, cloud cover, wind speed and temperature and all possible two-way interactions as explanatory variables.

For pollinator abundance spring and summer models were fitted separately and included management type, flower abundance, cloud cover, wind speed and temperature as explanatory variables. We again tested for collinearity between variables using variance inflation factors (VIFs) and removed all variables with VIFs >1.4 (see Appendix I). Flower diversity was excluded, as it was correlated with flower abundance. Both Poisson distributed models of the count data were overdispersed, therefore we used negative binomial models. All possible two-way interactions between the explanatory variables were again included.

Study area was included as a random effect and not as a fixed effect in all three models to account for the spatial dependency between parcels in the same area and because the inherent variation between the eleven study areas was not of interest. The final models for both pollinator species richness and abundance were selected based on the lowest AIC (Akaike, 1987) using dredge in the MuMIn package in R statistics (version 1.15.6; Barton, 2016). All models with a difference in AIC of less than 2 are presented in the results, since models within this range have similar strength in explaining the variation observed. Additionally, we tested for differences in flower abundance per management type with a Kruskal-Wallis test combined with a pairwise comparison test using Wilcoxon rank sum.

Finally, to visualize the community composition across types, Venn diagrams were constructed. These show how many pollinator species are unique to certain management types and how many species overlap between the management types. Non-metric multidimensional scaling (NMDS) was used to visualise the similarity in pollinator species composition between the different management types. Lastly, we calculated a beta-diversity value to see if any differences between sites were significant.

Results

Pollinator species richness

Four models (ΔAIC < 2) were selected explaining pollinator species richness (Table 1). Management type was included in all four models with a statistically clear effect: pollinator

Table 1. The best four GLMM models (ΔAIC < 2) explaining species richness. "Type" refers to which grassland types were tested. "HRB" = herb-rich grasslands, "HM" = hay meadows and "MBG" = meadow bird grasslands. The estimates (exp = exponential) refer to the rate ratios of a poisson distributed model. The 95% confidence interval of the log rate ratios are presented for each model covariate.

		Model 1				Model 2				Model 3				Model 4			
Explanatory variables		Est.	Est. (exp)	2.5%	97.5%	Est.	Est. (exp)	2.5%	97.5%	Est.	Est.(exp)	2.5%	97.5%	Est.	Est.(exp)	2.5%	97.5%
Type	HRG-HM	0.07	1.07	−0.16	0.29	0.03	1.03	−0.19	0.25	0.01	1.01	−0.22	0.23	0.01	1.01	−0.20	0.24
	MBG-HM	−0.27	0.76	−0.53	−0.01	−0.33	0.72	−0.58	−0.07	−0.35	0.70	−0.61	−0.09	−0.35	0.70	−0.62	−0.12
	MBG-HRG	−0.34	0.71	−0.59	−0.09	−0.36	0.70	−0.61	−0.11	−0.36	0.70	−0.61	−0.11	−0.36	0.70	−0.64	−0.13
Flower diversity		0.30	1.35	−0.01	0.62	X				X				X			
Temperature		−0.51	0.60	−0.89	−0.12	−0.46	0.63	−0.84	−0.02	−0.56	0.57	−0.96	−0.13	X			
Cloud cover		X				X				−0.26	0.77	−0.64	0.11	X			
AIC		186.2				186.7				187.8				188.1			

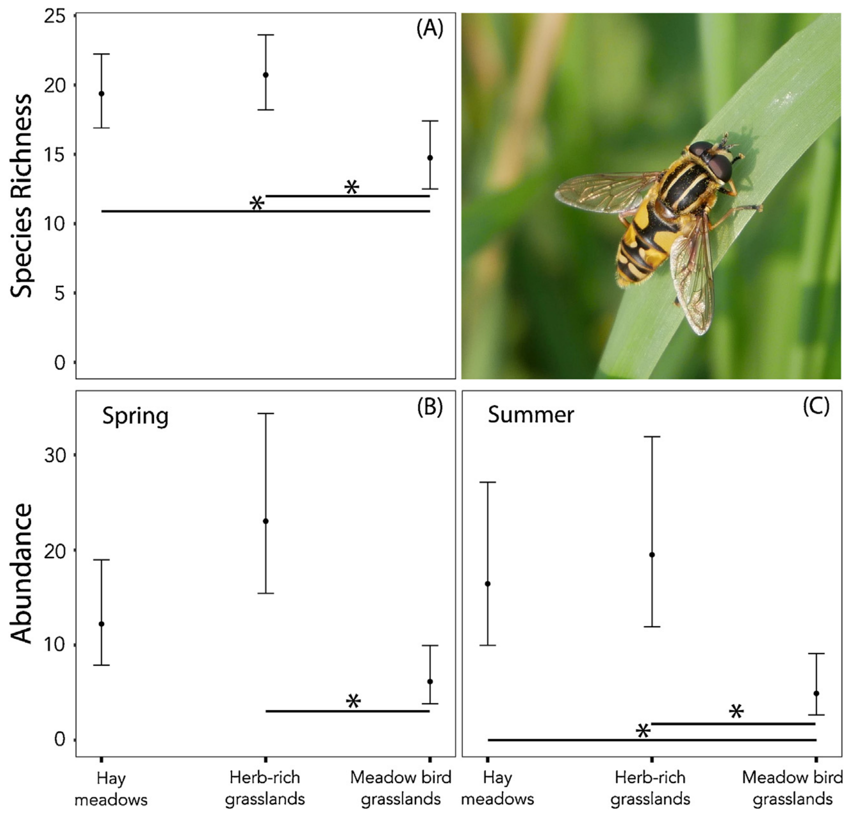

Fig. 2. Model coefficient estimates with 95% confidence intervals showing influence of grassland management on (A) pollinator species richness, (B) pollinator abundance in spring, and (C) summer per management type. All models represent the best model as chosen by AIC (see Tables 1–3). Asterisks represent pairwise comparison where the 95% confidence interval of the mean difference does not include zero. Photo of *Helophilus pendulus*, common hoverfly on these grasslands (photo by author).

species richness was lower on meadow bird grasslands than on other types, and similar on hay meadows and herb rich grasslands (Fig. 2A; Table 1). In addition, species richness increased with higher flower diversity (in one of the best models), lower temperatures (in three out of four models), and less cloud cover (in the third best model) (Table 1; Appendix J). No two-way interactions were included in the best models.

Pollinator abundance

Spring

The single best model included management type, flower abundance and cloud cover (Table 2). Again, management type had a statistically clear effect on pollinator abundance (Table 2): abundance was lower on meadow bird grasslands than on both other types, and was slightly higher on herb-rich grasslands than on hay meadows (Fig. 2B; Table 2). Moreover, flower abundance and cloud cover had a positive effect on pollinator abundance (Table 2; Appendix K).

Summer

All three top models explaining pollinator abundance in summer (Table 3) included a statistically clear effect of management type: meadow bird grasslands had lower pollinator abundance than both hay meadow and herb-rich grasslands

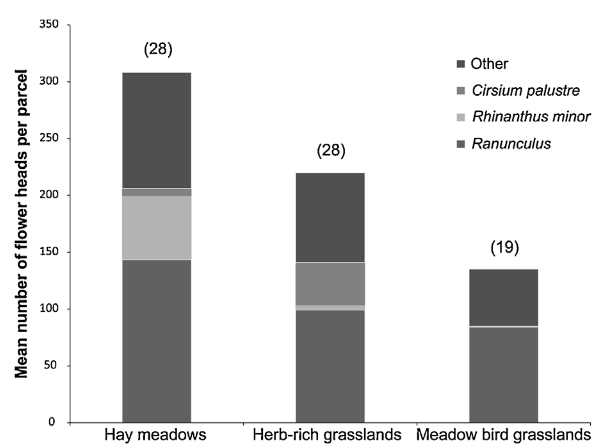

Fig. 3. Mean flower abundance of major forage plants per parcel across management types. In brackets: total number of plant species found per management type. Ranunculus species were pooled. Flower species with less than 30 flower heads per parcel were included in the category other (see Appendix L).

(Fig. 2C). Pollinator abundance was also slightly higher on herb-rich grasslands than on hay meadows. Flower abundance was included in all three models, with a clear positive effect on pollinator abundance. Furthermore, temperature was included in all models, and had a negative effect, just

Table 2. The best GLMM-Model (AIC) explaining spring pollinator abundance. "Type" refers to which grassland types were tested. "HRB" = herb-rich grasslands, "HM" = hay meadows and "MBG" = meadow bird grasslands. The estimates (exp = exponential) refer to the rate ratios of a negative binomial distributed model. The 95% confidence interval of the log rate ratios are presented for each model covariate.

	Model 1				
Explanatory variables		Estimate	Estimate. (exp)	2.5%	97.5%
	HRG-HM	0.63	1.88	−0.10	1.37
Type	MBG-HM	−0.68	0.50	−1.48	0.11
	MBG-HRG	−1.32	0.27	−2.06	−0.58
Flower abundance		1.40	4.05	0.31	2.48
Cloud cover		1.23	3.41	0.36	2.10
AIC		236.8			

as cloud cover, which was included in one model. No two-way interactions were included in the best models for both summer and spring.

Pollinator species composition

A total of 1688 pollinators were recorded or collected in this research. Of these, 447 were bees, 1146 hoverflies or soldier flies, and 95 butterflies. In total, 75 pollinator species were found, including 43 hoverfly species, 14 bee species, 12 butterfly species, 5 soldier fly species and one burnet moth species (see Appendix M). Almost half of the species (36 spp.) were found at least once in all management types. Of the remaining species, most were either unique to hay meadows (9 spp.), herb rich grasslands (11 spp.), or both (11 spp.), while meadow bird grasslands had only three unique species (Fig. 4A).

The NMDS (stress < 0.1) output shows that overall the pollinator communities were highly similar across the different types. This was confirmed by a beta-diversity analysis, which showed the communities to be similar ($p = 0.336$). Based on visual inspection of the output (Fig. 4B), the species community found on hay meadows possessed the most species-rich community, which is similar to that on herb-rich grasslands. Meadow bird grassland communities harbour a subset of the other two types (Fig. 4B).

Flower abundance & composition

Hay meadows had the highest flower abundance, followed by herb-rich grasslands and meadow bird grasslands (Fig. 3). The difference between the three types was significant (Kruskal Wallis test: $p < 0.05$), as was the difference between hay meadows and meadow bird grasslands ($p = 0.01$), but not between hay meadows and herb-rich grasslands ($p = 0.133$) or meadow bird grasslands and herb-rich grasslands ($p = 0.197$). The most abundant nectar plants on all three types of grasslands were members of the genus *Ranunculus*, consisting of *R. repens* and *R. acris* on meadow bird and herb-rich grasslands and of *R. flammula* and *R. acris* on hay meadows (see Appendix L). *Rhinanthus minor* was common on hay meadows, while *Cirsium palustre* was common on herb-rich grasslands. Meadow bird grasslands had no particular common species apart from *Ranunculus repens* (Fig. 3).

Discussion

The type of management applied on protected, semi-natural grasslands in the Netherlands affects both pollinator species richness and abundance as well as their floral resources. Meadow bird grasslands have fewer pollinator species, which occur in lower abundance, and fewer unique species than either herb-rich grasslands or hay meadows. These results indicate that meadow bird grasslands are a comparatively poor habitat for pollinators.

Impacts of mowing and grazing on pollinators

Mowing (or grazing) is necessary to maintain semi-natural grasslands, that otherwise develop into forests, which explains why all three management regimes include regular mowing or grazing. However, mowing can have a negative effect on arthropods (Morris, 2000), both through direct mortality (Humbert, Ghazoul, & Walter, 2009), and removal of forage and reproduction habitat (Cizek, Zamecnik, Tropek, Kocarek, & Konvicka, 2012). Partial mowing may mitigate these negative effects, as it leaves refuge areas (de Vries & Knotters, 2000; Humbert et al., 2009; Buri, Arlettaz, & Humbert, 2013) and improves grassland heterogeneity, which is advantageous to insects (Cizek et al., 2012) and birds (Verhulst, Kleijn, Loonen, Berendse, & Smit, 2011). Low intensity grazing also creates favourable habitat for pollinator species (Kruess & Tscharntke, 2002).

Both partial mowing and low intensity grazing are regularly used in hay meadows and herb-rich grassland management. Most meadow bird grasslands are mowed shortly after the end of the breeding season in late June. No insect refuges or flowers are left after mowing which renders large areas of meadow bird grasslands uninhabitable for pollinators after late June, precisely when pollinators are most abundant and diverse. Bees are particularly affected, as they need

Table 3. The best three GLMM models (ΔAIC<2) explaining summer pollinator abundance. “Type” refers to which grassland types were tested. “HRB” = herb-rich grasslands, “HM” = hay meadows and “MBG” = meadow bird grasslands. The estimates (exp = exponential) refer to the rate ratios of a negative binomial distributed model. The 95% confidence interval of the log rate ratios are presented for each model covariate.

	Model 1			Model 2				Model 3					
Explanatory variables		Est.	Est. (exp)	2.5%	97.5%	Est.	Est. (exp)	2.5%	97.5%	Est.	Est. (exp)	2.5%	97.5%
	HRG-HM	0.17	1.19	−0.65	0.99	0.22	1.25	−0.59	1.04	0.04	1.04	−0.80	0.89
Type	MBG-HM	−1.21	0.30	−2.18	−0.23	−1.19	0.30	−2.16	−0.23	−1.40	0.25	−2.43	−0.40
	MBG-HRG	−1.38	0.25	−2.36	−0.40	−1.42	0.24	−2.38	−0.45	−1.44	0.24	−2.41	−0.47
Flower abundance		2.34	10.42	0.74	3.95	2.41	11.12	0.87	3.95	2.21	9.16	0.66	3.77
Temperature		−2.72	0.07	−4.27	−1.16	−2.44	0.09	−3.99	−0.89	−3.07	0.05	−4.70	−1.43
Cloud cover		X				X				−0.68	0.51	−1.77	0.42
Wind speed		X				0.64	1.90	−0.35	1.63	X			
AIC		242.4				244.2				244.3			

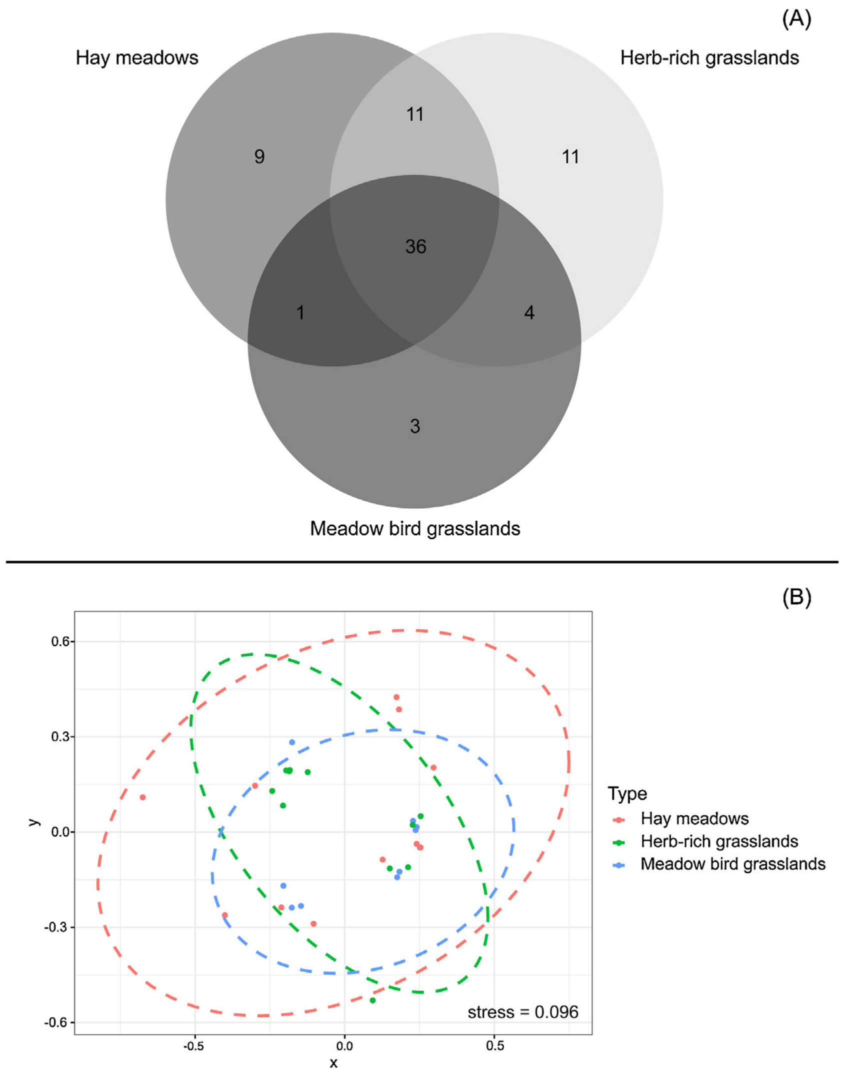

Fig. 4. Pollinator community structure in different grassland management types. (A) Venn diagram of the overlap in pollinator species. (B) Non-metric multidimensional scaling output for pollinator species community.

continuous forage in close proximity to their nests (Potts et al., 2010). Management of herb-rich grasslands and hay meadows, on the other hand, involves partial mowing or grazing (see Appendix B), which leaves part of the vegetation standing and thus supports pollinator populations throughout the year. This difference in mowing practice is the most likely explanation for the differences in pollinators between meadow bird grasslands and the other two types.

Lack of floral resources in meadow bird grasslands limits pollinators

Flower abundance and diversity are major factors shaping pollinator communities (Biesmeijer et al., 2006; Scheper et al., 2014). In our study, flower abundance had a positive effect on pollinator abundance and flower diversity on pollinator species richness. Of all the three management types, meadow bird grasslands have the lowest flower abundance and richness, possibly explaining why meadow bird grasslands are poor in pollinators.

In addition, floral composition of meadow bird grasslands was dominated by just two *Ranunculus* species, whereas many additional flower species were found in other grasslands. Thus, meadow bird grasslands constitute an extremely poor habitat and offer very limited choice to pollinators, with the exception of a small number of mobile hoverfly species. Hay meadows offer more choice, as a wide array of pollinator food plants are found regularly, e.g. *Rhinanthus minor*, *Lotus pedunculatus, Cardamine pratensis, Bellis perennis* and *Cerastium fontanum* (see Appendix M). This could explain why hay meadows have the most diverse pollinator communities. The third grassland management type, herb-rich grasslands, is also comparatively rich in pollinators. Here two excellent pollinator forage plants, *Cirsium palustre* and *Trifolium repens* (Vray, Lecocq, Roberts, & Rasmont, 2017), are often found. This may explain the similar pollinator abundance in hay meadows and herb-rich grasslands, despite hay meadows having on average more flowers.

A landscape suitable for pollinators?

Another result of this research is the apparent lack of bee species on all three types of grasslands. This is counter-intuitive, as pollinator diversity can be very high in open (semi-)natural grasslands (Öckinger & Smith, 2007) and many bee species used to thrive in these same regions (Peeters et al., 2012). However, the sampled grasslands tend to be part of open, monotonous landscapes, because of the overall intensification and homogenization of grasslands combined with the focus of nature management mostly on meadow birds, which favour breeding in open landscapes to avoid predators. They lack the small landscape elements, trees, buildings and dykes, (see Appendix N) that bees need as nesting sites and refuges, as the meadows themselves are often too wet for nesting. Wild bees need nesting sites in close proximity to their feeding sites, due to their relatively small forage range (Zurbuchen et al., 2010). Notably, the only species which was found regularly, *Macropis europaea*, is able to nest in wet soil (Peeters et al., 2012). The combination of large-scale mowing and landscape homogenization has led to low and intermittent forage resources, low nesting availability with a severely impoverished bee community as a result (only 14 of 51 possible bee species; Appendix O).

The apparent lack of bee species is in stark contrast with the hoverfly species found (43 of 66 possible species). The reason may be that all fly species are highly mobile and that many have aquatic larvae, and can reproduce in the ditches and wetlands in the area. The same goes for 8 of the 12 butterfly species found, which are migratory species unlikely to be bound to the grasslands. In contrast, species likely to be affected by mowing, such as stationary butterflies (4 species, out of 8 possible species) and phytophagous hoverfly species (3 species) were rarely found.

The pollinator fauna on all three types of grasslands consists almost completely of common species; only two recorded species could be considered of conservation priority: *Bombus jonellus* (Reemer, 2018) and *Neoascia geniculata* (Reemer et al., 2009). This indicates that the species of conservation interest have disappeared completely, even though they could still be found in these areas a few decades ago (Peeters et al., 2012; Reemer et al., 2009).

A place for pollinators in (meadow bird) grassland reserves in the Netherlands?

The Grassland nature reserves may fail to provide essential habitat requirements for bees and a number of hoverfly and butterfly species, with meadow bird grasslands being particularly poor habitat for bees. Currently about a third of the nature reserves in the Groene Hart and Midden-Delfland are managed as meadow bird grassland (App B.). This focus on a few species of meadow birds has clearly been detrimental to pollinating insects, which, under current regimes, must be conserved elsewhere. This may, however, be detrimental to the meadow birds themselves, as a varied pollinator community could also benefit them. Many flowering plants depend on insects for their pollination and seed set (Ollerton et al., 2011), and risk pollination failure if pollinators are lacking (Wilcock & Neiland, 2002). Therefore, a varied and abundant community of pollinators is important for maintaining flower-rich grasslands, which are rich in insects, an important food source for meadow birds (Beintema et al., 1991; Vickery et al., 2001).

Our results also emphasize the relative importance of hay meadows and herb-rich grasslands. Herb-rich grasslands are often seen as an intermediate stage towards another type of 'nature'. Nonetheless, pollinators are most abundant in these grasslands, likely due to the presence of *Cirsium* thistles. Hay meadows, on the other hand, harbour diverse plant communities on which the most diverse pollinator communities are maintained, underlining their importance for pollinator conservation.

In summary, our findings highlight the need for a more balanced approach for the conservation of wet grasslands of the Netherlands and their fauna, as they indicate that a single focus on meadow birds is unfavourable for bees, butterflies and hoverflies. An improvement could be to: include a larger proportion of hay meadows in the landscape, implement rotational mowing and increase heterogeneity within and between parcels. This could lead to a friendlier landscape for both birds and pollinators, which would be broadly supported by societal partners in the Netherlands (see Deltaplan Biodiversity Recovery, 2018).

Acknowledgements

We thank Maarten van't Zelfde for the map, Nieke Knoben for general assistance, Vincent Kalkman for helping develop the idea and John Smit for specimen identification. Thanks also to Ninouk Vermeer, Sietse Kleinjan, Rene Garskamp (Zuid-Hollands Landschap), Martijn van Schie, Guus van Oostwaard and Gerard Haak (Natuurmonumenten), Cor Noorman (Groenzoom), Nico de Bruyn and Casper Zuyderduin (Staatsbosbeheer) for access to the sites and their assistance, and to Lucas Alferink, Dimmy van Ruiten and Hans van der Kooij for field assistance.

Appendix A-P Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.baae.2019.12.002.

References

Akaike, H. (1987). Factor analysis and AIC. In *Selected papers of Hirotugu Akaike*. pp. 371–386. New York, NY: Springer.

Ausden, M., & Hirons, G. J. M. (2002). Grassland nature reserves for breeding wading birds in England and the implications for the ESA agri-environment scheme. *Biological Conservation*, *106*(2), 279–291.

Barton, K. (2016). *MuMIn: Multi-model inference. R package version 1.15.6*.

Batáry, P., Baldi, A., Sarospataki, M., Kohler, F., Verhulst, J., Knop, E., ... & Kleijn, D. (2010). Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agriculture, Ecosystems & Environment*, *136*(1–2), 35–39.

Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, *29*(4), 1006–1016.

Benton, T. G., Bryant, D. M., Cole, L., & Crick, H. Q. (2002). Linking agricultural practice to insect and bird populations: A historical study over three decades. *Journal of Applied Ecology*, *39*(4), 673–687.

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, *18*(4), 182–188.

Beintema, A. J., Thissen, J. B., Tensen, D., & Visser, G. H. (1991). Feeding ecology of charadriiform chicks in agricultural grassland. In *Breeding ecology of meadow birds (Charadriiformes); Implications for conservation and management*. , 85.

Biesmeijer, J. C., Roberts, S. P., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., ... & Settele, J. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, *313*(5785), 351–354.

Buri, P., Arlettaz, R., & Humbert, J. Y. (2013). Delaying mowing and leaving uncut refuges boosts orthopterans in extensively managed meadows: Evidence drawn from field-scale experimentation. *Agriculture, Ecosystems & Environment*, *181*, 22–30.

Chamberlain, D. E., Fuller, R. J., Bunce, R. G. H., Duckworth, J. C., & Shrubb, M. (2000). Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, *37*(5), 771–788.

Cizek, O., Zamecnik, J., Tropek, R., Kocarek, P., & Konvicka, M. (2012). Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. *Journal of Insect Conservation*, *16*(2), 215–226.

Deltaplan Biodiversity Recovery, 2018. https://www.samenvoorbiodiversiteit.nl.

de Vries, M. W., & Knotters, J. C. (2000). Effecten van gefaseerd maaibeheer op de ongewervelde fauna van graslanden. *De Levende Natuur*, *101*(2), 37–41.

Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*(1462), 25–29.

Falk, S., & Lewington, R. (2017). *Veldgids Bijen voor Nederland en Vlaanderen*. Utrecht/Antwerpen: Kosmos Uitgevers.

Falk, S. (24-10-2018). retrieved on 24-10-2018, from Flickr: https://www.flickr.com/photos/63075200@N07/albums/with/72157629248800794.

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., ... & Bartomeus, I. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, *339*(6127), 1608–1611.

Gossner, M. M., Lewinsohn, T. M., Kahl, T., Grassein, F., Boch, S., Prati, D., ... & Arndt, H. (2016). Land-use intensification causes multitrophic homogenization of grassland communities. *Nature*, *540*(7632), 266.

Goulson, D., Hanley, M. E., Darvill, B., Ellis, J. S., & Knight, M. E. (2005). Causes of rarity in bumblebees. *Biological Conservation*, *122*(1), 1–8.

Goulson, D., Lye, G. C., & Darvill, B. (2008). Decline and conservation of bumble bees. *Annual Review of Entomology*, *53*, 191–208.

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., ... & Goulson, D. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, *12*(10), e0185809.

Humbert, J. Y., Ghazoul, J., & Walter, T. (2009). Meadow harvesting techniques and their impacts on field fauna. *Agriculture, Ecosystems & Environment*, *130*(1–2), 1–8.

Inter Provinciaal Overleg. (2018). *Informatiemodel natuurbeheer (IMNAB): Index Natuur en Landschap*. https://www.bij12.nl/onderwerpen/natuur-en-landschap

Kleijn, D., Baquero, R. A., Clough, Y., Diaz, M., De Esteban, J., Fernández, F., ... & Knop, E. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, *9*(3), 243–254.

Kleijn, D., Rundlöf, M., Scheper, J., Smith, H. G., & Tscharntke, T. (2011). Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology & Evolution*, *26*(9), 474–481.

Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., ... & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London B: Biological Sciences*, *274*(1608), 303–313.

Kosior, A., Celary, W., Olejniczak, P., Fijał, J., Król, W., Solarz, W., ... & Płonka, P. (2007). The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. *Oryx*, *41*(1), 79–88.

Krebs, J. R., Wilson, J. D., Bradbury, R. B., & Siriwardena, G. M. (1999). The second silent spring? *Nature*, *400*(6745), 611.

Kruess, A., & Tscharntke, T. (2002). Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology*, *16*(6), 1570–1580.

Matson, P. A., Parton, W. J., Power, A. G., & Swift, M. J. (1997). Agricultural intensification and ecosystem properties. *Science*, *277*(5325), 504–509.

Morris, M. G. (2000). The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation*, *95*(2), 129–142.

Öckinger, E., & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, *44*(1), 50–59.

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326.

Osborne, J. L., Williams, I. H., & Corbet, S. A. (1991). Bees, pollination and habitat change in the European community. *Bee World*, *72*(3), 99–116.

Peeters, T. M., Nieuwenhuijsen, H., Smit, J., Van der Meer, F., Raemakers, I. P., Heitmans, W. R. B., . . . & Roos, M. (2012). *De Nederlandse bijen (Hymenoptera: Apidae S.L.)Nederlandse Fauna 11*. Naturalis Biodiversity Center & European Invertebrate Survey.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353.

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., . . . & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220.

Reemer, M., Renema, W., Van Steenis, W., Zeegers, T., Barendregt, A., Smit, J. T., . . . & Van der Leij, L. J. J. M. (2009). *De Nederlandse Zweefvliegen (Diptera: Syrphidae). Nederlandse Fauna 8*. Nationaal Natuurhistorisch Museum Naturalis & European Invertebrate Survey.

Reemer, M. (2014). *Veldtabel wapen-en bastvliegen van Nederland*. Leiden: EIS Kenniscentrum Insecten.

Reemer, M. (2018). *Basisrapport voor de Rode Lijst Bijen*. Leiden: EIS Kenniscentrum Insecten.

Scheper, J., Reemer, M., van Kats, R., Ozinga, W. A., van der Linden, G. T., Schaminée, J. H., . . . & Kleijn, D. (2014). Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proceedings of the National Academy of Sciences*, *111*(49), 17552–17557.

Schulten, A. (2018). *Zweefvliegen van Nederland en België*. 's Gravenland: Jeugdbondsuitgeverij.

Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, *27*(3), 379–423.

Thomas, J. A., Telfer, M. G., Roy, D. B., Preston, C. D., Greenwood, J. J. D., Asher, J., . . . & Lawton, J. H. (2004). Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, *303*(5665), 1879–1881.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters*, *8*(8), 857–874.

van Egmond, P. M., & de Koeijer, T. J. (2006). Weidevogelbeheer bij agrariers en terreinbeheerders. *De Levende Natuur*, *107*(3), 118–120.

Van Swaay, C., Van Strien, A., Aghababyan, K., Astrom, S., Botham, M., Brereton, T., . . . & Feldmann, R. (2015). *The european butterfly indicator for grassland species: 1990–2013*.

Van Swaay, C. A. M., Bos-Groenendijk, G. I., van Deijk, J. R., van Grunsven, R. H. A., Kok, J. M., Huskens, K., . . . & Poot, M. (2018). *Handleiding landelijke meetnetten vlinders, libellen en nachtvlinders. Rapport VS2018.011*. De Vlinderstichting, Wageningen.

Van Veen, M. P. (2004). *Hoverflies of Northwest Europe: Identification keys to the Syrphidae*. Utrecht: KNNV Publishing.

Vickery, J. A., Tallowin, J. R., Feber, R. E., Asteraki, E. J., Atkinson, P. W., Fuller, R. J., . . . & Brown, V. K. (2001). The management of lowland neutral grasslands in Britain: Effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology*, *38*(3), 647–664.

Vray, S., Lecocq, T., Roberts, S. P., & Rasmont, P. (2017). Endangered by laws: Potential consequences of regulations against thistles on bumblebee conservation. *Annales de la Société entomologique de France (NS)*, *53*(1), 33–41. Taylor & Francis.

Verhulst, J., Kleijn, D., Loonen, W., Berendse, F., & Smit, C. (2011). Seasonal distribution of meadow birds in relation to in-field heterogeneity and management. *Agriculture, Ecosystems & Environment*, *142*(3–4), 161–166.

Wilcock, C., & Neiland, R. (2002). Pollination failure in plants: Why it happens and when it matters. *Trends in Plant Science*, *7*(6), 270–277.

Winfree, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., & Gibbs, J. (2018). Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science*, *359*(6377), 791–793.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., & Dorn, S. (2010). Maximum foraging ranges in solitary bees: Only few individuals have the capability to cover long foraging distances. *Biological Conservation*, *143*(3), 669–676.