

# The effect of contrasting management types on two distinct taxonomic groups in a large-scaled windthrow

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Received: 27 February 2010 / Revised: 22 September 2010 / Accepted: 20 October 2010 / Published online: 19 November 2010  
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**Abstract** Improving ways of managing disturbed areas is in urgent need of further research. We assessed the effect of two contrasting management types—salvage logging and set aside for natural regeneration—applied to a large-scale windthrow in NE Poland on two distinct taxonomic groups of animals: scuttle flies and birds. In total, 5,368 individual scuttle flies were trapped and 1,649 individual birds were recorded. In both taxonomic groups, we recorded the “winners and losers” of the effects of salvage logging. The responses of particular species in both groups were independent of their body size. Species diversity, assessed by rarefaction, increased as a result of the logging in birds and declined in scuttle flies. The species richness, corrected for unseen species of scuttle flies and birds, was higher on the managed windthrow when compared to the natural one. Comparison of the results obtained with published data from the intact stands of Białowieża Primeval Forest suggests that salvage logging reduced the similarity of the fly and bird community to those reported from undisturbed, natural forest areas. Our results concern mostly the common species. We conclude that salvage logging has considerable influence on assemblages of common species in the post-disturbance forests. Birds and flies did not respond similarly to salvage logging in term of species diversity, although both groups included species that were attracted to either managed or unmanaged windthrow sites.

**Keywords** Birds · Disturbances · Salvage logging · Scuttle flies · Windstorm

## Introduction

Since the origins of forest management aimed at timber production, natural disturbances such as fires, windstorms, or outbreaks of folivorous insects have been regarded as undesirable. This view was driven by the fact that the disturbances can significantly reduce the quality and quantity of timber (Hanewinkel et al. 2008). Treatments applied by forest managers aimed at reducing the probability of the occurrence of natural disturbances (e.g., monitoring of folivorous insect populations, chemical protection against insects or fungi, removal of decaying trees and dead wood, regulations concerning fire prevention, and many others) have played an important role in forestry (Niemelä 1999). As a consequence, the role of disturbances and importance of disturbing agents (e.g., natural fires) in managed stands has been largely suppressed in comparison with those which are not managed (Kuuluvainen 2002).

However, the perception of natural disturbances in forest ecosystems has changed considerably during the last few decades (Niemelä 1999). The importance of disturbances as natural drivers of successional dynamics, stand development, and stand replacement has increasingly been stressed (Shorohova et al. 2009; Müller et al. 2010). Disturbances transform the closed-canopy structure of forests and create new habitats that are settled by many organisms atypical for closed stands (Fuller 2000). As a consequence, the species richness and species diversity of the disturbed patches may increase relative to intact stands (e.g., Faccio 2003). Moreover, great attention has recently been paid to

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Communicated by J. Müller.

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mimic natural disturbances by newly developed harvesting techniques applied in managed stands (Niemelä 1999).

In light of this change in the perception of natural disturbances in the forest ecosystem, the current management practices in disturbed areas need to be evaluated. Silvicultural practices applied to disturbed areas most commonly rely on previous perceptions of disturbances as undesirable events and widely include salvage logging of damaged timber (Lindenmayer et al. 2008). Legislation supporting salvage logging in Poland is a good example of this conservative thinking irrespective of current knowledge in this field. Moreover, the paucity of research studies and recommendations concerning different management regimes applied in disturbed forests in Central Europe is becoming a problem and appears to contradict the extensive literature addressing this subject in other regions, e.g., North America, Scandinavia, and Germany (Lindenmayer et al. 2008 and references therein; Müller et al. 2010). Therefore, improving methods of forest management in disturbed areas is in urgent need of further study, especially as climate changes may affect the intensity of disturbances in the future (Schelhaas et al. 2003). In this study, we evaluate the effect of two contrasting management options applied in a large-scaled windthrow in Poland (Central Europe) on two distinct taxonomic groups of animals. We used scuttle flies (Diptera: Phoridae), trapping by yellow plastic pans, and birds (Aves), sampled with a fixed-radius point counts, as taxonomically distant and ecologically unrelated groups that are considered to be important in measuring the habitat quality and sustainable forest management (Venier and Pearce 2004; Disney and Durska 2008). Using these two groups of animals, we attempt to assess the biological consequences of salvage logging of the windthrow, which was applied in accordance with prescribed forest management regulations. We put forward hypothesis stating that despite distinct ecological differences between the studied groups, effect of salvage logging on scuttle flies and birds is similar.

## Materials and methods

### Study area

The study was conducted in north-eastern Poland, in the Pisz Forest, which is a ca. 90,000 ha forest complex. The Pisz Forest is located in a young glacial landscape with predominantly sandy soil, hence the prevailing forest associations are conifers. Its forest stands are covered by fresh coniferous stands (Peucedano-Pinetum, Matuszkiewicz 2001) managed for timber production and are composed mainly of pine (*Pinus sylvestris*), with a lower proportion of Norway spruce (*Picea abies*), and oak (*Quercus robur*).

Forest floor's vegetative understory is dominated by mosses (*Polytrichum* spp.), grasses (*Deshampsia flexuosa*), and shrubs (*Vaccinium* spp.).

On July 4, 2002 a windstorm (12 of Beaufort notation, wind speed up to 170 km/h) destroyed ca. 33,000 ha of stands in NE Poland and 15,000 ha in the Pisz Forest and created one of the largest windthrows ever recorded in Poland. In the Pisz area, total amount of dead wood denoted 12,000 m<sup>3</sup>. The forest was transformed into a mosaic of open areas (completely damaged stands covered ca. 40% of the windthrow area), partially destroyed stands with single trees or groups of trees and also small areas covered by undisturbed forest (ca. 10% of the forest affected by the windstorm).

Field work was performed in two different habitats situated in the Pisz Forest. The habitats were natural windthrow allowed to regenerate naturally (hereafter natural windthrow) and managed windthrow where salvage logging was applied (hereafter managed windthrow, Fig. 1). The natural windthrow covered a 445-ha area, which had been excluded from post-disturbance salvage logging. This site abounded in fallen logs, leaning trees, and broken trunks, among which were numerous seedlings of pines, birches, and oaks (Fig. 1a). There were also some partially or completely undisturbed forest patches (up to several ha). The managed windthrow habitat covered an extensive part of the damaged forest, where all the fallen, leaning, and broken trees had been removed (Fig. 1b). In general, stands in the natural and managed windthrow were quite similar in term of pre-windthrow age structure and further windstorm damages. In the natural windthrow area, pre-windstorm age structure of the tree stand was as follows: age class 0–20 years covered 49.0% of stands, class 21–40 years—12.2%, 41–60 years—23.9%, 61–80 years—7.5%, and >80 years—7.3%. Analogical values for the managed windthrow area denoted 57.9, 12.0, 10.0, 5.0, and 15.1%, respectively (Zajaczkowski and Dzierża 2007). In the natural windthrow, 4.3% of stands remain undisturbed (stands with no visible damages), 30.4% were partially damaged (up to 50% of trees damaged), and 65.3% were totally damaged (51–100% of trees damaged). Analogical values for the managed windthrow area were similar and denoted 12.1, 31.5, and 56.5%. In respect to age classes, disturbances in the two habitats were also similar: in natural windthrow, 12.2% of stands from 0 to 20 years age class were undamaged, whereas 62.6% were totally damaged. In managed windthrow, the proportion was similar: 20.2 and 62.0%, respectively. In natural windthrow, 20.0% of the oldest stands ( $\geq 61$  years old) remain undamaged and 22.2% were totally damaged, and analogical values for the managed windthrow denoted 25.0 and 30.4%, respectively (Zajaczkowski and Dzierża 2007). The forest management activities on the managed windthrow started in 2002. In the

**Fig. 1** Two habitats in the Pisz Forest, NE Poland: natural windthrow left to regenerate naturally (fallen logs, leaning trees and broken trunks left) and managed windthrow (dead wood removed, artificial replanting applied). Both pictures were taken in 2007, 5 years after the windstorm



following years, most damaged stands were logged and replanted, in accordance with prescribed forest management regulations. A program of artificial replanting, partially fenced against ungulates, had been applied there. The natural and the managed windthrow habitats were adjacent to each other. For that reason, the sampling stations were arranged far from the edge of both habitats and sampling range was restricted in the case of birds (see below).

#### Scuttle fly sampling

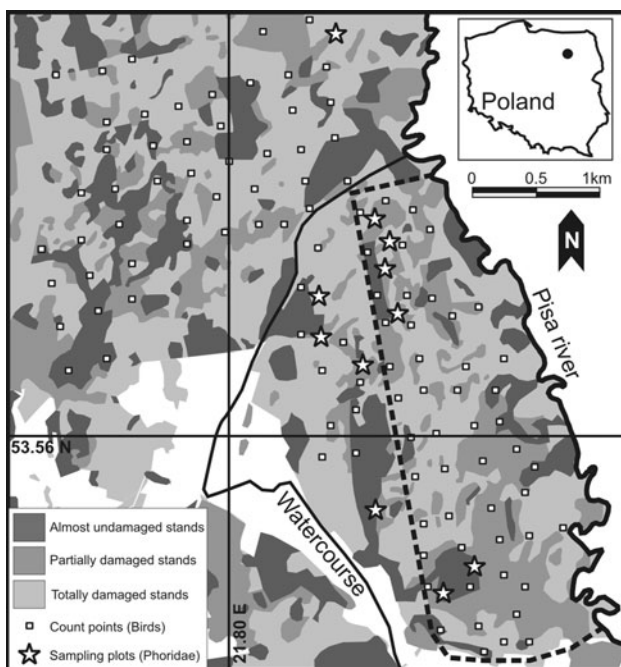
Scuttle flies were collected (5,368 individuals) in 2005 at five sampling sites in managed windthrow and at 6 sampling sites in natural windthrow (Fig. 2). The trapping was continuous from May to September, with traps emptied every 3–4 weeks. We used yellow plastic pans, ca. 18 cm

in diameter, containing a water solution of 75% ethylene glycol (for preserving the insects) and some detergent (surface active agent) (Bańkowska and Garbarczyk 1982). At each sampling site, flies were collected using three such traps (a total of 33 traps) situated one meter above the ground. Such placement of the pans reduces disturbance by small mammals, capture of slugs and others.

Identifications were made under a dissecting microscope with the material transferred to 75% ethanol. Analyses were based solely on male individuals (2,715 individuals) as most females of *Megaselia* spp. and *Phora* spp. are not identifiable to the species level. Consequently, these have only been identified to the genus level and are not included in the analysis. A lot of the *Megaselia* spp. males (about 10%) were left unidentified because they were damaged and diagnostic features were no longer available. The keys of Disney (1983, 1989), Schmitz (1938–1958) and Schmitz et al. (1974–1981) were used for determinations. All materials from this study are deposited in the Museum and Institute of Zoology Polish Academy of Sciences in Warsaw and at the University of Cambridge.

#### Bird sampling

Bird counts were conducted in spring 2007. In the two habitats, we selected 106 census points (49 in the natural windthrow and 57 in the managed windthrow). Census points were selected at the intersections of a 300 m × 300 m grid superimposed on the study area (the points were situated 300 m from one another, see also Ralph et al. (1995) who recommended 250 m between point counts as a minimum distance). The exact location of each point was marked with GPS (Fig. 2). Birds were counted using a fixed-radius point count (Gregory et al. 2004), which is one of the most common methods used for monitoring and ecological research of birds (see Gregory et al. 2007). At each point, we conducted two 10-min counts, one in April and one in June (Venier and Pearce 2007). This method allowed for the detection of both early sedentary breeders and tropical migrants that start to breed later in the spring. The points were sampled in a random order. During each 10-min count, we recorded all the individuals heard and



**Fig. 2** The distribution of the sample stations for scuttle flies (stars) and birds (squares) in the natural windthrow (bordered with dashed line) and the managed windthrow (remaining area) in the Pisz forest. The gray color indicates the forest at different levels of damage and the white indicates open areas

seen within a radius of 100 m (Giraud et al. 2008). In order to exclude migrants, we did not record birds flying above the canopy since they do not use windthrow being sampled (Faccio 2003). All counts were performed in the morning (before 10 a.m. in April and before 9 a.m. in June) and only in good weather conditions (no strong wind or rainfall). Of the two censuses carried out at a given point, the maximum number recorded for each species was used for further analysis (Barbaro et al. 2007).

#### Statistical analysis

We used redundancy analysis (RDA) implemented in CANOCO software (Lepš and Šmilauer 2003) in order to discriminate between species that show negative and positive response to the salvage logging. We used the locations of each sampling station (natural vs. managed windthrow) as an explanatory variable in RDA and performed the Monte Carlo test with 5,000 permutations for the assessment of the significance of the canonical axes (Lepš and Šmilauer 2003). We restricted the computation to only those species whose abundance in the two habitats pooled was equal to or exceeded ten individuals in order to exclude accidental species and to keep the output of the RDA as clear as possible.

We also investigated whether the response of each species to the salvage logging depended on its body size, since body mass- and size-related response to disturbances was previously reported for carabids and saproxylic beetles (Skłodowski 2006; Müller and Brandl 2009). For each species of scuttle fly and bird, we used scores for the first axis of the RDA as a measure of response to the logging. The location of a given species along the first axis of the RDA describes the importance of the habitat type (natural vs. managed windthrow) for the species distribution and abundance. As a measure of the body size of scuttle flies and birds, we adopted body length as a proxy (Schmitz 1938–1958; Schmitz et al. 1974–1981; Szczepski and Kozłowski 1953, respectively). Body length was then correlated with the RDA scores for flies and birds, respectively. In addition, we correlated body length with module of the RDA score to check whether species size is related to the strength of the response to the logging (irrespective of the direction of this response, i.e., positive or negative). SPSS 13.0 was used for the correlations.

We applied the rarefaction method in order to compare the diversity of scuttle fly and bird communities across the two habitats using EstimateS 800 software (Colwell 2005). We draw the expected cumulative species number as a function of the number of randomly chosen individuals, which should be interpreted as a measure of diversity (individual-based rarefaction, see Colwell 2005). Since bird density is higher in the natural windthrow relative to

the managed windthrow (Żmihorski 2010), we used individual-based rarefaction that is independent of possible differences in mean number of individuals per sample between the comparing habitats (Gotelli and Colwell 2001). For this purpose, we used Coleman curves (Colwell 2005). We prepared the curves for each habitat type independently. Total species richness of scuttle flies and birds in the two habitats was also estimated. For this purpose, we used the abundance-based coverage estimator (ACE) that is corrected for species unseen in the samples (Chao et al. 2006). 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).

Finally, for the discussion purposes, we also attempted to relative comparison the scuttle fly and bird communities recorded in our study to those reported from an intact, natural forest. For this purpose, we used the data available from Białowieża Forest as reference material. Białowieża Forest (BF), located ca. 150 km SE from the Pisz Forest, is a large woodland, the last surviving fragment of primeval temperate forest in the European lowland (Tomiałojć and Wesołowski 2004; Wesołowski 2005 and references therein). We used available data for scuttle flies from BF collected in 1986 and 1987 in BF (Durska 2001). As a reference for ornithological observations, we used the results of the long-term study on avifauna conducted by Tomiałojć and Wesołowski on the “NW” and “NE” plots (2004; see also Wesołowski et al. 2006 for detailed description and results). In the case of both groups, the reference material from BF was collected in intact, closed-canopy stands covering precisely the same forest association as in the Pisz Forest (i.e., Peucedano-Pinetum). In the case of birds, the methods differed (census in BF, point counts in Pisz Forest); however, this should not bias the results since we conducted relative comparison and put special attention to differences between the two types of windthrow rather than between BF and Pisz Forest. We used detrended correspondence analysis (DCA) implemented in CANOCO software to visualize the similarity of both taxonomic groups (in respect to species composition and abundance) in the managed and natural windthrow in the Pisz Forest in relation to those reported from the more natural and intact stands of Białowieża Forest.

## Results

### General characteristics of the two groups

In total, we recorded 2,715 scuttle fly male individuals representing 69 species (within two morphospecies: *Megaselia pulicaria*- complex and *M. giraudii*-complex)



and 1,649 birds from 66 species. In the case of the scuttle flies, nine species of the genus *Megaselia* (*M. verralli*, *M. pleuralis*, *Megaselia fumata*, *M. pusilla*, *M. pulicaria*—complex, *M. diversa*, *M. nigriceps*, *M. flavicoxa*, *M. altifrons*), *Borophaga femorata* and *Phora artifrons* were the dominants (> 10 specimens in each habitat) in both habitats (Appendix 1). Most of the dominant species are known as open area species.

The chaffinch *Fringilla coelebs* was the most abundant bird species in both habitats. Three other species had at least one hundred individuals (when pooled for both habitats): the woodlark *Lullula arborea*, the great spotted woodpecker *Dendrocopos major*, and the tree pipit *Anthus trivialis*. Twenty-one bird species were recorded in only one habitat, and ten species were represented by only one individual (Appendix 2).

### Winners and losers

Among the 26 scuttle fly species represented by at least ten individuals, exactly half were more common in the managed windthrow over the natural windthrow, while the remaining 13 showed an opposite tendency (Fig. 3). *Megaselia verralli*, *M. pleuralis*, *M. propinqua*, and *Phora atra* showed a distinct preference for the managed windthrow, while *M. pulicaria*—complex, *M. subnudipennis*, *M. emarginata* and *M. ciliata* preferred the left windthrow. The distribution of some species seemed to be independent of the salvage logging (e.g., *Megaselia nigriceps*). *Megaselia speiseri* was the one species with abundance exceeding 1% of the whole community without any captures on the natural windthrow, whereas *M. hyalipennis* showed reverse pattern. The distribution of scuttle fly species in relation to the canonical axes extracted by RDA was not random (Monte Carlo test, trace = 0.271;  $F$ -ratio = 3.339;  $P = 0.028$ ).

The majority of bird species showed preferences for the natural windthrow. Among the 33 bird species included in the analysis (i.e., represented by at least ten individuals), 20 were recorded as being more abundant in the natural windthrow, while the remaining 13 showed the opposite tendency (Fig. 3). The skylark *Alauda arvensis*, the yellowhammer *Emberiza citrinella*, the wagtail *Motacilla alba*, and the woodlark *Lullula arborea* showed strong preferences for the managed windthrow. In contrast, the winter wren *Troglodytes troglodytes*, the spotted flycatcher *Muscicapa striata*, the blackcap *Sylvia atricapilla*, and the chiffchaff *Phylloscopus collybita* preferred the natural windthrow. The great tit *Parus major*, the tree pipit *Anthus trivialis*, and several other species showed no clear response to the salvage logging (Fig. 3). In general, the variability of bird abundances strongly depended on the

canonical axes (Monte Carlo test, trace = 0.052;  $F$ -ratio = 5.665,  $P = 0.0002$ ).

### Body size versus response to the salvage logging

Preference for the managed or natural windthrow expressed as the species-specific score for the first axis of the RDA was correlated with the species body length neither in scuttle flies (Linear regression,  $R^2 = 0.002$ ;  $F = 0.057$ ;  $n = 26$ ;  $P = 0.813$ ) nor in birds (Linear regression,  $R^2 = 0.018$ ;  $F = 0.572$ ;  $n = 33$ ;  $P = 0.455$ ). Also the strength of the response expressed as the module of the score for the first axis of the RDA showed no linear relationship with the body length of scuttle flies (Linear regression;  $R^2 = 0.078$ ;  $F = 2.026$ ;  $n = 26$ ;  $P = 0.167$ ) or birds (Linear regression;  $R^2 = 0.086$ ;  $F = 2.932$ ;  $n = 33$ ;  $P = 0.097$ ).

### Species diversity and species richness

The species diversity of scuttle fly communities expressed as cumulative number of fly species for a given number of randomly chosen individuals was higher in the natural windthrow when compared to the managed windthrow. For example, in order to record 53 fly species (the smallest number of species in one habitat), one had to collect 1,337 individuals in the managed windthrow or just 697 individuals in the natural windthrow (Fig. 4).

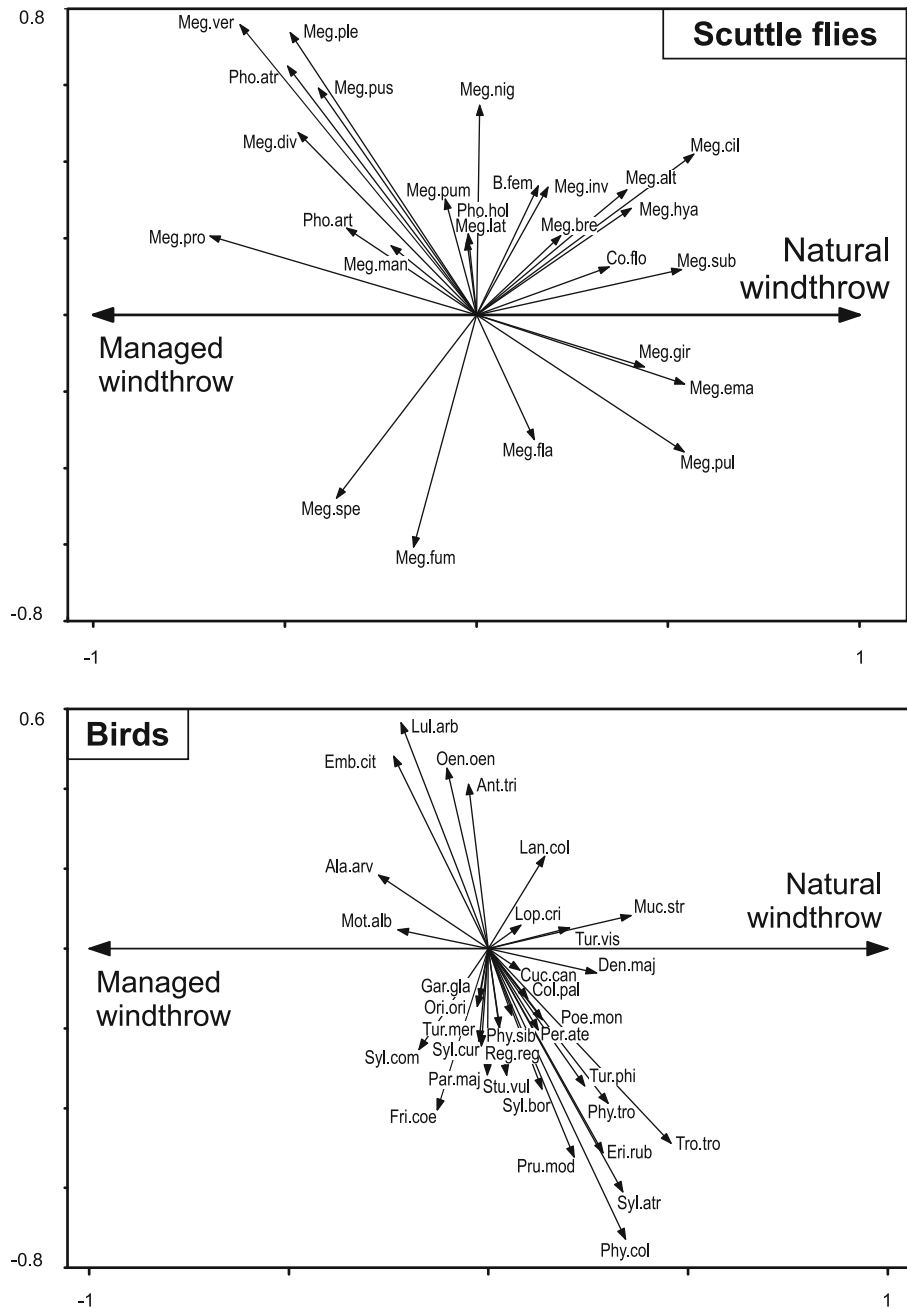
The species diversity of the bird community recorded in the natural windthrow was lower than in the managed windthrow. In order to see 52 bird species, one needed to record 853 randomly selected individuals in the natural windthrow or just 497 individuals in the managed windthrow (Fig. 4).

The total species richness corrected for unseen species was higher in the managed windthrow relative to the natural windthrow, both for scuttle flies (70.75 vs. 67.14 species, respectively) and for birds (73.17 vs. 56.91 species, respectively)(Fig. 5).

### Discussion

Our analysis is based on data from only one windthrow, although occurring over a large area, is in fact one replication (*sensu* Hurlbert 1984). Therefore, the observed patterns of abundance of scuttle flies and birds in relation to management options should be treated with caution. However, studies concerning the effects of natural disturbances on wildlife are often based on limited material since the disturbances are spatially and temporally unpredictable (e.g., Faccio 2003; Grimbacher and Stork 2009). Moreover, pre-treatment (pre-windstorm) similarities in the forest

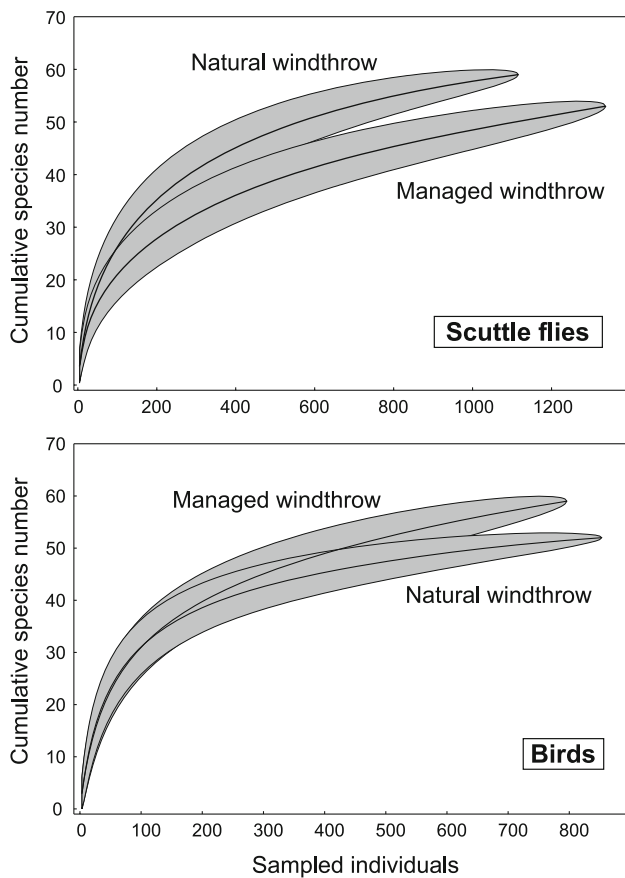
**Fig. 3** Ordination diagram of redundancy analysis (RDA) with 26 of the most common scuttle fly species (sampled 2005) and 33 of the most common bird species (sampled 2007) recorded in sampling stations in the Pisz Forest (NE Poland) explained by the placement of the stations in one of the two habitats: the managed windthrow and natural windthrow. The directions of the vectors along the horizontal axis show the preference for the two habitat types, vertical vectors indicate species not showing a preference for either habitat, the length of the vectors indicates the strength of the associations. Abbreviations of species names include the first three letters of the genus and species scientific names



structure and habitat type of managed and natural plots allow us to assume that the patterns described in this study do in fact reflect the effect of the salvage logging.

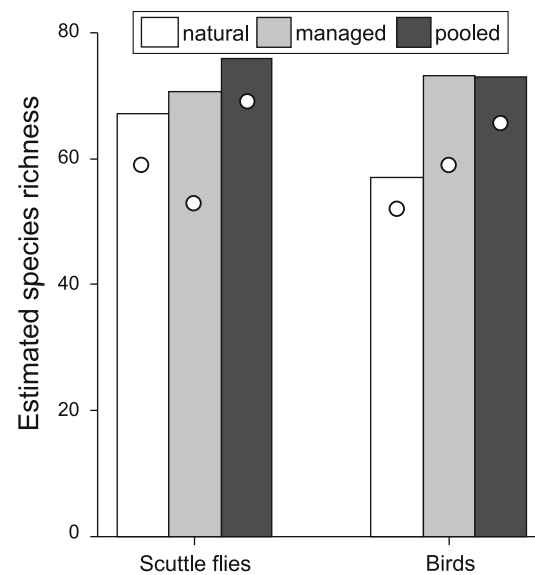
The study confirms the results of previous work showing that *Megaselia* species make an extremely major contribution to communities of Phoridae (Disney 1994; Durska 1996, 2001, 2006, 2009). Two of the dominants in the scuttle fly communities of natural and managed windthrow (i.e., the pyrophilous *Megaselia verralli* and the polysaprophagous *M. brevicostalis*) are also dominants in other forests of the Polish Lowland (Durska 2006, 2009). The bird community recorded during the study was composed mainly of small

passerines. We did not collect detailed data on large species, e.g., diurnal and nocturnal raptors. Also we did not record very rare species, e.g., rare woodpeckers, which possibly could be present in the windthrow in the Pisz Forest. This may be due to the method used—fixed-radius point count, as rare and shy species are difficult to detect with this method (Gregory et al. 2004). It should also be noted that the size of the natural windthrow (445 ha) may be less than is required by some species, such as raptors or galliform birds. Hence, the obtained results may not be reliable for all bird species and the effect of the salvage logging on rare species needs more detailed analysis.



**Fig. 4** The expected cumulative number of scuttle fly species and bird species (solid lines, 2 × SD bounds marked in gray) as a function of the number of sampled individuals in two habitat types (i.e., managed windthrow and natural windthrow)

In both taxonomic groups, one may identify the “winners” and “losers” of the salvage logging. This highly diversified reaction for different disturbing regimes or silvicultural treatments seems to be a common pattern (Greenberg and Lanham 2001; Venier and Pearce 2007; Kolbin 2008; Grimbacher and Stork 2009; Žmihorski 2010). In general, it seems that dead wood and natural structure of the windthrow left for natural regeneration positively affected forest dwelling species and saproxylic organisms (Bässler and Müller 2010; Müller et al. 2010), whereas abundance of open-area specialists increased as a result of windthrow management. Moreover, the response of scuttle flies and birds recorded in this study may indicate that leaving disturbed forest for natural regeneration has positive effect on forest specialists and saproxylic species in other taxonomic groups. In the case of scuttle flies, three of the dominant species in the Pisz Forest—*Megaselia verralli*, *M. pleuralis* and *M. pulicaria*—complex, are known as dominants in heterogeneous habitats afflicted by wildfires (a chestnut–belt in the Swiss Alps—Prescher et al. 2002) and in the pine plantations in Poland (Durska



**Fig. 5** Estimate of the total species richness of scuttle flies and birds in the two habitat types in the Pisz Forest. Bars denote the abundance-based coverage estimates (ACE) of a total species richness corrected for species unseen in the samples. Dots denote observed species richness

2001, 2006, 2009). However, the “disturbance specialists” *Megaselia verralli* and *M. pleuralis* preferred a managed windthrow over the natural one, whereas *M. pulicaria*-complex showed the opposite tendency. Our study confirms the results of previous work showing that *Megaselia* species, and especially these three open-area dominants mentioned above, make a major contribution to the communities of Phoridae after disturbance or stress (Durska 2009). In the case of birds, it seems that forest dwellers were more attracted by the natural windthrow, whereas species associated with open habitats preferred the managed windthrow. For instance, the winter wren, the great spotted woodpecker, and the blackcap, which showed strong preference for the natural windthrow, inhabit forests, whereas the skylark, the wagtail, and the yellowhammer, which preferred logged plot, are more typical for open or edge habitats (e.g., Moning and Müller 2008). Moreover, among six birds using tree holes for breeding (tits and the woodpecker), five preferred the natural windthrow, while the remaining one, the great tit, showed no clear preferences (see Fig. 4). Similar results were obtained by Germaine et al. (1997); Hutto and Gallo (2006); Koivula and Schmiegelow (2007). The authors recorded that post-disturbance harvesting negatively affected cavity-nesting birds; however, the effect of windstorm and its management on food resources of birds cannot be excluded.

We revealed clear transformation of scuttle fly and bird communities in response to the salvage logging. This result shows that the management of the disturbed plot had a strong impact on the wildlife characteristics of the

disturbed habitat. It should be stressed that the impact of logging is independent of the disturbing agent (i.e., windstorm)—in our case, both plots were disturbed in the same way. This effect of logging of the windthrow on the two taxonomic groups confirms that post-disturbance harvesting considerably affects the ecosystem (Lindenmayer and Noss 2006; Koivula and Spence 2006).

We did not find a significant relationship between the body size of scuttle flies and birds and the response to the logging. Skłodowski (2006) found that clear-cutting caused a drastic decrease in mean individual biomass in carabids in the forest of Białowieża and this response to disturbances seems to be common in carabids (Ribera et al. 2001). However, our results do not necessarily stand in contradiction to the findings of Skłodowski (2006) since he analyzed the effect of disturbance while our study concentrates on post-disturbance treatments. It is worth adding that almost all specimens of scuttle flies species recorded on the windthrow were clearly smaller (<2.5 mm) than the species previously recorded in the intact old-growth stands of the Polish Lowland (Durska 1996).

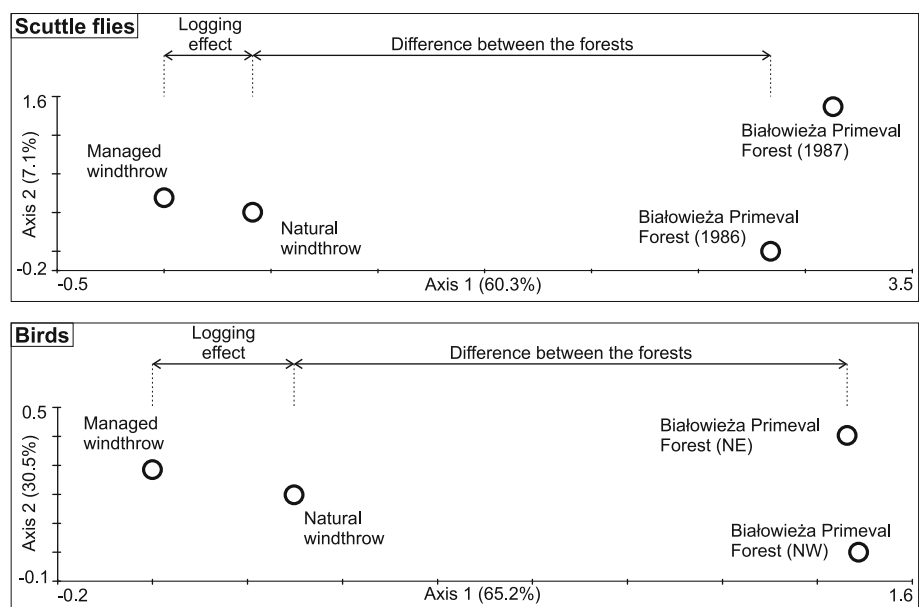
Characteristics of the natural windthrow were similar to those reported from natural conditions (dead wood, natural regeneration, etc.) while these of the logged plot were much more artificial. Despite this, we observed two opposite patterns of species diversity as a response to the salvage logging. Species diversity increased in birds while it decreased in scuttle flies as a reaction to the post-disturbance harvesting. Flies were counted 3 years and birds 5 years after the windstorm event; however, the two periods covered very similar stage of forest regeneration, and therefore, we believe that the differences did not contribute to the observed differences in ecological response of the studied communities. This discrepancy partially supports

former research showing that the diversity of one group is often a poor predictor of diversity in another (e.g., Davis et al. 2008 but see also Taboada et al. 2010). This finding seems to be important for the management of disturbances and one may conclude that species diversity is not a precise measure of the natural state of the habitat (Neumann and Starlinger 2001). Use of species diversity for assessment of the natural state may lead to contradictory conclusions and the final outcome depends strongly on the taxonomic groups taken into account. Estimated species richness should also be treated with caution when used as an important factor of habitat value: the estimated species richness of scuttle flies and birds was higher for the managed windthrow when compared to the natural windthrow. Again, this result suggests that species richness is not a universal indicator of the natural state of the habitat (Standovar et al. 2006). On the basis of the result, one may conclude that natural disturbances are not necessarily associated with higher species richness and species diversity relative to anthropogenic forest transformations. This in turn means that we failed to confirm our hypothesis concerning similar response of two distinct taxonomic groups for the salvage logging.

DCA showed that in respect to species composition of the scuttle fly community, the distance between the natural windthrow and the Białowieża Forest was less than that between the managed windthrow and BF (Fig. 6). A similar pattern was observed in birds. Bird species composition recorded in BF displayed greater similarity to that reported from the natural windthrow than to that computed for the managed windthrow (Fig. 6).

Comparison of our data to those available from the Białowieża Forest (BF) should be treated with caution because of some methodological differences and could be

**Fig. 6** Position of four samples (managed windthrow, natural windthrow, and two samples from Białowieża Forest) of scuttle flies (*upper*) and birds (*lower*) along the first two axes of detrended correspondence analysis (DCA)





used as a suggestion for further research. Despite this, the comparison leads to several important conclusions. First, the species composition of scuttle fly and bird communities in the two forest complexes differs. The difference can be due to a higher level of anthropogenic transformation in the Pisz Forest when compared to the BF. Moreover, the difference between the forest complexes may partially result from the windstorm since both habitats in the Pisz Forest were disturbed, while sample sites from the BF were intact. Therefore, one may interpret the difference between the forests along the first axis of DCA (besides possible effect of methodology and temporal separation of the data sets) as the windstorm effect and the difference between the stands. The second, and most important, DCA showed that communities from the natural conditions (BF) were more similar to those reported from the natural windthrow left for natural regeneration than to those recorded in the managed windthrow. In other words, salvage logging applied in the windthrow reduced the similarity of scuttle fly and bird communities found there to those in intact stands in a largely natural state (see also Żmihorski 2010). It should be underlined that the general aim of the salvage logging was to facilitate and hasten the regeneration of the forest (see also Lindenmayer et al. 2008). However, in light of our results, the post-disturbance harvesting, instead of hastening the regeneration of the forest ecosystem, reduces its similarity (expressed as bird and scuttle fly communities) to the intact forest. It is worth noting that the effect of the salvage logging is independent of the windstorm effect. As a result, the plot affected by the windstorm followed by the salvage logging displays less similarity to the natural stands in BF than the plot affected by the windstorm only.

**Acknowledgments** We are grateful to Prof. Jerzy Gutowski for the materials concerning flies. We would like to thank Dr. R. Henry L. Disney for determining some problematic scuttle fly species and also thank Krzysztof Gagla, M.Sc., for his invaluable assistance with the segregation of the material. We gratefully acknowledge valuable comments on the manuscript made by Prof. Joanna Gliwicz and by two anonymous referees. Ewa Durska has benefited from SYNTHESIS support made available by the European Community—Research Infrastructure Action under the FP6 Structuring the European Area Programme AT-TAF 543 and SE-TAF 1833, while Michał Żmihorski was supported by grant BLP-278 from the Polish State Forests National Forest Holding. Graham Carr kindly improved the English.

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## Appendix 1

See Table 1.

**Table 1** Percentage of number of individuals of scuttle fly (Diptera: Phoridae) species (males only) recorded for 2005 in the natural windthrow and the managed windthrow in the Pisz Forest, NE Poland

#	Species	Natural windthrow	Managed windthrow
1	<i>Megaselia pulicaria</i> -complex	22.60	3.90
2	<i>Megaselia verralli</i> (Wood, 1910)	14.86	29.87
3	<i>Megaselia fumata</i> (Malloch, 1909)	7.59	7.59
4	<i>Megaselia subnudipennis</i> (Schmitz, 1919)	4.23	0.27
5	<i>Megaselia nigriceps</i> (Loew, 1866)	3.99	2.80
6	<i>Megaselia pleuralis</i> (Wood, 1909)	3.35	12.99
7	<i>Phora artifrons</i> Schmitz, 1920	3.35	5.88
8	<i>Megaselia flavicoxa</i> (Zetterstedt, 1848)	3.12	1.37
9	<i>Borophaga femorata</i> (Meigen, 1830)	2.48	1.30
10	<i>Megaselia altifrons</i> (Wood, 1909)	2.40	1.23
11	<i>Megaselia giraudii</i> -complex	1.68	0.34
12	<i>Megaselia pusilla</i> (Meigen, 1830)	1.60	3.96
13	<i>Megaselia hyalipennis</i> (Wood, 1912)	1.44	0.00
14	<i>Megaselia brevicostalis</i> (Wood, 1910)	1.28	0.62
15	<i>Megaselia diversa</i> (Wood, 1909)	1.20	2.80
16	<i>Megaselia emarginata</i> (Wood, 1908)	1.20	0.07
17	<i>Conicera floricola</i> Schmitz, 1938	0.96	0.34
18	<i>Megaselia ciliata</i> (Zetterstedt, 1848)	0.80	0.21
19	<i>Megaselia pumila</i> (Meigen, 1830)	0.80	0.68
20	<i>Megaselia latifrons</i> (Wood, 1910)	0.72	0.55
21	<i>Megaselia involuta</i> (Wood, 1910)	0.64	0.21
22	<i>Megaselia manicata</i> (Wood, 1910)	0.64	0.68
23	<i>Phora holosericea</i> Schmitz, 1920	0.64	0.48
24	<i>Borophaga carinifrons</i> (Zetterstedt, 1848)	0.56	0.00
25	<i>Megaselia longicostalis</i> (Wood, 1912)	0.48	0.07
26	<i>Metopina oligoneura</i> (Mik, 1867)	0.48	0.21
27	<i>Megaselia elongata</i> (Wood, 1914)	0.40	0.27
28	<i>Megaselia minor</i> (Zetterstedt, 1848)	0.40	0.07
29	<i>Anevrina thoracica</i> (Meigen, 1804)	0.32	0.07
30	<i>Conicera tarsalis</i> Schmitz, 1920	0.32	0.00
31	<i>Conicera tibialis</i> Schmitz, 1925	0.32	0.27
32	<i>Megaselia coccyx</i> Schmitz, 1965	0.32	0.00
33	<i>Megaselia spinicincta</i> (Wood, 1910)	0.32	0.00
34	<i>Borophaga subsultans</i> (Linné, 1767)	0.24	0.21
35	<i>Conicera dauci</i> (Meigen, 1830)	0.24	0.00
36	<i>Megaselia campestris</i> (Wood, 1908)	0.24	0.07
37	<i>Megaselia lata</i> (Wood, 1910)	0.24	0.27
38	<i>Pseudacteon fennicus</i> Schmitz, 1927	0.24	0.07
39	<i>Conicera similis</i> (Haliday, 1833)	0.16	0.27
40	<i>Megaselia breviseta</i> (Wood, 1912)	0.16	0.00
41	<i>Megaselia curvicapilla</i> Schmitz, 1947	0.16	0.00
42	<i>Megaselia propinqua</i> (Wood, 1909)	0.16	1.71
43	<i>Megaselia styloprocta</i> (Schmitz, 1921)	0.16	0.00

**Table 1** continued

#	Species	Natural windthrow	Managed windthrow
44	<i>Megaselia tarsalis</i> (Wood, 1910)	0.16	0.00
45	<i>Megaselia unicolor</i> (Schmitz, 1919)	0.16	0.34
<b>46</b>	<b><i>Phora atra</i> (Meigen, 1804)</b>	<b>0.16</b>	<b>3.21</b>
47	<i>Phora obscura</i> (Zetterstedt, 1848)	0.16	0.00
48	<i>Triphleba papillata</i> (Wingate, 1906)	0.16	0.21
49	<i>Anevrina unispinosa</i> (Zetterstedt, 1860)	0.08	0.07
50	<i>Megaselia aculeata</i> (Schmitz, 1919)	0.08	0.07
51	<i>Megaselia affinis</i> (Wood, 1909)	0.08	0.07
52	<i>Megaselia albicans</i> (Wood, 1908)	0.08	0.00
53	<i>Megaselia coei</i> (Schmitz, 1938)	0.08	0.00
54	<i>Megaselia hibernans</i> (Schmitz, 1934)	0.08	0.00
55	<i>Megaselia hilaris</i> Schmitz, 1927	0.08	0.00
56	<i>Megaselia picta</i> (Lehmann, 1822)	0.08	0.07
57	<i>Megaselia protarsalis</i> Schmitz, 1927	0.08	0.00
58	<i>Triphleba intermedia</i> (Malloch, 1908)	0.08	0.07
59	<i>Triphleba opaca</i> (Meigen, 1830)	0.08	0.14
60	<i>Anevrina curvinervis</i> (Becker, 1901)	0.00	0.07
61	<i>Megaselia basispinata</i> (Lundbeck, 1920)	0.00	0.07
62	<i>Megaselia flava</i> (Fallen, 1823)	0.00	0.27
63	<i>Megaselia gregaria</i> (Wood, 1910)	0.00	0.07
64	<i>Megaselia meconicera</i> (Speiser, 1925)	0.00	0.14
65	<i>Megaselia scutellaris</i> (Wood, 1909)	0.00	0.41
<b>66</b>	<b><i>Megaselia speiseri</i> (Schmitz, 1929)</b>	<b>0.00</b>	<b>4.24</b>
67	<i>Megaselia stigmatica</i> (Schmitz, 1920)	0.00	0.07
68	<i>Megaselia subpleuralis</i> (Wood, 1909)	0.00	0.07
69	<i>Phora dubia</i> (Zetterstedt, 1848)	0.00	0.07
	<i>Megaselia</i> spp. (males)	10.86	8.61
	Total individuals	1,252	1,463

Dominant species (with abundance exceeding 1% of overall community) are shown in bold type

## Appendix 2

See Table 2.

**Table 2** Percentage of number of individuals of bird species recorded in the natural windthrow and the managed windthrow in the Pisz Forest, NE Poland

#	Species	Natural windthrow	Managed windthrow
<b>1</b>	<b><i>Fringilla coelebs</i></b>	<b>11.37</b>	<b>15.70</b>
<b>2</b>	<b><i>Dendrocopos major</i></b>	<b>7.39</b>	<b>5.53</b>
<b>3</b>	<b><i>Erithacus rubecula</i></b>	<b>6.10</b>	<b>4.65</b>
<b>4</b>	<b><i>Phylloscopus trochilus</i></b>	<b>5.98</b>	<b>3.89</b>
<b>5</b>	<b><i>Phylloscopus collybita</i></b>	<b>5.98</b>	<b>3.02</b>
<b>6</b>	<b><i>Turdus philomelos</i></b>	<b>5.28</b>	<b>3.89</b>

**Table 2** continued

#	Species	Natural windthrow	Managed windthrow
<b>7</b>	<b><i>Anthus trivialis</i></b>	<b>5.16</b>	<b>7.04</b>
<b>8</b>	<b><i>Troglodytes troglodytes</i></b>	<b>4.81</b>	<b>0.88</b>
<b>9</b>	<b><i>Lullula arborea</i></b>	<b>4.57</b>	<b>8.79</b>
<b>10</b>	<b><i>Prunella modularis</i></b>	<b>3.87</b>	<b>2.39</b>
<b>11</b>	<b><i>Lanius collurio</i></b>	<b>3.05</b>	<b>2.39</b>
<b>12</b>	<b><i>Sylvia atricapilla</i></b>	<b>3.05</b>	<b>0.88</b>
<b>13</b>	<b><i>Garrulus glandarius</i></b>	<b>2.93</b>	<b>3.89</b>
<b>14</b>	<b><i>Emberiza citrinella</i></b>	<b>2.81</b>	<b>6.53</b>
<b>15</b>	<b><i>Muscicapa striata</i></b>	<b>2.34</b>	<b>0.38</b>
<b>16</b>	<b><i>Parus major</i></b>	<b>1.99</b>	<b>2.51</b>
<b>17</b>	<b><i>Turdus merula</i></b>	<b>1.76</b>	<b>2.39</b>
<b>18</b>	<b><i>Turdus viscivorus</i></b>	<b>1.76</b>	<b>0.88</b>
<b>19</b>	<b><i>Lophophanes cristatus</i></b>	<b>1.41</b>	<b>1.26</b>
<b>20</b>	<b><i>Poecile montanus</i></b>	<b>1.41</b>	<b>0.88</b>
<b>21</b>	<b><i>Oenanthe oenanthe</i></b>	<b>1.29</b>	<b>2.64</b>
<b>22</b>	<b><i>Phylloscopus sibilatrix</i></b>	<b>1.29</b>	<b>1.26</b>
<b>23</b>	<b><i>Periperus ater</i></b>	<b>1.29</b>	<b>0.88</b>
<b>24</b>	<b><i>Sturnus vulgaris</i></b>	<b>1.17</b>	<b>1.13</b>
<b>25</b>	<b><i>Sylvia communis</i></b>	<b>1.06</b>	<b>2.64</b>
26	<i>Cuculus canorus</i>	0.94	0.75
27	<i>Columba palumbus</i>	0.94	0.63
28	<i>Sylvia borin</i>	0.94	0.50
29	<i>Sylvia curruca</i>	0.82	1.13
30	<i>Regulus regulus</i>	0.82	0.88
31	<i>Dryocopus martius</i>	0.82	0.25
32	<i>Certhia familiaris</i>	0.70	0.13
33	<i>Oriolus oriolus</i>	0.59	0.88
34	<i>Phoenicurus phoenicurus</i>	0.59	0.00
35	<i>Corvus corax</i>	0.47	0.25
36	<i>Poecile palustris</i>	0.35	0.00
<b>37</b>	<b><i>Alauda arvensis</i></b>	<b>0.23</b>	<b>2.26</b>
38	<i>Pyrrhula pyrrhula</i>	0.23	0.25
39	<i>Upupa epops</i>	0.23	0.13
40	<i>Jynx torquilla</i>	0.23	0.13
41	<i>Anas platyrhynchos</i>	0.23	0.13
42	<i>Streptopelia turtur</i>	0.23	0.13
43	<i>Hippolais icterina</i>	0.23	0.13
44	<i>Loxia curvirostra</i>	0.23	0.00
45	<i>Buteo buteo</i>	0.23	0.00
46	<i>Accipiter nisus</i>	0.12	0.25
47	<i>Tringa ochropus</i>	0.12	0.25
48	<i>Turdus pilaris</i>	0.12	0.13
49	<i>Lanius excubitor</i>	0.12	0.13
50	<i>Carduelis spinus</i>	0.12	0.00
51	<i>Dendrocopos minor</i>	0.12	0.00
52	<i>Cyanistes caeruleus</i>	0.12	0.00
53	<i>Motacilla alba</i>	0.00	1.51

**Table 2** continued

#	Species	Natural windthrow	Managed windthrow
54	<i>Gallinago gallinago</i>	0.00	0.50
55	<i>Anthus pratensis</i>	0.00	0.38
56	<i>Corvus corone</i>	0.00	0.38
57	<i>Fringilla montifringilla</i>	0.00	0.25
58	<i>Falco subbuteo</i>	0.00	0.25
59	<i>Ficedula hypoleuca</i>	0.00	0.25
60	<i>Turdus iliacus</i>	0.00	0.13
61	<i>Carduelis chloris</i>	0.00	0.13
62	<i>Coccothraustes coccothraustes</i>	0.00	0.13
63	<i>Aquila pomarina</i>	0.00	0.13
64	<i>Saxicola rubetra</i>	0.00	0.13
65	<i>Miliaria calandra</i>	0.00	0.13
66	<i>Columba oenas</i>	0.00	0.13
	Total individuals	853	796

Dominant species (with abundance exceeding 1% of overall community) are marked in bold

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