

Chapter 5

Saproxylic Diptera



Michael D. Ulyshen

Abstract Diptera rivals Coleoptera as perhaps the most abundant and diverse order of saproxylic insects, with saproxylic habits known from at least 75 (48%) of the 157 fly families recognized globally. Some fly families are mostly if not entirely saproxylic including Aulacigastridae, Axymyiidae, Canthyloscelidae, Clusiidae, Pachyneuridae, Pantophthalmidae, Periscolididae, Xylomyidae, and Xylophagidae. Saproxylic flies are common inhabitants of virtually all moist to wet microhabitats including sap flows, under bark, in rotting wood, tree hollows, and fungal fruiting bodies. Most species are saprophagous or fungivorous although many predatory species exist as well, including some of the most important natural enemies of bark beetles. Although very poorly studied compared to beetles, it is clear that many saproxylic fly species are declining due to forest loss or degradation, and some taxa (e.g., mycetophilids) are good indicators of forest continuity. The dependence of flies on wet or even saturated substrates suggests they need special consideration when developing conservation strategies. Studies addressing their sensitivity to various management interventions are urgently needed.

5.1 Introduction

Originating approximately 270–251 million years ago (Bertone and Wiegmann 2009), flies belong to one of the four most taxonomically diverse insect orders, Diptera, with approximately 157 extant families and over 160,000 named species (Marshall 2012). They are also the most ecologically diverse, occurring in virtually all terrestrial and freshwater habitats where they exploit an unmatched variety of food resources. Although sometimes overshadowed by beetles and other groups, flies are ubiquitous and are often among the most numerous insects encountered in saproxylic habitats (Swift et al. 1984; Krivosheina 2006; Teskey 1976; Derksen

M. D. Ulyshen (✉)

USDA Forest Service, Southern Research Station, Athens, GA, USA

e-mail: mulyshen@fs.fed.us

This is a U.S. government work and its text is not subject to copyright protection in the United States; however, its text may be subject to foreign copyright protection 2018 M. D. Ulyshen (ed.), *Saproxylic Insects*, Zoological Monographs 1, https://doi.org/10.1007/978-3-319-75937-1_5

167

1941; Vanderwel et al. 2006; Schiegg 2001). Hövemeyer and Schauer mann (2003) collected nearly 12,000 flies from 37 families and 163 species from decomposing beech logs in Germany, for example, and flies accounted for over 90% of insects emerging from decaying wood in a Canadian study (Vanderwel et al. 2006). As members of the saproxylic insect community, flies are second only to beetles in functional and taxonomic diversity (Figs. 5.1 and 5.2) and may prove to be even more species rich than beetles in some regions [e.g., Nordic countries, see Stokland et al. (2012)]. The diversity of saproxylic flies is generally underappreciated due to

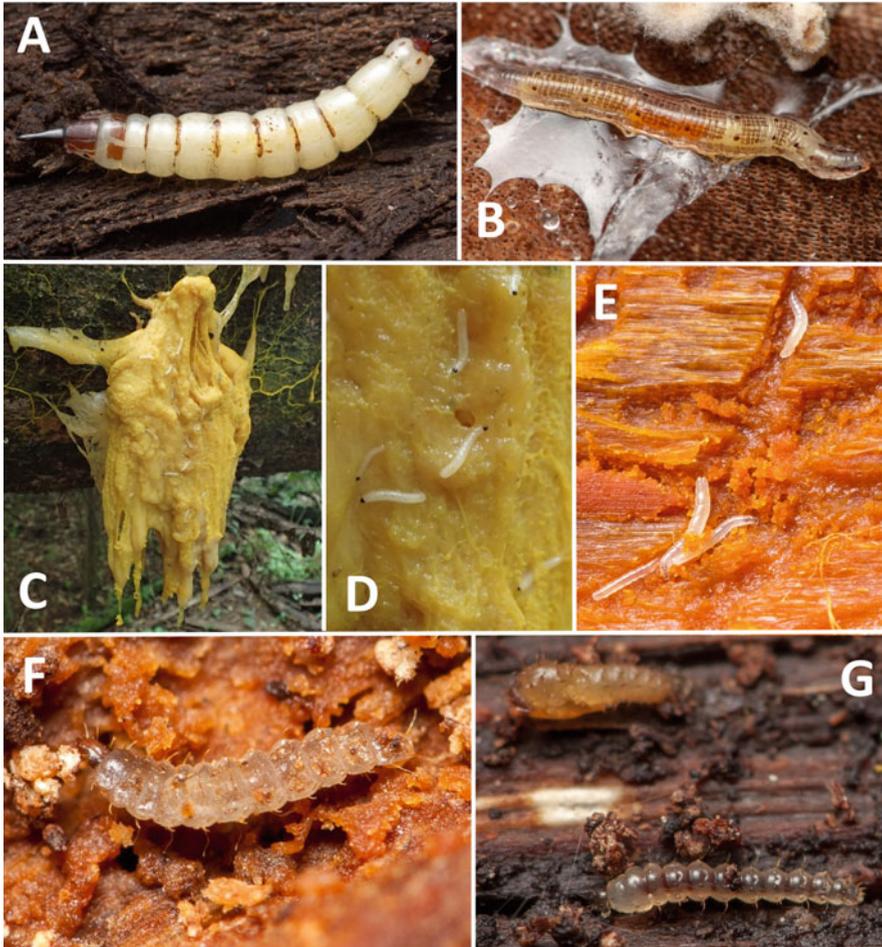


Fig. 5.1 Examples of larval saproxylic flies. (a) *Xylophagus lugens* Loew (Xylophagidae) in rotting wood, North Carolina; (b) Keroplatidae on a polypore, North Carolina; (c) Sciaroidea on the plasmodium of a slime mold (*Physarum*) atop the rotting fruiting bodies of *Pleurotus*, South Carolina; (d) close-up view of the same larvae shown in the previous image; (e) *Medetera* (Dolichopodidae) in bark beetle galleries, Florida; (f) Stratiomyidae under bark, North Carolina; (g) Forcipomyiinae ceratopogonids (pupa and larva) under bark, North Carolina. Images (a), (b), and (e-g) by Matthew Bertone and images (c) and (d) by Michael Ulyshen

their small size and the difficulty of identifying many families to species. Efforts to study the most challenging families have revealed an incredible diversity of species associated with dead wood, however. In Canada, for instance, Selby (2005) collected 323 cecidomyiid species or morphospecies from rotting logs in an old-growth forest.

Flies are typically saproxylic only as larvae (Fig. 5.1), whereas adults (Fig. 5.2) usually function away from dead wood as nectar feeders, predators, etc. Certain

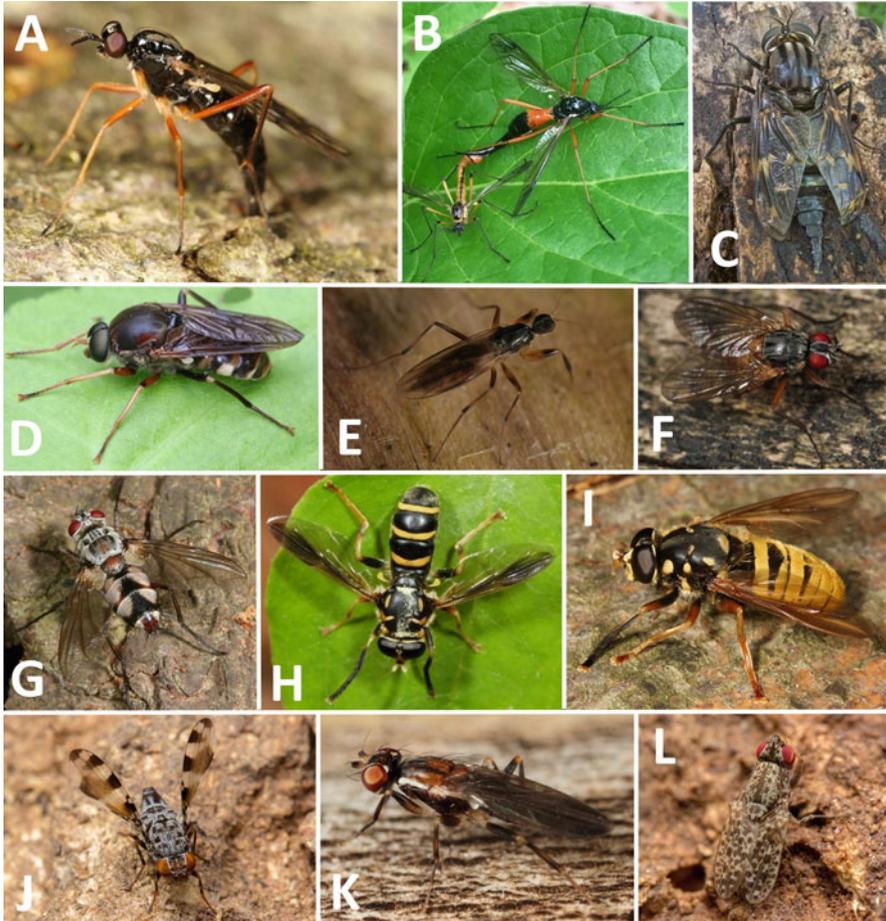


Fig. 5.2 Examples of adult saproxylic flies. (a) *Xylophagus compeditus* Meigen (Xylophagidae), Germany; (b) *Tanyptera dorsalis* (Walker) (Tipulidae), New York; (c) *Pantophthalmus bellardii* (Bigot) (Pantophthalmidae), Costa Rica; (d) *Coenomyia ferruginea* (Scopoli) (Xylophagidae), Illinois; (e) *Tachypeza* sp. (Hybotidae), Germany; (f) *Phaonia rufiventris* (Scopoli) (Muscidae), Germany; (g) *Zelia vertebrata* (Say) (Tachinidae), North Carolina; (h) *Temnostoma balyras* (Walker) (Syrphidae), North Carolina; (i) *Temnostoma vespiforme* (L.) (Syrphidae), Germany; (j) *Pseudotephritis vau* (Say) (Ulidiidae), North Carolina; (k) *Clusiodes albimanus* (Meigen) (Clusiidae), Germany; (l) *Traginops irroratus* Coquillett (Odiniidae), North Carolina. Images (a), (e), (f), (i), and (k) by Frithjof Kohl; (b) by Brandon Woo; (c) by Piotr Naskrecki; (j) and (l) by Matthew Bertone; (d) by Thomas Bentley; and (g) and (h) by Patrick Coin

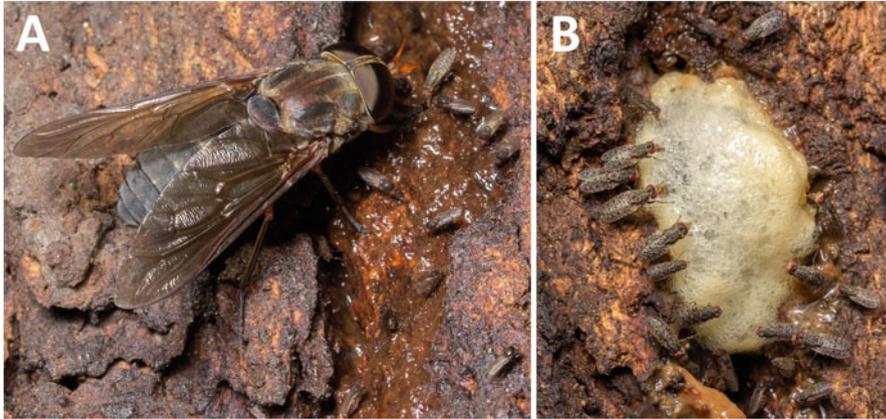


Fig. 5.3 Flies on slime flux in North Carolina, USA. Members of Aulacigastridae, Drosophilidae, Odiniidae, and Tabanidae are shown in image (a), and Odiniidae (*Traginops*) and Drosophilidae are shown in image (b). Images by Matthew Bertone

syrrhids and other species that feed exclusively on sap runs (Fig. 5.3) are some of the few taxa that are saproxylic as adults (Speight 1989). As with other insect orders, many non-saproxylic fly taxa also benefit from the conditions and resources provided by dead wood. In Germany, for instance, Hövemeyer and Schauer mann (2003) found that many fly species benefit from the moss layer that sometimes forms on rotting logs, with moss coverage being one of the two strongest determinants (the other being water content) of fly diversity associated with dead wood. A number of non-saproxylic predatory fly taxa also benefit from dead wood. One example, *Pherbellia annulipes* (Zetterstedt), is a specialist predator of snails in Europe that is rarely found away from rotting logs due to the high numbers of snails to be found there (Speight 1989).

Compared to beetles, the habits of saproxylic flies remain poorly studied. Many species are presumed to be saproxylic due to their close association with dead wood (Roháček and Marshall 2017), but little or nothing is known about their larval habits or requirements. The threatened status of saproxylic flies is thus likely to be underestimated (Jonsell et al. 1998). Unlike beetles and other groups, saproxylic flies typically prefer moist to wet microhabitats and often dominate assemblages in saturated or submerged wood (Hövemeyer and Schauer mann 2003; Braccia and Batzer 2008). Many saproxylic fly species develop within fermenting sap, either flowing from wounds on trees or under the bark, where they function as microbial grazers or predators of other insects (Marshall 2012). Many other species feed within wet or saturated wood at various stages of decomposition and can best be described as saprophagous, benefiting more from the microbes associated with rotting wood than from the wood itself. Species that are restricted to water-filled tree holes, including many mosquito taxa, are also saproxylic. Saproxylic flies associated with the wettest environments commonly have special morphological structures to aid in respiration. Axymyiid larvae, for example, have tail-like respiratory syphons

ending in a pair of spiracles that allow them to maintain contact with the surface of wood partially submerged in streams (Marshall 2012) (see Fig. 22.3e, this volume). Larval sap flies belonging to the family Aulacigastridae also breathe through long respiratory tubes as do many syrphid larvae (Marshall 2012).

There is some disagreement over family-level divisions among flies, creating uncertainty about the total number of fly families. Whereas crane flies are typically divided into four families in Europe (Tipulidae, Limoniidae, Cylindrotomidae, and Pediciidae), for example, others give these groups subfamily status within Tipulidae (Petersen et al. 2010). Here I follow the classification system used by Marshall who listed 157 extant fly families. As summarized in Table 5.1, saproxylic habits are known from at least 75 (48%) of these families although this probably underestimates the true number given that the habits of many species, genera, and even families (e.g., Lygistorrhinidae, Rangomaramidae, Syringogastridae, etc.) remain entirely unknown. While many of the families listed in Table 5.1 contain relatively few saproxylic species, other families are mostly if not entirely saproxylic. Examples of the latter include Aulacigastridae, Axymyiidae, Canthyloscelidae, Clusiidae, Pachyneuridae, Pantophthalmidae, Perisclididae, Xylomyidae, and Xylophagidae. The most well-studied group of saproxylic flies are those belonging to the family Syrphidae. Although only a small proportion of syrphid species are saproxylic [e.g., ~14% of European species (Reemer 2005)], this still amounts to many hundreds of species including most members of the largest subfamily, Eristalinae. Fungus gnats belonging to a variety of families are perhaps the most diverse members of the saproxylic community. They are also among the least understood, with most species awaiting discovery and description. In the Neotropics, for example, the ratio of undescribed to known species of mycetophilids is thought to exceed 10:1 (Amorim 2009).

This chapter aims to promote the appreciation for and conservation of saproxylic flies. My main objectives are to (1) summarize the family-level diversity of saproxylic flies globally (Table 5.1), (2) describe the main resources utilized by saproxylic flies, and (3) discuss the conservation status of these insects and how best to protect them in managed forests.

5.2 Feeding Groups and Microhabitats

Most saproxylic flies are either saprophagous, fungivorous, or predatory as larvae. The saprophagous species feed on a variety of decomposing substrates including fermenting sap near tree wounds or under bark, rotting wood and the frass or nest material of saproxylic insects. Fungivorous species are commonly associated with the fruiting bodies of wood-rotting fungi. Predatory taxa, including parasitoids, can be found in all of these microhabitats and attack a wide range of species including other fly species, wood-boring beetles, termites, etc. According to Krivosheina (2006), predatory habits are much more widespread among brachyceran (especially Orthorhapha) saproxylic flies than among the lower families of Diptera. Some fly

Table 5.1 Alphabetical list of fly families of the world known to include saproxylic species, their habits, and distribution

Family	Habits of saproxylic members
Acartophthalmidae	Rotting wood, presumably saprophagous (Marshall 2012) (Holarctic)
Anisopodidae	Saprophagous in decaying wood, roots, wet tree holes, beetle galleries, or sap flows (e.g., <i>Mycetobia</i>) on wounded trees (Marshall 2012; Teskey 1976) (widespread)
Anthomyiidae	Saprophagous in rotting wood or under bark and predators of cavity nesting bees and wasps (e.g., <i>Eustalomyia</i>) (Teskey 1976; Speight 1989; Marshall 2012) (widespread but mostly Holarctic)
Asilidae	Predatory in rotting wood (especially Laphriinae) including within beetle burrows, often in light gaps (Speight 1989; Rotheray et al. 2001; Teskey 1976) (widespread)
Asteiidae	Saprophagous in tree hollows, fungi, etc. (Marshall 2012) (widespread)
Aulacigastridae	Saprophagous on sap flows (<i>Aulacigaster</i>) (Rotheray et al. 2001; Teskey 1976) (widespread but concentrated in Neotropics)
Axymyiidae	Develop only in partially submerged rotting wood in small forest streams (Wihlm and Courtney 2011) (northern hemisphere, temperate)
Bibionidae	Saprophagous in rotting wood (e.g., Hesperinae) (Marshall 2012) (widespread)
Bolitophilidae	Fungivorous, some monophagous on wood-rotting fungi [e.g., <i>Bolitophila (C.) retangulata</i> Lundström on <i>Laetiporus sulphureus</i> (bull.) Murrill.] (Ševčík 2010) (Holarctic and Taiwan)
Braulidae	Inquiline of honey bee hives (widespread)
Calliphoridae	Saprophagous or predatory within termite nests (e.g., Bengaliinae and Prosthetosomatinae) (Marshall 2012). Also reported under bark (Rotheray et al. 2001) (widespread)
Canthylosceldidae	Saprophagous in wet decaying wood (e.g., <i>Synneuron</i>), especially in “ancient” forests (Teskey 1976; Marshall 2012) (Holarctic, South America and New Zealand)
Cecidomyiidae	Saprophagous, fungivorous, or predatory in rotting wood, under bark (e.g., <i>Miastor</i>), fungal fruiting bodies, beetle galleries, or termite nests (Økland 1995a; Ševčík 2010; Marshall 2012; Teskey 1976; Selby 2005) (widespread)
Ceratopogonidae	Saprophagous or predatory, in tree holes (e.g., <i>Dasyhelea</i>), under bark, and rotting wood (Marshall 2012; Teskey 1976; Kitching 1971). Other species are fungivorous (Ševčík 2010) (widespread)
Chaoboridae	Predators in tree holes (e.g., <i>Corethrella</i>) (Yanoviak 2001)
Chironomidae	Saprophagous in soggy or submerged rotting wood (Braccia and Batzer 2008; Teskey 1976) or water-filled tree holes (e.g., <i>Metriocnemus</i>) (Kitching 1971) and a few terrestrial species are fungivorous (e.g., <i>Bryophaenocladus</i>) (Ševčík 2010) (widespread)

(continued)

Table 5.1 (continued)

Family	Habits of saproxylic members
Chloropidae	Saprophagous or rarely predatory in rotting wood and tree holes; some species fungivorous on fungal fruiting bodies (Ševčík 2010; Teskey 1976) (widespread)
Chyromyidae	Saprophagous in tree holes (Teskey 1976) (widespread)
Clusiidae	Predatory in rotting wood, under bark, and beetle galleries (Rotheray et al. 2001; Teskey 1976; Marshall 2012) (widespread)
Corethrellidae	Predatory in water-filled tree holes (Marshall 2012) (widespread but mostly tropical)
Culicidae	Saprophagous or predatory (e.g., <i>Toxorhynchites</i>) in water-filled tree holes (Teskey 1976) (widespread)
Cypselosomatidae	Under bark (Krivosheina 1979) (widespread)
Diadocidiidae	Fungivorous in decaying wood (Jakovlev 2011) (widespread)
Ditomyiidae	Fungivorous (e.g., <i>Ditomyia</i>) on bracket fungi or saprophagous in relatively hard (e.g., <i>Symmerus</i>) or rotting wood (Ševčík 2010; Krivosheina 2006) (widespread but concentrated in Australasia and South America)
Dolichopodidae	Predatory (or necrophagous) in rotting wood, sap flows, tree holes (e.g., <i>Systemus</i>), under bark, and in beetle burrows (e.g., <i>Medetera</i>) (Rotheray et al. 2001; Teskey 1976; Marshall 2012; Kishi 1969) (widespread)
Drosophilidae	Saprophagous in rotting wood, under/in bark, wet tree holes, sap flows, and in the tunnels of ambrosia beetles (<i>Amiota</i>) (Rotheray et al. 2001; Teskey 1976; Krivosheina 2006); other species are fungivorous (Ševčík 2010; Jonsell et al. 1999) (widespread)
Empididae	Saprophagous in rotting wood (e.g., <i>Rhamphomyia</i> , <i>Drapetis</i> , and <i>Platypalpus</i>) and under bark (Rotheray et al. 2001); other species are predatory (Hövmeyer and Schauer mann 2003) (widespread)
Fanniidae	Fungivorous in fungal fruiting bodies (Ševčík 2010) or saprophagous in rotting wood or in tree holes (e.g., <i>Fannia</i>) (Hövmeyer and Schauer mann 2003) (widespread)
Heleomyzidae	Fungal fruiting bodies and in wood-boring beetle tunnels (e.g., the Australian <i>Cairnsimya</i>) (Marshall 2012) (widespread)
Hybotidae	Predators in rotting wood, under bark, and rarely in fungi (Rotheray et al. 2001; Ševčík 2010) (widespread)
Keroplastidae	Fungivorous or predatory on bracket fungi, under bark, or in rotting wood (Speight 1989; Marshall 2012; Ševčík 2010) (widespread)
Lauxaniidae	Saprophagous or fungivorous in rotting wood (e.g., <i>Lyciella</i>) (Rotheray et al. 2001) (widespread)
Lonchaeidae	Saprophagous or predatory in rotting wood, under bark, and in beetle galleries (Rotheray et al. 2001; Wegensteiner et al. 2015). <i>Lonchaea</i> is particularly common in dead or dying wood (Marshall 2012) (widespread but most diverse in north temperate region)

(continued)

Table 5.1 (continued)

Family	Habits of saproxylic members
Lonchopteridae	Saprophagous “surface scrapers” on rotting wood (Hövmeyer and Schauer mann 2003)
Megamerinidae	Predatory under bark (Marshall 2012) (Palearctic and oriental)
Micropezidae	Saprophagous in rotting wood and under bark (especially Taeniapterinae) (Teskey 1976) (widespread)
Milichiidae	Saprophagous? In tree holes (e.g., <i>Stomosis</i>) and under bark (Teskey 1976; Krivosheina 2006) (widespread)
Muscidae	Predatory of saprophagous or predatory in rotting wood (e.g., <i>Phaonia</i>), tree holes, or at sap flows (Rotheray et al. 2001; Ševčík 2010; Marshall 2012; Teskey 1976) (widespread)
Mycetophilidae	Fungivorous or predatory in rotting wood, tree holes, under bark, and in fungal fruiting bodies (Ševčík 2010; Marshall 2012; Jakovlev 2011) (widespread)
Mydidae	Predatory in rotting wood (e.g., <i>Mydas</i>) (Teskey 1976) (widespread)
Neriidae	Rotting wood and sap flows (Marshall 2012) (widespread but mostly tropical)
Odiniidae	Saprophagous or predatory in sappy wood, beetle and Lepidoptera galleries, and fungus (Rotheray et al. 2001; Teskey 1976; Marshall 2012) (widespread)
Opetiidae	Rotting wood (Marshall 2012) (Palearctic only)
Pachyneuridae	Saprophagous or fungivorous in rotting wood (Marshall 2012; Krivosheina 2006) (Holarctic)
Pallopteridae	Predatory under bark (<i>Palloptera</i>) (Rotheray et al. 2001; Teskey 1976) (mostly Holarctic)
Pantophthalmidae	Saprophagous on fermenting sap within their galleries (Neotropical)
Periscelididae	Saprophagous in sap flows (e.g., <i>Periscelis</i>), (Teskey 1976) (widespread)
Phoridae	Saprophagous in rotting wood and under bark; fungivorous (e.g., <i>Megaselia</i>) and parasitoids or inquiline of termites (Marshall 2012; Ševčík 2010; Matthewman and Pielou 1971) (widespread)
Pipunculidae	Predatory in rotting wood (e.g., <i>Chalarus</i>) (Hövmeyer and Schauer mann 2003)
Platypezidae	Fungivorous in rotting logs, under bark (<i>Callomyia</i>), and on fungal fruiting bodies (e.g., <i>Agathomyia</i> , <i>Bertamyia</i> , and <i>Polyporivora</i>) (Marshall 2012; Krivosheina 2006) (widespread)
Platystomatidae	Saprophagous in rotting wood and root-feeders (Marshall 2012) (mostly Australasian, oriental, and Afrotropical but also in new world)
Pseudopomyzidae	Under bark (Marshall 2012) (widespread except for the Afrotropics)

(continued)

Table 5.1 (continued)

Family	Habits of saproxylic members
Psilidae	Under bark or in sappy wood (e.g., <i>Chyliza</i>) (Teskey 1976) (mostly Holarctic and Afrotropical)
Psychodidae	Saprophagous in rotting wood (e.g., Trichomyiinae), tree holes (e.g., <i>Telmatoscopus</i> , <i>Brunettia</i> , and <i>Psychoda</i>), sap flows, and decaying fungal fruiting bodies (Rotheray et al. 2001; Ševčík 2010; Marshall 2012; Teskey 1976) (widespread)
Rhagionidae	Rotting wood (Rotheray et al. 2001) (widespread)
Richardiidae	Saprophagous, wet dead wood (e.g., <i>Omomyia</i>) (Marshall 2012) (new world only, especially Neotropics)
Ropalomeridae	Rotting wood and tree wounds (Marshall 2012) (Neotropics)
Sarcophagidae	Predatory on termites, honey bees, etc. (Marshall 2012; Hövemeyer and Schauer mann 2003) (widespread)
Scatopsidae	Saprophagous in rotten wood (e.g., <i>Ectaetia</i>), tree holes, under bark (e.g., <i>Rhexoza</i>), or decaying fungi (Rotheray et al. 2001; Ševčík 2010; Marshall 2012) (widespread)
Scenopinidae	Predatory in rotting wood, wood-boring insect galleries, under bark, and termite nests (Marshall 2012; Teskey 1976) (widespread)
Sciaridae	Saprophagous in rotting wood, under bark, at sap runs, or fungivorous (Ševčík 2010; Sokoloff 1964) (widespread)
Sphaeroceridae	Fungivorous on fungal fruiting bodies (Ševčík 2010) or saprophagous in rotting wood (Roháček and Marshall 2017) (widespread)
Stratiomyidae	Saprophagous or predatory (or necrophagous) under bark (e.g., Pachygastrinae), rotting wood, tree holes (Rotheray et al. 2001; Marshall 2012; Krivosheina 2006). Occasionally fungivorous (<i>Beris</i>) (Krivosheina 2006) (widespread)
Strongylophthalmyiidae	Under bark (Rotheray et al. 2001) (mostly old world but also North America)
Syrphidae	Saprophagous in rotting wood, under bark (<i>Hammerschmidtia</i>), in tree holes (<i>Blera</i> , <i>Callicera</i> , <i>Ceriana</i> , <i>Eristalis</i> , <i>Mallota</i> , <i>Myathropa</i> , <i>Spilomyia</i> , <i>Pocota</i> , etc.), sap runs (<i>Brachyopa</i>), or insect tunnels (<i>Brachyopa</i>) (Rotheray et al. 2001; Reemer 2005; Krivosheina 2006). Most members of Eristalinae are saproxylic (Marshall 2012) (widespread)
Tabanidae	Predatory in tree holes and rotting wood (e.g., <i>Leucotabanus</i>) (Teskey 1976) (widespread)
Tachinidae	Predatory in rotting wood or in fungal fruiting bodies (e.g., <i>Elodea</i> and <i>Phytomyptera</i>) (Jonsell et al. 2001) (widespread)
Tanyderidae	Saprophagous in submerged wood (Marshall 2012) (widespread)
Tephritidae	Saprophagous in rotting wood (e.g., Phytalmiinae) or under bark (<i>Lenitovena</i>), predatory in termite nests (Marshall 2012; Krivosheina 2006) (widespread)

(continued)

Table 5.1 (continued)

Family	Habits of saproxylic members
Therevidae	Predatory in rotting wood (e.g., <i>Psilocephala</i> and <i>Thereva</i>) or tree hollows (e.g., <i>Pandivirilia</i> , <i>Thereva</i>) (Marshall 2012; Stokland et al. 2012) (widespread)
Tipulidae (including Tipulinae, Limoniinae, Cylindrotominae, and Pediciinae)	Saprophagous, predatory, or fungivorous in rotting wood (e.g., <i>Ctenophora</i>), under bark (e.g., <i>Gnophomyia</i>), in tree holes (e.g., <i>Sigmatomera</i> , <i>Ctenophora</i>), or fungal fruiting bodies (Rotheray et al. 2001; Ševčík 2010; Marshall 2012; Yanoviak 2001) (widespread)
Trichoceridae	Saprophagous in rotting wood and sometimes fungivorous in fruiting bodies (Ševčík 2010) (widespread)
Ulidiidae	Saprophagous in rotting wood or under bark, including the frass of wood-boring beetles (e.g., <i>Callopistromyia</i>) (Rotheray et al. 2001; Teskey 1976; Marshall 2012) (widespread)
Xylomyidae	Saprophagous or predacious (or necrophagous) under bark (e.g., <i>Solva</i>) and in tree holes (e.g., <i>Xylomya</i>) (Krivosheina 2006; Teskey 1976) (widespread)
Xylophagidae	Predatory under bark and in rotting wood (e.g., <i>Xylophagus</i> , <i>Rachicerus</i> , and <i>Coenomyia</i>) (Teskey 1976) (widespread)

species appear to function primarily as necrophages, feeding on dead rather than living insects, including various xylomyids, stratiomyids, and dolichopodids (Krivosheina 2006; Kishi 1969). Other flies are inquilines of saproxylic termites and bees, and there are aquatic species that require water-filled tree holes. Major microhabitats utilized by saproxylic flies are summarized below.

5.2.1 Sap Runs

Trees wounded by insects [e.g., cossids; see Yoshimoto and Nishida (2007)], vertebrates, or other factors typically ooze sap, sometimes chronically, and this sugary substance is quickly colonized by bacteria and yeasts. The term “slime flux” is often used to refer to sap overgrown with microbes (Fig. 5.3). Sap runs (also referred to as flows or exudations) attract a wide range of insects, including species that breed in fermenting sap and those that opportunistically feed on this material as adults or prey upon other insects (Speight 1989). Diptera are typically by far the most abundant and diverse insects associated with these habitats (Wilson and Hort 1926; Yoshimoto et al. 2005) (Fig. 5.3). Wilson and Hort (1926) reported 10 families and at least 20 species from sap runs in Britain, with anthomyiids and muscids being present in the highest numbers. Sokoloff (1964) similarly reported 12 families and 21 species from sap runs in California, including 6 families and at least 8 species that were present as larvae. Some families of flies are mostly or

entirely restricted to sap runs such as Aulacigastridae, Odiniidae, and Periscelididae, and many other families (e.g., Anisopodidae, Cecidomyiidae, Ceratopogonidae, Dolichopodidae, Drosophilidae, Syrphidae) include species known only from this microhabitat. Sap-feeding flies are essentially saprophagous, grazing on the microbes present in this material.

5.2.2 *Subcortical Zone*

The zone between the bark and wood provides a variety of resources for saproxylic flies. Many researchers have reported flies from fermenting sap beneath bark, and this was one of the most productive habitats reported by Rotheray et al. (2001) in their search for saproxylic flies in Scotland. This resource appears to support a number of species also found breeding in sap runs, such as *Hammerschmidia ferruginea* (Fallén), an endangered syrphid in Europe (Rotheray et al. 2009). Krivosheina (2006) listed a number of fly taxa associated with the phloem layer in Russia, including various tipulids (*Libnotes*, *Gnophomyia*), Scatopsidae, syrphids (*Graptomyza*), tephritids (*Lenitovena*), and ulidiids (*Pseudoseioptera*). Most of these species are associated with decomposing phloem and are presumably saprophagous although several cecidomyiids primarily occur beneath the bark of dying trees. Other families found under bark include Pseudopomyzidae, Strongylophthalmyiidae, and Megamerinidae, but the habits of these taxa remain mostly unresolved (Krivosheina 2006). Some of the fly taxa found under bark (e.g., tipulids of the genera *Discobola* and *Ula*) appear to be largely fungivorous, feeding primarily on growths of mycelia.

In addition to the many saprophagous and fungivorous species, a number of predatory fly taxa occur under bark, and they often exceed other subcortical predators in both number and importance (Wegensteiner et al. 2015). Among these are important natural enemies of bark beetles including genera like *Phaonia* (Muscidae) (Fig. 5.2f), *Lonchaea* (Lonchaeidae), *Palloptera* (Pallopteridae), and *Medetera* (Dolichopodidae) (Fig. 5.1e) (Krivosheina 2006). Species of *Medetera* in particular are widely considered to be among the most valuable natural enemies of bark beetles in many areas (Wegensteiner et al. 2015). Other zoophagous species occurring beneath bark are thought to be primarily necrophagous, including various stratiomyids (*Neopachygaster*, *Pachygaster*, *Zabrachia*) (Fig. 5.1f), xylomyids, and dolichopodids (Kishi 1969; Krivosheina 2006). Some scavenging flies function as saprophagous detritivores, feeding on the mixture of rotting wood particles, fungi, bacteria, insect frass, and dead body parts that accumulates under bark and in insect tunnels. This group includes various species of Scatopsidae, Psychodidae, Tipulidae, etc. (Krivosheina 2006).

5.2.3 Wood

Members of many fly families tunnel through wood but are generally more saprophagous than xylophagous, benefiting primarily from the microbial biomass within wood rather than from the plant matter itself. One of the few exceptions is the phytophagous family Agromyzidae which includes species that feed on the cambium of living trees (Teskey 1976). Because they feed on healthy tissues, however, agromyzids are not truly saproxylic and are therefore not listed in Table 5.1. Certain cecidomyiids also feed on living wood tissue, but this family also includes many saproxylic species found under bark, in beetle galleries, or in rotting wood (Teskey 1976; Krivosheina 2006). Famous for their large size (20–55 mm in length), timber flies of the Neotropical family Pantophthalmidae (Fig. 5.2c) bore through the sound wood of dying or recently dead trees and are sometimes considered pests of living trees (e.g., *Casuarina* introduced into Central America) (Zumbado 2006). Rather than being xylophagous, the larvae of these flies feed primarily on fermenting sap within their galleries and are thus saprophagous. According to Zumbado (2006), pantophthalmids typically attack trees that produce latex or mucilaginous sap such as *Ficus* or *Ceiba pentandra* (L.) in Central America. Tipulidae is among the most significant families of wood-borers and can be found in all stages of decomposition. Swift et al. (1984) reported that *Tipula flavolineata* Meigen was the most common invertebrate present in branches from the forest floor in England, with evidence of the species in 39% of the sampled branches. The largest and most colorful tipulid genera (e.g., *Ctenophora*, *Dictenidia*, *Phoroctenia*, *Tanyptera*, and *Pselliophora*), belonging to the subfamily Tipulinae (or Ctenophorinae, depending on the classification system), all develop in dead wood, and many have become rare (Oosterbroek et al. 2006). Although some tipulid genera are capable of penetrating hardwood (e.g., *Ctenophora* and *Epiphragma*), many others (e.g., *Austrolimnophila*, *Elephantomyia*, *Limonia*) feed primarily in rotting logs and, in some cases (e.g., *Lipsothrix*), in saturated rotten logs (Teskey 1976; Dudley and Anderson 1987; Krivosheina 2006). Members of other fly families also tunnel in relatively fresh wood [e.g., *Temnostoma* syrphids (Fig. 5.2h, i)], but rotting logs generally support a greater variety of species from families including Bibionidae, Canthylloscelidae, Cecidomyiidae, Ditomyiidae, Pachyneuridae, Psychodidae, Scatopsidae, and Syrphidae (Krivosheina 2006). Some species have very specific substrate requirements with respect to moisture levels. For example, axymiids tunnel into logs partially submerged in streams and only use wet portions of the log exposed to the air (Wihlm and Courtney 2011). Wood with a high moisture content is generally preferred by saproxylic flies, and many taxa are more abundant in downed than in standing trees, as Dennis et al. (2017) recently reported from Canada. Some species are known to occur in snags, however. For example, Krivosheina (2006) reported that *Pachyneura oculata* Kriv. et Mam. (Pachyneuridae) can be found within the relatively dry wood of standing dead trees in Russia.

Although flies associated with dying and dead wood in tropical forests have been less studied than those in temperate regions, they include some of the most

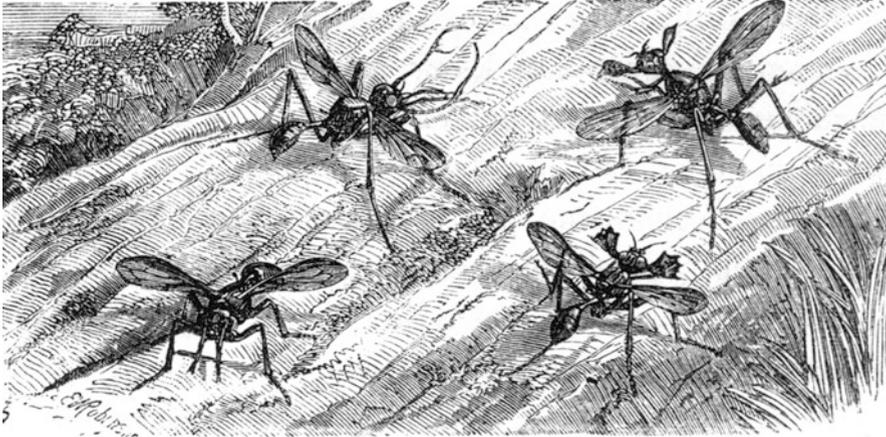


Fig. 5.4 An illustration of four “horned fly” species (Tephritidae: Phytalmiinae) from New Guinea observed by Alfred Russel Wallace in the mid-1800s. Wallace (1869) was the first naturalist to report on their association with dead wood (Glaubrecht and Kotrba 2004). Species shown include *Phytalmia cervicornis* Gerstaecker (top left), *P. alvicornis* (Saunders) (top right), and *P. megalotis* Gerstaecker (lower right) (Gary Dodson, personal communication)

remarkable fly species in the world. Among these are 6 genera and 15 species of Phytalmiinae tephritids that breed in rotting logs in New Guinea, Northern Australia, Borneo, and Sulawesi (Dodson 2000). The males of these taxa have dramatic forward-curving cheek projections that are, depending on the species, often paddle-shaped, sometimes resembling the antlers of a moose, or thin and branch-like (Fig. 5.4). The males use these structures to signal body size and, if necessary, to fight over breeding sites and females (Wilkinson and Dodson 1997). Similar examples of sexual dimorphism are seen in other saproxylic fly species associated with rotting logs. The males of many clusiid species, for example, have broadened heads, cheek projections (e.g., certain *Hendelia* and *Procerosoma*), or elongated antennae (e.g., *Hendelia* from Australia) used to defend mating territories from rivals (Marshall 2012). These examples are reminiscent of the exaggerated mandibles of lucanids and the horns of dynastine scarabs, certain ciids, tenebrionids, and other saproxylic beetle taxa, underscoring the frequency of resource-defense mating systems and associated sexually dimorphic structures among saproxylic insects (Hamilton 1978).

Fungivorous flies, especially those belonging to the families Mycetophilidae, Sciaridae, and Cecidomyiidae, are among the most abundant and diverse fly taxa associated with rotting wood (Derksen 1941; Hövemeyer and Schauer mann 2003; Krivosheina 2006) where they are thought to primarily feed on mycelia (see Sect. 5.2.5 on associates of fungal fruiting bodies). These flies remain mostly undescribed throughout much of the world (Amorim 2009), and the habits of most described species remain unknown. Stokland et al. (2012) suggest that saproxylic flies may prove to be more diverse than saproxylic beetles in Scandinavia once the habits of

these fungus gnats are more fully known. Given the same uncertainties, it should not be assumed that all fungus gnats and other fly taxa that emerge from rotting wood are saproxylic as many taxa may also breed in other decomposing plant material. A study of Collembola in North America, for example, found that species occurring in rotting stumps represented just a subset of the soil-dwelling fauna (Setälä and Marshall 1994). However, this does not appear to be the case for fungus gnats based on a comparison of flies associated with rotting wood and leaf litter. In Germany, Irmeler et al. (1996) found that 46% and 32% of mycetophilid species were found only in association with wood and leaf litter, respectively, with the remainder occurring in both substrate types. The respective figures for sciarids in that study were 30% and 45%. These findings indicate that many but not all of the fly species associated with dead wood are in fact saproxylic and underscore the need for more life history information.

In addition to the many saprophagous fly species found in dead wood, a wide variety of predatory taxa are present as well. Some predatory taxa have a wide host range. The North American tachinid, *Zelia vertebrata* (Say) (Fig. 5.2g), for instance, is known to parasitize a wide range of wood-boring beetle taxa including passalids, tenebrionids, and lucanids, etc.

5.2.4 Tree Holes

Tree holes are highly variable habitats depending on their age, position relative to the ground, opening size, water content, and insect community composition. All of these factors have been shown to influence saproxylic fly assemblages (Sánchez-Galván et al. 2014). Water content is a particularly important determinant, ranging from hollows that are usually or seasonally water-filled to those that are always dry. Flies typically dominate insect assemblages in the wettest tree holes, as Yanoviak (2001) observed in Panama, Majumder et al. (2011) reported from India, and Blakely et al. (2012) reported from New Zealand. Although some of these species are opportunists that utilize a wide range of water bodies, many of them are restricted to these structures (Blakely et al. 2012). Of the 25 species of Syrphidae collected by Ricarte et al. (2009) in Spain, 23 were collected from trunk cavities or tree holes and 12 of these were found nowhere else. Fly species dependent on water-filled tree cavities are perhaps best exemplified by Culicidae. In North America alone, for example, there are 21 species of mosquitoes from four genera (*Aedes*, *Anopheles*, *Orthopodomyia*, and *Toxorhynchites*) that are found only in these habitats and are thus saproxylic (Teskey 1976). Other fly taxa found only in or at the edge of water in wet tree holes include ceratopogonids (e.g., *Dasyhelea*, *Culicoides*, and *Atrichopogon*), syrphids (e.g., *Callicera*, *Mallota*, and *Myathropa*), chironomids (e.g., *Metriocnemus*), and dolichopodids (e.g., *Systemus*, a predator of ceratopogonids), whereas other fly genera (e.g., *Brachyopa*, *Fannia*, *Forcipomyia*, and *Phaonia*) are found in drier parts of the hole away from the water surface (Teskey 1976; Speight 1989). Syrphids exhibit a wide range of variation with respect

to their affinity to water in tree hollows, with some species requiring it and others being restricted to drier substrates (Sánchez-Galván et al. 2014). Moreover, Rotheray (2013) showed that four species of syrphids that coexist within pine stump rot holes in Scotland inhabit distinct depths, as permitted by differences in behaviors and lengths of their respiratory tubes. In addition to water content, Sánchez-Galván et al. (2014) showed cavity height, size, and orientation to also be important determinants of hollow-dwelling syrphid assemblages in Spain. The most important predictor in that study was cetoniine beetle activity, however, and the frass from these beetles was shown to enhance the larval growth rate and adult wing length of *Myathropa florea* (L.). In addition, scolytine galleries were particularly important for one species, *Criorhina pachymera* Egger. While these findings suggest interspecific interactions may strongly influence the occurrence and abundance of hollow-dwelling insect assemblages, not all studies have shown this to be the case (Schmidl et al. 2008). Fly taxa dependent on tree hollows are probably among the most vulnerable of all saproxylic fly species due to the rarity of hollow-bearing old trees and the length of time required for these structures to form. Although similar estimates for flies are lacking, Floren and Schmidl (2008) estimated that 86% of beetle species dependent on rot holes in Germany are threatened.

5.2.5 Fungal Fruiting Bodies

Elton (1966b) distinguished between the fruiting bodies of non-saproxylic and saproxylic fungi and noted that, whereas flies dominate the insect fauna associated with the former, beetles more commonly dominate the fruiting bodies of saproxylic fungi. A survey of insects utilizing *Fomes fomentarius* (L. ex Fr.) in Canada largely supports this conclusion, at least for this species of hard sporocarp. Matthewman and Pielou (1971) reported Diptera from only 4.7% of the sporocarps inspected in that study, and they accounted for just 18% and 14% of the total numbers of species and individuals collected, respectively (Fig. 5.5). Beetles, by contrast, were found in 34% of all sporocarps and made up about 33% and 37% of all species and individuals collected. Although flies make up a smaller proportion of the fauna in fungal fruiting bodies than in some other saproxylic habitats, they are nevertheless represented by a wide variety of taxa and are generally thought to be more numerous in fruiting bodies that are softer and that decompose more rapidly [i.e., annual vs. perennial species; see Komonen et al. (2001)]. In a survey of Diptera associated with fungi (including saproxylic fungi) in the Czech and Slovak Republics, Mycetophilidae was the most diverse family, accounting for 41% of species, followed by Phoridae (9%), Cecidomyiidae (8%), Drosophilidae (6%), Bolitophilidae (4%), Platypezidae (4%), and Muscidae (4%) (Ševčík 2010).

Once established, all wood-rotting basidiomycetes produce fruiting bodies. In some cases these are short-lived and soft, whereas in perennial species harder fruiting bodies continue to grow for several years before dying and slowly decomposing (Gilbertson 1984). Elton (1966b) recognized that fungal fruiting

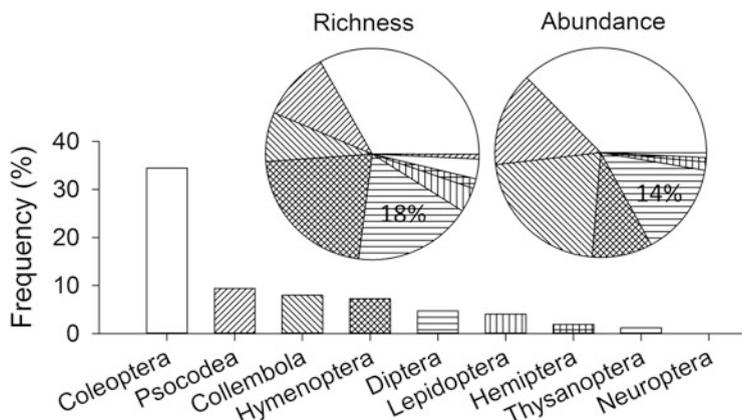


Fig. 5.5 Relative richness, abundance, and occupancy rates of Diptera and other insect orders reported by Matthewman and Pielou (1971, see Table 3) from sporocarps of *Fomes fomentarius* in Canada

bodies provide insects with four main resources: (1) spores, (2) living fungal tissue, and (3–4) aging or dead fungal tissue which, depending on the species, can be hard and long-lasting or soft and ephemeral. There are saproxylic flies specific to all four of these categories. An example of a spore-feeding species is the threatened European keroplaid, *Keroplatus tipuloides* Bosc, which feeds on the spores of *Fomes fomentarius* (L. ex Fr.) within mucilaginous webs they construct beneath the sporocarps (Speight 1989). A variety of fly species feed on living fungal tissue (e.g., Cecidomyiidae, Platypezidae, Mycetophilidae, Sciariidae, etc.), and these taxa tend to be more host specific, but fewer in number, than those feeding on decomposing fungi (Matthewman and Pielou 1971; Marshall 2012; Jonsell et al. 2001). Most sporocarp-inhabiting fly species are found in dead rather than living fruiting bodies. Those associated with dead soft fungi (Fig. 5.1c, d) are generally less host specific than those utilizing hard perennial sporocarps. Graves (1960) distinguished between dying or recently dead sporocarps and those that are dead and decomposing and suggested the former support the greatest diversity of insects. A variety of intrinsic and extrinsic factors are important in influencing the occurrence of saproxylic flies in fungal fruiting bodies. In a comparison of insect assemblages associated with *Fomitopsis pinicola* and *Fomes fomentarius*, for example, Jonsell et al. (2001) showed that most common fly taxa correlated positively with sporocarp size. Height above the ground was also important for some species (e.g., mycetophilids) as was tree diameter and sun exposure.

Predatory flies can often be found inhabiting fungal fruiting bodies. Jonsell et al. (2001) reported two species of Tachinidae (*Elodia* and *Phytomyptera*), both parasitoids, from sporocarps in Sweden, for example. Similarly, Komonen et al. (2001) found another tachinid, *Elfia cingulata* (Robineau-Desvoidy), parasitizing a tineid moth in fungal fruiting bodies in Finland. Keroplaidids are often associated with spores from polypore fungi, but will also feed on small invertebrates trapped in their webs, sometimes very efficiently (Mansbridge and Buston 1933) (Fig. 5.1b).

5.2.6 *Insect Galleries*

Many fly taxa are predators within the tunnels of wood-boring beetles and other insects. Pachygasterine stratiomyids can be found wherever their hosts occur, including their tunnels. Laphriinae asilids are active predators within the tunnels of xylophagous beetles and are morphologically adapted for this habitat (Krivosheina 2006). Dolichopodids of the genus *Medetera* are also confined to the galleries of various bark beetle species (Fig. 5.1e). Clusiids and odiniids are also among the predators found within the tunnels of wood-boring insects. Not all fly species found in beetle tunnels are predators, however. For instance, species of Ulidiidae associated with dead wood are also thought to feed on frass and other particulate matter in beetle galleries (Marshall 2012).

5.2.7 *Social Insect Nests*

A number of flies exist as inquilines within the nests of social saproxylic insects. The family Braulidae consists of two genera and eight species that are wingless, mite-like inquilines of honey bees. The larvae live in honeycombs where they feed on pollen, and the adults can be found clinging to the hairs of their hosts (Marshall 2012). Species from at least six fly families (Calliphoridae, Cecidomyiidae, Phoridae, Sarcophagidae, Scenopinidae, and Tephritidae) are known to be associated with termite nests. Within the family Phoridae alone, there are 190 species known to associate with termites (Dupont and Pape 2009), including parasitoids, opportunistic scavengers, and inquilines. The inquilines are often highly specialized, either protected by armor or by a physical or chemical similarity to their termite hosts (e.g., see Fig. 1 in Dupont and Pape 2009).

5.3 *Substrate Requirements*

5.3.1 *Successional Patterns*

As with beetles and other insects, there is a succession of flies as decomposition proceeds, with many species exhibiting distinct preferences for fresh or highly decomposed wood. An excellent demonstration of this was provided by Hövemeyer and Schauer mann (2003) who studied the emergence of flies from decomposing beech wood over a 10-year period in Germany. Consistent with other studies (Derksen 1941; Irmeler et al. 1996; Kleinevoss et al. 1996; Selby 2005), they showed that fly abundance and richness generally increased as the logs decomposed. While many fly taxa were more abundant later in the decomposition process (e.g., species of *Tipula*, *Caenosciara*, *Euthyneura*, *Cordyla*, and *Neolimonia*), some were

restricted to medium-aged logs (*Symmerus*), and others were more strongly associated with younger logs including predatory taxa such as *Medetera* and *Xylophagus*. In Canada, Vanderwel et al. (2006) also found predatory flies (Dolichopodidae and Lonchaeidae but not Empididae, which showed the opposite pattern) to be more abundant in younger decay classes, whereas saprophagous and fungivorous taxa were generally more abundant in later stages of decomposition. The higher abundance of predatory flies in younger decay classes probably reflects the higher abundance of phloem- and wood-feeding beetle prey in young logs as was shown in the same study. The pattern of greater saprophage and fungivore abundance in highly decomposed wood is complicated by the migration of leaf litter fauna into the wood as decomposition proceeds, as found by Irmiler et al. (1996) in Germany. Clearly, more detailed information on habitat associations will be needed to better understand the successional patterns of saproxylic Diptera.

Some saproxylic fly taxa are restricted to ephemeral resources or microhabitats present only at the beginning of the decomposition process. Fermenting sap under bark, for example, is a breeding substrate for many fly taxa but dries out and disappears quickly (Rotheray et al. 2009). The subcortical space itself is an important microhabitat for many species but lasts only as long as the bark remains in place. Among the North American taxa of *Forcipomyia* (Ceratopogonidae), for example, some species are restricted to wood prior to bark loss, whereas others occur only in highly decomposed wood (Teskey 1976).

Living sporocarps support a different fly fauna than dead sporocarps, and the hard sporocarps produced by perennial fungal species decompose slowly and host a succession of fly species. As summarized by Elton (1966a), mycetophilids associated with the living sporocarps of *Piptoporus betulinus* (Bull.) P. Karst. in England were replaced, soon after the death of the fungus, by the larvae of cecidomyiids and other taxa. Jonsell et al. (2001) reported a similar pattern for flies associated with *Fomitopsis pinicola* in Sweden. Økland and Hågvar (1994) showed that living *F. pinicola* sporocarps support few species before, compared to after, the development of hymenium and that dead sporocarps support the most species. Graves (1960) suggested that dying or recently dead sporocarps support more insects than those at latter stages of decomposition. Those associated with decomposing fungi (Fig. 5.1c, d) are generally believed to exhibit less host specificity. In Canada, Matthewman and Pielou (1971) found a species of *Gaurax* (Chloropidae) to be found only in dead sporocarps of *Fomes fomentarius*.

5.3.2 Diameter Preferences

Wood diameter probably matters for saproxylic fly communities just as it does for other insect taxa, but few studies have tested this. In Switzerland, Schiegg (2001) collected a significantly greater number of species from beech limbs than from beech trunks, with only a 55.3% similarity between the two diameter classes compared to 82.6% for beetles. Halme et al. (2013) found nematoceran fly communities emerging

from the bases and tops of aspen trunks to be highly variable in Finland and attributed compositional differences between these locations to random assembly rather than to diameter preferences. They suggested that the difference in diameters compared in that study was not large enough to detect strong differences.

5.3.3 *Host Specificity*

Host tree specificity is common among saproxylic insects, and many saproxylic fly taxa are largely or entirely restricted to a single genus of trees. Among the species of *Phytalmia* (Tephritidae) associated with the wood of decaying rainforest trees, for example, two are restricted to a single tree species (Dodson 2000). Irmiler et al. (1996) reported a fairly high degree of host specificity among fungus gnats (mycetophilids and sciarids) in a comparison of three wood genera in Germany. About 71% and 30% of mycetophilid and sciarid taxa, respectively, were collected from beech wood but not from the *Alnus* or *Picea* wood included in that study. By contrast, Rotheray et al. (2001) found fly diversity to vary widely among tree species in Scotland, but relatively few species were restricted to a single genus or species. Taken together, these findings indicate that the degree of host specificity exhibited by saproxylic flies varies widely among species but that some species depend on the presence of particular host tree taxa.

Although some tree species are more likely to form hollows than others, Kitching (2000) suggested that tree species has little influence on the composition of the insect fauna occupying a hollow. This appears to be true for many hollow-dwelling fly species (Ricarte et al. 2009), but some species are known to be strongly associated with particular tree taxa. The European syrphid species *Blera fallax* (L.), for example, is found in water pockets or rot holes of *Pinus sylvestris* L. stumps (Rotheray et al. 2016). Another threatened syrphid, *Callicera rufa* Schummel, also appears to be restricted to tree holes in conifers (Rotheray and MacGowan 2000).

Saproxylic flies associated with fungal fruiting bodies, especially with living sporocarps, often exhibit a high degree of host specificity. According to Jonsell et al. (2001), living fungal species that produce soft ephemeral sporocarps tend to support a less distinct fauna than those producing perennial sporocarps. Perennial sporocarps are thought to contain more secondary compounds used in defense, and this likely gives rise to specialization among fungivorous insects. In a comparison of insects associated with six species of sporocarps in Norway, Økland (1995b) found some cecidomyiid species to be restricted to particular genera or species. In Finland, Komonen et al. (2001) found that species of annual and perennial fungal fruiting bodies (*Amylocystis lapponica* (Romell) and *Fomitopsis rosea* (Alb. et Schw.: Fr.) Karst., respectively) supported distinct communities of flies and other insects.

5.3.4 *Effects of Sun Exposure*

Saproxylic flies prefer wetter substrates than many other saproxylic insect taxa, and many are adapted to aquatic or semiaquatic microhabitats. Rotheray et al. (2001) conducted perhaps the single greatest effort to describe the microhabitat associations of saproxylic Diptera. Over a 10-year period in Scotland, they collected 32 families and 258 species from sap runs, tree holes, loose bark, and dead wood from a variety of tree species. They found that some tree genera supported more species than others and that the occurrence of key microhabitats varied among tree taxa. Saproxylic fly larvae were almost always collected from damp or wet conditions in that study, with most coming from decaying sap under bark and decaying sapwood on the ground. In a study of saproxylic fly succession in Germany, Hövemeyer and Schauer mann (2003) found that flies were most numerous the year following very moist summers and suggested that log conditions, particularly moisture content, may be more important than log age in determining substrate suitability. Indeed, of the six saproxylic fly species abundant enough to analyze individually in that study, the abundances of all but one were positively and significantly correlated with wood water content.

Such findings suggest that saproxylic flies may be sensitive to sun exposure. In a study of insects associated with fungal fruiting bodies in Sweden, Jonsell et al. (2001) found *Medetera* to be significantly less frequent under open conditions, whereas the frequency of Cecidomyiidae and Mycetophilidae did not differ among exposure categories. Some saproxylic fly taxa are considered thermophilic, however, such as the European syrphid *Mallota dusmeti* Andréu (Quinto et al. 2014). Moreover, open conditions may provide important resources for the adult stage of many saproxylic fly species, such as those that visit flowers.

5.4 Status and Conservation

The literature is full of examples of saproxylic fly species known or suspected to be in decline if not already extirpated across much of their historic range. Stubbs (1972) highlighted seven such species from Britain in his early report on the conservation value of dead wood. Threatened flies also featured prominently in Speight's later assessment of the status of saproxylic insects in Europe (Speight 1989). Jonsell et al. (1998) reported 46 species of saproxylic flies red-listed in Sweden (making up nearly half of all red-listed Diptera for the country), but noted that this probably underestimates the number of threatened species due to limited knowledge. Some saproxylic fly species have the potential to serve as indicators of habitat quality. Many of the largest and most charismatic tipulid species are saproxylic, for example, and these are sensitive to the amount and continuity of dead wood (Oosterbroek et al. 2006). In some cases, flies are suspected of being saproxylic and limited to old-growth forests even though their biology remains incompletely known. In northeastern North

America, for example, the rare sphaerocerid *Volumosina voluminosa* (Marshall) has been collected only from old-growth forests and almost exclusively from large woody debris (Roháček and Marshall 2017).

The question of how much dead wood is needed to sustain diverse saproxylic insect assemblages remains an active area of study. This question has received less attention for flies than for beetles, however. Vanderwel et al. (2006) showed that the abundance of fungivorous flies (Cecidomyiidae, Mycetophilidae, and Tipulidae, which were also combined with the beetle family Melandryidae for the analysis) emerging from decomposing logs was positively correlated with the volume of dead wood present within both the surrounding 20 ha and the surrounding 79 ha. It was not possible to determine which spatial scale was more relevant in that study, however. As discussed in that paper, these patterns may be due to fungal richness correlating with coarse woody debris abundance and influencing the richness of fungivorous insects as has been shown in previous studies (Vanderwel et al. 2006 and references therein). Similarly, Schiegg (2000) found a positive correlation between the richness of flies emerging from dead wood and the average volume of subplots within a 150 m radius in Switzerland. In Norway, Økland (1994) found mycetophilid diversity to be much higher in seminatural forests when compared to managed forests (clear-cut 70–120 years previously) or recent clear-cuts (2–3 years previously), suggesting this family may be especially sensitive to the temporal continuity of forests. Økland (1996) also found a positive correlation between mycetophilid species richness and the amount of old-growth forests in the surrounding 100 km² in Norway. It was suggested in the same article that because mycetophilids must wait until late summer or early autumn for sporocarps suitable for oviposition to become available, they generally conserve energy by waiting in humid microhabitats such as under logs rather than wasting energy on dispersal. Later work by the same author found mycetophilids to be largely unaffected by harvests that removed, on average, 26% of the basal area (Økland et al. 2008). Taken together, these findings indicate that mycetophilids may be less impacted by partial harvests than clear-cuts.

Although rarely studied, the dispersal abilities of saproxylic flies probably vary widely among taxa as have been shown for beetles and other groups. Species that utilize ephemeral and infrequent resources are generally expected to be capable of travelling long distances. Support for this was provided by a mark-recapture study by Rotheray et al. (2014) which showed that the syrphid *Hammerschmidtia ferruginea* can disperse at least 5 km in Scotland. More limited dispersal abilities have been reported for other species, however. Jonsell et al. (1999) studied the ability of insects to colonize fungal fruiting bodies placed at various distances from source populations in Sweden and found two fly taxa, *Leucophenga* and *Medetera* (Drosophilidae and Dolichopodidae, respectively) to be more affected by distance than beetles in that study. Jonsell and Nordlander (2002) also found *Medetera* to be generally more common in forests with a long history of dead wood continuity compared to forests with a shorter history, although there were too few records for statistical analysis. In Finland, Komonen et al. (2000) found *Elfia cingulata*, a

tachinid that parasitizes larval tineids in fungal fruiting bodies, to be completely absent from forest fragments that had been isolated for the longest period of time.

In the Netherlands, Reemer (2005) found that 59% of saproxylic syrphid species have increased in recent years, whereas 26% have decreased. The increases are thought to be due to an increase in forest cover since the 1950s, the presence of more large diameter trees, and efforts to protect dying trees and dead wood. These numbers suggest that efforts to protect old trees and dead wood in forests can be expected to benefit saproxylic flies, although the specific requirements of declining species need to be taken into account. The protection of old trees is likely to be particularly beneficial to flies dependent on tree hollows (Blakely et al. 2012; Ricarte et al. 2009). Because these structures take such a long time to develop naturally (Micó 2018), management interventions that promote their formation are of great interest. Traditional pruning practices such as pollarding and coppicing have been shown to do so in Europe where orchards, parks, old forest pastures, and similar habitats provide some of the most important habitats for hollow-dependent insects (Sebek et al. 2013). Indeed, Quinto et al. (2014) suggest that pollarding may benefit vulnerable hollow-dependent syrphids such as *Mallota dusmeti* in Spain. Suitable breeding sites for some species (e.g., *Callicera rufa* in Europe) can be created more directly and immediately by simply cutting holes into trees or stumps (Rotheray and MacGowan 2000). Active recovery efforts for *Blera fallax*, a syrphid species on the edge of extinction in Scotland, involve captive rearing of the fly and reintroducing it into areas where pine stump rot holes have been artificially created (Rotheray et al. 2012).

Efforts to conserve saproxylic Diptera should recognize that these insects typically exhibit a stronger affinity for moist or wet habitats than most beetles or other saproxylic groups. Quinto et al. (2014) found syrphid abundance to be positively correlated with the amount of water in tree cavities, for example, whereas the opposite was the case for beetles. Rotheray et al. (2001) showed that even small young trees can provide breeding habitat for many flies, including red-listed species, provided that the necessary wet microhabitats are provided. Whereas the results from beetle studies often suggest that more open forests and sunnier conditions will promote the conservation of saproxylic insects, this may not be true for other groups, including flies. In Scotland, the endangered syrphid *Hammerschmidia ferruginea* is known to breed in the wet fermenting sap beneath bark as well as in sap runs. The former resource is more productive but is also more ephemeral. The speed at which fermenting sap beneath bark dries out is thought to be one of the major challenges facing efforts to conserve this species (Rotheray et al. 2009), suggesting such taxa may be sensitive to efforts aimed at creating more open conditions.

Finally, aquatic flies dependent on submerged wood are thought to be sensitive to forest clearance. In Brazil, for instance, Valente-Neto et al. (2015) showed that deforestation decreased the abundance and richness of saproxylic flies (chironomids) in wood submerged in streams. The researchers attributed these effects to increased sedimentation caused by the harvesting operations.

5.5 Conclusions

Flies are extremely diverse members of saproxylic insect assemblages and commonly exceed even beetles in abundance and richness. This is especially true in the wettest microhabitats including sap runs, wet tree holes, and submerged wood. Although the diversity, ecology, and conservation status of these insects have received little attention, it is clear that many species are declining or have experienced significant range contractions. Because saproxylic Diptera exhibit a strong affinity for wet or even saturated substrates, they deserve special consideration when developing conservation strategies for saproxylic insects. Studies addressing their sensitivity to forest management interventions are urgently needed.

Acknowledgments I thank Matt Bertone, Ellen Rotheray, and Jessica Mou for providing comments on an early draft of the manuscript and Gary Dodson for sharing information on *Phytalmia*. I also thank Thomas Bentley, Matthew Bertone, Patrick Coin, Frithjof Kohl, Piotr Naskrecki, and Brandon Woo for providing images used in some of the figures.

References

- Amorim DS (2009) Neotropical Diptera diversity: richness, patterns and perspectives. In: Pape T, Bickel D, Meier R (eds) *Diptera diversity: status, challenges and tools*. Brill, Boston
- Bertone MA, Wiegmann BM (2009) True flies (Diptera). In: Hedges SB, Kumar S (eds) *The timetree of life*. Oxford University Press, Oxford, pp 270–277
- Blakely TJ, Harding JS, Didham RK (2012) Distinctive aquatic assemblages in water-filled tree holes: a novel component of freshwater biodiversity in New Zealand temperate rainforests. *Insect Conserv Divers* 5(3):202–212
- Braccia A, Batzer DP (2008) Breakdown and invertebrate colonization of dead wood in wetland, upland, and river habitats. *Can J For Res* 38:2697–2704
- Dennis RWJ, Malcolm JR, Smith SM, Bellocq MI (2017) Response of saproxylic insect communities to logging history, tree species, stage of decay, and wood posture in the central Nearctic boreal forest. *J For Res*. <https://doi.org/10.1007/s11676-017-0543-z>
- Derksen W (1941) Die succession der pterygoten insekten im abgestorbenen buchenholz. *Z Morphol Ökol Tiere* 37:683–734
- Dodson GN (2000) Behavior of the Phytalmiinae and the evolution of antlers in tephritid flies. In: Aluja M, Norrbom A (eds) *Fruit flies (Tephritidae): phylogeny and evolution of behavior*. CRC, New York, pp 175–186
- Dudley TL, Anderson NH (1987) The biology and life cycles of *Lipsothrix* spp. (Diptera: Tipulidae) inhabiting wood in Western Oregon streams. *Freshw Biol* 17(3):437–451
- Dupont ST, Pape T (2009) Termitophile and termite-associated scuttle flies (Diptera: Phoridae). *Terr Arthropod Rev* 2:3–40
- Elton CS (1966a) *Dying and dead wood. The pattern of animal communities*. Wiley, New York
- Elton CS (1966b) *The pattern of animal communities*. Methuen, London
- Floren A, Schmid J (2008) Introduction: canopy arthropod research in Europe. In: Floren A, Schmid J (eds) *Canopy arthropod research in Europe*. Bioform Entomology, Nuremberg, pp 13–20
- Gilbertson RL (1984) Relationships between insects and wood-rotting basidiomycetes. In: Wheeler Q, Blackwell M (eds) *Fungus-insect relationships*. Columbia University Press, New York, pp 130–165

- Glaubrecht M, Kotrba M (2004) Alfred Russel Wallace's discovery of "curious horned flies" and the aftermath. *Arch Nat Hist* 31:275–299
- Graves RC (1960) Ecological observations on the insects and other inhabitants of woody shelf fungi (Basidiomycetes: Polyporaceae) in the Chicago area. *Ann Entomol Soc Am* 53:61–78
- Halme P, Vartija N, Salmela J, Penttinen J, Norros V (2013) High within- and between-trunk variation in the nematoceran (Diptera) community and its physical environment in decaying aspen trunks. *Insect Conserv Divers* 6(4):502–512
- Hamilton WD (1978) Evolution and diversity under bark. In: Mound LA, Waloff N (eds) *Diversity of insect faunas*. Symposia of the Royal Entomological Society of London, No. 9. Blackwell Scientific, Oxford, pp 154–175
- Hövmeyer K, Schauerermann J (2003) Succession of Diptera on dead beech wood: a 10-year study. *Pedobiologia* 47(1):61–75
- Irmiler U, Heller K, Warning J (1996) Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). *Pedobiologia* 40:134–148
- Jakovlev J (2011) Fungus gnats (Diptera: Sciaroidea) associated with dead wood and wood growing fungi: new rearing data from Finland and Russian Karelia and general analysis of known larval microhabitats in Europe. *Entomol Fennica* 22:157–189
- Jonsell M, Nordlander G (2002) Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of dead wood. *For Ecol Manag* 157:101–118
- Jonsell M, Weslien J, Ehnström B (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodivers Conserv* 7:749–764
- Jonsell M, Nordlander G, Jonsson M (1999) Colonization patterns of insects breeding in wood-decaying fungi. *J Insect Conserv* 3(2):145–161
- Jonsell M, Nordlander G, Ehnström B (2001) Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. *Ecol Bull* 49:173–194
- Kishi Y (1969) A study on the ability of *Medetera* sp. (Diptera: Dolichopodidae) to prey upon the bark and wood boring Coleoptera. *Appl Entomol Zool* 4:177–184
- Kitching RL (1971) An ecological study of water-filled tree-holes and their position in the woodland ecosystem. *J Anim Ecol* 40:281–302
- Kitching RL (2000) *Food webs and container habitats: the natural history and ecology of phytotelmata*. Cambridge University Press, Cambridge
- Kleinevoss K, Topp W, Bohac J (1996) Buchen-Totholz im Wirtschaftswald als Lebensraum für xylobionte Insekten. *Z Ökologie u Naturschutz* 5:85–95
- Komonen A, Penttilä R, Lindgren M, Hanski I (2000) Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos* 90(1):119–126
- Komonen A, Siitonen J, Mutanen M (2001) Insects inhabiting two old-growth forest polypore species. *Entomol Fennica* 12(1):3–14
- Krivosheina NP (1979) A new representative of the family Pseudopomyzidae from the Palaearctic Fauna and the taxonomic position of this family in the system of Diptera. *Entomol Rev* 58(1):179–189
- Krivosheina MG (2006) Taxonomic composition of dendrobiontic Diptera and the main trends of their adaptive radiation. *Entomol Rev* 86(5):557–567
- Majumder J, Goswami R, Agarwala BK (2011) A preliminary study on the insect community of phytotelmata: an ephemeral ecosystem in Tripura, Northeast India. *NeBio* 2:27–31
- Mansbridge GH, Buston HW (1933) On the biology of some Ceroplatinae and Macrocerinae (Diptera, Mycetophilidae). *Ecol Entomol* 81:75–92
- Marshall SA (2012) *Flies: the natural history and diversity of Diptera*. Firefly Books, Richmond Hill
- Matthewman WG, Pielou DP (1971) Arthropods inhabiting the sporophores of *Fomes fomentarius* (Polyporaceae) in Gatineau Park, Quebec. *Can Entomol* 103:775–847
- Micó E (2018) Saproxylic insects in tree hollows. In: Ulyshen MD (ed) *Saproxylic insects: diversity, ecology and conservation*. Springer, Heidelberg, pp 693–727

- Økland B (1994) Mycetophilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forests in southern Norway. *Biodivers Conserv* 3(1):68–85
- Økland B (1995a) Description of the female and the breeding habitat of *Excrementia mutuatata* Mamaev and Berest (Diptera: Cecidomyiidae). *Fauna Norvegica Serie B* 42(1):27–30
- Økland B (1995b) Insect fauna compared between six polypore species in a southern Norwegian spruce forest. *Fauna Norvegica Serie B* 42:21–26
- Økland B (1996) Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). *Biol Conserv* 76(3):297–310
- Økland B, Hågvar S (1994) The insect fauna associated with carpophores of the fungus *Fomitopsis pinicola* (Fr.) Karst. In a southern Norwegian spruce forest. *Fauna Norvegica Serie B* 41:29–45
- Økland B, Götmark F, Nordén B (2008) Oak woodland restoration: testing the effects on biodiversity of mycetophilids in southern Sweden. *Biodivers Conserv* 17(11):2599–2616
- Oosterbroek P, Bygebjerg R, Munk T (2006) The west Palearctic species of Ctenophorinae (Diptera: Tipulidae): key, distribution and references. *Entomologische Berichten* 66:138–149
- Petersen MJ, Bertone MA, Wiegmann BM, Courtney GW (2010) Phylogenetic synthesis of morphological and molecular data reveals new insights into the higher-level classification of Tipuloidea (Diptera). *Syst Entomol* 35(3):526–545
- Quinto J, Micó E, Martínez-Falcón AP, Galante E, Marcos-García Mdl Á (2014) Influence of tree hollow characteristics on the diversity of saproxylic insect guilds in Iberian Mediterranean woodlands. *J Insect Conserv* 18(5):981–992
- Reemer M (2005) Saproxylic hoverflies benefit by modern forest management (Diptera: Syrphidae). *J Insect Conserv* 9(1):49–59
- Ricarte A, Jover T, Marcos-García MA, Micó E, Brustel H (2009) Saproxylic beetles (Coleoptera) and hoverflies (Diptera: Syrphidae) from a Mediterranean forest: towards a better understanding of their biology for species conservation. *J Nat Hist* 43(9–10):583–607
- Roháček J, Marshall SA (2017) *Volumosina*, a new Nearctic genus for the rare old-growth forest fly *Herniosina voluminosa* Marshall (Diptera: Sphaeroceridae). *Can Entomol* 149:444–460
- Rotheray EL (2013) Differences in ecomorphology and microhabitat use of four saproxylic larvae (Diptera, Syrphidae) in scots pine stump rot holes. *Ecol Entomol* 38(3):219–229
- Rotheray GE, MacGowan I (2000) Status and breeding sites of three presumed endangered Scottish saproxylic syrphids (Diptera, Syrphidae). *J Insect Conserv* 4(4):215–223
- Rotheray GE, Hancock G, Hewitt S, Horsfield D, MacGowan I, Robertson D, Watt K (2001) The biodiversity and conservation of saproxylic Diptera in Scotland. *J Insect Conserv* 5(2):77–85
- Rotheray EL, MacGowan I, Rotheray GE, Sears J, Elliott A (2009) The conservation requirements of an endangered hoverfly, *Hammerschmidtia ferruginea* (Diptera, Syrphidae) in the British Isles. *J Insect Conserv* 13(6):569–574
- Rotheray EL, Lepais O, Nater A, Krützen M, Greminger M, Goulson D, Bussière LF (2012) Genetic variation and population decline of an endangered hoverfly *Blera fallax* (Diptera: Syrphidae). *Conserv Genet* 13(5):1283–1291
- Rotheray EL, Bussière LF, Moore P, Bergstrom L, Goulson D (2014) Mark recapture estimates of dispersal ability and observations on the territorial behaviour of the rare hoverfly, *Hammerschmidtia ferruginea* (Diptera, Syrphidae). *J Insect Conserv* 18(2):179–188
- Rotheray EL, Goulson D, Bussière LF (2016) Growth, development, and life-history strategies in an unpredictable environment: case study of a rare hoverfly *Blera fallax* (Diptera, Syrphidae). *Ecol Entomol* 41(1):85–95
- Sánchez-Galván IR, Quinto J, Micó E, Galante E, Marcos-García MA (2014) Facilitation among saproxylic insects inhabiting tree hollows in a Mediterranean Forest: the case of Cetonids (Coleoptera: Cetonidae) and Syrphids (Diptera: Syrphidae). *Environ Entomol* 43:336–343
- Schiegg K (2000) Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecoscience* 7:290–298
- Schiegg K (2001) Saproxylic insect diversity of beech: limbs are richer than trunks. *For Ecol Manag* 149:295–304

- Schmidl J, Sulzer P, Kitching RL (2008) The insect assemblage in water filled tree-holes in a European temperate deciduous forest: community composition reflects structural, trophic and physicochemical factors. *Hydrobiologia* 598(1):285–303
- Sebek P, Altman J, Platek M, Cizek L (2013) Is active management the key to the conservation of saproxylic biodiversity? Pollarding promotes the formation of tree hollows. *PLoS One* 8(3): e60456
- Selby RD (2005) Diversity of saproxylic Cecidomyiidae (Diptera) in a Quebec hardwood forest. McGill University, Montréal, QC
- Setälä H, Marshall VG (1994) Stumps as a habitat for Collembola during succession from clear-cuts to old-growth Douglas-fir forests. *Pedobiologia* 38:307–326
- Ševčík J (2010) Czech and slovak Diptera associated with fungi. Slezské zemské muzeum, Opava
- Sokoloff A (1964) Studies on the ecology of *Drosophila* in the Yosemite region of California. V. A preliminary survey of species associated with *D. pseudobscura* and *D. persimilis* at slime fluxes and banana traps. *Pan Pac Entomol* 40:203–218
- Speight MCD (1989) Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg
- Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in dead wood. Cambridge University Press, Cambridge
- Stubbs AE (1972) Wildlife conservation and dead wood. A supplement to the Journal of Devon Trust for Nature Conservation
- Swift MJ, Boddy L, Healey IN (1984) Wood decomposition in an abandoned beech and oak coppiced woodland in SE England II. The standing crop of wood on the forest floor with particular reference to its invasion by *Tipula flavolineata* and other animals. *Holarct Ecol* 7:218–228
- Teskey HJ (1976) Diptera larvae associated with trees in North America. *Mem Ent Soc Can* 108:1–53
- Valente-Neto F, Koroiva R, Fonseca-Gessner AA, Roque FO (2015) The effect of riparian deforestation on macroinvertebrates associated with submerged woody debris. *Aquat Ecol* 49 (1):115–125
- Vanderwel MC, Malcolm JR, Smith SM, Islam N (2006) Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. *For Ecol Manag* 225:190–199
- Wallace AR (1869) The Malay Archipelago. Macmillan, London.
- Wegensteiner R, Wermelinger B, Herrmann M (2015) Natural enemies of bark beetles: predators, parasitoids, pathogens and nematodes. In: Vega FE, Hofstetter RW (eds) Bark beetles: biology and ecology of native and invasive species. Elsevier, San Diego, pp 247–304
- Wihlm MW, Courtney GW (2011) The distribution and life history of *Axymyia furcata* McAtee (Diptera: Axymyiidae), a wood inhabiting, semi-aquatic fly. *P Entomol Soc Wash* 113 (3):385–398
- Wilkinson GS, Dodson GN (1997) Function and evolution of antlers and eye stalks in flies. In: Choe J, Crespi B (eds) The evolution of mating systems in insects and arachnids. Cambridge University Press, Cambridge, pp 310–328
- Wilson GF, Hort ND (1926) Insect visitors to sap-exudations of trees. *T Roy Ent Soc London* 74:243–254
- Yanoviak SP (2001) The macrofauna of water-filled tree holes on Barro Colorado Island, Panama. *Biotropica* 33(1):110–120
- Yoshimoto J, Nishida T (2007) Boring effect of carpenterworms (Lepidoptera: Cossidae) on sap exudation of the oak, *Quercus acutissima*. *Appl Entomol Zool* 42(3):403–410
- Yoshimoto J, Kakutani T, Nishida T (2005) Influence of resource abundance on the structure of the insect community attracted to fermented tree sap. *Ecol Res* 20(4):405–414
- Zumbado MA (2006) Diptera of Costa Rica and the new world tropics. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica