

FUNCTIONAL DIVERSITY OF TACHINID PARASITOIDS IN MANAGED BOREAL FORESTS

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INTENSIVE FOREST MANAGEMENT is characterized by clear-cut harvesting, artificial regeneration, short rotation cycles, and fire suppression. This management poses a threat to forest multi-functionality and biodiversity, leading to forest simplification and reducing the provision of ecosystem services other than the steady supply of wood for fuel, pulp and timber (Bengtsson *et al.* 2000, Puettmann *et al.* 2009). Although negative effects of intensive forestry are widely acknowledged for saproxylic species diversity (species dependent on dead or decaying wood, Niemelä 1997), much less is known about its effects on other groups. There is especially a dearth of information about the effect of intensive forest management on insect parasitoid diversity and function, despite their staggering diversity (Heraty 2009), and their key role on the maintenance of forest biological control (Peralta *et al.* 2014).

In this contribution, I outline the main findings from Rodríguez *et al.* (2019), in which we assessed the effect of diversifying forest management practices on tachinid diversity and functional composition (the organization of groups of species according to traits related to ecosystem functioning and response to disturbances). We take advantage of a large-scale and replicated ecological experiment established in 2000 in Eastern Finland, where forest structure was manipulated with several harvesting regimes and prescribed fire according to a factorial design (Fig. 1).

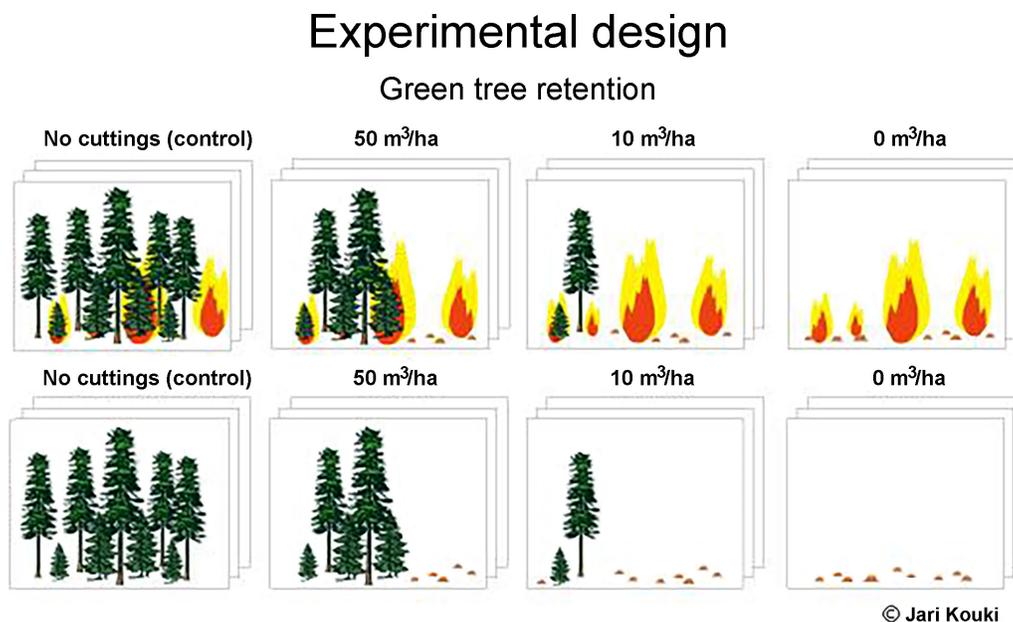


Figure 1. Experimental design. No cuttings (control) refers to old-growth forests, 50 m³/ha of tree retention, 10 m³/ha of tree retention, and 0 m³/ha refers to clear-cut. Flames in the upper row refer to prescribed burning. Number of replicates in each treatment combination was three. Reproduced here with permission from J. Kouki.

We sampled 750 individuals of 59 tachinid species parasitizing herbivorous insects with pan-traps (Appendix 1) and documented the understory vegetation functional diversity (trait diversity) as a measure of vegetation complexity for each study site, 13 years after the onset of the experiment. Tachinid species were identified by Jaakko Pohjoismäki (University of Eastern Finland). We compiled tachinid traits related to dispersal ability (body size), resource use (host taxonomic order, degree of specialization, host micro-habitat, host concealed or exposed habit), phenology and life-history (oviposition strategy, oviposition location, gregariousness) for the calculation of tachinid functional diversity and mean trait value in relation to forest habitats defined by forest management.

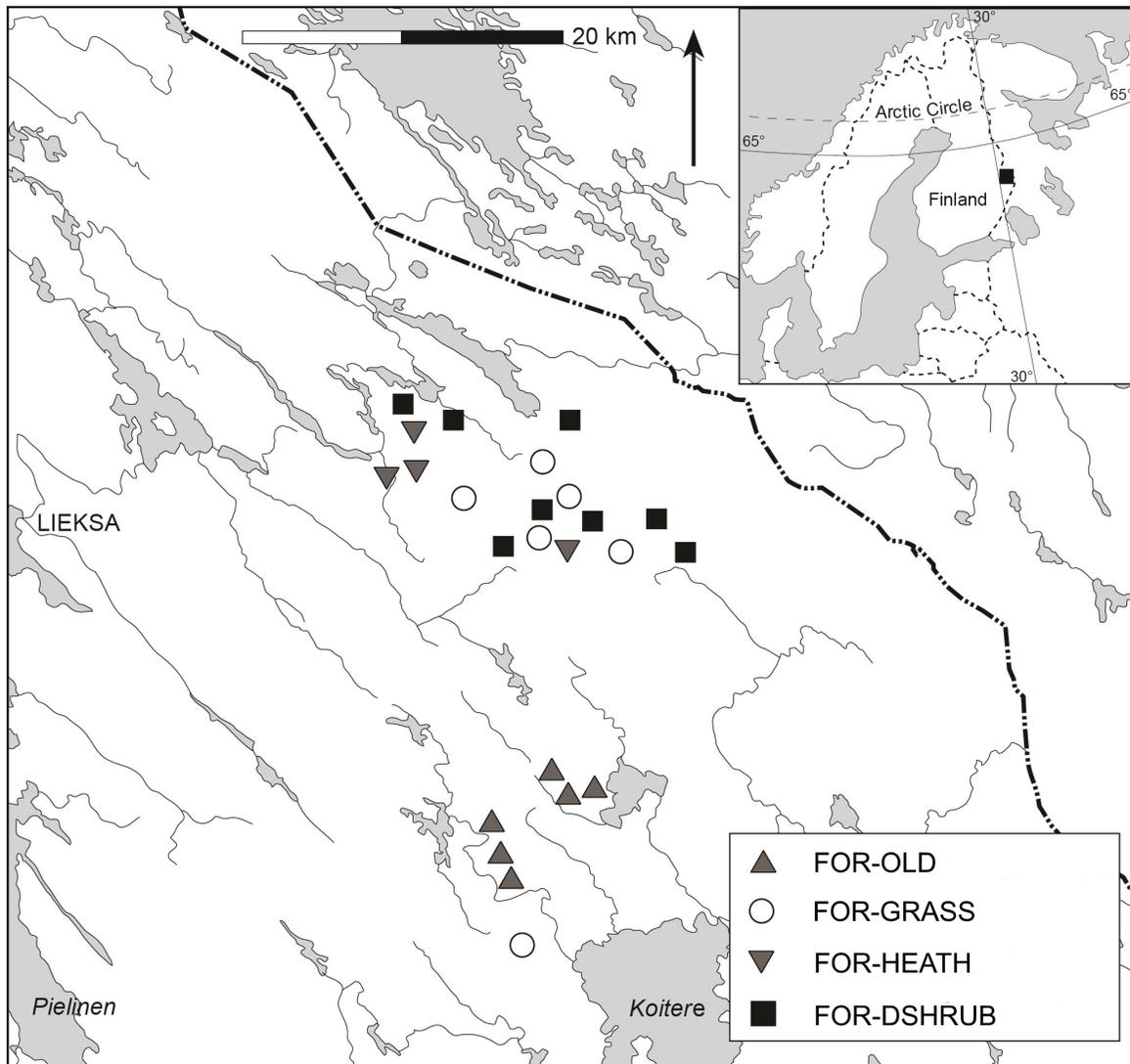


Figure 2. Map of the experimental area. The location of study sites is indicated by grey-filled triangles (old-growth forests), white-filled circles (early successional forests rich in grass), inverted grey-filled triangles (early successional forests rich in heather), and black-filled squares (early successional forests with mixed cover of ericaceous dwarf shrubs).

The combination of different levels of tree retention (retention of individual trees or forest patches at the time of clear-cut harvesting) and prescribed burning gave rise to four distinct vegetation communities (Figs. 2, 3): old-growth forests (FOR-OLD, Fig. 3a), early successional forests rich in grass (FOR-GRASS, Fig. 3b), early successional forests rich in heather (FOR-HEATH, Fig. 3c), and early successional forests with mixed cover of ericaceous

dwarf shrubs (FOR-DSHRUB, Fig. 3d). At the local scale, FOR-DSHRUB habitats contained higher tachinid diversity than most habitats, in connection with their higher level of understory vegetation complexity.



Figure 3. Pictures of the four different forest habitats taken 13 years after treatments. **a.** Old-growth forests (FOR-OLD). **b.** Early successional forests rich in grass (FOR-GRASS). **c.** Early successional forests rich in heather (FOR-HEATH). **d.** Early successional forests with mixed cover of ericaceous dwarf shrubs (FOR-DSHRUB). All photos courtesy of M. Ramos.

FOR-DSHRUB habitats correspond to burnt harvested forest stands with high levels of tree retention, which show high levels of heterogeneity caused by variability in fire intensity and augmented structural heterogeneity from retention trees. Enhanced vegetation complexity has profound implications for parasitoid behavior and development, providing diversity of physical and chemical oviposition cues (Kaiser *et al.* 2017), structural refuges for herbivores against parasitoids (Lill *et al.* 2002), refuge for parasitoids against predators (Murphy *et al.* 2014), and higher niche diversity and insect host availability.

At the landscape scale, diversity of forest management, involving prescribed fire, variable tree retention and the preservation of old-growth forest, increased habitat diversity, diversifying parasitoid trait composition (Figs. 4, 5). FOR-HEATH habitats contained on average the largest tachinid species (Fig. 4a), including *Tachina grossa* (Fig. 5a), attacking large caterpillars on heather and deciduous trees. Open areas from early successional boreal forests (FOR-GRASS, FOR-HEATH & FOR-DSHRUB) have higher vegetation functional diversity than old-growth forests, enabling higher herbivore host diversity for tachinid parasitoids. These early successional habitats contain more

specialized tachinids (Fig. 4b), like *Staurochaeta albocingulata* (Fig. 5c), and tachinids attacking a great diversity of host herbivores on herbs, grasses, shrubs and tree saplings (Figs. 4c, 4d, 5b, 5d, 5e).

Boreal old-growth (FOR-OLD), Scots pine dominated forests (Fig. 3a) provide a stable environment for generalist caterpillars feeding on bilberry (*Vaccinium myrtillus*), which is exploited by generalist tachinids attacking caterpillars on woody vegetation, like *Oswaldia muscaria* (Fig. 5f). These tachinid species may spill over to neighboring habitats (Inclán *et al.*, 2015), providing potential biological control services to forest plantations.

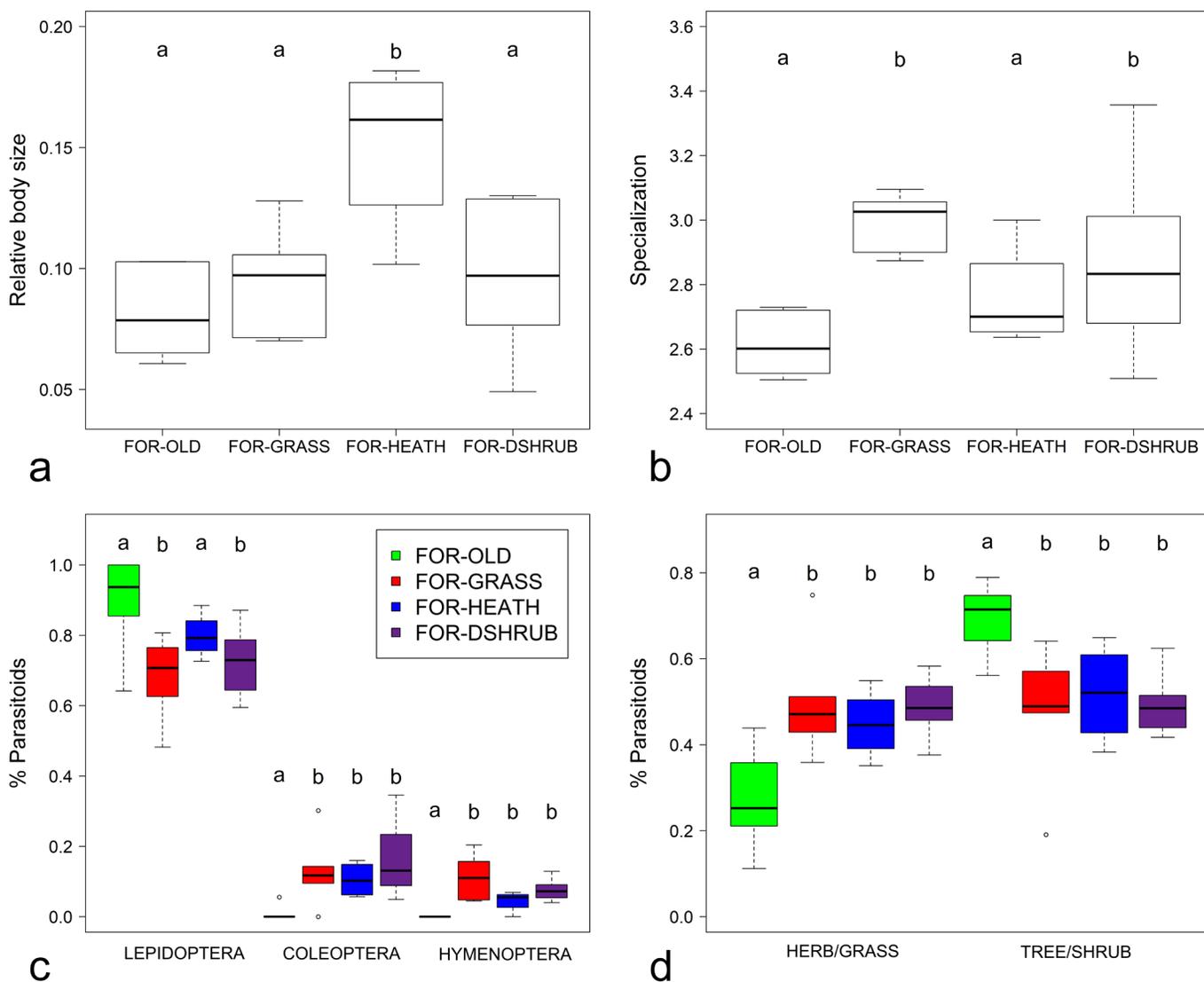


Figure 4. Relationship between mean trait values and habitats defined by forest management: **a.** Relative body size in reference to the largest species, which was scored as 1.0. **b.** Specialization (coded as 1, host species in several orders; 2, host species within one order; 3, host species within one family; 4, host species within one genus; and 5, species specific). **c.** Percentage of parasitoids attacking different host orders. **d.** Percentage of parasitoids known to attack herbivores associated with a particular plant type (herb/grass or tree/shrub). Significant differences indicated by letters relative to old-growth forest as the baseline habitat for comparison with other habitats. Habitat labels as in Fig. 2.

In conclusion, the conservation of old-growth forests, together with the diversification of harvesting practices within the forest plantation matrix, generate forest heterogeneity at the landscape scale. Within forest stands, the application of practices based on natural disturbance (fire and increased tree retention), increases heterogeneity at the local scale. Both strategies increase functional heterogeneity at several spatial scales (Odion & Sarr 2007), leading to the conservation of Tachinidae functional diversity and the maintenance of biological control in managed boreal forests.

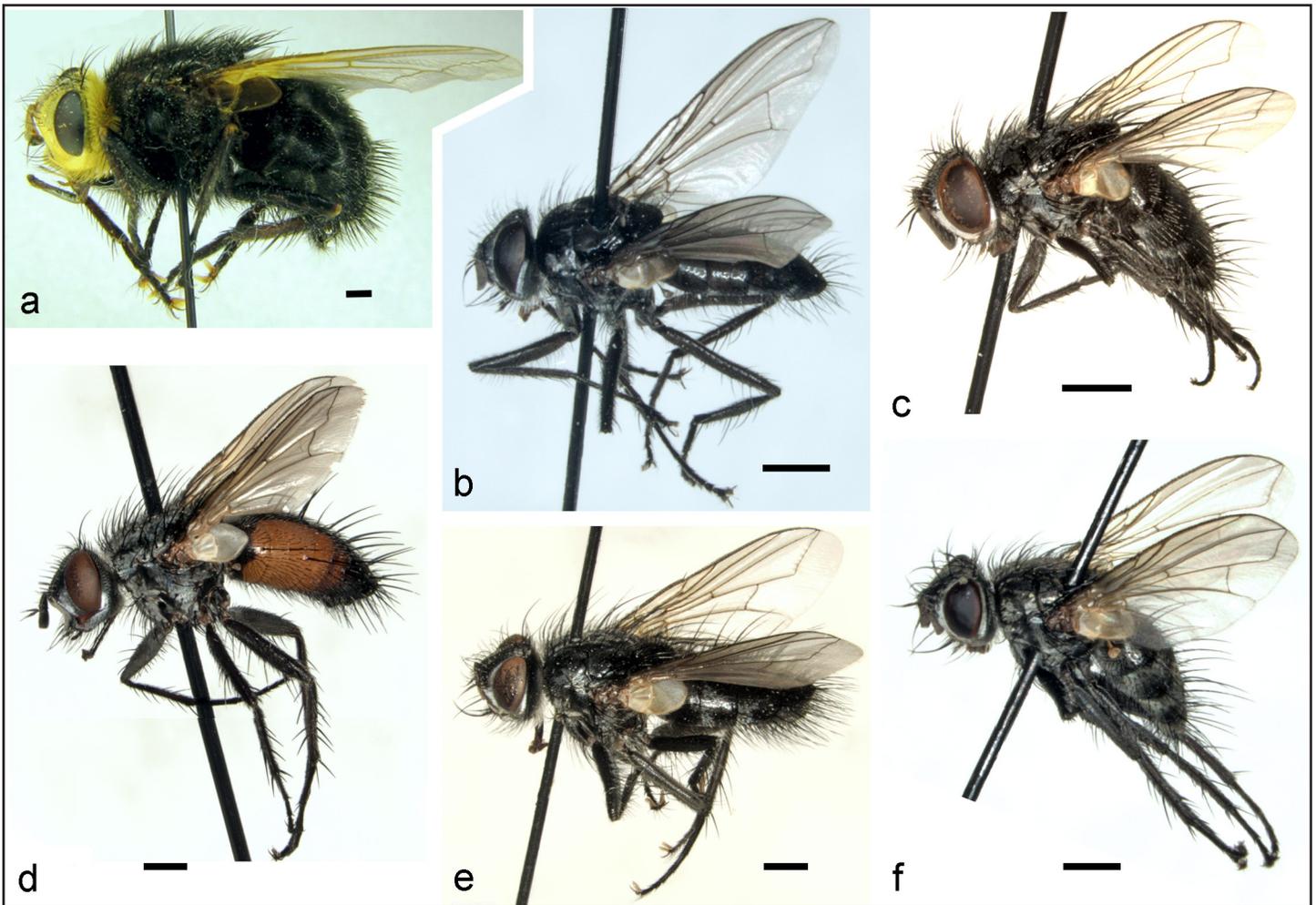


Figure 5. Examples of Tachinidae species from this study illustrating morphological, taxonomic, resource use and life-history trait diversity of tachinid parasitoids. **a.** *Tachina grossa* (Tachininae, Tachinini), the largest European tachinid (15–18 mm), ovolarviparous parasitoid of Lasiocampidae caterpillars. **b.** *Medina luctuosa* (Exoristinae, Blondelliini), the most abundant tachinid parasitoid on Coleoptera (oviparous on Chrysomelidae larvae) in our study sites. **c.** *Staurochaeta albocingulata* (Exoristinae, Blondelliini), oviparous parasitoid species-specific on *Monoctenus juniperi* (L.) larvae (Hymenoptera, Diprionidae). **d.** *Eriothrix rufomaculata* (Dexiinae, Voriini), the most abundant tachinid parasitoid in early successional forests rich in grass in our study sites; an ovolarviparous parasitoid attacking concealed Crambidae caterpillars in grasses. **e.** *Belida angelicae* (Exoristinae, Blondelliini), one of the most abundant tachinid parasitoids on Hymenoptera (oviparous on Argidae larvae) in our study sites. **f.** *Oswaldia muscaria* (Exoristinae, Blondelliini), the most abundant tachinid parasitoid in old-growth forests in our study sites; an oviparous generalist parasitoid attacking Geometridae and Noctuidae caterpillars. For all pictures, scale bar represents 1 mm.

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Appendix 1. Tachinid species abundances in different habitats (sum of observations). Habitat names as in Figure 2.

Species*	FOR-OLD	FOR-GRASS	FOR-HEATH	FOR-DSHRUB
SUBFAMILY DEXIINAE				
Tribe Dexiini				
<i>Trixa conspersa</i> (Harris)	1	0	0	1
Tribe Dufouriini				
<i>Microsoma exiguum</i> (Meigen)	0	1	0	4
Tribe Voriini				
<i>Athrycia impressa</i> (van der Wulp)	0	3	0	6
<i>Athrycia trepida</i> (Meigen)	0	2	7	14
<i>Blepharomyia piliceps</i> (Zetterstedt)	1	0	0	0
<i>Campylocheta inepta</i> (Meigen)	3	1	0	1
<i>Eriothrix rufomaculata</i> (De Geer)	1	57	3	9
<i>Klugia marginata</i> (Meigen)	0	0	0	1
<i>Ramonda prunaria</i> (Rondani)	0	0	0	1
<i>Ramonda ringdahli</i> (Villeneuve)	1	0	0	1
SUBFAMILY EXORISTINAE				
Tribe Blondeliini				
<i>Admontia blanda</i> (Fallén)	0	0	1	0
<i>Belida angelicae</i> (Meigen)	0	9	1	2
<i>Blondelia nigripes</i> (Fallén)	0	0	0	5
<i>Medina collaris</i> (Fallén)	1	6	0	5
<i>Medina luctuosa</i> (Meigen)	0	29	12	28
<i>Oswaldia eggeri</i> (Brauer & Bergenstamm)	0	0	0	1
<i>Oswaldia muscaria</i> (Fallén)	57	10	6	18
<i>Oswaldia spectabilis</i> (Meigen)	0	0	0	1
<i>Staurochaeta albocingulata</i> (Fallén)	0	3	0	2
<i>Trigonospila ludio</i> (Zetterstedt)	3	0	0	0
Tribe Eryciini				
<i>Aplomya confinis</i> (Fallén)	16	22	18	44
<i>Carcelia atricosta</i> Herting	3	0	0	1
<i>Carcelia bombylans</i> Robineau-Desvoidy	1	0	0	0
<i>Hubneria affinis</i> (Fallén)	0	0	0	1
<i>Nilea hortulana</i> (Meigen)	7	7	10	20
<i>Nilea innoxia</i> Robineau-Desvoidy	0	0	0	1
<i>Phebellia strigifrons</i> (Zetterstedt)	0	1	0	0
<i>Senometopia pollinosa</i> Mesnil	0	0	0	1
<i>Tlephusa cincinna</i> (Rondani)	0	8	0	8
<i>Paratryphera barbatula</i> (Rondani)	17	14	4	23
<i>Paratryphera bisetosa</i> (Brauer & Bergenstamm)	9	1	0	1

Species*	FOR-OLD	FOR-GRASS	FOR-HEATH	FOR-DSHRUB
Tribe Exoristini				
<i>Exorista fasciata</i> (Fallén)	0	1	1	2
<i>Exorista rustica</i> (Fallén)	0	3	0	0
<i>Exorista</i> nr. <i>tubulosa</i> Herting	0	4	2	7
<i>Parasetigena silvestris</i> (Robineau-Desvoidy)	0	0	0	1
Tribe Goniini				
<i>Allophorocera ferruginea</i> (Meigen)	3	3	1	9
<i>Cyzenis jucunda</i> (Meigen)	2	0	0	0
<i>Gonia picea</i> (Robineau-Desvoidy)	0	1	0	1
<i>Onychogonia flaviceps</i> (Zetterstedt)	1	2	2	7
<i>Platymya fimbriata</i> (Meigen)	0	13	1	12
Tribe Winthemiini				
<i>Smidtia amoena</i> (Meigen)	1	2	2	6
SUBFAMILY PHASIINAE				
Tribe Catharosiini				
<i>Catharosia pygmaea</i> (Fallén)	0	1	0	0
Tribe Cylindromyiini				
<i>Cylindromyia interrupta</i> (Meigen)	0	6	0	15
<i>Cylindromyia pusilla</i> (Meigen)	0	0	1	3
<i>Phania thoracica</i> Meigen	1	0	0	0
SUBFAMILY TACHININAE				
Tribe Linnaemyini				
<i>Appendicia truncata</i> (Zetterstedt)	0	1	0	1
<i>Cleonice callida</i> (Meigen)	0	0	0	3
<i>Eurithia vivida</i> (Zetterstedt)	0	3	0	2
<i>Gymnocheta viridis</i> (Fallén)	0	1	0	0
<i>Linnaemya haemorrhoidalis</i> (Fallén)	1	1	0	0
<i>Linnaemya rossica</i> Zimin	1	2	4	3
<i>Panzeria rudis</i> (Fallén)	5	0	2	1
Tribe Polideini				
<i>Lydina aenea</i> (Meigen)	0	4	0	0
<i>Lypha dubia</i> (Fallén)	5	2	3	0
Tribe Siphonini				
<i>Actia nigroscutellata</i> Lundbeck	0	0	0	1
<i>Ceromya silacea</i> (Meigen)	1	0	0	0
Tribe Tachinini				
<i>Nowickia marklini</i> (Zetterstedt)	2	2	4	2
<i>Tachina fera</i> (Linnaeus)	1	3	3	3
<i>Tachina grossa</i> (Linnaeus)	0	2	3	5
Totals	145	231	91	283

* Tachinidae names and classification follow Pohjoismäki & Kahanpää (2014).