

Saproxylic hoverflies benefit by modern forest management (Diptera: Syrphidae)

Menno Reemer

European Invertebrate Survey – The Netherlands, Postbus 9517, 2300 RA, Leiden, The Netherlands (e-mail: reemer@naturalis.nl)

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Abstract

Saproxylic organisms are regarded as threatened in many European countries. Nevertheless, there have been some signals indicating a recent increase of saproxylic hoverflies in the Netherlands. This paper examines the change in occurrence of saproxylic hoverflies compared to other ecological groups of the same family. The trend analysis is based on the database of an extensive recording programme carried out in the Netherlands. The results show an increase in occupied grid cells for a majority of saproxylic species in relation to other ecological groups. This positive trend occurs among all five ecological subcategories of saproxylic hoverflies recognized in this paper. It is suggested that this increase could be attributed to the changes in the Dutch forests during the past 50 years. Important aspects of these changes are: the increase in forest area (including an increase in area of forest with large and very large trees), the increase in age of forests and the changes in forest management in favour of a more natural approach towards dead and ill trees. In the discussion the possible influence of climate change and the method of trend calculation are discussed.

Introduction

Saproxylic organisms are 'species that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics' (Speight 1989). The conservation of saproxylic organisms has recently gained recognition as an important issue in the protection of European biodiversity (Mason et al. 2003). Many saproxylic species have suffered from loss and degradation of their habitats all over Europe, so there is great concern for their survival. Among this group of organisms, insects are particularly rich in species. In several European countries, special projects

have been initiated to promote the study and conservation of saproxylic insects (Versteirt et al. 2000; Cavalli and Mason 2003; Fayt et al. 2003). Some of these projects focus on particular taxonomic groups, like Diptera, or even more specifically on hoverflies (Diptera: Syrphidae) (Rotheray and MacGowan 2000; Rotheray et al. 2001).

Of the circa 800 species of Syrphidae known from Europe, 115 are considered to be saproxylic (Speight et al. 2003a, b). In some parts of Europe, many of these saproxylic Syrphidae are regarded as declining or even threatened. For instance, in Great Britain many species associated with dead wood are under threat (Ball and Morris 2000), and Speight and Good (2003) express their worries about the European saproxylic Syrphidae fauna as

a whole. Although there can hardly be any doubt about the negative effects on these insects of deforestation and the disappearance of old trees all over Europe, there also seem to be some positive signals, apparently resulting from changes in forest management. This has for instance been noted for the German Syrphidae fauna by Ssymank and Doczkal (1998).

In recent years, data on the occurrence of Syrphidae in the Netherlands suggested that many saproxylic species had increased. This has been attributed to the tendency of leaving dead wood and ill trees in the forests (Reemer et al. 2003). Speight and Good (2003) reason that this is no satisfactory explanation for the increase of saproxylic Syrphidae, because most of these species are dependent on microhabitats associated with over-mature and senescent trees, instead of microhabitats provided by 'coarse woody debris, defined as: 'dead woody material (...), occurring detached from trees that are alive'.

This paper gives the results of a study on the trends of saproxylic Syrphidae in the Netherlands, which have been analysed in more detail than in the previous study by Reemer et al. (2003). The aim of it was mainly to find out whether all ecological sub-groups of saproxylic Syrphidae have increased, or if there is only an increase among the species associated with 'coarse woody debris'. The results will be discussed in the light of what is known about changes in the Dutch forests in the past 50 years.

The analysis presented in this paper has been conducted by European Invertebrate Survey (EIS) – the Netherlands on behalf of the National Institute of Public Health and the Environment (Bilthoven, the Netherlands). A report in Dutch containing the same results has been produced by Reemer (2003).

Material and methods

Database

Distributional data of Syrphidae in the Netherlands have been collected in a database by the Netherlands Syrphidae Recording Scheme, a cooperation between the EIS – the Netherlands (EIS – the Netherlands), the Netherlands Youth federation for the study of Nature (NJN) and the 'sectie Diptera' of the Netherlands Entomological Society (NEV). At the time of the analysis

presented in this paper, the database contained 261.126 records of 324 species of Syrphidae in the Netherlands, of which 253.106 were suitable for the analysis. The database covers all parts of the country and the oldest records date back to the 19th century. Table 1 summarises the contents of the database in May 2003.

Calculation of trends

The data are divided into two periods: before 1988 and 1988–2002. Both the number of records and the number of investigated 5 km squares are approximately equal in both periods (Table 1). By doing this, differences in recording effort between the period can be minimalised. Other potential biases in the dataset will be addressed in the discussion. Figure 1 shows that the spatial distribution of the records is similar in both periods.

For each species in each of the two periods, the relative abundance (RA) has been calculated by dividing the number of 5 km squares in which a species has been found by the total number of investigated squares ($\times 100\%$). Subsequently, the trend has been calculated as follows:

$$\text{trend} = \frac{(\text{'RA before 1988'} - \text{'RA in 1988–2002'})}{\text{'RA before 1988'} \times 100\%}$$

Based on the calculated trends, the species have been divided into three trend categories:

- Decreased, negative trend of less than – 25%
- 0 Stable, trend between – 25 and 25%
- + Increased, positive trend of more than 25%

Statistical tests

The results of the analysis have been tested on statistical significance with a χ^2 -test, provided by Microsoft Excel 2000. Calculated *p*-values are considered to be significant below 0.05.

Table 1. Summary of the database of the Netherlands Syrphidae Recording Scheme (May 2003).

	Before 1988	1988–2002
Number of records	127.830	131.423
Number of investigated 5 km squares	1281	1233
Average number of records per square	100	107



Figure 1. Distribution of records of Syrphidae in the Netherlands before 1988 (squares) and in 1988–2002 (dots). The grid consists of 5×5 km squares.

Definition of ecological groups

All Dutch hoverfly species have been categorized into ecological groups, using information in the databases of Speight and Castella (2003a) and Speight et al. (2003a, b). The definitions of the ecological categories are given in Table 2. Note that the categories are partly overlapping. For instance, some species associated with rot-holes can also be found in sap runs. This is why the sum of the species numbers in the different saproxylic categories (Table 3(D)) is higher than the total number of saproxylic species (58).

Results

The results of the trend calculations are summarized in Table 3(A–E) and Figure 2. Of all 324

Dutch species of Syrphidae, approximately equal numbers have increased (35%), remained stable (30%) and decreased (35%). Different comparisons of ecological groups have been made to provide insight in the trends of saproxylic species in the Netherlands. The next paragraphs will deal with these comparisons.

Splitting up the forest species

All species of Syrphidae from the Netherlands have been divided into forest species and non-forest species, and subsequently the forest species have been divided into saproxylic forest species and non-saproxylic forest species. The trend calculations for these categories have resulted in the percentages in Table 3(A) and (B), which are illustrated in Figure 2.

Table 2. Ecological categories of hoverflies, based on information in [1] Speight and Castella (2003a), [2] Speight et al. (2003a) and [3] Speight et al. (2003b).

Categories	Definitions
Habitat categories	Species with a preference or maximal preference for [2]:
Forest species	'Forest macrohabitat – general'
Non-forest species	All other species not in the above category
Forest categories	Species with a preference or maximal preference for [2]:
Species of deciduous forest	'Deciduous forest – general'
Species of coniferous forest	'Coniferous forests – general'
Larval food categories	Species feeding on [1]:
Saproxylic	Micro-organisms and categorized as 'saproxylic' in [1]
Aquatic	Micro-organisms and not categorized as 'saproxylic' in [1] ^a
Predacious	Living animals (mostly soft-bodied Homoptera)
Phytophagous	Living plants
Saproxylic categories	Species with a preference or maximal preference for [3]:
Timber ^b	'Timber general' (e.g. stumps, trunks)
Overmature/senescent trees	'Overmature/senescent trees' (microhabitats which occur in relation to old (but living) trees)
Sap runs	'Sap runs/lesions' (tree wounds from which sap is flowing)
Rot-holes	'Rot-holes' (tree-holes, partly filled with rain water and decaying matter)
Insect workings	'Insect workings' (wood that has been infested with other wood-dwelling insects, like the caterpillar of the goat moth <i>Cossus cossus</i>)

^aWith exception of the genera *Eumerus* and *Merodon*, which have been considered to be phytophagous in the present study.

^bTimber can be regarded as synonymous with 'coarse woody debris' as used by Speight and Good (2003).

While 41% of the forest species has increased, only 25% of the non-forest species has increased, which is a significant difference ($p < 0.001$). A comparison of the trends within saproxylic forest species and non-saproxylic forest species shows that 59% of the saproxylic species has increased, while in the non-saproxylic species this percentage is only 34% ($p < 0.001$). The proportions of trend categories within non-saproxylic forest species are similar to those of the total Dutch hoverfly fauna. This shows that the observed increase of forest species can be totally explained by the increase of saproxylic species.

Saproxylic species and other ecological groups

Four major ecological groups of Syrphidae can be recognized based on the larval feeding habits: saproxylic species, aquatic species, predacious species and phytophagous species. The results of the trend calculations for these groups of species are given in Table 3(C). When compared with the trends within all the species of Syrphidae together, the trends within the saproxylic species ($p < 0.001$) and the aquatic species ($p = 0.04$) turn out to differ significantly. Among the saproxylic group the increased species form a majority, while in the aquatic group there are slightly more decreased species. The

increased saproxylic species and their ecological characteristics are listed in Table 4.

Splitting up the saproxylic species

Table 3(D) gives the results of the trend calculations for the five subcategories of saproxylic Syrphidae. In each of these groups, the proportion of increased species is much, and significantly, larger than among all species of Syrphidae together (compare with Figure 2). The only exception is the group of species associated with insect workings, but this can be due to the low number of species in this group (12).

A comparison of the trends of the five subcategories with those of the total group of saproxylic species reveals that there are no significant differences (Table 3(D)). So there does not seem to be a saproxylic subcategory in which the species show different trends than the other saproxylic Syrphidae. Species associated with 'coarse woody debris' (here called 'timber') do not show a stronger increase than the other species.

Deciduous vs. coniferous

There are no differences in the trends of species associated with deciduous forests in comparison

Table 3. Numbers and percentages of hoverfly species per trend category: decreased (–), stable (0), increased (+).

	Numbers			Percentages			Expected numbers			Total numbers	<i>p</i>
	–	0	+	–	0	+	–	0	+		
(A) Forest species/non-forest species^a											
Forest species	63	60	85	30	29	41	87.9	68.1	52	208	< 0.001
Non-forest species	49	38	29	42	33	25	–	–	–	116	–
(B) Saproxylic forest species/non-saproxylic forest species^b											
Saproxylic forest species	15	9	34	26	16	59	–	–	–	58	–
Non-saproxylic forest species	48	52	51	32	34	34	38.8	23.3	87.9	150	< 0.001
(C) Larval food categories^c											
Saproxylic	15	9	34	25.86	15.52	58.62	20.0	17.5	20.4	58	< 0.001
Aquatic	21	27	14	33.87	43.55	22.58	21.4	18.8	21.8	62	0.04
Predacious	48	42	47	35.04	30.66	34.31	47.5	41.4	48.2	137	0.98 (n.s.)
Phytophagous	21	15	17	39.62	28.30	32.08	18.3	16.0	18.6	53	0.74 (n.s.)
(D) Subcategories of saproxylic Syrphidae^d											
Timber	4	2	17	17.39	8.70	73.91	5.9	3.6	13.5	23	0.33 (ns.)
Overmature/senescent trees	15	8	31	27.78	14.81	57.41	13.9	8.4	31.7	54	0.95 (n.s.)
Sap runs/lesions	8	3	17	28.57	10.71	60.71	7.2	4.3	16.4	28	0.77 (n.s.)
Rot-holes	7	6	20	21.21	18.18	60.61	8.5	5.1	19.3	33	0.80 (n.s.)
Insect workings	6	1	5	50	8.33	41.67	3.1	1.9	7.1	12	0.16 (n.s.)
(E) Deciduous forest species compared with coniferous forest species, and saproxylic species of deciduous forest compared with saproxylic species of coniferous forest^e											
Deciduous forest	53	57	77	28.34	30.48	41.18	–	–	–	187	–
Coniferous forest	29	30	42	28.71	29.70	41.58	28.6	30.8	41.6	101	0.99 (n.s.)
Deciduous & saproxylic	12	8	29	24.49	16.33	59.18	–	–	–	49	–
Coniferous & saproxylic	3	3	13	15.79	15.79	68.42	4.7	3.1	11.2	19	0.65 (n.s.)

The *p*-value is the result of a χ^2 -test, based on a comparison between the observed and expected numbers.

^aExpected numbers of forest species are based on the proportions of trend categories within non-forest species.

^bExpected numbers of non-saproxylic forest species are based on the proportions of trend categories within saproxylic forest species.

^cExpected numbers are based on the proportions of trend categories within all species of Syrphidae together (Figure 2).

^dExpected numbers are based on the proportions of the trend categories within the total group of saproxylic forest-species (see Table 3(B) and Figure 2).

^eExpected numbers of species of coniferous forest are based on the proportions of trend categories within the species of deciduous forest.

with species associated with coniferous forests (Table 3(E)). When this comparison is limited to saproxylic species, the proportion of increased species is 9% higher among the species of coniferous forest. However, this difference is not significant.

Decreased saproxylic species

Although a large proportion of saproxylic species has increased, there is a small group of species which has decreased. Somehow, whatever the causes of the increase of saproxylic Syrphidae might be, not every saproxylic species seems to benefit by them. It would be interesting to find out if these 15 decreased saproxylic species share any ecological characteristics. These species and their characteristics are listed in Table 5. The last two

columns in this table indicate whether the species is on the Red List of Germany (Ssymank and Doczkal 1998) and if it is considered as threatened at European level by Speight and Castella (2003b).

Three of the species in Table 5 (those marked with an asterisk) will not be considered here. *Ceriana vespiformis* has been found only twice in the Netherlands and the origins of the specimens of this mediterranean species are questionable. *Psarus abdominalis* has been considered as saproxylic based on ‘best expert opinion’, but recently evidence increases that this is species is not saproxylic (pers. comm. M.C.D. Speight). *Sphiximorpha subsessilis* has recently been rediscovered on a number of localities in the Netherlands (records not yet in database), so the species can not be considered as decreased. So there are 12 decreased species of saproxylic Syrphidae left to be considered here.

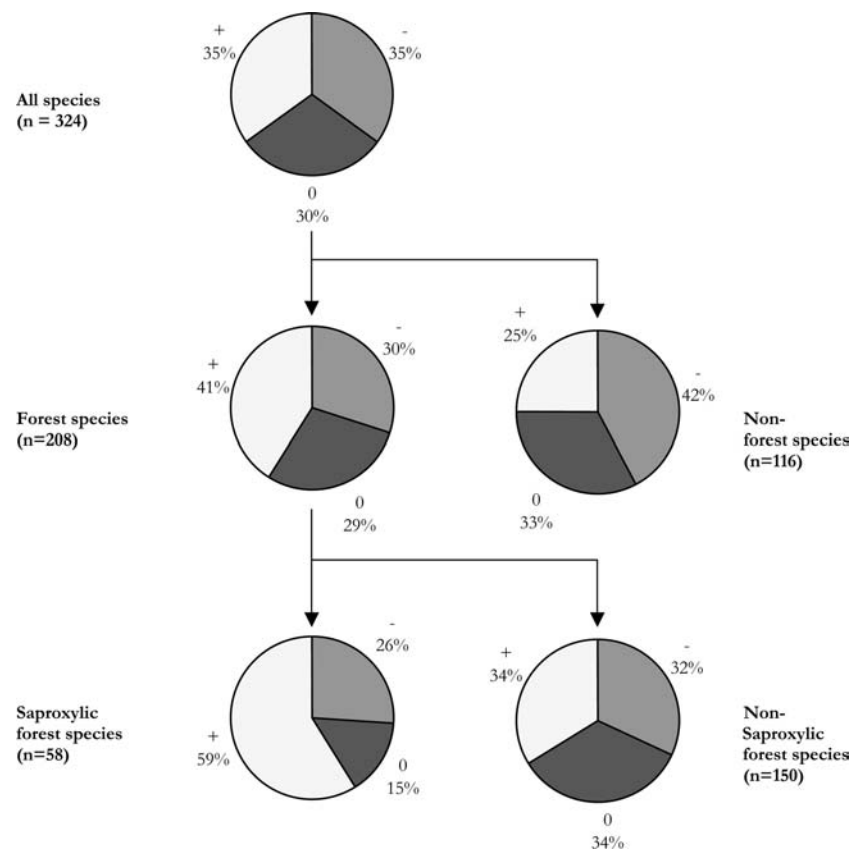


Figure 2. Distribution of hoverfly species over the trend categories 'decreased' (-), 'stable' (0) and 'increased' (+), based on a comparison between the periods before 1988 and 1988–2002. In this figure, all Dutch species of Syrphidae are divided into forest species and non-forest species, and subsequently the forest species are divided into saproxylic forest species and non-saproxylic forest species.

The only ecological characteristic occurring more in this group of species than in other saproxylic species, is the association with insect workings. Among the 12 decreased saproxylic species there are five with a maximal preference for this microhabitat feature, while among the 33 increased saproxylic species there are also only five which are associated with insect workings. So it seems that the species which are dependent on other insects have suffered disproportionately.

Ferdinanda ruficornis and *Volucella inflata* have been found in association with the goat moth *Cossus cossus* (Lepidoptera: Cossidae), *Chalcosyrphus piger* has been found in humus formed from the frass of *Acanthocinus* (Coleoptera: Cerambycidae) and *Ips* (Coleoptera: Scolytidae) (Rotheray 1999; Speight et al. 2003b). The codings of *Chalcosyrphus curvipes* and *C. femoratus* by Speight et al. (2003b) have been based on 'best

expert opinion', and no evidence has yet been found for a relation of these species with other saproxylic invertebrates.

Discussion

Changes in the forests as an explanation for the increase of saproxylic Syrphidae

Of the 58 species of saproxylic Syrphidae occurring in the Netherlands, 34 have increased (59%). In other ecological groups of Syrphidae the proportion of increased species is much and significantly smaller. It seems logical to try to find the cause of this increase in the changes in the forests of the Netherlands. No special measures have been taken to conserve saproxylic insects in the Netherlands, as has been done in England (Rotheray

Table 4. Ecological characteristics of increased saproxylic Syrphidae, according to Speight et al. (2003a, b).

Species	Overmat gen	Rot holes	Insect workings	Sap runs	Timber gen	Deciduous gen	Coniferous gen	Red List	Germany	Threatened Europe	Indicator species
<i>Blera fallax</i>	2	2	2		2		3				
<i>Brachyopa bicolor</i>	2		2	2		3		x			x
<i>B. panzeri</i>	2	2		1		3		x			x
<i>B. pilosa</i>	3			3		3					
<i>B. scutellaris</i>	3			3		3					
<i>B. testacea</i>	2	2			2		3				
<i>B. vittata</i>	2	2		2	2		3				x
<i>Brachypalpus lentus</i>	2				2	3	2				
<i>Brachypalpus laphriformis</i>	2	2		2		3		x			
<i>Callicera aenea</i>	3	3				3	3	x		x	x
<i>C. fagesii</i>	3	3				3				x	x
<i>Caliprobola speciosa</i>	2					3		x			x
<i>Chalcosyrphus eunotus</i>					2	3		x			x
<i>C. nemorum</i>					2	3	1				
<i>Criorhina berberina</i>	3	3			3	3	3				
<i>C. floccosa</i>	3	3			2	3					
<i>C. pachymera</i>	3	3				3		x		x	x
<i>C. ranunculi</i>	3	3				3		x			
<i>Ferdinandea cuprea</i>	2	2	2	2		3	2				
<i>Myolepta dubia</i>	2	2	2	2		3		x			
<i>Psilota anthracina</i>	2			2	2	3	3	x		x	
<i>Sphegina clavata</i>	2			2		2		x			
<i>S. clunipes</i>	2			2	2	3	2				
<i>S. sibirica</i>					2		3				
<i>S. verecunda</i>	2			2		3					
<i>Temnostoma bombylans</i>	3				3	3					
<i>T. vespiforme</i>	3				3	3	1	x			
<i>Xylota jakutorum</i>	3	2		2	2		2				
<i>X. meigeniana</i>	3	3				3		x			x
<i>X. segnis</i>	2	2	1	1	2	3	3				
<i>X. sylvarum</i>	3	2		2	2	3	3				
<i>X. tarda</i>	3	1		3		3	1	x			
<i>X. xanthocnema</i>	3	2		2	2	3		x			

3: Maximally preferred (micro) habitat.

2: Preferred (micro) habitat.

1: Can occur in (micro) habitat, but not normally expected. The last three columns indicate whether a species is on the German Red List or not (Ssymank and Doczkal 1998), if it is considered as threatened on a European scale by Speight and Castella (2003b) and if it is considered to be an indicator species of forests of European conservation value by Good and Speight (1996).

and MacGowan 2000), but still much has changed in the Dutch forests since the 1950s. The following aspects of these changes could be relevant in explaining the increase of saproxylic Syrphidae.

1. The total area occupied by forests has increased from 260.320 ha in the 1950s to 359.845 ha in 2000, an increase of 38% (Dirkse et al. 2003). This increase is mainly caused by the plantation of deciduous forest, consisting of indigenous trees, for purposes of recreation and nature-development. The area of coniferous forest has slightly decreased with – 5% during the period 1984–1997, while the area of mixed deciduous/coniferous forest has increased with 20% during this period (Duuren et

al. 2003). An increase in area occupied by forests does not only enlarge the area of potential habitat for saproxylic Syrphidae, it could also make the landscape more ‘permeable’ to these insects, thus facilitating them in their dispersal.

2. The area of forest with ‘large trees’ (defined as trees with a diameter of 40–60 cm) has increased from 44.481 ha in 1984–1985 to 83.257 ha in 2001–2002. The area of forest with ‘very large trees’ (trees with a diameter of more than 60 cm) has increased from 7.901 ha in 1984–1985 to 20.069 ha in 2001–2002 (Dirkse et al. 2003).

3. The average age of the Dutch forests has increased. When comparing the period 1980–1984

Table 5. Ecological characteristics of decreased saproxylic Syrphidae, according to Speight et al. (2003a, b).

Species	Overmat gen	Rot holes	Insect workings	Sap runs	Timber gen	Deciduous gen	Coniferous gen	Red List Germany	Threatened Europe	Indicator species
<i>Brachypalpus valgus</i>	2	2		2		3		x	x	x
<i>Ceriana conopsoides</i>	2	2		2		3		x		x
<i>C. vespiformis</i> *	2	2		2		2			x	
<i>Chalcosyrphus curvipes</i>	3		3	2	1	3		x	x	x
<i>C. femoratus</i>	3		3	2	1		3	x	x	x
<i>C. piger</i>	3		3	2	2		3	x	x	x
<i>Ferdinandea ruficornis</i>	3		3			2		x	x	x
<i>Mallota fuciformis</i>	3	3				3		x	x	x
<i>Pocota personata</i>	3	3				3		x		x
<i>Psarus abdominalis</i> *	3		3			2		x	x	x
<i>Sphiximorpha subsessilis</i> *	2	2		2		3		x	x	x
<i>Spilomyia manicata</i>	2	2				3		x	x	x
<i>Volucella inflata</i>	3		3	2		3		x		
<i>Xylota florum</i>	3					3				
<i>X. ignava</i>	3				2		3	x		

*Species not considered, for reasons explained in the text.

3: Maximally preferred (micro) habitat.

2: Preferred (micro) habitat.

1: Can occur in (micro) habitat, but not normally expected. The last three columns indicate whether a species is on the German Red List or not (Ssymank and Doczkal 1998), if it is considered as threatened on a European scale by Speight and Castella (2003b) and if it is considered to be an indicator species of forests of European conservation value by Good and Speight (1996).

with the year 2000, the increase in average age is 10 years (Dirkse et al. 2003). This is a consequence of a shift in the use of forests from forestry to recreation and nature (Duuren et al. 2003).

4. The attitude in forest management has strongly changed in favour of a 'natural approach' towards dead and ill trees, which – in many forests – are no longer being removed (Duuren et al. 2003). This is probably beneficial for saproxylic Syrphidae, especially those associated with timber (or 'coarse woody debris'). Species associated with overmature trees might benefit as well, because the same types of habitats could be produced by ill trees as are provided by overmature trees. No data on the increase of dead wood are available yet, but governmental institutions have recently started to monitor the amount of dead wood in the forests, both standing and fallen (Dirkse et al. 2003).

5. There is a tendency towards a more natural 'age-composition' of forests, to be achieved by thinning out the forests instead of logging entire parts of them. This could allow for a more natural variation in microhabitats to develop (Duuren et al. 2003).

6. Environmental factors like acidification and eutrophication also have their effects on forests, although nothing is known about their influence on saproxylic insects. The recent decrease in sul-

phur- and nitrogen-deposition has been beneficial for other organisms, like macrofungi and lichens (Duuren et al. 2003).

Which of the factors named above would provide the most satisfactory explanation for the increase of saproxylic Syrphidae is hard to say, but it seems likely that all six of them will have a certain influence. Studies on other groups of flora and fauna in the Netherlands have also revealed an increase of species associated with old forests, e.g. birds (SOVON 2002) and macrofungi (Duuren et al. 2003). For these groups, the same factors are mentioned in explaining the increase.

It is surprising that, while the area of coniferous forest in the Netherlands has slightly decreased, the group of species associated with coniferous shows the same positive trend as the group of species of deciduous forests. This might be explained by the increase of the area of mixed deciduous/coniferous forest.

Alternative explanations

Climatic changes have an important influence on the distribution of insects. Many southern species have expanded their ranges in northern direction during the past decades (Burton 2003). If the

proportion of southern species is larger among the saproxylic Syrphidae than among the other ecological groups, this might be an alternative explanation for the increase of saproxylic Syrphidae. This has been examined by Reemer et al. (2003), who demonstrated that 15% of the saproxylic Syrphidae from the Netherlands have a southern distribution, and that this percentage does not differ significantly from the proportion of southern species in other ecological groups (ranging from 7 to 31%). This does not rule out the possibility that climate change somehow affects saproxylic hoverflies stronger than other ecological groups, but so far there are no signs indicating that this is happening.

Another possible explanation for the observed increase of saproxylic Syrphidae might be that hoverfly recorders have concentrated greater effort in woodland habitats, or that they have somehow focused stronger on saproxylic species. Considering the distribution of investigated grid cells in both periods (Figure 1), there does not seem to be an important difference in the coverage of the database. Besides, hoverfly recorders traditionally have always had a preference for recording in or near woodland habitats, since this is the habitat in which the hoverfly fauna is most diverse (64% of the Dutch species can be considered as forest species; Table 3(A)). Many saproxylic hoverfly species are large and conspicuously coloured mimics of aculeate Hymenoptera. These species must have been as attractive to hoverfly recorders in earlier years as they are now, so it is unlikely that these species are somehow under-represented in the first period. Methods for collecting saproxylic hoverflies do not differ from those for collecting other groups of hoverflies. Their ecological and ethological characteristics are very different during the immature stages, but very similar in the adult stage.

Notes on the trend analysis

The method used for the trend analysis is a very rough one. It is based on a comparison between two periods, one of which is much longer than the other. These periods have been chosen because the average total number of records per grid cell is equal in both periods. This is an important condition for being able to compare the abundance of

species between two periods, for the chance of finding a certain species in a certain number of grid cells will change according to the number of records available from these grid cells.

There are disadvantages of comparing a long period with a short one. During a long period, many species will fluctuate in their abundance, so the calculated relative abundance for both periods only reflects an 'average' indication for the abundance of a species. This disqualifies the used method for calculating trends of single species, because in many species there will not be a simply positive or negative trend. Rather there will be a complicated pattern of periods of increase and decrease. However, when large groups of species are being compared, as is the case in this paper, this method provides a rough indication of the differences in average relative abundance between these groups of species. Accordingly, the fact that the proportion of increased species is much higher in the saproxylic group than in other ecological groups, reflects an increase in the average relative abundance of saproxylic species in relation to the other groups.

In this paper grid cells have been chosen to base the analysis on, instead of numbers of records. One disadvantage of using numbers of records in the trend analysis, is that the bias due to differences in recording habits is much larger. In recent years, the proportion of field records in the database has become much larger than the proportion of records from collections. Since hoverfly recorders tend to collect mainly the less abundant species, common species are over-represented in the recent part of the database because of the large proportion of field records in recent years. So, when calculating the relative abundance based on records, in general common species will show an increase and scarce species will show a decrease. This recording effect will be much less important in an analysis based on grid cells, because only presence or absence are considered and numbers of records do not matter.

Another disadvantage of using numbers of records in the trend analysis, is that the relative abundance of a species influences the relative abundance of other species. When the number of records of a certain species increases, the relative abundance of other species will decrease, even when these other species actually remain stable. In an analysis based on grid cells, this does not happen. An increase in number of grid cells in which a certain

species has been found, is unlikely to affect the total number of investigated grid cells, so relative abundances of other species will remain the same.

Why not carry out an analysis of a large number of shorter periods, and calculate the trends with a regression analysis? When the database is split into, for instance, several periods of 10 years, the recording intensity (average number of records per grid cell) will differ strongly between the periods, so the relative abundances of species will not be comparable between the periods. It is not possible to compensate for these differences. This would require an adaptation of the number of records in each period in order to obtain equal recording intensities, which would mean that certain records can not be used. But how to choose which records to use and which not?

Conclusion

The saproxylic Syrphidae in general are on the increase in the Netherlands, and it seems that this can most likely be attributed to changes in the Dutch forests and their management. Still a small group of decreased saproxylic species remains, which gives reason for concern. Most of these species are also on the Red List of Germany (Ssymank and Doczkal 1998) and are considered to be threatened all over Europe by Speight and Castella (2003b). Besides, they are listed by Good and Speight (1996) as indicator species for the identification of forests of European conservation value. These species should be subject to research on their ecology and their faunistics, to find out the causes of their decline.

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