

# Forest hoverfly community collapse: Abundance and species richness drop over four decades

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## Abstract

1. To study insect decline, an important threat to biodiversity, long-term datasets are needed. Here we present a study of hoverfly (Diptera: Syrphidae) abundance and diversity in a Dutch forest, surrounded by other forests, and analyse the variation in insect numbers over four decades.
2. Between 1982 and 2021, abundance decreased by 80%. Until 1990, abundance showed a strong decrease of 10.9% per year, mainly in nationally rare species with carnivorous larvae exposed to air. From 1990, abundance stabilised, whereas from 2000, a second period of strong decline of 9.0% per year occurred, mainly in very common species.
3. Species richness also declined strongly between 1979 and 2021: the total number of species observed in five monitoring days dropped by 44% over those 43 years. The characteristic set of dry-forest hoverfly species disappeared over four decades.
4. The number of nationally rare species observed at the study site declined from 19 to 9 early on, in a period (1979–1984) that coincided with intense nitrogen input and acidification caused by agriculture in the same region. The more recent decline is likely also caused by factors from outside the forest, as forest management and conditions remained constant.
5. Continued influx of nutrients and pesticides at a regional level, as well as climate change are possible causes of the decline. Research is needed to quantify their relative effects.

## KEYWORDS

decreased diversity, defaunation, forest, insect decline, Syrphidae

## INTRODUCTION

Animal diversity is decreasing in the world (Dirzo et al., 2014; Goulson, 2019) and Red Lists are a formalised tool to illustrate declines (IUCN, 2019). Knowledge on former and present populations is needed for Red Lists, and with well-studied species such as mammals and birds this tool has been successful. However, datasets to evaluate declines of insects are less available, due to the enormous diversity in these smaller species, the specialism required to identify

them, and as a consequence fewer people to monitor species groups. Since 2000 long-term research in insects illustrated declines in distribution in well-studied insects such as butterflies, bumblebees, moths, bees, and flies (Biesmeijer et al., 2006; Bourn & Thomas, 2002; Carvell et al., 2006; Conrad et al., 2006; Shortall et al., 2009). In more recent years, many case studies and reviews prove that the distribution and abundance of many other insect groups have declined by 30%–75% within a few decades (Bell et al., 2020; Dirzo et al., 2014; Fox et al., 2014; Grabener et al., 2020; Hallmann et al., 2017, 2020;

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Homburg et al., 2019; van Strien et al., 2019). Society realises that these insects are an essential link in the food web, and that they facilitate essential processes such as pollination and nutrient recycling (Habel & Schmitt, 2018; Raven & Wagner, 2021).

Because so many insect species exist, with a wide range of life history strategies, a decline in numbers can be explained with many hypotheses (Wagner et al., 2021), for instance, due to the disappearance of a specific habitat or landscape structure (Keil et al., 2011; Moquet et al., 2018; Seibold et al., 2019). Many hypotheses focus on general changes in the environment by human activities like nutrient inputs, spread of pesticides used in agriculture, drought and climate change (Christopher et al., 2021; Wagner et al., 2021), pointing at regional rather than local drivers (Habel et al., 2019; Seibold et al., 2019). Mostly these hypotheses cannot be tested due to the absence of datasets on the spatial and temporal variation in insect abundance and/or equally detailed information on relevant environmental factors (but see Hallmann & Jongejans, 2021 for a spatiotemporal analysis of effects of weather, land use and micropollutants on aquatic insects). However, as an alternative, traits of species with either stable or declining populations can be analysed to see whether these are consistent with hypothesised mechanisms due to certain environmental changes. For instance, Bowler et al. (2021) found that German dragonfly species that are generally known to be cold-adapted or preferring standing waters had decreasing distributional ranges, whereas those of warm-adapted and stream-preferring species increased.

Within Diptera, the hoverflies (Syrphidae) are among the best investigated families with many records. They are mostly not difficult to identify, and the species are observed by relatively many people, resulting in knowledge of their distribution and links with ecosystems (e.g. Reemer et al., 2009; Speight et al., 2020). Biesmeijer et al. (2006) compared pre- and post-1980 species richness of Syrphidae (and bees) per  $10 \times 10$  km grid cells with rarefaction. They did find comparable numbers of grid cells with decreasing and increasing species richness of Syrphidae in the Netherlands. However, they found a significant decrease in rare species and an increase in common species. More recently, Powney et al. (2019) studied the distribution of Syrphidae in Britain and concluded that the average occupancy of 214 hoverfly species in 1 km grid cells decreased in the period 1986–2010. However, little is known about changes in the number of individuals. Only Gatter et al. (2020) and Hallmann et al. (2021) published results on abundance of hoverflies at a single location over time. These authors only had data from the start and the end of their research periods. They calculate a decline of 80% over 40 and 25 years, respectively.

In this article, we present a long-term (1979–2021) study on hoverfly abundance and species richness in a Dutch forest ('Boeschoten') with little human disturbance for many decades, meaning that local drivers for changes are absent. Most previous insect studies concentrate on agricultural landscapes and miss combined data on abundance and species richness over several decades. There are relatively few studies on insect trends in forests (e.g. Habel et al., 2019; Roth et al., 2021), while forest-dwelling hoverflies remain particularly understudied. Preliminary results from Boeschoten are discussed by Barendregt (2001). Here, the data are extended 21 years and used to answer the following research

questions: Are there trends in forest hoverfly abundance and species richness, and do trends vary over the years? Do trends depend on species traits? Can environmental drivers of change be indicated based on the traits of declining hoverfly species?

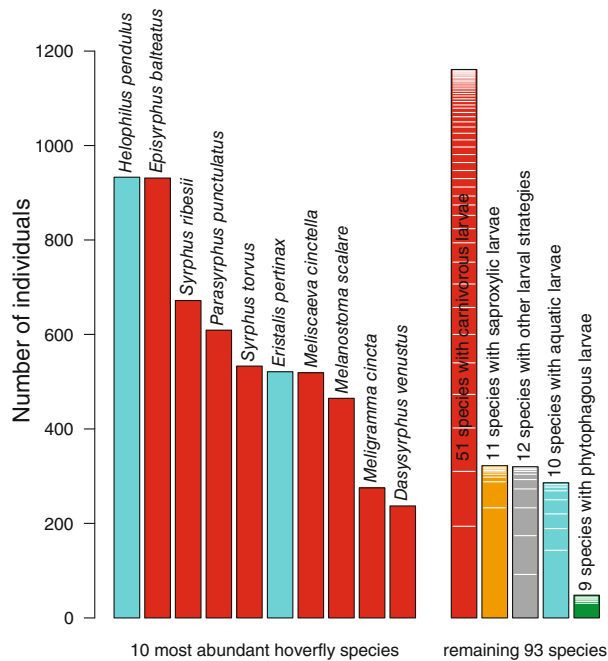
## MATERIALS AND METHODS

### Study site

Boeschoten is an (extensively used) agricultural enclave within large mixed deciduous-coniferous forests in the centre of The Netherlands, 40–50 m a.m.s., west of the village of Garderen ( $52^{\circ}13'24''N$ ,  $5^{\circ}40'31''E$ ). The sandy soil is very dry and open water is only available in some small pools. The selected forest sections (ca. 20 ha) are partly dominated by *Quercus* for hundreds of years, partly former heathlands planted with *Pinus* and *Pseudotsuga* in the period 1900–1950. Locally, other tree species (*Fagus*, *Larix*) dominate; in the shrub layer, *Sorbus*, *Amelanchier*, and *Rhamnus* are important. In the ground layer, *Vaccinium myrtillus* dominates at many locations, next to some *Rubus* along paths. The forest did not change for at least 60 years in land use or management: only the trees matured further (no new planting) and in the ground layer the vegetation changed in some species after the period of intense acid rain ('Waldsterben') around 1985, when *Galium saxatile* and *Deschampsia flexuosa* decreased and *Rubus* increased in abundance. This forest was selected because it was representative of forests in the Veluwe region, because it was (and still is) a rather homogeneous old forest (i.e. no large roads, no disturbance due to recreation, no nearby intensive agriculture), and because of its proximity to the home of the first author. The hoverfly community in this forest did not appear to be richer or poorer than in other parts of the Veluwe region in 1975–1985. This Veluwe region ( $50 \times 25$  km) is the largest forest-heathland area in the Netherlands. In the surroundings of Boeschoten, there are some smaller arable fields; 5 km to the south and west there is intensive livestock farming.

### Data collection

Within the 'Boeschoten' forest, the same permanent route of approximately 3 km has been inspected for the presence of hoverflies (Diptera: Syrphidae) in the second half of the morning (10:00–13:00), for a duration of approximately 2 h. The forest was included up to 30 m from the route to obtain a complete inventory of the ecosystem; a complete list of all present hoverflies was aimed for each time. Monitoring was done only on sunny days, independent from temperature. All observed specimens have been counted and collected with an insect net, species and sex identified in the field, or preserved for identification later on (with e.g. Barendregt, 1978; van der Goot, 1981; Bot & van de Meutter, 2019; Speight et al., 2020). Vouchers are deposited in the first author's collection. During the survey, *Syrphus nitidifrons* was found for the second time ever, only after the original description by Becker in 1921 (Barendregt, 1983). While



**FIGURE 1** Distribution of 7832 observed individuals over 103 hoverfly species, based on monitoring in 1982–2021. Separately shown are the top 10 most abundant species (together 72.7% of the individuals; red bars indicate species with carnivorous larvae, cyan bars species with aquatic larvae). The remaining 93 species are grouped per larval type. White lines separate those remaining species within their groups. Counts per species can be found in Appendix E of Data S1

monitoring started in 1974, it was only from 1979 onwards that complete species lists were kept, and from 1982 onwards that the number of observed individuals per species was recorded (Figure 1). The sampling days were irregularly distributed over the years (Appendix A of Data S1) and throughout the whole flight season (April–October, with September slightly under-sampled).

## Abundance trend analysis

Daily totals of the number of observed hoverflies were analysed to test whether there was a trend in total hoverfly abundance over the years. As total hoverfly counts showed a clear bimodal pattern throughout the season (with peaks in spring and summer), we first fitted a generalised additive model (GAM) to all daily counts as a function of the day of the year (irrespective of year and weather). This GAM was then used to predict day-of-the-year-specific relative hoverfly abundance ('season score'), from 0 in winter to 1 at the time of the highest peak (summer). This season score, and a continuous year variable, were included in a generalised linear mixed-effect model of the daily counts (Figure 2). Year was also a random (categorical) factor to account for the nestedness of multiple visits within a year. We assumed a negative binomial distribution, as the variance of the daily counts was much larger than the mean.

Because flight activity of Syrphidae is known to vary with weather (Gilbert, 1985), we also explored models that included sets of

weather variables, to study whether potential weather effects on daily counts could have affected trend estimates. These weather variables and analyses are explained in detail in Appendix B of Data S1.

All visits since 1982 were included in the hoverfly abundance trend analysis (Figure 3). A large number of these visits date from the first 9 years (139 = 55% in 1982–1990). No visits were done in the periods 2001–2009 and 2012–2019, resulting in two temporal gaps in the dataset. In addition to the main analysis of all data in the 1982–2021 period, we also fitted the same type of model to the 1982–1990, 1982–2000 and 1982–2011 subsets (to study whether the trend estimate changed with the increasing length of the time series; Didham et al., 2020) and 1990–2000 and 2000–2021 subsets (to see whether trends in total counts differed among time periods). We also performed trend analyses of total hoverfly abundance separately for data from the spring peak period (19 April to 3 June) and summer peak period (13 June to 8 September). Hoverflies can be univoltine or bi- or polyvoltine, and we studied the combined abundance trend of all univoltine species, as well as that of the group of bi- and polyvoltine species.

The same model structure was used to quantify trends for subsets of the species. For instance, all species were categorised (according to the non-zero fuzzy scores of Speight et al., 2020) into one of five larval feeding strategies: carnivorous (mainly on aphids; living in either trees and shrubs or the herb layer), phytophagous, saproxylic, aquatic, and 'other' (see Appendix C of Data S1). The 'other' group included species with larvae living in rotting plants, manure, or insect nests. Species were also grouped depending on whether their larvae are mainly (i) exposed to water, (ii) exposed to air, or (iii) hidden within plants or insect nests. Furthermore, we fitted separate models for rare (including very rare and fairly rare), common (including fairly common), and very common species in the Netherlands. Rarity was based on classification by Reemer et al. (2009). And finally, abundance trends were analysed separately for the 10 hoverfly species with the highest number of individuals observed over the 1982–2021 period (Table 1).

## Species richness trend analysis

For each of the 105 hoverfly species recorded since 1979, we noted whether it was observed in each of six time periods: 1979–1982, 1983, 1984–1987, 1988–1994, 1995–2011, and 2020–2021. These combinations of years were chosen to minimise the variation among the periods with respect to the number of monitoring days: 45, 45, 45, 45, 36, and 63 days, respectively. This allowed us to visualise the turnover of species.

Since monitoring days were differently distributed over the seasons in different years, while also the number of monitoring days differed between study years, standard methods for estimating and comparing species richness among years were not applicable (i.e. the assumptions of methods like Chao2 (Béguinot, 2014; Chao et al., 2017) were not met). Instead, we visually inspected differences in species accumulation curves between years (starting in 1979), and performed simple statistical trend analyses, as explained below (Figure 4). First, we created year-specific species accumulation curves by randomly reordering the monitoring days of a particular year and

**TABLE 1** Summary of abundance trend analyses for different subsets of the hoverfly species and time periods.

Hoverfly group	Annual abundance change				Spp	Indiv	Spring (%)
	1982–1990	1982–2000	1982–2011	1982–2021			
Total	–10.9% <sup>**</sup> (–14.3% to –7.4%)	–2.0% <sup>ns</sup> (–3.8% to –0.1%)	–2.5% <sup>(*)</sup> (–3.7% to –1.2%)	–4.1% <sup>***</sup> (–4.8% to –3.3%)	103	7832	44
Larval feeding strategies							
Carnivorous	–14.4% <sup>***</sup> (–17.5% to –11.1%)	–3.1% <sup>ns</sup> (–5.1% to –1.1%)	–4.0% <sup>*</sup> (–5.5% to –2.5%)	–4.4% <sup>***</sup> (–5.2% to –3.6%)	59	5402	53
Aquatic	–1.9% <sup>ns</sup> (–9.0% to +5.8%)	–1.2% <sup>ns</sup> (–3.8% to +1.4%)	–0.9% <sup>ns</sup> (–2.7% to +0.9%)	–3.8% <sup>***</sup> (–4.9% to –2.7%)	12	1740	24
Saproxyllic	+1.9% <sup>ns</sup> (–6.8% to +11.4%)	+6.7% <sup>*</sup> (+3.3% to +10.1%)	+2.2% <sup>ns</sup> (–0.7% to +5.2%)	–0.6% <sup>ns</sup> (–2.2% to +1.0%)	11	322	25
Phytophagous	–10.4% <sup>ns</sup> (–19.3% to –0.6%)	–1.2% <sup>ns</sup> (–5.2% to +2.9%)	+5.4% <sup>*</sup> (+2.8% to +8.1%)	+1.1% <sup>ns</sup> (–0.6% to +2.9%)	9	48	79
Other feeding strategies	+1.2% <sup>ns</sup> (–6.2% to +9.2%)	–0.3% <sup>ns</sup> (–3.2% to +2.7%)	+1.1% <sup>ns</sup> (–1.0% to +3.3%)	–3.8% <sup>*</sup> (–5.4% to –2.2%)	12	320	31
Larval exposure							
Exposed to air	–14.4% <sup>***</sup> (–17.6% to –11.2%)	–3.3% <sup>ns</sup> (–5.3% to –1.3%)	–4.1% <sup>**</sup> (–5.5% to –2.6%)	–4.5% <sup>***</sup> (–5.2% to –3.7%)	52	5336	52
Exposed to water	–1.9% <sup>ns</sup> (–9.0% to +5.8%)	–1.2% <sup>ns</sup> (–3.8% to +1.4%)	–0.9% <sup>ns</sup> (–2.7% to +0.9%)	–3.8% <sup>***</sup> (–4.9% to –2.7%)	12	1740	24
Hidden in plants, soil or insect nests	–2.6% <sup>ns</sup> (–8.7% to +4.0%)	+1.4% <sup>ns</sup> (–1.5% to +4.4%)	+2.6% <sup>ns</sup> (+0.6% to +4.6%)	–1.4% <sup>ns</sup> (–2.7% to –0.1%)	39	756	35
Peak period							
Spring (19 Apr to 3 Jun)	–14.9% <sup>***</sup> (–18.6% to –11.0%)	–4.4% <sup>*</sup> (–6.5% to –2.2%)	–3.4% <sup>*</sup> (–4.8% to –2.0%)	–3.9% <sup>***</sup> (–4.6% to –3.1%)	78	3326	100
Summer (13 Jun to 8 Sep)	–11.9% <sup>*</sup> (–16.6% to –7.0%)	+1.5% <sup>ns</sup> (–0.9% to +3.9%)	–0.5% <sup>ns</sup> (–2.7% to +1.7%)	–5.1% <sup>***</sup> (–6.3% to –3.8%)	75	4193	0
Generations per year							
1	–16.6% <sup>***</sup> (–19.6% to –13.4%)	–1.0% <sup>ns</sup> (–3.6% to +1.7%)	–2.0% <sup>ns</sup> (–3.8% to –0.1%)	–2.9% <sup>**</sup> (–3.9% to –2.0%)	51	1691	83
2 or 3	–7.5% <sup>ns</sup> (–12.9% to –1.8%)	–1.8% <sup>ns</sup> (–4.1% to +0.5%)	–2.5% <sup>ns</sup> (–4.0% to –0.9%)	–4.3% <sup>***</sup> (–5.2% to –3.4%)	52	6141	34
Abundance classes							
Rare	–26.8% <sup>***</sup> (–31.8% to –21.4%)	–7.6% <sup>(*)</sup> (–11.4% to –3.7%)	–5.1% <sup>(*)</sup> (–7.9% to –2.2%)	–5.1% <sup>**</sup> (–6.8% to –3.5%)	26	287	64
Common	–13.5% <sup>*</sup> (–18.3% to –8.3%)	–3.3% <sup>ns</sup> (–5.6% to –0.9%)	–3.6% <sup>*</sup> (–5.3% to –2.0%)	–4.6% <sup>***</sup> (–5.5% to –3.7%)	56	2928	59
Very common	–5.1% <sup>ns</sup> (–9.6% to –0.4%)	–0.3% <sup>ns</sup> (–2.3% to +1.8%)	–1.2% <sup>ns</sup> (–2.7% to +0.2%)	–3.6% <sup>***</sup> (–4.5% to –2.8%)	21	4617	34
Ten most abundant spp							
<i>Helophilus pendulus</i>	+1.4% <sup>ns</sup> (–6.6% to +10.0%)	–3.8% <sup>ns</sup> (–7.3% to –0.2%)	–2.7% <sup>ns</sup> (–5.0% to –0.3%)	–4.7% <sup>***</sup> (–6.1% to –3.3%)	1	933	26
<i>Episyrphus balteatus</i>	–14.8% <sup>(*)</sup> (–22.0% to –6.9%)	–3.0% <sup>ns</sup> (–5.6% to –0.3%)	–4.6% <sup>(*)</sup> (–8.9% to +0.0%)	–0.6% <sup>ns</sup> (–1.7% to +0.5%)	1	931	3
<i>Syrphus ribesii</i>	–15.8% <sup>ns</sup> (–24.7% to –5.8%)	–9.2% <sup>*</sup> (–13.1% to –5.2%)	–11.5% <sup>**</sup> (–14.8% to –8.0%)	–4.5% <sup>*</sup> (–6.2% to –2.6%)	1	672	49
<i>Parasyrphus punctulatus</i>	–28.1% <sup>ns</sup> (–42.2% to –10.6%)	–0.6% <sup>ns</sup> (–7.1% to +6.4%)	–3.4% <sup>ns</sup> (–8.0% to +1.4%)	–1.3% <sup>ns</sup> (–3.9% to +1.3%)	1	609	99
<i>Syrphus torvus</i>	–19.7% <sup>ns</sup> (–33.9% to –2.4%)	–4.0% <sup>ns</sup> (–11.0% to +3.5%)	–10.0% <sup>ns</sup> (–15.6% to –4.0%)	–10.3% <sup>**</sup> (–13.5% to –6.9%)	1	533	44

(Continues)

**TABLE 1** (Continued)

Hoverfly group	Annual abundance change				Spp	Indiv	Spring (%)
	1982–1990	1982–2000	1982–2011	1982–2021			
<i>Eristalis pertinax</i>	–6.1% <sup>ns</sup> (–16.1% to +5.1%)	+1.8% <sup>ns</sup> (–1.9% to +5.6%)	+1.2% <sup>ns</sup> (–1.3% to +3.8%)	–2.1% <sup>ns</sup> (–3.7% to –0.6%)	1	521	26
<i>Meliscaeva cinctella</i>	+1.5% <sup>ns</sup> (–22.4% to +32.9%)	<b>–17.1%<sup>***</sup></b> (–17.4% to –16.8%)	<b>–11.8%<sup>***</sup></b> (–12.1% to –11.5%)	<b>–15.7%<sup>**</sup></b> (–20.7% to –10.4%)	1	519	25
<i>Melanostoma scalare</i>	+2.5% <sup>ns</sup> (–10.6% to +17.5%)	+3.0% <sup>ns</sup> (–2.4% to +8.8%)	–0.8% <sup>ns</sup> (–4.5% to +3.2%)	–3.3% <sup>ns</sup> (–5.4% to –1.1%)	1	465	89
<i>Meligramma cincta</i>	–5.8% <sup>ns</sup> (–13.3% to +2.5%)	<b>+12.3%<sup>**</sup></b> (+7.4% to +17.4%)	+4.2% <sup>ns</sup> (+0.0% to +8.6%)	–2.4% <sup>ns</sup> (–4.9% to +0.1%)	1	275	80
<i>Dasysyrphus venustus</i>	+6.8% <sup>ns</sup> (–2.7% to +17.2%)	–9.8% <sup>(*)</sup> (–14.7% to –4.5%)	–4.5% <sup>ns</sup> (–7.9% to –1.0%)	<b>–8.8%<sup>**</sup></b> (–11.5% to –6.0%)	1	237	98

Note: Significant mean annual changes in abundances are indicated in bold. Confidence intervals are based on  $\pm 1$  standard error of the year slope in the regression analyses.

Abbreviations: Indiv, number of individuals; Spp, number of species; spring, percentage of individuals caught before 4 June.

noted the total number of unique species with increasing number of monitoring days. This random shuffling of the monitoring days was done a 1000 times per year, after which mean curves per year were plotted. We did this separately for (i) the whole season, (ii) the spring peak period, and (iii) the summer peak period.

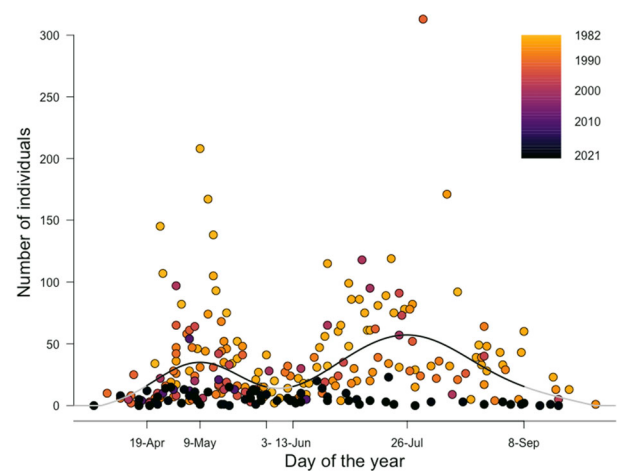
To statistically test for potential trends in species richness, we used the number of unique species observed during five randomly chosen monitoring days as a year-specific statistic of species richness. Generalised linear regression models (with Poisson distribution) were fitted using the mean estimates of year-specific species-richness in 5 days, based on a 1000 random draws of 5 days per year (Figure 5). The choice for a threshold of 5 days was the result of balancing the need for multiple monitoring days to arrive at a robust estimate of species richness, and the aim to include as many years as possible in the analyses (i.e. only excluding years with less than five monitoring days). We also plotted species accumulation curves based on the spring peak days only, and on the Summer peak days only. For each of the peak periods the same minimum of five monitoring days was required for a year to be included in a trend analysis of species richness.

## RESULTS

In 254 days (1982–2021), 7832 specimens of hoverflies have been observed, that is, 31 specimens per visit on average. The raw data are available in Appendix E of Data S1. Since 1979, a total of 105 species have been observed (31% of the Dutch hoverfly fauna). Most of the species are characteristic for this forest ecosystem, often rare species in the Netherlands.

### Abundance trends

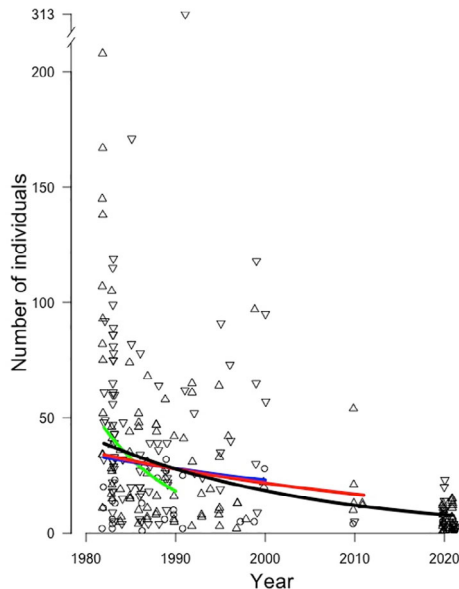
The GAM fitted to the daily total number of hoverfly individuals (as a function of day of the year), indeed showed a bimodal pattern with spring and summer peak periods (Figure 2). The GAM was then applied



**FIGURE 2** Total number of hoverfly individuals at each of 254 monitoring days in the 1982–2021 period. A generalised additive model (GAM) fitted to the daily totals (irrespective of year) predicts a bimodal pattern. The black sections of the line indicate the spring (19 April to 3 June) and summer (13 June to 8 September) peak periods for which the GAM predicts more than 15 individuals per day. A log-scale version of this graph can be found in Appendix D of Data S1

to predict relative hoverfly abundance ('season score') at the day-of-the-year of each of the 254 sampling dates (so irrespective of weather or year). This season score and a continuous year variable were included in a generalised linear mixed-effect model of the daily counts. Including weather variables like the precipitation, sun hours and temperature (i) at the time of the monitoring, (ii) in the 30 days leading up to each monitoring day, and (iii) in the preceding month of April, resulted in significant effects of most of these weather variables on the total hoverfly abundance (Appendix B of Data S1). However, these weather variables could not explain the negative trend in abundance; the effect of the continuous 'year' variable remained significantly negative in all cases. We therefore choose to continue without weather variables.

Separate models were fitted on increasingly large temporal subsets of the data to study how new years of data affected the total



**FIGURE 3** Number of hoverfly individuals caught during 254 days of monitoring. Four different models were fitted on different temporal subsets of the data (starting in 1982 and ending in 1990, 2000, 2011 and 2021). The fitted models account for seasonal patterns (Figure 2) and a random effect of year. Annual change (%) and statistical significance can be found in Table 1. Upward-pointing triangles indicate days during the spring-peak period, downward-pointing triangles indicate days during the summer-peak period. Monitoring days outside those periods are indicated with circles. A log-scale version of this graph can be found in Appendix D of the Data S1

abundance trend starting in 1982. The strongest decline was seen over the first 9 years (1982–1990): a statistically very significant  $-10.9\%$  per year (with a  $-14.3\%$  to  $-7.4\% \pm 1$  standard error range; Figure 3; significance levels given in Table 1). Daily numbers, although highly variable, appeared to stabilise and even slightly improve in the 1990s, leading to non-significant decline over the 1982–2000 period:  $-2.0\%$  per year ( $-3.8\%$  to  $-0.1\%$ ). Adding the low daily numbers of 2010 and 2011 reduced the trend to a nearly significant  $-2.5\%$  per year ( $-3.7\%$  to  $-1.2\%$ ). Over the entire study period (so including the very low numbers in 2020 and 2021), there was a highly significant decline in individuals:  $-4.1\%$  per year ( $-4.8\%$  to  $-3.3\%$ ), resulting in an overall loss in individuals of 80% over 40 years ( $-85\%$  to  $-74\%$ ).

We observed that this decline is varying over time. As indicated earlier, the strongest loss was found over the first 9 years, resulting in a loss of 60% over 9 years ( $-71\%$  to  $-46\%$ ). Looking at the 1990–2000 period, we see that the total number of hoverfly individuals was stable (i.e. slightly positive trend, but not significantly:  $+0.9\%$  per year [ $-3.1\%$  to  $+5.0\%$ ]; Table 2). On the other hand, the 2000–2021 period showed a highly significant negative decline of  $-9.0\%$  per year ( $-10.6\%$  to  $-7.3\%$ ). The differences in trend between observations in spring and summer were small: both followed the time-period-specific trend based on all monitoring days (Table 2), while in the 2000–2021 period, the negative trend was stronger in summer ( $-11.9\%$  per year [ $-15.2\%$  to  $-8.5\%$ ]) than in spring ( $-7.1\%$  [ $-9.4\%$  to  $-4.8\%$ ]). In the 1980s, the abundance of univoltine species declined more strongly

than that of species with more than one generation per year (Table 1). However, with new years of data added, the differences in the negative trends of these two groups of species disappeared.

To test whether species traits influenced responses, different subsets were compiled based on the feeding strategy of larvae (Speight et al., 2020) (Table 1). The larvae of the species have different food strategies; in the Boeschoten forest ecosystem 57% of the species is carnivorous (mainly on aphids), others are, for example, saprophagous, phytophagous, or aquatic filterers. It appeared that the main group with carnivorous larvae in trees/shrubs declined already before 1991 ( $-17.4\%$  per year [ $-20.9\%$  to  $-13.8\%$ ]) and this significant decline continued over the entire 1982–2021 period with  $-4.5\%$  per year ( $-5.3\%$  to  $-3.6\%$ ), more than in the whole dataset (Table 1). The carnivorous larvae in grass-herbs declined especially in the period 2010–2021 ( $-13.5\%$  per year [ $-17.2\%$  to  $-9.6\%$ ]); the same is true for the aquatic larvae ( $-9.4\%$  [ $-12.9\%$  to  $-5.8\%$ ]). The saproxylic larval type did not increase in abundance over time over the whole period of study ( $-0.6\%$  [ $-2.2\%$  to  $+1.0\%$ ]), but did increase significantly in the first half (1982–2000;  $+6.7\%$  [ $+3.3\%$  to  $+10.1\%$ ]). No trend could be detected in the other feeding strategies; this might come from the restricted number of observations in other strategies.

Additionally, subsets were compiled for larval exposure: in contact with air or water, or hidden in plants, soil or insect nests. The results indicate that the hidden larvae show no significant change, whereas the larvae exposed to air or water declined significantly with  $-4.5\%$  ( $-5.2\%$  to  $-3.7\%$ ) and  $-3.8\%$  ( $-4.9\%$  to  $-2.7\%$ ), respectively (Table 1).

Next, we fitted separate models for nationally rare (including very rare and fairly rare), common (including fairly common), and very common species. Rare can be used as an indication of special conditions and very common of the conditions that are generally present. The rare species especially declined significantly in the period 1982–1990 with  $-26.8\%$  ( $-31.8\%$  to  $-21.4\%$ ), and to 2021 with  $-5.1\%$  per year ( $-6.8\%$  to  $-3.5\%$ ; Table 1). The common species declined in all periods, and to 2021 by  $-4.6\%$  per year ( $-5.5\%$  to  $-3.7\%$ ), whereas the very common species only declined significantly when the whole study period was considered:  $-3.6\%$  per year ( $-4.5\%$  to  $-2.8\%$ ). Over any period of time studied starting 1982, the (relative) decline in numbers of rare species is the strongest, those of very common species the weakest. To illustrate that species respond individually in time, we added in Table 1 the modelling results of the 10 most abundant species from Figure 1.

## Species richness trends

The results in species richness from Boeschoten are summarised in Table 3. There appears to be a decline in species richness from 1979–1982 to 2021, with especially low values in 2020–2021. The full description with all species (including larval type) is presented in Appendix C of Data S1, also showing some species turnover: while 24 out of the total of 105 species were no longer recorded after 1987, 13 species were first recorded after 1987. During the last 20 years, no species with southern distribution were new to the forest. No shift in phenology was detected.

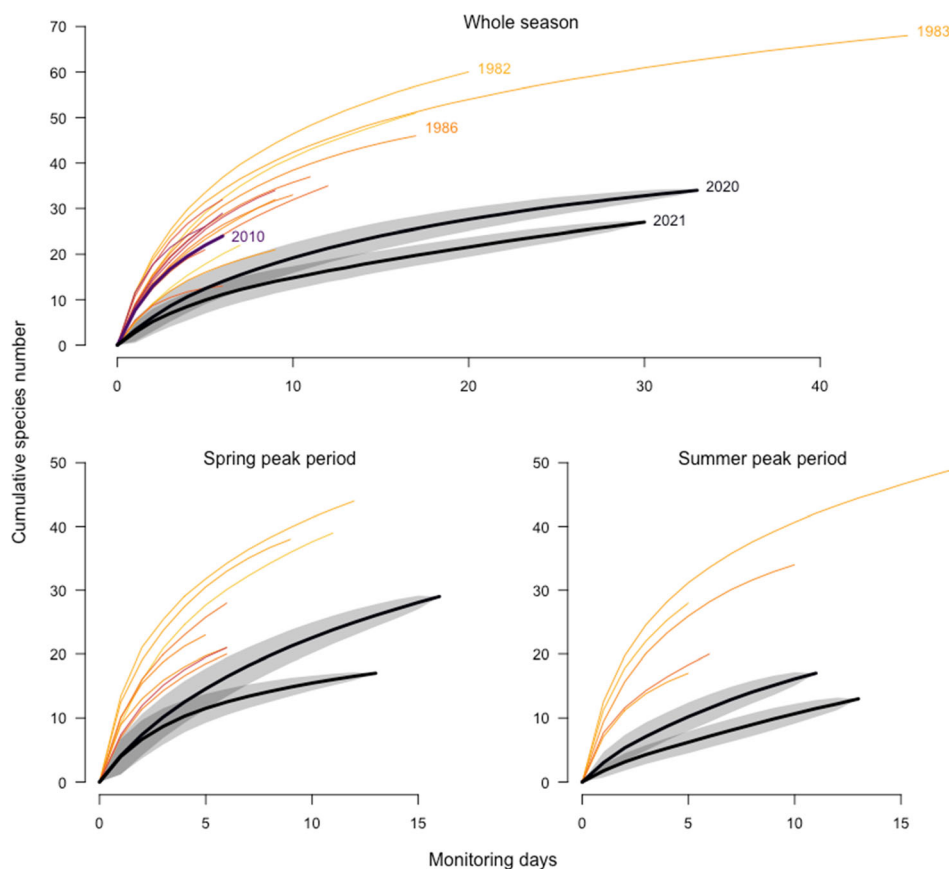
**TABLE 2** Summary of abundance trend analyses of the total number of hoverflies per monitoring day for three time periods.

Hoverfly counts	Annual abundance change		
	1982–1990	1990–2000	2000–2021
Total	<b>–10.9%**</b> (–14.3% to –7.4%)	+0.9% <sup>ns</sup> (–3.1% to +5.0%)	<b>–9.0%***</b> (–10.6% to –7.3%)
Spring (19 Apr to 3 Jun)	<b>–14.9%***</b> (–18.6% to –11.0%)	+1.4% <sup>ns</sup> (–3.4% to +6.4%)	<b>–7.1%**</b> (–9.4% to –4.8%)
Summer (13 Jun to 8 Sep)	<b>–11.9%*</b> (–16.6% to –7.0%)	–1.1% <sup>ns</sup> (–6.3% to +4.3%)	<b>–11.9%***</b> (–15.2% to –8.5%)

Note: Significant mean annual changes in abundances are indicated in bold. Confidence intervals are based on  $\pm 1$  standard error of the year slope in the regression analyses.

**TABLE 3** Summary of species numbers in six time periods with comparable numbers of sampling days

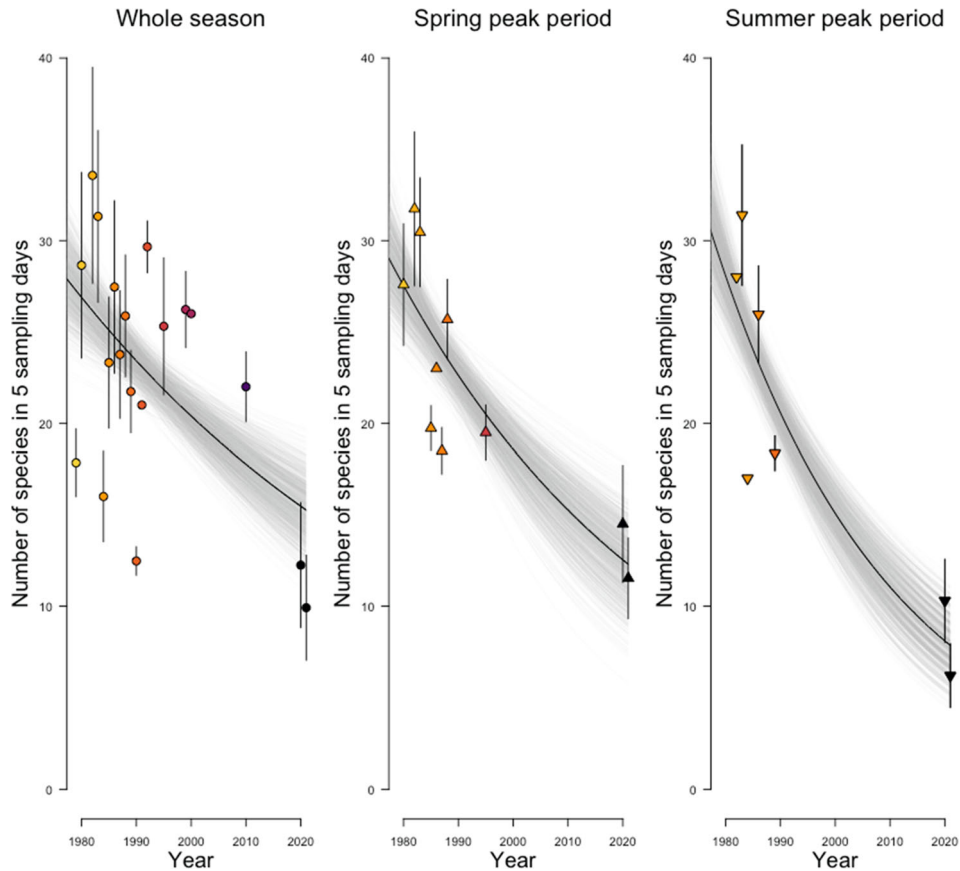
Time period	1979–1982	1983	1984–1987	1988–1994	1995–2011	2020–2021
Number of days	45	45	45	45	36	63
Number of (fairly) rare species	19	15	9	9	5	4
Number of (very) common species	54	54	50	51	50	39
Total number of species	73	69	59	60	55	43



**FIGURE 4** Species accumulation plots. Per year the order of the monitoring days is shuffled a 1000 times. Each curve shows the year-specific mean accumulation of species over an increasing number of monitoring days. For 2020 and 2021, the shaded area gives the standard deviation among the 1000 perturbations. Only years with at least five monitoring days are shown (either for the whole season in the top panel or per season in the bottom panels). Colours as in Figure 2. The axes in the bottom right panel are cut off (to be directly comparable to the bottom left panel). However, the 1983 summer curve continues to go up to 58 species in 29 sampling days. See Figure A1 (Appendix A) for the number of sampling days in each of the years

To test the species richness by year, species accumulation plots were calculated (Figure 4). For 2020 and 2021, the shaded area gives the standard deviation among the permutations. Especially the early years (to 1986) show higher species numbers with

increasing number of sampling days, whereas the Year 2021 is absolutely on a lower level, including the standard deviation. The results for spring or summer give the same results as the whole year.



**FIGURE 5** Species richness (in five randomly selected sampling days) estimated as a function of year. Error bars represent standard deviations calculated from a 1000 estimates based on separate random draws of sets of five sampling days. The black, interrupted line represents a regression model fitted to the mean estimates ( $-1.37\%$  [ $-1.81\%$  to  $-0.94\%$ ],  $-1.96\%$  [ $-2.52\%$  to  $-1.40\%$ ] and  $-3.03\%$  [ $-3.74\%$  to  $-2.33\%$ ] per year for the whole season, spring peak period and summer peak period, respectively, with  $p < 0.002$  in all cases). The 1000 grey lines in each panel represent models fitted to each of the 1000 sets of obtained estimates by randomly selecting five sampling days each time. In all cases, the year effect was negative. In 95.5%, 99.8% and 100% of the cases, respectively, the  $p$ -value was below 0.05

Another test was whether the cumulative number of unique species encountered in five sampling days showed a significant trend over the years, or not (Figure 5). The results indicate a significant lowering in species numbers of  $-0.9\%$  per year; the results from spring and summer periods are comparable (even more significant).

## DISCUSSION

The recent defaunation in invertebrates is summarised by Shortall et al. (2009), Dirzo et al. (2014) and van Klink et al. (2020), among many others. On Diptera, few studies are published, but they too show strong declines. Most insect studies focus on agricultural land or open natural habitats, while forests have been found to be the most species-rich ecosystems (Seibold et al., 2019; Uhler et al., 2021). Here, we add a detailed long-term case study on the hoverflies at Boeschoten forest, reporting significant declines in both total abundance and species richness at a landscape level. A species-rich community with nationally rare, characteristic species was present around 1980, but has now been reduced to a restricted number of species

that are mostly common to the Netherlands. This decline in species richness is not only caused by the loss of the rare species in Boeschoten. Many of the disappeared characteristic species were common around 1980. For instance, the genera *Didea*, *Dasysyrphus* and *Parasyrphus* totalled 16 species with (at least, due to imperfect monitoring before 1982) 609 specimens in 1979–1982 (44 days), and only five species with 65 specimens in 2020–2021 (63 days).

In this dry mixed forest, we observed two waves of decline in species richness. In the 1980s, the diversity of rare, characteristic species decreased by 27%. Most common species remained present at least until 2000, after which the number of observed species in that category also declined. In recent years, the total number of individuals has decreased dramatically, mainly due to decreased abundance of the previously common species (Table 1). It appears that in this process of overall collapse of the hoverfly community, the specialised species are already lost in an early stage (accompanied by a decrease in overall abundance), while a severe decline in abundance occurred many years later. Powney et al. (2019) indicate that losses in UK hoverfly diversity are concentrated in rare species. For butterflies, another well-studied



insect group, it is known that specialist species decline first, whereas generalists stabilise or increase (Habel et al., 2016). Beside the important ecological role of rare species in an ecosystem (Jain et al., 2014; Leitao et al., 2016; Mouillot et al., 2013), our data suggest that the loss of rare species may be an indicator of ecosystem development many years before the number of individuals in common species is reduced.

The decline in species richness at Boeschoten cannot be explained by local changes in land use and management: this forest and its surroundings have not changed for decades. A clue to the explanation could be that in the period 1979–1984 especially the rare hoverflies with carnivorous larvae living on aphids in open air declined, but not the species with hidden larvae that live in plants, dead trees or the ground. It seems that the origin of the change in hoverfly fauna is due to air-borne transport; this period is known for the extreme emissions of nitrogen (acid rain) from agriculture, which was reduced by national legislation in 1986. Intensive agriculture is present 5–30 km to the southwest of Boeschoten forest. The direct and indirect effects of nitrogen for animals (e.g. eutrophication, acidification, changes in food quality and microclimates) are discussed in Nijssen et al. (2017), Stevens et al. (2018, 2020) and Carvalho et al. (2020).

In the years 1990–2000, we observed a period of no further decline in hoverfly abundance. After 2000 the decline continued (especially in the summer period, Table 2), and possible contributors could be continued nitrogen input, the application of new pesticides in agriculture and climate change. Data on the local presence of pesticides in the Boeschoten forest are not available, but air transport is not unlikely. Recent studies have found a range of pesticides in nature areas in the same Veluwe region (Buijs & Mantingh, 2020; van Eekeren et al., 2022). The negative impact of pesticides on the survival of insects in nature reserves is indicated by Ewald et al. (2015), Mancini et al. (2020) and Barmantlo et al. (2021).

Recent publications on the impact of climate change on ecosystems (Morris & Ball, 2021; Román-Palacios & Wiens, 2020; Wiens, 2016) indicate another possible cause for the decline of very common (non-critical) species at Boeschoten over the past two decades. While weather variables like precipitation and direct sunlight in the preceding month of April or the 30 days preceding a day of monitoring did have significant effects on the total number of active hoverflies, none of these variables could explain the negative trend at Boeschoten over the years (Appendix B of Data S1). It is of course possible that our a priori selected time windows for which we evaluated weather statistics were not the most informative ones, or that these analyses were limited due to the two gaps in data collection in the two most recent decades. However, it is also likely that climate change disrupts stable population dynamics by having intricate effects throughout the life cycle of these hoverflies, which would be difficult to quantify with simple weather statistics.

Two other long-term hoverfly studies are known to us. The first is that of Hallmann et al. (2021), who reported strong declines in hoverfly abundance and species diversity in the German Wahnbachtal, based on six Malaise traps that operated in the 1989 and 2014 seasons. The species composition at Boeschoten (this study) differed considerably from

that in the Wahnbachtal, clearly indicating that the hoverfly communities in dry forests (Boeschoten) and in semi-open nature reserves with wet meadows and tall perennial meadows (Wahnbachtal) are different ecosystems. In Wahnbachtal frequently observed genera were *Cheilosia*, *Melanogaster*, *Neoascia*, *Orthonevra* and *Platycheirus* (total 46 species, 6007 specimen), that are almost absent in Boeschoten (total 10 species, 284 specimen). Frequent genera at Boeschoten are *Dasysyrphus*, *Didea*, *Neocnemodon*, *Parasyrphus* and *Syrphus* (total 24 species, 2839 specimen), different from Wahnbachtal (13 species, 415 specimen). The ecology of the hoverfly larvae is primarily carnivorous in Boeschoten, whereas in Wahnbachtal phytophagous and aquatic larvae are more common. Notwithstanding the different aspects (ecosystem, management, hydrology, species, ecology of larvae) and different methods (Malaise traps versus insect net, 2 trapping years vs. 30 years) the total decline in hoverfly fauna is comparable between the studies: 80% in Wahnbachtal and 80% in Boeschoten. Hallmann et al. (2021) give as possible explanation a change in human management (agriculture, hydrology) in Wahnbachtal. Our study at Boeschoten, an isolated location in the dry forests without human management, suggests that the decline in hoverflies is general.

The second study with which we compare our results is that of Gatter et al. (2020). They report on migrating hoverflies in the Schwäbische Alb uplands in southwest Germany, where a big Malaise trap was active on a mountain top in 1978–1987 and 2014–2019. In that period the landscape remained unaltered, as did the local conditions. They report an enormous decline in abundance; especially the hoverflies with carnivorous larvae fall to under 10% of the earlier numbers. In addition, they published data from research by visual counting in a standardised narrow corridor, without attempting to identify specimens at the species level. When they compare their results from 1970 to 1974 with 2014 to 2019, the loss of individuals of migrating species in July/August is about 97%. The loss in migrating hoverflies with aquatic or saprophagous larval development is not so extreme as in the carnivorous species. The decline of species at Boeschoten, especially in the carnivorous larvae free in the air, is the same as in the results in the study by Gatter et al. (2020). Moreover, a comparable decline is also observed in Belgium: comparing the species list from Boeschoten with the Red List of Flemish hoverflies (van de Meutter et al., 2021), 29 species observed at Boeschoten are (critically) endangered or vulnerable in Flanders (based on declining distributions). The majority of these 29 species belong to the group of species with carnivorous larvae that was decimated at Boeschoten.

In conclusion, we can add hoverflies to the groups of insects that have recently declined by 70%–80% in western Europe (e.g.: Bell et al., 2020; Hallmann et al., 2020; Homburg et al., 2019; van Strien et al., 2019). The fact that we cannot pinpoint an obvious direct effect of local human interference in our forest study, can only lead to the conclusion that large-scale processes such as influx of nutrients and pesticides, acidification and/or climate change contribute to insect declines (Wagner et al., 2021). To substantiate these strong suspicions with data, it is critical that long-term monitoring of insect populations and potential environmental drivers is conducted at a multitude of locations, for

instance, through well-coordinated citizen-science programmes (Didham et al., 2020; Harvey et al., 2020; Montgomery et al., 2020).

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## CONFLICT OF INTEREST

The authors declare no competing interests.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Barendregt et al. (2022).

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**Appendix S1.** Supporting Information.

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