

# Pollinating Flies (Diptera): A major contribution to plant diversity and agricultural production

Axel Ssymank<sup>1</sup>, C.A. Kearns<sup>2</sup>, Thomas Pape<sup>3</sup> and F. Christian Thompson<sup>4</sup>

**Abstract.** Diptera are one of the three largest and most diverse animal groups in the world. As an often neglected but important group of pollinators, they play a significant role in agrobiodiversity and the biodiversity of plants everywhere. Flies are present in almost all habitats and biomes and for many medicinal, food and ornamental plants, pollinating flies guarantee or enhance seed and fruit production. They are important in the natural landscape, in agriculture and in greenhouses, and have recently come into use in the production of seeds for seed banks. The São Paulo Pollinator Initiative, the CBD, and Pollinator secretariats were important starting points in the international recognition of pollinator importance. However, large gaps in our knowledge of the role of Diptera in pollination networks need to be addressed in order to sustain agriculture and to enable appropriate responses to climate change. At this 9<sup>th</sup> Conference of the Parties we would like to draw attention to the role of often-neglected Dipteran pollinators, to stress their current importance and potential future use as pollinators in agriculture. A case study on flower flies that act as important pollinators, as adults, and major biocontrol agents, as larvae, illustrates their double importance for agriculture.

**Keywords.** Diptera, Agrobiodiversity, Pollination, Flower Flies, Bio-Control, medicinal plants, ornamental plants

## AUTHORS' ADDRESSES:

<sup>1</sup> Corresponding author: Axel Ssymank c/o Federal Agency for Nature Conservation (BfN, I.2.2), Kantantinstrasse 110, 53179 Bonn/Germany. E-mail: Ssymanka@bfn.de Phone +49 228 8491 1540

<sup>2</sup> C.A. Kearns, Baker Residential Academic Program UCB 176, Ecology and Evolutionary Biology, University of Colorado, Boulder, CO USA 80309

<sup>3</sup> Thomas Pape, Natural History Museum of Denmark, Zoological Museum, Universitetsparken 15, DK - 2100 Copenhagen, Denmark

<sup>4</sup> F. Christian Thompson, Systematic Entomology Lab., ARS, USDA, c/o Smithsonian Institution MRC-0169 PO Box 37012, Washington, D. C. USA 20013-7012

## THE SÃO PAULO POLLINATOR INITIATIVE – AND SUBSEQUENT STEPS

The International Initiative for the Conservation and Sustainable Use of Pollinators (later referred to as International Pollinators Initiative IPI) was established by the 5th Conference of the Parties (COP) to the Convention on Biological Diversity (CBD) as a cross cutting initiative within its work on agriculture under the lead of FAO. Starting with Decision VI/5 of the 6th COP and the “São Paulo Pollinator Declaration” (<http://biodiv.org/decisions/default.asp?m=cop-06&d=05>), coordinated action has been encouraged to monitor pollinator declines, address the lack of taxonomic information on pollinators, assess the economic value of pollination and to promote the conservation, restoration and sustainable use of pollinator diversity in agriculture and related ecosystems. A number of regional initiatives have been organized: the European Pollinators Initiative, the African Pollinators Initiative; the International Centre for Integrated Mountain Development Initiative from South Asia, the North American Pollinators Campaign (also NRC 2007 assessment of pollinator status) and the Brazilian Pollinators Initiative. In the Pollinators plus 5 Forum (2003), participants collaborated to discuss information technology within the Pollinators Initiatives. With the 8<sup>th</sup> Conference of the Parties in 2006, the activities were also linked to the Global Taxonomy Initiative (GTI) and in a side event on the COP 8 major works of the Brazilian and the African Pollinators Initiative (e.g. API

2004) were presented. These initial programs focused on the pollination services of bees. Dipteran pollination, which is less well understood and often underestimated, was largely ignored. In view of the 2010 target of the CBD, to reduce the rate of loss of biodiversity worldwide, and to address the risk of major reductions in pollination capacity due to climate and land use change, it will be necessary for the COP 9 Pollinator Initiative to broaden its scope in addressing pollinator systems.

## POLLINATION ON TWO WINGS

Diptera probably were among the first important angiosperm pollinators and may have, as such, been instrumental in the early angiosperm radiation (Endress 2001; Labandeira 1998). Today Diptera are one of the three largest and most diverse animal groups in the world (Skevington and Dang 2002), comprised of over 160,000 named species in about 150 families (Evenhuis *et al.* 2008). At least seventy-one families of Diptera contain flower-visiting flies, and flies are pollinators of, or at least regular visitors to, at least 555 flowering plant species (Larson *et al.* 2001) and pollinators of more than 100 cultivated plants including such important crops as mango, cashew, tea, cacao, onions, strawberries (Larson, Inouye and Kevan, unpubl.; Heath 1982), cauliflower, mustard, carrots, apples (Mitra and Banerjee 2007), leek (Clement *et al.* 2007) and cassava (Hansen 1983). Calliphorid flies are raised commercially for use as pollinators of crops including many of the above-mentioned plants, as well as canola, sunflower, buckwheat, garlic, lettuce and peppers, and to increase the production of greenhouse tomatoes and peppers ([www.forkedtreeranch.com/index.html](http://www.forkedtreeranch.com/index.html)). *Eristalis* sp. (Syrphidae) is used in greenhouse pollination of peppers (Jarlan *et al.* 1997), and *Musca* sp. (Muscidae) and *Calliphora* sp. will pollinate umbelliferous plants in greenhouses (USDA 2007). *Eristalis* sp. and other flower flies are laboratory-reared and used in the production of seeds for seed banks (Rosso *et al.* 1994; Gladis 1994). Diptera are thus one of the most important groups of pollinating organisms, second only to the Hymenoptera.

Flies visit flowers for several reasons (Kearns 2002), the predominant one being for food. Nectar provides a good source of energy, and pollen protein is essential for reproduction in at least some fly species (Kevan 2002). Flowers can also provide species-specific rendezvous sites for mating. Flowers oriented towards the sun may provide warmth, and certain types of flowers temporarily trap flies, or deceive female carrion flies to visit by mimicking scents and visual cues of rotting flesh.

The tremendous diversity in flower-visiting flies is reflected in the large variation in effectiveness of fly pollinators, which range from specialists such as the long-tongued flies of southern Africa (Goldblatt *et al.* 1995) to generalists that are likely to visit many types of plants. Variation in size and hirsuteness (related to pollen adhesion) is great. Nonetheless, even generalist flies have been demonstrated to contribute to plant reproductive success, and in some instances plants are dependent upon them as pollinators (Kearns 2001; Kevan 2002). Fly pollination has not been the subject of as many studies as pollination by bees. Unlike bees, which are dependent on floral rewards during all stages of development, flies do not need to make continual visits to flowers to provision a brood, and most lack specialized structures for pollen transport, although some syrphids (e.g., *Platycheirus* spp.) have enlarged tarsi on their front legs, which they use to squeeze pollen out of anthers, and others have a thick "fur" which effectively accumulates pollen (e.g., *Cheilosia canicularis*, *Mallota* spp.). However, flower-visiting flies are abundant in numbers and diversity, and are found in all habitats. They seem to be particularly important as pollinators of flat to bowl-shaped flowers in habitats and under conditions where bees are less active. For example, flies seem to be among the most important pollinators of many arctic and alpine flowers (Kevan 1972; Kearns 2001) and for some early season flowering plants (Motten 1986; Goldblatt *et al.* 2004). Also, small flies may be instrumental pollinators in the forest understory, especially for shrubs with numerous small, inconspicuous, often dioecious flowers (Larson *et al.* 2001; Borkent and Harder 2007). Pollination by these very small flies (e.g., Phoridae, Sciaridae, Mycetophilidae, Piophilidae, etc.) deserves further study (Kevan 2002). An increasing number of flowering plants are discovered to be entirely dependent on dipteran pollinators, sometimes with surprising relationships like the 'seed-for-seed' mutualism found in species of the anthomyiid genus *Chiastocheta*, which pollinate *Trollius europaeus* (Pellmyr 1989), or the gall midge pollination of *Artocarpus*, which is a mutualism mediated by a parasitic fungus (Sakai *et al.* 2000). As fly pollinators are studied more systematically, more of these amazing and specific relationships are likely to be discovered.

The relative importance of fly and bee pollinators in particular situations may relate to differences in their basic biology (Kearns 2001). Unlike most bees, many flies thrive in moist and cool habitats, and flies are relatively more abundant in habitats like cloud forests and the shady understory. Compared to bees, flies have low energy requirements and by not provisioning a brood, flies may be able to depend on less rewarding flowers, and to spend more time basking in flowers. In addition, many

flies are active at low ambient temperatures, and Diptera dominate in high altitude and high latitude plant-flower visitor systems (Kearns 1992; Elberling and Olesen 1999, see Fig. 1). Flies exhibit marked diurnal activity patterns of flower-visiting (Gilbert 1985; Herrera 1988; Ssymank 1991, 2001). While in some regions in Central Europe, bees are most active late morning and noon, flower flies visit flowers in highest abundances and diversity early in the morning or late afternoon. Diptera activity patterns and the timing of nectar production and anthesis is a potentially rewarding research topic.

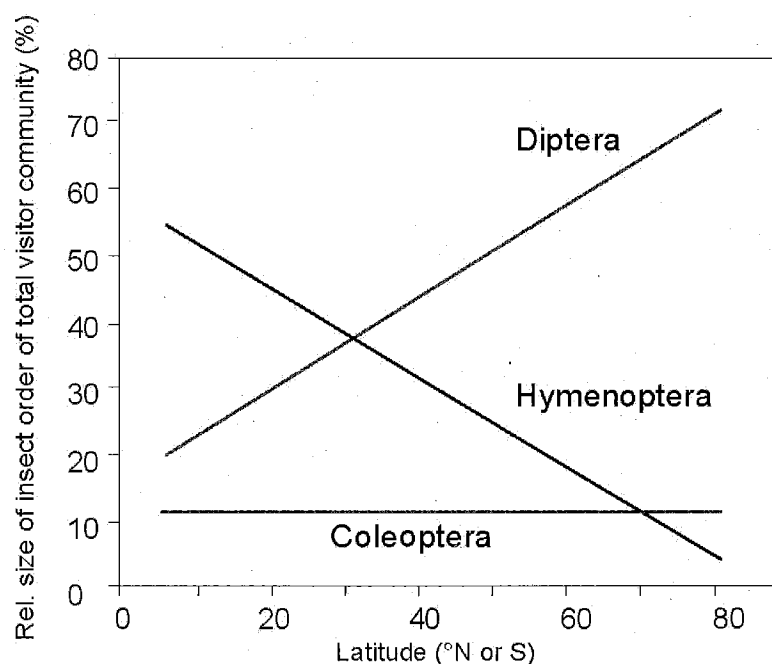
Most entomophilous flowers are visited by multiple types of insects. Because populations of insect species fluctuate temporally, the relative importance of a particular pollinator may differ from year to year or season to season. Conditions affecting bee populations could be quite different from those affecting fly populations due to the differences in larval requirements (Kearns 2001). Thus the relative contributions of bees and flies to plants with redundant pollination systems are likely to vary over time.

### FLOWER FLIES FOR POLLINATION AND BIOCONTROL

Flower flies, family Syrphidae, play a particularly important role among all the flower-visiting flies. Of the approximately 6,000 species and 300 genera and subgenera, most species are likely to play a major role in pollination (Fig. 2). Studies from around the globe have documented their importance. In Europe, Ssymank's (2001) regional studies in Germany, conducted over 10 years with more than 21,000 flower observations, showed that 80% of the total flowering plants in the area were visited by flower flies, including a number of plants previously thought to be visited by bees only. Over 600 plant species are known to be visited by syrphids in Germany (Ssymank 2007, unpublished data).

In Belgium De Buck (1990, 1993) lists more than 700 plant species in 94 families visited by syrphids, including 57

Figure 1. Relative importance of flies (Diptera), bees (Hymenoptera) and beetles (Coleoptera) in plant-flower visitor systems depending on latitude, modified from Kanstrup and Olesen (2000).



“anemophilous” species. In light of the COP 9 attempts to reduce the loss of biodiversity, we should note that Bañkowska’s five year study in Poland (Bañkowska 1980) documented that the syrphid fly fauna was dramatically different in natural versus disturbed areas. Species diversity was low in areas with intensive human activity, and those species that occurred in these areas were generalists with broad ranges and good colonizing abilities. In contrast, undisturbed areas had more species and a higher representation of specialists (Bañkowska 1980, 1981, in Germany; Ssymank 2001, 2002).

In Japan, Kakutani *et al.* (1990) observed insect visitors to the flowers of 113 plant species on the Kyoto University campus. Diptera visited 57% of these plants, and 20 species of syrphid flies visited 35%. Representatives of at least 25 Diptera families have been reported visiting flowers in the Oriental Region (Corlett 2004). Syrphids are the dominant flower-visiting flies in the forests of Yakushima and are common on winter flowering plants in Hong Kong. Syrphids are important flower visitors in the northern temperate areas of the Oriental Region, becoming less conspicuous at lower latitudes where they are still important visitors to specific plants (Corlett 2004). Mitra and Banerjee (2007) list several species of syrphid flies as pollinators of agricultural, horticultural and medicinal plants. In North America, a regional study of grassland pollinators in Colorado showed that roughly 65% of flowering plant species studied were visited by flies, and 44% were visited by sixteen species of syrphid flies (Kearns and Oliveras, unpubl.).

Flower flies are not only important as pollinators in agroecosystems, but they also serve as biocontrol agents. About 40% of the world species belong to groups which have

zoophagous larvae, mostly eating aphids, scales and other homopteran pests. They can be quite effective in preventing outbreaks of crop-damaging aphids, especially in landscapes with mosaics of seminatural vegetation like hedgerows and crops. In lettuce fields in California, they successfully control aphids (Smith and Chaney 2007). So, managing agricultural fields to encourage aphidophagous flower flies, and/or potentially rearing syrphids for release into crop fields are important applications that demand further attention.

### LARGE GAPS IN SPECIES KNOWLEDGE

Of all the Diptera on our planet, we have probably named less than a tenth, and the large majority of those named are still unknown biologically. As incidental flower visitors and opportunistic pollinators, Diptera have received much less attention than more specialized pollinators with a more predictable behaviour such as bees and hummingbirds. Diptera are too often ignored as pollinators due to their supposed inefficiency, yet by their numbers and their ubiquity in all ecosystems their role in pollen transfer may be considerably underestimated. A systems ecology approach to fly pollination is strongly needed in order to quantify the structural importance of Diptera to pollination networks.

### PLANT-POLLINATOR INTERACTIONS – A KEY FOR BIODIVERSITY

Mobile and migratory species can be efficient pollinators of abundant flower-resources and ensure long distance exchange of pollen and genetic variation. For example abundant late-flowering plants are often used for “fuelling-up” during annual fall migration of flower flies crossing the Alps in Europe.

Transitions between anemophilous and entomophilous plants/ plant-populations are known in fly-pollinated systems. Evolutionary plasticity of plant-pollinator relationships may play an important role in the co-evolution of plants and fly pollinators. The same anemophilous plant can be wind-pollinated in exposed localities, while sheltered populations can be pollinated by flies (e.g. Syrphidae in *Plantago*: Stellemann 1978).

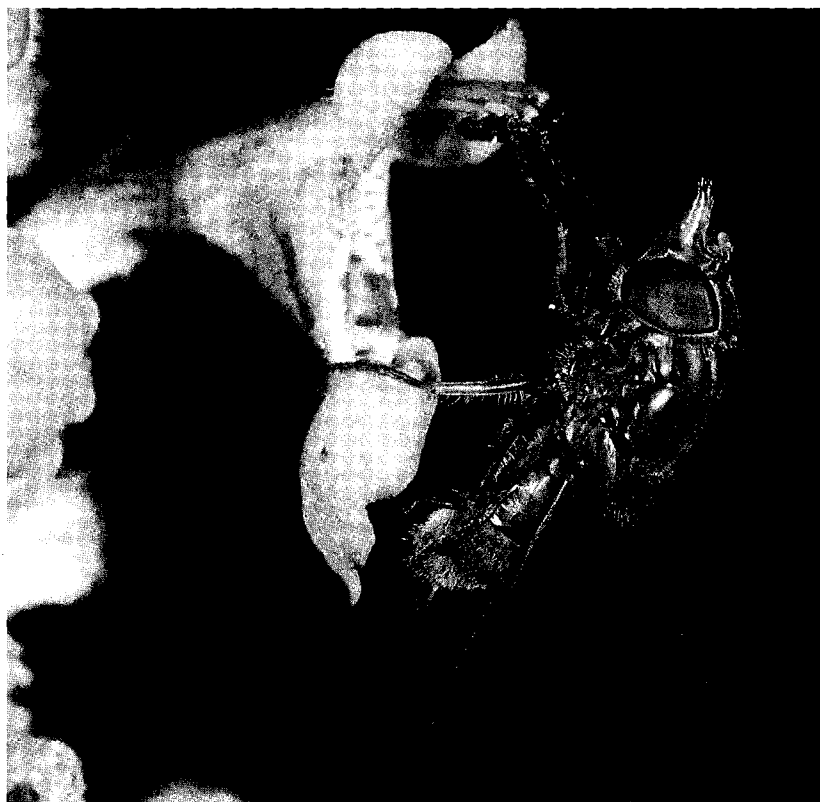
Relatively high flower constancy ensures good pollination efficiency, even with moderate plant specialisation. Flowering phenology (low number of simultaneously flowering plants), in combination with a preference of flower types (based on colour, height, inflorescence type, etc. (Ssymank 2003) is a key issue, at least in flower flies, to ensure flower constancy.

Pollination services of bees may be absent in some areas (arctic, high mountains and small or oceanic islands) or under certain conditions (time of day, humidity) be partly or completely replaced by flies. Large gaps in the knowledge both on taxonomy of Diptera and on the functional systems of pollination (worldwide, even in central Europe) demand more attention to support agriculture, maintain biodiversity and to be able to react on climate change.

### MAJOR CONCLUSIONS

The importance of Diptera as pollinators has been largely neglected, and basic studies on the taxonomy and natural history

Figure 2. Specialized flower visitor in flower flies, *Rhingia campestris*, able to exploit deep corollae with its proboscis longer than body length (Photo: A. Ssymank).



of many dipteran pollinator groups are urgently needed. Selected dipteran groups like certain flower flies play a double role in agroecosystems as both pollinators and biocontrol agents.

Applied and pure research with the aim of better understanding plant – pollinator interactions is a necessary precondition for long-term sustainable agrobiodiversity and for biodiversity at large. Dipteran pollinator shifts or population decline due to climate change or (other) human interference need to be monitored and analysed locally (Biesmeijer *et al.* 2006) as well as globally in order to maintain plant diversity with its importance for food production, therapeutic drug development and cultural values. We therefore recommend broadening the scope of the International and Regional Pollinator Initiatives within the CBD to all major ecosystems and other important pollinator groups such as flies (Diptera).

## REFERENCES

- API (African Pollinators Initiative, Secretariat). 2004. Crops, Browse and Pollinators in Africa: An Initial Stock-taking. - <http://www.fao.org/ag/AGPS/C-CAB/Castudies/pdf/apist.pdf>. Nairobi, Kenya. 62 pp.
- Bańkowska, R. 1980. Fly communities of the family Syrphidae in natural and anthropogenic habitats of Poland. *Memorabilia Zoologica* 33:3-93.
- Bańkowska, R. 1981. Hover flies (Diptera, Syrphidae) of Warsaw and Mazovia. *Memorabilia Zoologica* 35: 57-78.
- Biesmeijer, J. C., S. P. M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A.P. Schaffers, S. G. Potts, R. Kleukers, C.D. Thomas, J. Settele, and W. E. Kunin. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313 (5785): 351-354.
- Borkent, C.J. and L.D. Harder. 2007. Flies (Diptera) as pollinators of two dioecious plants: Behaviour and implications for plant mating. *Canadian Entomologist* 139(2): 235-246
- Brazilian Ministry of the Environment. 1999. International Pollinators Initiative: The São Paulo Declaration on Pollinators, Brasilia, 79 pp., <http://www.cbd.int/doc/case-studies/agric/agr-pollinator-rpt.pdf>.
- Clement, S.L., B.C. Hellier, L.R. Elberson, R.T. Staska, and M.A. Evans. 2007. Flies (Diptera: Muscidae: Calliphoridae) are efficient pollinators of *Allium ampeloprasum* L. (Alliaceae) in field cages. *Journal of Economic Entomology* 100: 131-135.
- Corlett, R. T. 2004. Flower visitors and pollination in the Oriental (Indomalayan) Region. *Biol. Rev.* 79: 497-532.
- De Buck, N. 1990. Bloembezoek en bestuivingsecologie van zweefvliegen (Diptera, Syrphidae) in het bijzonder voor België. - Studiendocumenten Royal Belgian Institute of Natural Sciences. 60: 1-167, Brussels.
- De Buck, N. 1993. Bloembezoek en bestuivingsecologie van zweefvliegen (Diptera, Syrphidae) in het bijzonder voor België. Appendix to working document '60' of the Royal Belgian Institute of Natural Sciences. - unpublished, 56 pp.
- Elberling, H., and J. M. Olesen. 1999 The structure of a high latitude plant-flower visitor system: The dominance of flies. *Ecography* 22: 314-323.
- Endress, P.K. 2001. The Flowers in Extant Basal Angiosperms and Inferences on Ancestral Flowers. *International Journal of Plant Sciences* 162: 1111-1140.
- Evenhuis, N. L., T. Pape, A.C. Pontand, F.C. Thompson (Eds.). 2008. Biosystematic Database of World Diptera, Version 10. <http://www.diptera.org/biosys.htm>, accessed on 20 January 2008.
- Gilbert, F.S. 1985. Diurnal activity patterns in hoverflies (Diptera, Syrphidae). *Ecol. Ent.* 10(4): 385-392.
- Gladis, T. 1994. Zuchtmethoden und Nutzungsmöglichkeiten für einheimische Insekten als Bestäuber allogamer Kulturpflanzenarten. - Schriftenreihe Länderinst. für Bienenkunde 1: 10-23.
- Goldblatt, P., P. Bernhardt, P. Vogan, and J.C. Manning. 2004. Pollination by fungus gnats (Diptera: Mycetophilidae) and self-recognition sites in *Tolmiea menziesii* (Saxifragaceae). *Plant Syst. Evol.* 244: 55-67.
- Goldblatt, P., J.C. Manning, and P. Bernhardt. 1995. Pollination biology of *Lapeirousia* subgenus *Lapeirousia* (Iridaceae) in Southern Africa: Floral divergence and adaptation for long-tongued fly pollination. *Ann. Missouri Bot. Gard.* 82: 517-534.
- Hansen, M. 1983. *Yuca* (Yuca, Cassava), pp. 114-117. In Janzen, D. (Ed.). *Costa Rican Natural History*. The University of Chicago Press, Chicago, xi + 816.
- Heath, A. C. G. 1982. Beneficial aspects of blowflies (Diptera: Calliphoridae). *New Zealand Entomologist* 7: 343-348.
- Herrera, C.M. 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biol. J. Linn. Soc.* 35: 95-125.
- Jarlan, A., D. DeOliveira, and J. Gringras. 1997. Pollination by *Eristalis tenax* (Diptera : Syrphidae) and seed set of greenhouse sweet pepper. *Horticultural Entomology* 90: 1646-1649.
- Kakutani, T., T. Inoue, M. Kato, and H. Ichihashi. 1990. Insect-flower relationship in the campus of Kyoto University, Kyoto: An overview of the flowering phenology and the seasonal pattern of insect visits. *Contributions from the Biological Laboratory, Kyoto University* 27(4): 465-521.
- Kanstrup, J. and J.M. Olesen. 2000. Plant-flower visitor interactions in a neotropical rain forest canopy: community structure and generalisation level. Pp. 33-41 in Totland, Ø., W. S. Armbruster, C. Fenster, U. Molau, L. A. Nilsson, J. M. Olesen, J. Ollerton, M. Philipp and J. Ågren (Eds.). The Scandinavian Association for Pollination Ecology honours Knut Fægri. The Norwegian Academy of Science and Letters, Oslo.
- Kearns, C. A. 1992. Anthophilous fly distribution across an elevation gradient. *Am. Midl. Nat.* 127: 172-182.
- Kearns, C. A. 2001. North American dipteran pollinators: assessing their value and conservation status. *Conservation Ecology* 5(1): 5. [online] URL: <http://www.consecol.org/vol5/iss1/art5/>
- Kearns, C. A. 2002. Flies and flowers: an enduring partnership. *Wings* (The Xerces Society) 25(2):3-8.
- Kevan, P.G. 1972. Insect pollination of high arctic flowers. *J. Ecology* 60: 831-847.
- Kevan, P. 2002. Flowers, pollination, and the associated diversity of flies. *Biodiversity* 3(4):16-18.
- Kluser, S. and P. Peduzzi. 2007. Global pollinator decline: A literature review. UNEP/GRIDEurope, Geneva; 10 pp.
- Labandeira, C. C. 1998. How old is the flower and the fly? *Science* 280: 85-88.
- Larson, B. M. H., P. G. Kevan and D. W. Inouye. 2001. Flies and flowers: I. The taxonomic diversity of anthophiles and pollinators. *Canadian Entomologist* 133(4): 439-465.
- Mitra, B. and D. Banerjee. 2007. Fly pollinators: assessing their value in biodiversity conservation and food security in India. *Rec. zool. Surv. India* 107(Part 1): 33-48.
- Motten, A. F. 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecological Monographs* 56: 21-42.
- NRC: National Research Council, National Academy of Science. 2007. Status of pollinators in North America. Xiv + 307 pp., Washington.
- Pellmyr, O. 1989. The cost of mutualism: interactions between *Trollius europaeus* and its pollinating parasites. *Oecologia* 78:53-59.
- Rosso, H., V.R. Rao, and T. Gladis. 1994. Laborzucht von *Eristalis tenax* (Diptera: Syrphidae) zur kontrollierten Bestäubung von Kulturpflanzen. [Laboratory rearing of *Eristalis tenax* (Diptera: Syrphidae) for controlled pollination of cultivated plants]. -Mitt.bl. EVSA e.V. 2(1): 6-9, Schönebeck.
- Sakai, S., M. Kato, and H. Nagamasu. 2000. *Artocarpus* (Moraceae)-gall midge pollination mutualism mediated by a male-flower parasitic fungus. *American Journal of Botany* 87(3): 440-445.
- Skevington, J. H. and P.T. Dang (Eds). 2002. Exploring the diversity of flies (Diptera). *Biodiversity* 3(4): 3-27.
- Smith, A. A. and W.E. Chaney. 2007. A survey of syrphid predators of *Nasonovia ribisnigri* in organic lettuce on the central coast of California. *Journal of Economic Entomology* 100(1): 39-48.
- Stellemann, P. 1978. The possible role of insect visits in pollination of reputedly anemophilous plants, exemplified by *Plantago lanceolata* and syrphid flies. *Linnaean Society Symposium* 6: 41-46.
- Ssymank, A. 1991. Die funktionale Bedeutung des Vegetationsmosaiks eines Waldgebietes der Schwarzwaldvorbergzone für blütenbesuchende Insekten - untersucht am Beispiel der Schwebfliegen (Diptera, Syrphidae). *Phytocoenologia* 19(3): 307-390.
- Ssymank, A. 2001. Vegetation und blütenbesuchende Insekten in der Kulturlandschaft [Vegetation and flower-visiting insects in cultivated landscapes] - Schriftenreihe Landschaftspflege und Naturschutz 64, 513 pp., Bonn-Bad Godesberg.
- Ssymank, A. 2002. Patterns of habitat use by Syrphidae (Diptera) in the valley of the river Strom in north-east Brandenburg. - Stuttgart. - *Volucella* 6: 81-124.
- Ssymank, A. 2003. Habitatnutzung blütenbesuchender Schwebfliegen (Diptera, Syrphidae) in Wald-Offenland-Vegetationsmosaik. - Ber. d.Reinh.-Tüxen-Ges. 15: 215-228, Hannover.
- USDA, US Department of Agriculture, North Central Regional Plant Introduction Station 2007. Pollinators at PI. <http://www.ars.usda.gov/Main/docs.htm?docid=13442&page=5>