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ORIGINAL PAPER

Effects of disturbances on scuttle flies (Diptera: Phoridae) in Pine Forests

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Abstract I investigated the ecological consequences of disturbances (anthropogenic and natural) on the scuttle fly communities in four large Pine Forests in Poland. I used data on 17,547 male individuals representing 183 species. Communities found in pine plantations (established in clear-cut areas) and in differently treated post-windstorm (with windthrow logs being left or removed) were less diverse than those found in old-growth forest. The communities recorded in the same habitat types in different forest complexes (ca. 300 km apart) were found to display greater similarity than those recorded on adjacent plots in a given forest (ca. 1 km apart), but covering different habitats. The species-specific preference for habitats after disturbances (clear-cuts and post-windstorm areas) was highly correlated between the forests. The abundance of the species with saprophagous larvae was distinctly higher in the disturbed areas than in the old-growth stands. Also, the body length of the scuttle flies was significantly related to their preference for disturbed or undisturbed habitats: smaller species preferred clear-cuts and post-windstorm areas, whereas larger species were related to intact stands.

Keywords Phoridae · Clearcutting · Windstorm · Salvage logging · Pine Forests · Body size

Introduction

Transformations associated with environmental disturbances can cause changes in global, regional, and local patterns of species composition, their abundance, and the biodiversity in various ecosystems. Natural disturbances (hurricanes, floods, wildfires) are necessary components of ecosystems worldwide by providing the open areas of habitat required by

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many species (Sousa 1984; Platt and Connell 2003) and creating a range of habitat patches that increase spatial heterogeneity and, thus, contribute to biodiversity (Fox 1979). Anthropogenic disturbances may have both beneficial and detrimental impacts on habitats and can be used for the development of management strategies and forest protection (Knisley 2011 and literature therein).

In Central and Eastern Europe salvage logging is one of the most commonly applied activities of forest managers related to natural disturbances—after windstorms or fires. Salvaging is commonly used to save at least part of the wood and reduce the probability of the occurrence of other disturbances (Lindenmayer et al. 2008). Both legislation and official forest management rules in many countries support salvaging. Unfortunately, the ecological effect of this treatment is still insufficiently explored, especially in the case of less studied groups of organisms (Økland 1994; Grove 2002; Żmihorski and Durska 2011). Moreover, the picture obtained from scant research in this area is unclear and depends on a particular taxonomic group, study area etc. As a consequence, it is very difficult to propose a set of appropriate management rules concerning disturbed areas in the context of biodiversity conservation in the forest ecosystem. Nevertheless, this issue needs urgent research as the frequency of disturbances is expected to increase in the future (Schelhaas et al. 2003).

The differences between clear-cutting and salvage-logging are obvious. Clearcutting is associated with intact forest areas; salvaging with disturbed stands. Despite the obvious differences one may expect that the effect of salvage logging is to some extent similar to the effect of clearcutting because both types of harvesting lead to a considerable reduction of the number of standing trees, a reduction of the amount of dead wood and the creation of open or partially open areas in the forest. Moreover, seedlings of trees are either planted or occur naturally in both clear-cut and salvage-logged areas. The new habitats created after such anthropogenic disturbances are very similar to those created after natural disturbances: both are short-lived and remain suitable for open-area species for several years (Southwood 1962; Travis and Dytham 1999).

My studies on Phoridae inhabiting areas after disturbances shows that the disturbed areas are remarkably diverse and species rich as to this group of insects. Many of these are a major component of the pioneer faunas recolonizing habitats devastated by episodes such as clearcutting, windstorms or forest fires (Durska 1996, 2001, 2003, 2006, 2009; Durska et al. 2010; Żmihorski and Durska 2011).

The aim of my study was to evaluate the similarities of the scuttle fly communities colonizing forest habitats after anthropogenic and natural disturbances. Scuttle flies, due to their highly diversified life cycles and environmental requirements, as well as relatively high number of species, are considered to be good indicators of habitat quality (Disney 1983a; Disney 1994; Disney and Durska 1998, 2008, 2011).

Methods

Study area

The study is based on material collected in four large forest complexes in northern Poland (Fig. 1): The Białowieża Primeval Forest (BPF) (52°30′–52°50′ N, 23°40′–24°00′ E), the Tuchola Forest (TF) (53°30′–53°50′ N, 18°15′–18°40′ E), the Biała Forest (BF) (52°30′–53°00′ N, 20°40′–21°30′ E) and the Pisz Forest (PF). The forest complexes are extensive;

they cover areas ranging from 50,000 ha (BF) to 120,000 ha (TF). The forests, mostly on sandy soils, comprise nutrient-poor to semi-rich habitats, with understorey vegetation dominated by mosses (*Polytrichum* spp.), grasses (*Calamagrostis* spp., *Deschampsia flexuosa*) and shrubs (*Rubus* spp., *Vaccinium* spp.). Moist Pine Forests found in the BPF, BF and PF were represented by *Peucedano-Pinetum* in its subboreal variety, and in the TF by its western equivalent, *Leucobryo-Pinetum* (Matuszkiewicz et al. 1993). In all cases, tree stands are composed mainly of Scots pine (*Pinus sylvestris*), with a lower proportion of Norway spruce (*Picea abies*), oaks (*Quercus* spp.), birches (*Betula* spp.) and occasional other species. The stand age in the forests was highly diversified and ranged from 0 years on fresh clearcuts to 100–150 years in the oldest patches. In general, forest stands are characterized as being, generally speaking, unmanaged however, most of the areas (where the scuttle-flies sampling was conducted) have been managed for timber production for decades. Clearcutting is commonly used in the four complexes as the main harvesting technique and new stands are regrown as the result of man-made afforestation.

Clearcutting is the main kind of disturbance in the four forest complexes. However, in the Pisz Forest also a natural disturbance recently occurred. On the 4th of July, 2002 a windstorm destroyed ca. 15,000 ha of the Pisz Forest and created one of the largest windthrows ever recorded in Poland. The windthrow was cleared (fallen, leaning and otherwise damaged trees were removed) and artificial replanting, partially fenced to protect against ungulates, was applied there. However, a small area (445 ha) of the windthrow was left to regenerate naturally and was, consequently, excluded from salvage logging and artificial replanting. This site abounded in fallen logs, leaning trees and broken trunks, among which were numerous seedlings of pines, birches and oaks.

I set up sampling stations in BPF, TF and BF in recently clear-cut stands and in old, closed-canopy stands (95–145 years old). In the case of PF, however, I conducted the scuttle fly sampling 3 years after the windstorm mentioned above, in the windthrow left for natural regeneration (referred to as “left-windthrow”) and in the windthrow where salvage logging was applied (referred to as “logged-windthrow”).

Scuttle fly sampling

Scuttle flies in BPF, TF and BF were collected in 1986 and 1987. In each of these three forest complexes the plots were randomly selected within even-aged pine plantations as well as within old-growth stands. In the case of the pine plantations the following were chosen: a 4 year old clear-cut in BPF (1 plot: 538 Bf-1986), 3 year old clear-cuts in TF

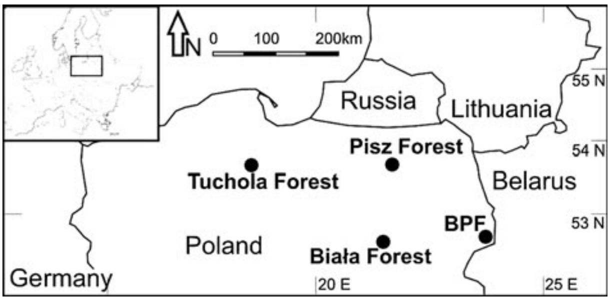

Fig. 1 Location of the study plots in Poland: Biała Forest, Tuchola Forest, Białowieża Primeval Forest (BPF) and Pisz Forest (Żmihorski and Durska 2011)

(2 plots: 3c and 15c—1986) and 3 year old clear-cuts in BF (3 plots: 62 g and 32n—1986; 34f—1987). In the case of mature forest stands I collected samples in 1986 and 1987 from three plots per each of the three forest complexes (BPF: 667Bf—140 years old, 668Af—140 years old, 538Bf—145 years old; TF: 306b—105 years old, 340a—100 years old, 346a—95 years old; BF: 34f—125 years old, 38b—100 years old, 62 g—140 years old) (for details see Durska 1996, 2001, 2006, 2009). In PF scuttle flies were collected in 2005 from six stations in the natural windthrow (i.e. left-windthrow as habitat type) and from five stations in the managed windthrow (i.e. logged-windthrow as habitat type) (for details see Żmihorski and Durska 2011). To avoid possible problems of spatial autocorrelation of particular samples all the samples from each forest and habitat type were pooled.

Scuttle flies were collected using yellow plastic pans, 18 cm in diameter, containing water, 75 % ethylene glycol (for conservation of the insects) and some detergent (Bańkowska and Garbarczyk 1982). In BPF, TF and BF flies were sampled using five such traps located at ground level on each clear-cut, and five traps (1 per tree) that were suspended within the crowns of Scots pines in old-growth stands. The trapping lasted from April to October in BPF and BF, and to mid-November in the TF, with traps emptied fortnightly. In PF very similar methods were used: at each sampling site (total = eleven sites) flies were collected using three such traps (a total of 33 traps) situated one meter above ground level and the traps were emptied every 3–4 weeks.

Identification was conducted under a dissecting microscope with the material transferred to glycerol. Analyses were based solely on male individuals, as most females of *Megaselia* spp. and *Phora* spp. are not identifiable at species level. For determination the keys of Disney (1983a, b, 1989), Schmitz (1938–1958) and Schmitz et al. (1974–1981) were used. The material from this study is deposited at the Museum and Institute of Zoology, PAS, Warsaw and the Department of Zoology, University of Cambridge.

Statistical analysis

To assess the similarity of the scuttle fly communities of the forest habitats studied, three indices were calculated: Sørensen (operating only in the number of common and separated species), Baroni-Urbani (operating only in the number of common, separated and absent species), and Morisita-Horn (operating in the number of individuals of each species) (Wolda 1981). Cluster analysis was performed by using the said indices as similarity functions and an agglomeration method: group of k samples with $n_{i,j}$ individuals of i species in j sample was treated as one sample with $n_{i,j1} + n_{i,j2} + \cdots + n_{i,jk}$ individuals of i species. Finally, the three similarity dendrograms were created.

Species diversity of the scuttle fly community recorded in the clear-cuts, the old-growths, the left and logged-windthrow plots was assessed with the help of rarefaction curves implemented in EstimateS 800 software. Coleman rarefaction curves were used in order to estimate the expected cumulative number of species for a given number of sampled individuals. In addition, the total species richness, corrected for unseen species in the samples was also assessed. For this purpose an abundance-based coverage estimator (ACE) and Chao1 estimator (Colwell 2005, Chao et al. 2006) was applied. This method uses the abundance of rare species ($P \leq 10$ individuals) in samples to estimate the number of unseen species and is commonly used in faunistic research (Chao et al. 2006).

Following this an attempt was made to define the relationship between disturbances (anthropogenic or natural) and the abundances of scuttle fly species with different food habits. For this analysis I used data on all recorded scuttle fly species with known biology.

I assessed if the number of individuals of each species with saprophagous (including necrophagous and polysaprophagous), mycophagous, zoophagous and polyphagous larvae, differs on clear-cut and old-growth plots, and left- and logged-windthrow plots. For this purpose the species-specific preference for the four different habitats (clear-cuts, old-growths, left-windthrow and logged-windthrow plots) was quantified with the χ^2 statistic.

Finally, I examined whether size of scuttle flies is associated with their preferences for the distinguished habitats (clear-cuts, old-growths, left-windthrow and logged-windthrow plots). I used analysis of variance (ANOVA) and post hoc Tukey's test to compare mean body length of species occurring in particular habitats. Information on the average size of males of particular species is taken from various sources (Lundbeck 1922; Schmitz 1938–1958; Schmitz et al. 1974–1981; Disney 1991 and references therein, Disney personal comm.).

Results

General characteristics of scuttle-fly communities

Altogether, 17, 547 male individuals of scuttle flies belonging to 183 species (including two morphospecies: *Megaselia giraudii*-complex and *M. pulicaria*-complex) were analyzed (Table 1). In the disturbed habitats (pine plantations vs. post-windstorm plots) the number of species (S) and specimens (N) were almost the same (clear-cuts plots: S = 71 and N = 2,481; left- and logged-windthrow plots: S = 67 and N = 2,450). However, in the old-growth habitats of three forest complexes (BF, TF, BPF), total number of the scuttle fly species was more than twice as high and their abundance was more than five times as high (S = 154 and N = 12,616) comparing to the scuttle fly communities inhabiting pine plantations and post-windstorm habitats (Table 1). In the material under study, the species from the genus *Megaselia* constituted almost 70 % (S = 123) of all recorded species and the individuals of this giant genus accounted for 80–90 % of the scuttle fly community associated with each plot after disturbance (Table 1).

In pine plantations of BF, TF, BPF fourteen species of the genus *Megaselia*, and *Conicera similis*, *Metopina oligoneura* and *Triphleba opaca* were found in relatively high numbers (more than 10 male individuals in at least one sampling plot). Among these dominants, nine species (polysaprophagous *Megaselia brevicostalis*, saproxylic: *M. giraudii*-complex, *M. minor*, *M. nigriceps*, *M. pleuralis*, sapro/mycophagous *M. pulicaria*-complex, mycophagous *M. pumila*, pyrophilous *M. verralli* and polysaprophagous *Metopina oligoneura*) were found not only in all young pine plantation plots, but also in all remaining habitats, including the two habitats in PF. The majority of the dominant species in pine plantations were sapro/mycophages with multivoltine life cycle, which are most active during spring and autumn. In the scuttle fly communities of old-growth stands in BF, TF and BPF, six species of the genus *Megaselia* (*M. giraudii*-complex, *M. meconicera, M. nigriceps*, *M. pleuralis*, *M. pulicaria*-complex and *M. woodi*) were found in high numbers. Some species of the genus *Phora* (*Ph. obscura* and *Ph. holosericea* in BPF; *Ph. artifrons* in TF) and *Borophaga* (*B. carinifrons* in BPF, *B. subsultans* in TF) were also abundant. Seven species of the genus *Megaselia* (*M. brevicostalis*, *M. campestris*, *M. giraudii*-complex, *M. nigripes*, *M. pleuralis*, *M. pulicaria*-complex and *M. pumila*), as well as *Metopina oligoneura* and *Triphleba opaca* were recorded in each habitat under study. The most characteristic autumn species in the old-growth stands (BF, TF, BPF) was a univoltine

Megaselia woodi, a species with an unknown trophic position (probably mycophagous) (Table 1).

Changes in the scuttle fly communities related with the disturbances in four localities allow one to distinguish the species gaining from the stand transformation from closed into open habitat. Twelve species, i.e. *Conicera floricola*, *C. similis*, *Diplonevra funebris*, *Megaselia altifrons*, *M. brevicostalis*, *M. latifrons*, *M. minor*, *M. pumila*, *M. scutellaris*, *M. verralli*, *M. xanthozona* and *Metopina oligoneura*, have been observed in pine plantations in clearly higher numbers than in old growth stands. The species most characteristic of the open areas of young pine plantations (BF, TF, BPF) are the pyrophilous *Megaselia verralli*, whose food habits are unknown, and the polysaprophagous *M. brevicostalis* and *Metopina oligoneura*. These three species were also found in the samples from the post-windstorm habitats in PF. *M. verralli* was a dominant in left- and logged-windthrow plots, but its abundance was more than twice as high in the latter habitat. In old-growth pine stands in BF, TF and BPF, five species of the genus *Megaselia* (*M. giraudii*-complex, *M. meconicera*, *M. pleuralis*, *M. pulicaria* and *M. woodi*), seven species of the genus *Phora* (*Ph. artifrons*, *Ph. atra*, *Ph. dubia*, *Ph. holosericea*, *Ph. obscura*, *Ph. penicillata* and *Ph. tincta*) and *Borophaga subsultans* were found in high numbers in comparison to the numbers of these species in the pine plantations (Table 1).

The scuttle fly species, with a known biology, accounted for 43.2 % (S = 79) of the compared species. The losers of the transformation after disturbances, were the species with mycophagous (S = 21) and zoophagous (S = 19) larvae. Among the species of fungus-feeding/fungus-breeding larvae (twenty species of the genus *Megaselia* and *Triphleba minuta*) inhabiting Pine Forests (BF, TF, BPF and PF), only six were found in clear-cuts and four in left- and logged-windthrow plots. In clear-cut plots I have found five zoophagous species (*Megaselia ciliata*, *M. major*, *M. mallochi*, *Phalacrotophora fasciata* and *Triphleba lugubris*). Also, in the left-windthrow plots in PF I have found five species with zoophagous larvae (*M. ciliata*, *M. elongata*, *M. flavicoxa*, *Phora holosericea* and *Pseudacteon fennicus*), and in the logged-windthrow plots, the same zoophagous species, except *M. flavicoxa*. In the old-growth stands, I have found nearly three times more (S = 17) species with zoophagous larvae, compared to disturbed habitats.

Among the species with polyphagous larvae (S = 3), *M. giraudii*-complex reached very high abundance in the old-growths plots of all compared forest complexes (BF, TF and BPF) (Table 1).

Similarity of the scuttle fly communities

Within-locality similarity of the scuttle fly communities was much higher for the Pisz Forest (Sørensen index between left- and logged-windthrow plots amounts to 0.76) than for the three remaining forest complexes (0.41, 0.39 and 0.39 for old-growths vs. clear-cuts in BF, TF, and BPF, respectively). In general, the communities recorded in the same habitat type-clear-cuts or old-growths stands—in different forest complexes (up to 300 km apart) were found to display greater similarity than those recorded on adjacent plots in a given forest complex (c.a. 1 km apart), but covering different habitats. As a result, data from old-growth and clear-cut plots constituted separated clusters. The scuttle fly communities recorded in Pisz Forest (both left- and logged-windthrow plots) show greater similarity to those from clear-cut stands than that from old-growth stands (indices of similarity: Sørensen, Baroni-Urbani and Morisita-Horn) (Table 1; Fig. 2).

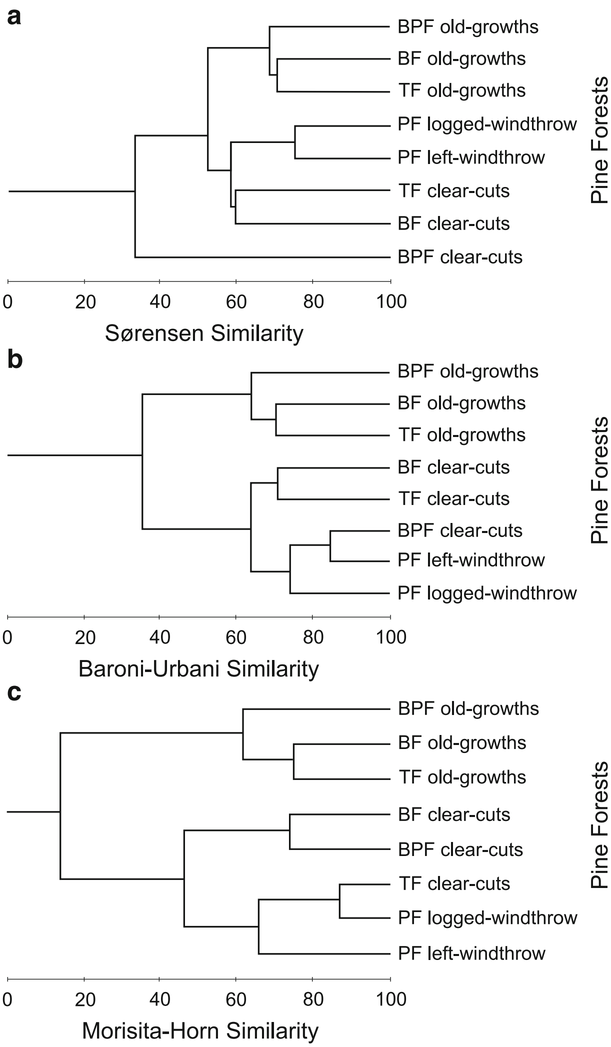

Fig. 2 a, b, c Claster analyses, using the indices of similarity (presence/absence species), showed that young pine plantations (BPF clear-cuts, BF clear-cuts and TF clear-cuts) and post-windstorm habitats (PF left-windthrow and PF logged-windthrow) shared similar scuttle fly communities, while intact forest stands (BPF old-growths, BF old-growths and TF old-growths) composed a second group (unpublished material)

Diversity of the scuttle fly communities

The scuttle fly communities found in clear-cut plots appeared to be distinctly less diverse in terms of the number of species for a given number of sampled individuals, relative to old-growth habitats (data for the three localities pooled). Estimations of total species richness corrected for unseen species in samples (ACE and Chao1) confirms this result and estimated richness for the old-growth is ca. twice as high than for the clear-cut plots (Fig. 3).

Of the two post-windstorm habitats in PF, the left-windthrow habitat was more diverse (diversity expressed as the cumulative number of fly species) than the logged-windthrow one. Among twenty-two species, common to both post-windstorm habitats, almost all (S = 20) reached a higher abundance in left- windthrow plots (Table 1). However, the total species richness, corrected for unseen species, was higher in the logged-windthrow relative to the left- windthrow habitats. (Table 1; Fig. 3).

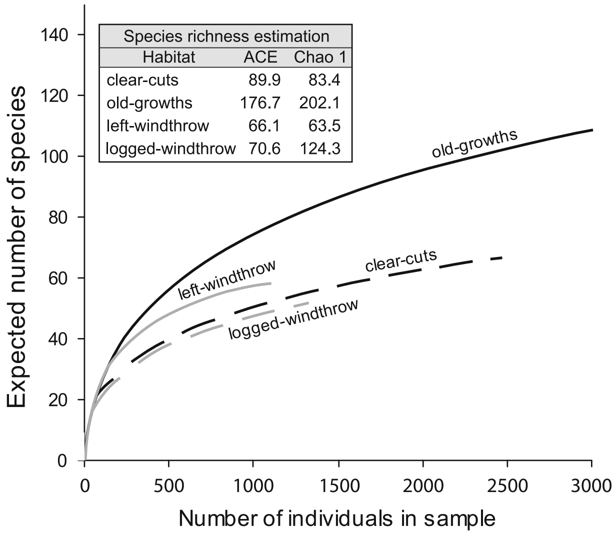

Fig. 3 The expected cumulative number of scuttle fly species as a function of number of sampled individuals in four habitat types. Estimated species richness, corrected for species unseen in samples, is given in the box. Data from BF, TF and BPF are pooled (unpublished material)

Scuttle fly trophic structure in disturbed and intact habitats

The abundance (N) of the species with saprophagous, polysaprophagous and necrophagous larvae (all as saprophagous group: S = 36) was distinctly higher (N = 82–87 %) in the scuttle fly communities inhabiting disturbed plots, than the communities of the old-growth (N = 53.2 %) habitats. The abundance of six mycophagous species, inhabiting clear-cuts (N = 8.9 %) and four species of logged-windthrow (N = 7.8 %) plots, was significantly higher compared to the mycophagous species of old-growths (N = 3.5 %) and left-windthrow (5.3 %) areas. In contrast, the species with zoophagous larvae reached the highest abundance in the left-windthrow (N = 9.6 %) and old-growths (N = 5.6 %) habitats. The reaction, expressed as Chi square values computed for the species with known biology, showed a significant and positive correlation between the forests ($\chi^2 = 1940.8$, $df = 15$, $P < 0.0001$) (Table 1; Fig. 4).

Body size and preferences for different habitats

Habitat preferences of the scuttle flies were found to be significantly correlated to their body size (Tukey' test: $P < 0.05$). Smaller species (mean length $\leq$ 1.35 mm) preferred disturbed habitats, whereas larger species preferred intact forests. In the case of both post-windstorm areas, the mean body length of the scuttle fly species was almost identical (Fig. 5).

Discussion

The study has one important flaw: the sampling in Pisz Forest and the remaining forests was conducted during different periods. As animal communities are not stable over time, the time shift mentioned above may have resulted in different fly communities having been analyzed for the clear-cutting effect and post-windstorm effect. However, in my opinion,

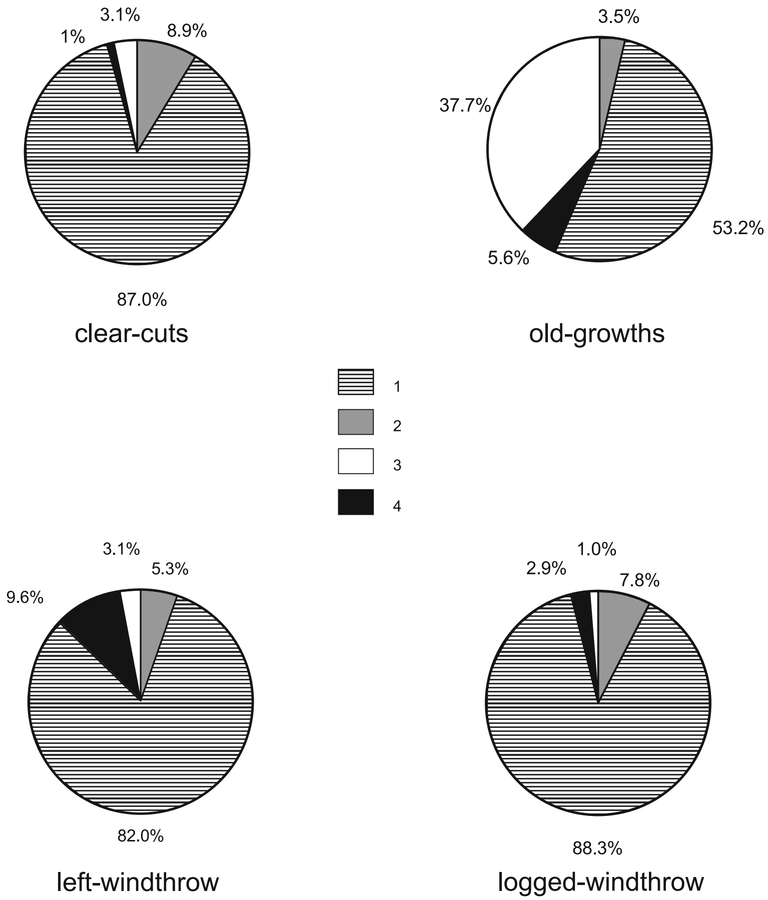

Fig. 4 Contribution to the scuttle fly communities of species with different larval diet, in the four habitat types. *1* Saprophagous larvae; *2* mycophagous larvae; *3* polyphagous larvae; *4* zoophagous larvae (unpublished material)

this issue has little consequence on the results obtained as the clear-cutting effect and post-windstorm effect were compared only for the species that were present in the two study periods. This leads to the conclusion that possible changes in the structure of the communities should not influence the comparison. It is also significant that the data on the scuttle fly communities were obtained ca. 3 years after disturbances (a similar stage of secondary succession with similar aboveground-belowground interactions) in all the study plots (De Deyn, Van der Putten 2005). Changes in species-specific habitat preferences over the 20 year period are also rather unlikely. Therefore, it is assumed that the species-specific similarity in response to disturbances remains reliable.

Several species were present that preferred the disturbed areas and several others were found to be more numerous in the intact forest. Similar patterns of diversified responses were recorded for several other taxonomic groups that inhabit disturbed forest areas (Garbalińska and Skłodowski 2008; Koivula et al. 2006; Maeto and Sato 2004; Żmihorski and Durska 2011).

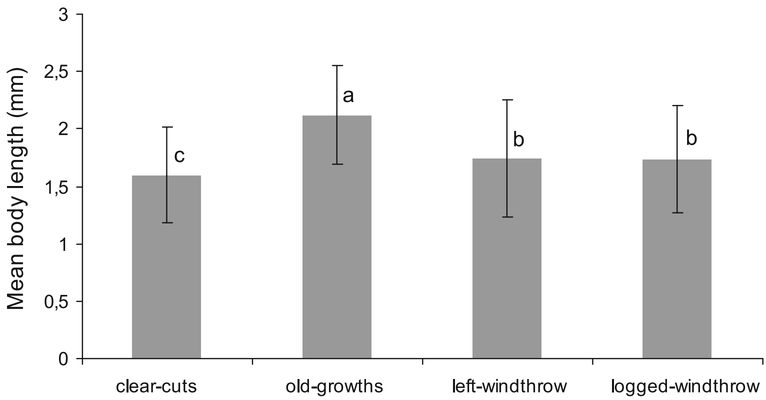

Fig. 5 Mean body length and its standard error of the scuttle fly species in different habitats; Different letters denote statistically significant differences (Tukey's test, $P < 0.05$) (unpublished material)

The results showed that clearcutting and windstorm (open-area plots) had a major ecological impact on the scuttle fly communities and divided them into two separate groups compared to intact forest (old-growth plots) (see Fig. 2). As a consequence, the plots covering the same habitat in different forest complexes and located hundreds of kilometers apart displayed greater similarity than adjacent plots (less than 1 km apart) covering different habitats. The conclusion remains in accordance with results obtained from similar research on carabids (Heliöla et al. 2001; Brouat et al. 2004; Skłodowski 2006); ants (Maeto and Sato 2004) and spiders (Halaj et al. 2008; Mallis and Hurd 2005). In a broader ecological context the results seem to confirm the major impact of forest management on the biodiversity of the ecosystem (Huston 1994; Maeto and Sato 2004).

The response of the flies to disturbances (anthropogenic and natural) was species-specific. The species richness of the scuttle fly communities of young pine plantations and post-windstorm habitats was remarkably similar and less than half that of the old-growth stands of the forests (Table 1; Fig. 3). This leads to a suggestion that the groups of winners and losers of the clearcutting and post-windstorm effects can be predicted. A similar pattern seems to be borne out for other groups of insects of disturbed habitats, e.g. ants (Maeto and Sato 2004) and carabids (Skłodowski and Garbalińska 2007). It is worth noting that both the females (not included in the analyses) of scuttle flies and two species complexes (*M. giraudii*-complex and *M. pulicaria*-complex) could conceal a large number of unidentified species.

The scuttle fly species that increased in number as a result of disturbances predominantly comprised habitat generalists and species preferring open areas. The characteristic dominants of scuttle fly communities in pine plantations were *Megaselia verralli*, *M. brevicostalis* and *Metopina oligoneura*. Sapro/mycophagous and saproxylic *M. giraudii*-complex has been found in the greatest abundance in each community of the three old-growth forests. Also the autumn breeding *M. woodi*-probably connected with fungi, is a characteristic species of old-growth forests. In my previous studies on scuttle fly communities in BPF, a distinct change of dominant species has been observed even in young-growth (Durska 1996; Durska 2001, 2002).

However, despite these general trends some of the species showed different reactions to habitat disturbances in particular forest complexes. For instance, polysaprophagous and saproxylic *M. pleuralis* (Godfrey and Disney 2002) was much more numerous in the clear-cuts in relation to the intact forest in the Tuchola forest, while an opposite pattern was observed in the Biała Forest. *M. pleuralis* has been found to be an extraordinarily abundant species after the wildfire in Tyresta Forest near Stockholm (Durska et al. 2010; Bonet et al. 2011).

In the Pisz Forest, a wide range of microhabitats (dead or dying stumps, snags, logs, branches, uprooted trees), suitable for saproxylic organisms, were created after the windstorm (Bouget and Duelli 2004; Jabin et al. 2004). Accordingly, it was discovered that the common saproxylic species (*M. giraudii*-complex, *M. minor*, *M. nigriceps*, *M. pulicaria*-complex and *Metopina oligoneura*) were more numerous in left-windthrow areas compared to logged-windthrow ones (Table 1).

Sahlin and Ranius (2009) found that for all species of beetle associated with coarse woody debris, the habitat availability was higher on clear-cuts than in the older stands. Fast growing deciduous trees or shrubs that colonize forest gaps after disturbances produce large amounts of dead wood contributing to an increase in the habitat diversity (Janssen et al. 2011). In my study, the mycophagous species reached a higher abundance in young pine plantations (clear-cut plots) and logged-windthrow habitats compared to the old-growth and left-windthrow plots (Fig. 4). The differences in species richness of the lichen and vascular plants and what is most relevant, the amount of dead wood with fungal habitats could be correlated with the species diversity (Økland 1994 and references therein). The sun exposed microhabitats arising after disturbances are suitable for those scuttle fly species which are predators/parasitoids of the abundant flies of the family Sciaridae. It seems that these lesser fungus gnats breed in the mycelia in the soil and in the fruiting bodies of the pioneering fungi (Ascomycetes: *Trichoderma* spp.) developing after disturbnaces (Durska unpubl.). *Megaselia flavicoxa*—a parasitoid of *Bradysia bicolor* (Sciaridae) (Disney 1994), have been found in the logged-windsthorm plots (Table 1).

In this study I found that the preferences for clearcutting and post-windstorm habitat were significantly related to the body length of scuttle flies. Open-area habitats resulted from disturbance were settled by smaller, multivoltine and mostly sapro/mycophagous species of Phoridae. This observation is in accordance with the general rule concerning habitat stability-species size relationship (Kingsolver 2009). These small species of a relatively fast development times that dominate scuttle fly communities in clear-cuts, but also in areas after windstorm and wildfire, are attracted by higher insolation and temperature, and also lower humidity (Durska 1996, 2001, 2006, 2009; Chown and Gaston 2010; Durska et al. 2010). Similar results were obtained for carabids in Białowieża Primeval Forest, Pisz Forest and in the south of Sweden (Skłodowski 2006; Garbalińska and Skłodowski 2008; Tyler 2010). Dajoz (1998) reported a smaller mean size of species of Coleoptera in fire-damaged areas in California and Arizona. In turn, McAbendroth et al. (2005) found that both habitat fractal complexity and allometry may control density-body size scaling in lentic macroinvertebrate communities. However, Hurd and Fagan (1992) found that in the cursorial spider community of herbaceous habitat the breadth of the distribution of adult body lengths was greater than in older woody stands. Those authors pointed out that a consequence of variation in body sizes of generalist arthropod predators is the tendency of larger individuals "to eat smaller ones, which would give the larger bodied species an advantage when other preys were scarce". In contrast, I detected that the dominant species in the old-growth stands, were of a larger-size than the dominant species in the habitats after disturbances. In my previous study (Durska 1996) the small-sized (mean length $\leq$1.35 mm) dominant in clear-cut and windstorm habitats, pyrophilous *M. verralli* was found only in a few individuals in the old-growth stand habitats. It is worth adding that this species also dominated in the scuttle fly communities after wildfires in the

Castanea sativa forests in the Swiss Alps (Prescher et al. 2002). Possibly, *M. verralli* is sensitive to shade and prefers exposure to the sun more than other scuttle flies (Durska 1996, 2001, 2006, 2009; Prescher et al. 2002; Żmihorski and Durska 2011). I have not found this species in scuttle fly material collected after a wildfire affecting hemiboreal forest in Tyresta near Stockholm (Durska et al. 2010). Probably, the range of this species does not reach the far north of Europe.

High similarity of the scuttle fly communities found in clear-cuts and logged-windthow areas is not surprising as these two habitat types have common features. Both experience a considerable reduction in the density of standing and felled trees. As a consequence, semi-open habitats with increased insolation are created. Clear-cuts and habitats after salvaging may harbor many species associated with sun-exposed habitats that initially occurred after forest fires (Sippola et al. 2002). Perhaps, the scuttle fly species inhabiting open-areas are evolutionary adapted at a genetic level (heat shock proteins) to high temperatures (Durska unpubl.).

Conclusions

The results indicate a high similarity of scuttle fly communities associated with disturbed habitats. Perhaps, the same stage of above- and belowground secondary succession (ca. 3 years after disturbance) may affect the open-area species in a similar way. Due to this conclusion, similar preferences for disturbed habitats could be explained by a similar matrix structure of the inhabited areas (De Deyn and Van der Putten 2005; Prevedello and Vieira 2010).

My study on Phoridae shows that the species favored by disturbance either survived during the disturbances or immigrated from the surrounding area. The resilience (i.e. recovery over time) and resistance (i.e. heat stress tolerance) of the scuttle flies to anthropogenic and natural disturbances indicate that the scuttle fly community could be a prime candidate for use in conservation evaluation exercises (Disney and Durska 2008; Griffiths et al. 2008). My results call for an increased interest in species associated with early successional stages.

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Appendix

See Table 1.

Table 1 Species abundance per site (numbers of specimens), larval diet and mean body length (mm) of males

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Anevrina curvinervis (Becker)				1		2		1	Unknown	2.80
***Anevrina thoracica* (Meigen)**		**26**		7		**22**	4	**1**	Necrophagous	3.00
Anevrina unispinosa (Zetterstedt)	2	2	1	5	1	4	1	1	Necrophagous	2.50
Anevrina urbana (Meigen)						1			Necrophagous	2.60
***Borophaga carinifrons* (Zetterstedt)**		2		1		**29**	7		Unknown	2.35
***Borophaga femorata* (Meigen)**		4		**28**		**13**	**31**	**19**	Unknown	2.80
Borophaga irregularis (Wood)			2			1			Unknown	3.10
***Borophaga subsultans* (Linné)**	**10**	**12**		**170**		7	3	3	Unknown	2.68
Conicera crassicosta Disney			1						Unknown	1.60
Conicera dauci (Meigen)		2		3	2	3	3		Saprophagous	1.30
***Conicera floricola* Schmitz**	1		2				**12**	5	Saprophagous	1.15
***Conicera similis* (Haliday)**	**73**		3				2	4	Necrophagous	1.25

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Conicera tarsalis Schmitz							4		Unknown	1.85
Conicera tibialis Schmitz		1					4	4	Necrophagous	1.45
***Diplonevra funebris* (Meigen)**	**20**		1						Polyphagous	2.00
Diplonevra glabra (Schmitz)					1				Unknown	2.50
Diplonevra nitidula (Meigen)				2		2			Polyphagous	2.40
Gymnophora nigripennis Schmitz	1								Unknown	2.50
Megaselia abdita Schmitz						1			Necrophagous	1.50
Megaselia aculeata (Schmitz)		2		1		2	1	1	Unknown	1.50
Megaselia aequalis (Wood)		3		7		1			Zoophagous	1.40
Megaselia affinis (Wood)	2			1			1	1	Unknown	1.20
Megaselia albicans (Wood)				3			1		Mycophagous	1.30
Megaselia albicaudata (Wood)				1					Unknown	1.10
Megaselia alticolella (Wood)					1	8			Unknown	2.00

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
***Megaselia altifrons* (Wood)**	**20**		1	1	5	4	**30**	**18**	Saprophagous[a]	1.90
Megaselia analis (Lundbeck)						1			Unknown	1.50
Megaselia angusta (Wood)					1	2			Saprophagous	1.80
Megaselia aristica (Schmitz)						1			Unknown	2.05
Megaselia basispinata (Lundbeck)	1							1	Unknown	1.58
Megaselia beckeri (Wood)			2						Unknown	2.50
Megaselia berndseni (Schmitz)		1		1					Mycophagous	1.50
Megaselia bovista (Gimmerthal)		2		2					Mycophagous	1.50
***Megaselia brevicostalis* (Wood)**	**459**	2	9	**31**	**63**	**16**	**16**	9	Polysaprophagous	1.30
Megaselia breviseta (Wood)			1				2		Unknown	1.85
***Megaselia campestris* (Wood)**	2	4	8	**23**	1	**33**	3	1	Unknown	2.25
Megaselia ciliata (Zetterstedt)		3		1	1	2	10	3	Zoophagous	1.90

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Megaselia cinereifrons (Strobl)		2		1		3			Mycophagous	1.30
Megaselia clara (Schmitz)						9			Unknown	2.00
Megaselia coccyx Schmitz							4		Unknown	1.60
Megaselia coei Schmitz			1				1		Unknown	1.00
Megaselia collini (Wood)						1			Unknown	1.70
Megaselia communiformis (Schmitz)		8				5			Unknown	1.80
***Megaselia conformis* (Wood)**		**35**				3			Unknown	1.40
Megaselia cothurnata (Schmitz)						1			Unknown	2.00
Megaselia crassipes (Wood)				5		3			Unknown	1.50
Megaselia curvicapilla Schmitz							2		Unknown	1.23
Megaselia dahli (Becker)	1								Unknown	2.00

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Megaselia differens Schmitz						1			Unknown	1.70
Megaselia discreta (Wood)						3			Mycophagous	1.20
***Megaselia diversa* (Wood)**	9			1		**21**	**15**	**41**	Saprophagous[a]	1.63
***Megaselia dubitalis* (Wood)**		**31**		**128**		**1**			Unknown	2.00
Megaselia eccoptomera Schmitz						5			Unknown	1.50
Megaselia eisfelderae Schmitz				2		2			Mycophagous	2.00
***Megaselia elongata* (Wood)**		2		**31**		2	5	4	Zoophagous	1.50
***Megaselia emarginata* (Wood)**		9	2	**39**	3	**13**	**15**	1	Unknown	1.30
***Megaselia errata* (Wood)**		**4**		**88**		**4**			Unknown	1.70
Megaselia fenestralis (Schmitz)				1					Unknown	1.50
***Megaselia flava* (Fallén)**		3				2		**20**	Mycophagous	1.90
***Megaselia flavicoxa* (Zetterstedt)**						1	**39**		Zoophagous	2.70

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Megaselia frameata Schmitz		1							Mycophagous	1.30
***Megaselia fumata* (Malloch)**				1			**95**	**111**	Unknown	2.40
***Megaselia giraudii*-complex**	**28**	**944**	**12**	**1425**	1	**846**	**21**	5	Polyphagous	2.50
***Megaselia gregaria* (Wood)**		**11**	1	**12**		1		1	Unknown	1.00
Megaselia henrydisneyi Durska			1						Unknown	*
Megaselia hortensis (Wood)						3			Unknown	1.80
Megaselia humeralis (Zetterstedt)		2				9			Zoophagous	2.20
***Megaselia hyalipennis* (Wood)**	9	**35**	1	**10**		**31**	**18**		Mycophagous	1.80
Megaselia indifferens (Lundbeck)						3			Unknown	1.80
Megaselia insons (Lundbeck)				1		1			Unknown	1.20
Megaselia intercostata (Lundbeck)						2			Unknown	1.70

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Megaselia intonsa Schmitz						3			Unknown	1.50
Megaselia involuta (Wood)	6				8	6	8	3	Unknown	1.55
***Megaselia lata* (Wood)**	1	9		**14**	1	2	3	4	Mycophagous	1.40
***Megaselia latifrons* (Wood)**	2		**46**	3	4	**13**	9	8	Unknown	1.10
***Megaselia longicostalis* (Wood)**	2	**13**		**26**		6	6	1	Necrophagous	1.25
***Megaselia lucifrons* (Schmitz)**				**10**		3			Unknown	1.20
Megaselia lutea (Meigen)		5		2		5			Mycophagous	2.00
***Megaselia major* (Wood)**		2	1	**18**		**10**			Zoophagous	1.60
Megaselia mallochi (Wood)	3		1		1				Zoophagous	2.00
***Megaselia manicata* (Wood)**	**33**	9		**281**	**15**	**36**	8	**10**	Unknown	1.36
Megaselia maura (Wood)						1			Mycophagous	2.00
***Megaselia meconicera* (Speiser)**		**89**		**1139**	2	**87**		2	Saprophagous[a]	1.70

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Megaselia meigeni (Becker)				2		3			Unknown	2.80
***Megaselia minor* (Zetterstedt)**	**23**	4	3	6	4	3	5	1	Necrophagous	1.65
Megaselia nasoni (Malloch)		5		4		7			Zoophagous	1.40
***Megaselia nigriceps* (Loew 1866)**	**77**	**39**	**68**	**247**	**71**	9	**50**	**41**	Saprophagous	2.20
Megaselia obscuripennis (Wood)				1					Zoophagous	2.10
Megaselia oligoseta Disney							1		Unknown	1.50
Megaselia palmeni (Becker)				2					Unknown	1.50
Megaselia paludosa (Wood)						5			Zoophagous	1.50
Megaselia parva (Wood)		5				7			Unknown	1.10
Megaselia pectoralis Schmitz		8				6			Saprophagous	1.20
***Megaselia picta* (Lehmann)**		6		**47**		**6**	1	1	Unknown	2.40
***Megaselia pleuralis* (Wood)**	**59**	**270**	**191**	**1284**	**16**	**14**	**42**	**190**	Polysaprophagous	1.95

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Megaselia plurispinulosa (Zetterstedt)	4								Mycophagous	1.70
Megaselia posticata (Strobl)				9					Unknown	2.00
***Megaselia propinqua* (Wood)**	4	6		**11**		**10**	2	**25**	Unknown	1.20
Megaselia protarsalis Schmitz						2	1		Unknown	2.05
Megaselia pseudogiraudii (Schmitz)				1		4			Zoophagous	3.00
***Megaselia pulicaria*-complex**	**92**	**89**	**74**	**514**	5	**90**	**283**	**57**	Polysaprophagous	1.50
***Megaselia pumila* (Meigen)**	**24**	**6**	1	1	2	4	**10**	**10**	Mycophagous	1.43
***Megaselia pusilla* (Meigen)**	5	3	1	**64**		**93**	**20**	**58**	Saprophagous	1.20
***Megaselia pygmaea* (Zetterstedt)**		1				**13**			Mycophagous	1.60
***Megaselia quadriseta* (Schmitz)**		**13**		**83**					Mycophagous	2.00
***Megaselia rubella* (Schmitz)**		**14**		2	1	6			Mycophagous	1.70
Megaselia rudis (Wood)						1			Unknown	1.60

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
***Megaselia ruficornis* (Meigen)**		6	1	9		**16**			Saprophagous	2.20
Megaselia rufipes (Meigen)				3					Polysaprophagous	1.80
Megaselia rupestris Schmitz				1					Unknown	1.20
***Megaselia scutellaris* (Wood)**	**115**	1			3	3		6	Mycophagous	1.95
***Megaselia septentrionalis* (Schmitz)**			1	**19**	1				Unknown	*
***Megaselia sepulchralis* (Lundbeck)**		**12**		**148**		**129**			Unknown	2.10
Megaselia serrata (Wood)						3			Unknown	0.50
Megaselia setulipalpis Schmitz						5			Unknown	1.50
Megaselia simplex (Wood)						2			Unknown	1.50
Megaselia sordida (Zetterstedt)				1		2			Unknown	1.90
***Megaselia speiseri* Schmitz**								**62**	Unknown	1.40
Megaselia spinicincta (Wood)						3	4		Mycophagous	1.50

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Megaselia spinigera (Wood)	1	5				3			Unknown	1.90
Megaselia stigmatica (Schmitz)								1	Saprophagous	2.00
Megaselia striolata Schmitz				5		3			Unknown	*
Megaselia styloprocta (Schmitz)					1		2		Unknown	2.00
Megaselia subcarpalis (Lundbeck)				4					Unknown	1.30
***Megaselia subnudipennis* (Schmitz)**	**14**	1		5		6	**53**	4	Necrophagous	1.05
Megaselia subpleuralis (Wood)								1	Unknown	1.95
Megaselia subtumida (Wood)		2				1			Necrophagous	1.50
Megaselia superciliata (Wood)				1		3			Unknown	1.10
Megaselia sylvatica (Wood)		2				1			Mycophagous	1.40
Megaselia tarsalis (Wood)			1			1	2		Unknown	1.30

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Megaselia tarsella (Lundbeck)		1		5					Unknown	1.40
Megaselia tergata (Lundbeck)		1							Unknown	2.00
Megaselia tumida (Wood)		1							Unknown	1.80
***Megaselia unicolor* (Schmitz)**	**32**	**22**	3	**20**		**41**	2	5	Saprophagous	2.00
Megaselia unguicularis (Wood)						1			Unknown	1.70
Megaselia valvata Schmitz						7			Unknown	1.60
Megaselia variana Schmitz						1			Unknown	1.60
***Megaselia verralli* (Wood)**	**185**		**218**	7	**47**	3	**186**	**437**	Unknown	1.35
***Megaselia woodi* (Lundbeck)**	5	**79**		**231**	4	**868**			Unknown	2.40
***Megaselia xanthozona* (Strobl)**	**23**				3	6			Saprophagous[a]	1.20
Megaselia zonata (Zetterstedt)		3			5	1			Unknown	*
Metopina braueri (Strobl)						6			Zoophagous	1.10

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Metopina crassinervis Schmitz						1			Unknown	1.10
Metopina crassinervis Schmitz				2	1				Unknown	1.10
Metopina heselhausi Schmitz	1	1	3	9		3			Unknown	1.10
***Metopina oligoneura* (Mik)**	**101**	7	**10**	2	**11**	5	6	3	Polysaprophagous	1.10
Metopina perpusilla (Six)				2					Unknown	1.10
Metopina pileata Schmitz		1		2					Unknown	1.00
***Phalacrotophora berolinensis* Schmitz**		**15**		**10**		**21**			Zoophagous	1.70
***Phalacrotophora fasciata* (Fallén)**		**32**	2	6		**11**			Zoophagous	1.70
***Phora artifrons* Schmitz**		**16**		**302**		**84**	**42**	**86**	Unknown	
***Phora atra* (Meigen)**		4	9	**145**			2	**47**	Unknown	2.35
Phora convallium Schmitz						3			Unknown	2.20
***Phora dubia* (Zetterstedt)**		1		**120**		**11**		1	Unknown	3.00
***Phora holosericea* Schmitz**		**17**		**77**		**146**	8	7	Zoophagous	2.50

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Phora indivisa Schmitz						1			Unknown	3.20
Phora obscura **(Zetterstedt)**		7		**92**		**366**	2		Unknown	2.25
Phora penicillata **Schmitz**					2	**41**			Unknown	2.25
Phora praepandens Schmitz						3			Unknown	2.10
Phora pubipes Schmitz						1			Unknown	2.70
Phora tincta **Schmitz**						**17**			Unknown	2.25
Plectanocnema nudipes (Becker)							2		Unknown	1.80
Poloniohora bialoviensis Disney					1				Unknown	1.05
Pseudacteon fennicus Schmitz							3	1	Zoophagous	1.50
Pseudacteon formicarum (Verrall)		1				4			Zoophagous	1.60
Triphleba aequalis (Schmitz)				1					Saprophagous	1.60
Triphleba antricola (Schmitz)				3					Saprophagous[a]	1.90
Triphleba bifida Schmitz	1								Unknown	2.70

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Triphleba crassinervis (Strobl)					1				Unknown	1.60
Triphleba distinguenda (Strobl)	1								Necrophagous	1.70
Triphleba hyalinata (Meigen)		2		5					Saprophagous	2.20
Triphleba intermedia (Malloch)				2			1	1	Unknown	2.35
Triphleba lugubris (Meigen)		5		1	5	4			Zoophagous	2.20
***Triphleba luteifemorata* (Wood)**		**13**		**34**		**12**			Necrophagous	1.70
Triphleba minuta (Fabricius)		4							Mycophagous	2.20
Triphleba nudipalpis (Schmitz)		2		1		2			Necrophagous	1.80
***Triphleba opaca* (Meigen)**	1	**21**	3	**26**	**37**	**18**	1	2	Saprophagous	2.85
Triphleba papillata (Wingate)				1			2	3	Saprophagous	2.90
Triphleba smithi Disney						1			Unknown	1.65

Table 1 continued

	Poland									
	Biała Forest clear-cuts	Biała Forest old-growths	Tuchola Forest clear-cuts	Tuchola Forest old-growths	Białowieża PF clear-cuts	Białowieża PF old-growths	Pisz Forest left-windthrow	Pisz Forest logged-windthrow	Larval diet	Male body length
Triphleba subcompleta Schmitz	1		1						Unknown	2.50
Triphleba trinervis (Becker)	4	2		6	4	5			Unknown	2.50
Trucidophora ewardurskae (Disney)						5			Zoophagous	*
Woodiphora retroversa (Wood)		1							Unknown	*
Total number of species per site	43	79	37	93	38	123	59	52		
Expected number of species - ACE	53.1	88.0	66.8	116.6	48.0	138.8	66.1	70.6		
Expected number of species - Chao1	52.0	85.5	61.6	115.0	57.1	145.3	63.5	124.3		
Expected number of species - Chao1 corrected	49.5	84.7	56.0	112.5	51.6	143.0	62.6	97.3		
Total number of individuals per site	1458	2037	687	7113	336	3466	1117	1333		

Dominant species, at least at one site of all habitat types ≥10 individuals, are shown in bold type (Lundbeck 1922; Schmitz 1938–1958; Schmitz et al. 1974–1981; Disney 1991 and references therein, Disney personal comm.; Durska (2006) and literature therein; Żmihorski and Durska (2011)and literature therein)

[a] Probable diet of larvae

*Species with missing data on body length are excluded from the pertinent analysis

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