

The effects of anthropogenic and natural disturbances on breeding birds of managed Scots pine forests in northern Poland

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Anthropogenic disturbance of habitats associated with clear-cut harvesting has replaced natural disturbances, such as wildfire and wind-throw, as initiators of succession in most European forests. Recently, however, forest management has begun to adopt techniques that better mimic natural disturbances, following the documentation of the negative effects of forestry activities, but less information exists on the relative similarity between man-caused and natural disturbances. This study aimed at comparing the bird faunas of windstorm, clear-cut and closed-forest areas in northern Poland. Following the two disturbances, species inhabiting open areas and edge habitats increased (e.g., Yellowhammer *Emberiza citrinella* and Woodlark *Lullula arborea*) while closed-forest specialists decreased (Wood Warbler *Phylloscopus sibilatrix*, Crested Tit *Parus cristatus* and Goldcrest *Regulus regulus*). Community density, rarefied diversity and estimated species richness were higher in the disturbed than in the intact, closed-canopy forests. The species-specific responses to windstorm and clear-cutting were positively correlated, i.e., a given species that increased in response to one disturbance regime also increased in response to the other. This finding indicates that man-made disturbances, such as logging, may act as substitutes for natural disturbances for some species.



1. Introduction

Forest management involves substantial decreases in the impacted area and frequency of natural disturbances, such as fires, wind-throws and outbreaks of folivorous insects (e.g., Esseen *et al.* 1997, Kohm & Franklin 1997). The reason for this trend is that these disturbances reduce the quality and quantity of timber (Schelhaas *et al.* 2003). As a result, the impact of natural disturbances in managed forests is largely suppressed relative to primeval conditions (Esseen *et al.* 1997, Kuuluvainen 2002, Schelhaas *et al.* 2003). On the other

hand, timber production creates open areas in forests, and in this sense this process can be considered a disturbance. But a question that is crucial for evaluating the impact of forest management on biodiversity in the forested ecosystem is whether clear-cuts can substitute for natural disturbances in managed forests (Niemelä 1999, Drever *et al.* 2006, Toivanen & Kotiaho 2007a)?

For various groups of organisms, clear-cuts do not substitute for the above-mentioned natural disturbances in managed forests (Bengtsson *et al.* 2000), simply because clear-cuts do not much resemble disturbed plots where all damaged trees re-

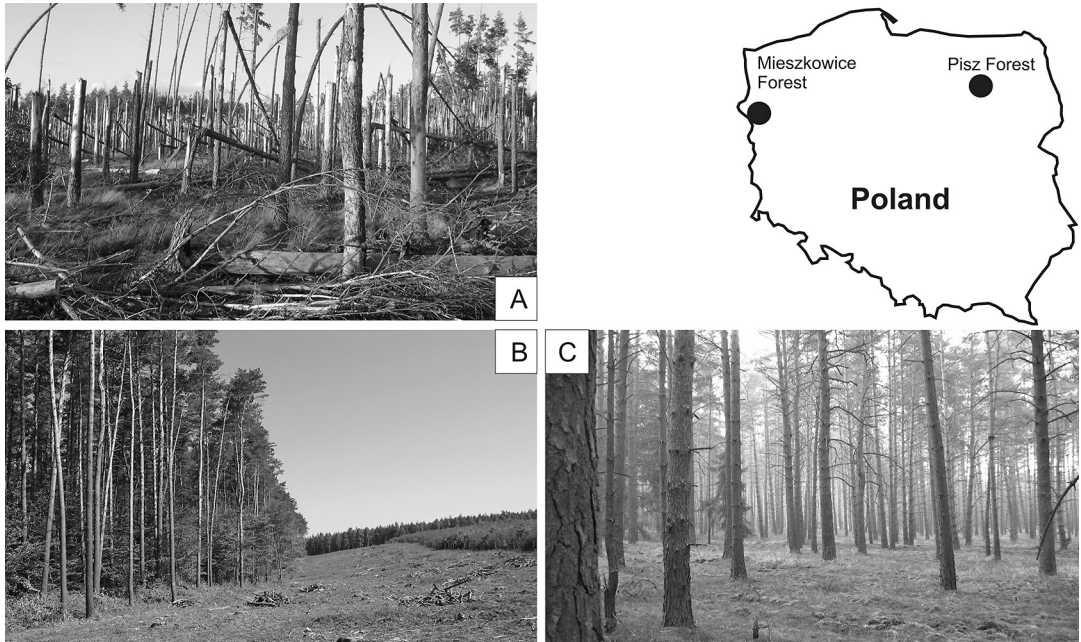


Fig. 1. The location of the two study areas (up, right) and studied habitat types (A–C) in northern Poland. A = naturally-regenerating wind-throw plot in the Pisz Forest; B = clear-cut in the Mieszkowice Forest; and C = managed mature forest in the Mieszkowice Forest.

main (Niemelä 1999). The presence of dead wood is crucial for dead-wood dependent (saproxylic) insects (Bouget & Duelli 2004, Lindbladh & Abrahamsson 2008). Moreover, Buddle *et al.* (2006) found remarkable differences in communities of epigeic invertebrates between natural (post-fire) and artificial (clear-cut) openings. Retention of fallen logs promotes the occurrence of late-successional species, while their removal favours pioneer plant communities (Fischer *et al.* 2002). Moreover, logs and branches lying on the ground protect seedlings from ungulates (Ramming *et al.* 2007), which facilitates forest regeneration. As the structural differences between naturally-disturbed and clear-cut forests affect plants and insects, one may assume that these in turn impact forest birds that use these resources for foraging and nesting. In Białowieża Forest, Tomiałojć and Wesołowski (2004) found that an important factor for bird assemblages was the origin of open areas in the forest, and several species (e.g., Yellowhammer *Emberiza citrinella*, Lesser Whitethroat *Sylvia curruca*, Red-backed Shrike *Lanius collurio* and Willow Warbler *Phylloscopus trochilus*) occurred commonly in clear-cuts but were less often en-

countered in gaps of natural origin (see also Fuller 2000). This pattern has been confirmed in other regions. Schieck and Song (2006) observed that the bird communities between areas affected by natural or man-made disturbances were different in North America. These authors concluded that post-fire plots are colonized by cavity-nesting and post-harvest plots are colonized by open-country species. Also Imbeau *et al.* (1999) found remarkable differences in abundance of neotropical migrants and cavity nesters between stands that were logged and stands that had burned.

One can expect that for species associated with open areas, clear-cuts are better than intact, closed-canopy stands (e.g., Faccio 2003). The substitute role of clear-cuts for birds may be especially important in managed stands where the role of natural disturbances is artificially suppressed (see also Forsman *et al.* 2010). Hence, in the present study, I investigated the effect of anthropogenic and natural disturbances in managed pine-dominated stands in northern Poland on the breeding bird community. I evaluated whether man-made clear-cuts can act as a substitute for natural windstorm in managed stands. More precisely I hypothesized

that, despite certain obvious differences between natural and anthropogenic disturbances, the two types of disturbances will result in rather similar breeding bird communities in managed stands.

2. Material and methods

2.1. Study area

The study was conducted in two locations of northern Poland separated by a distance of ca. 500 km: Pisz Forest and Mieszkowice Forest. The two locations differed by the type of disturbance. In Pisz Forest, a natural, large-scale windthrow occurred, whereas in Mieszkowice Forest, the main disturbing agent was clear-cutting. At both locations, I carried out bird counts in disturbed and undisturbed sections (see below).

Pisz Forest is a ca. 90,000-ha forest complex mostly managed for timber production by the State Forests National Forest Holding, and clear-cutting is the predominant source of disturbance there. The area is mainly composed of Scots pine (*Pinus sylvestris*) forests, with Norway spruce (*Picea abies*) and oak (*Quercus robur*) as a mixture. Pisz Forest is located in a young glacial landscape with predominantly sandy soil; hence the prevailing forest associations are conifers (Matuszkiewicz 2001). On July 4, 2002 a windstorm severely impacted ca. 15,000 ha of the area, which is one of the largest wind-throws ever recorded in Poland. This 15,000-ha area became a mosaic of open sites: completely damaged stands covered ca. 40% of the wind-throw area, while partially damaged stands, with single or groups of trees remaining undamaged, covered ca. 10%; the rest (50%) was either very little or not impacted by the storm. In the subsequent years, most damaged stands were cleared and planted through forestry operations. However, a 445-ha fraction of the wind-throw was excluded from forestry activities to regenerate naturally, i.e., was not subjected to post-storm salvage logging or tree planting or seedling. This site abounded in fallen logs, leaning trees and broken trunks, among which numerous seedlings of pine, birches (*Betula* sp.) and oak were growing (Fig. 1A). The height of the seedlings and young trees that appeared after windstorm reached up to 2–3 m at the time of bird inventories (see below). The

445-ha area also contained occasional partially or completely undisturbed sections (up to several ha).

Mieszkowice Forest is ca. 14,000 ha in size and managed by State Forests National Forest Holding for timber production; as in Pisz Forest, clear-cutting is the dominant disturbance (Fig. 1B), and afforestation is the rule after clear-cutting. Forests in the study area were dominated by Scots pine, with oak and birch as a mixture (Fig. 1C). The area is comprised of both semi-rich and poor habitats, with sandy soils and acidophilous oak stands as the potential vegetation type. Clear-cuts at this area are common; the studied ones (see below) were up to 4 ha in size, 0 to 10 years old and hosted single large, retained trees. The youngest clear-cuts had not been planted at the time of the study, but the older ones were planted with Scots pine, with deciduous trees added (mainly oaks and birches), and these trees were up to 2–3 m height in the oldest clear-cuts at the time of the study. The herbaceous plant community in these clear-cuts was dominated by *Calamagrostis* and *Senecio* species.

2.2. Bird sampling

I conducted bird counts in the spring of 2007 (Pisz and Mieszkowice Forests) and 2008 (Mieszkowice Forest). Data from the two seasons in Mieszkowice Forest were pooled prior to the analysis. Birds were counted using a fixed-radius point count (Gregory *et al.* 2004), which is a common method in avian research (e.g., Fuller 2000, Dunford & Freemark 2005, Paquet *et al.* 2006, Gregory *et al.* 2007, Venier & Pearce 2007, Greenberg *et al.* 2008, Uezu *et al.* 2008). At each point, two 10-minute counts were conducted, one in March or April, and another in May or June. This method allows detecting both early sedentary breeders and tropical migrants, which start to breed later on in the spring. The points were sampled in a random order, and the exact location of each point was mapped using GPS. During the 10-minute counts, all individuals heard and seen within a 100-m radius were recorded (Dunford & Freemark 2005, Giraudo *et al.* 2008). In order to exclude migrants, birds in flight were not recorded. All counts were performed between sunrise and 10:00 in March–April and 9:00 in May–June, on days with no or

light wind and free of precipitation. Out of the two censuses carried out at a given point, the maximum number of a given species was used in the analysis (e.g., Hausner *et al.* 2003, Barbaro *et al.* 2007).

In the Pisz Forest, counts were performed in two different habitats: the above-mentioned 445-ha wind-throw area and mature forests unaffected by the windstorm. These undisturbed forests were approximately 5 km west of the wind-throw, suggesting no impact of the windstorm on the bird community in that habitat, and represented managed forests typical of what had covered the entire Pisz Forest before the windstorm event. In the Mieszkowice Forest, counts were also performed in two different habitats: recent clear-cuts and mature forests. In both areas, no mature-forest counts were conducted in the vicinity of clear-cuts.

In the Pisz Forest, counts were done at 98 points, of which 49 were within the wind-throw and 49 were in mature forests. These points were 300 m apart (Ralph *et al.* 1995) and located at the intersections of regular grids placed within the wind-throw and within the mature forest. In the Mieszkowice Forest, a total of 371 points were sampled, of which 227 were in mature forests and 144 were placed at borders of clear-cuts (here, regenerating stands less than ten years old; see above). The placing of the point-count stations was regular in the managed forests (at intersections of a regular grid, 500 m apart) but was non-random at the clear-cut sites.

2.3. Statistical analysis

A simple spatial autocorrelation analysis was used to demonstrate that the sampling points could be treated as independent measures: the spatial distance and the similarity index (see below) for 50 randomly-chosen point pairs, within a given habitat type, were correlated against each other. Distance explained only 0.3–8.5% of the variation in the similarity index, confirming the independence of adjacent sampling points.

Redundancy analysis (RDA) implemented in CANOCO software (Lepš & Šmilauer 2003) was used to detect general patterns of distribution of bird species' records in disturbed and undisturbed forests. The analysis was conducted for the species represented by at least 10 individuals (hereafter

“common species”), and was done separately for Pisz and Mieszkowice forests. The significance of the canonical axes of RDA was tested by using the Monte Carlo test with 5,000 permutations. Species-specific scores were subsequently plotted on the first axis of RDA obtained for each of the two study areas to indicate whether a given species preferred or avoided disturbed habitat. The average number of individuals and the average species number per point were compared between the intact and disturbed habitats in Pisz and Mieszkowice forests using the unequal-variance *t*-test on ranked cases (Ruxton 2006).

Next, the diversity of the bird communities was evaluated using rarefaction curves. For this purpose the Mao Tau estimator, implemented in EstimateS 800 software (Colwell 2005), was used. This estimator presents the expected cumulative number of species for a given number of randomly-chosen individuals and is interpreted as a measure of diversity (Gotelli & Colwell 2001, Colwell 2005). The resulting curves for disturbed and undisturbed count points were compared for each of the two study areas independently, as well as for the pooled material. Moreover, the abundance-based coverage estimator (ACE) was used as an approximation of total species richness (i.e., mathematically including species not observed but assumed to be present; see Chao *et al.* 2006), independently for a given habitat type (wind-throw, clear-cut and mature forest).

Finally, the similarity in species composition between the two study areas and habitat types was examined by means of the shared-species function in EstimateS 8.00 (Colwell 2005). The similarity index for two points, chosen randomly from the two regimes of disturbance within a given study area (e.g., undisturbed versus disturbed within the Pisz Forest), as well as for two points chosen randomly from a given disturbance regime of the two forests (e.g., disturbed forests from Pisz versus Mieszkowice), was compared. In order to obtain the average similarity index for these comparisons, an improved Sørensen similarity index for 53,268 pairs of points (i.e., all combinations of point pairs) was first calculated. This index for species abundance was corrected for undetected species, which improves the reliability of the classical Sørensen index, especially when undetected species constitute an important fraction of all spe-

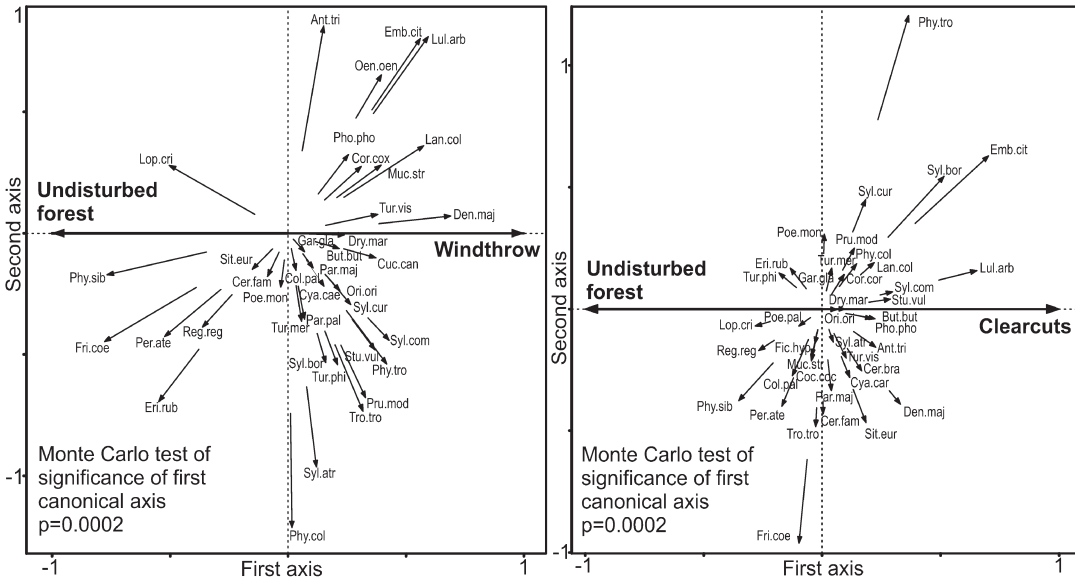


Fig. 2. Ordination diagram of the Redundancy Analysis (RDA) obtained from data on common bird species. Species associated with undisturbed forests are scattered to the left, and those associated with disturbed forests are clustered to the right. (a) Results for the Pisz forest. (b) Results for the Mieszkowice Forest. Species are indicated with 3+3-letter abbreviations; for example, *Syl.atr* = *Sylvia atricapilla*.

cies at the sampled area (Chao *et al.* 2005). This improved index is increasingly commonly used in ecological research (e.g., Ellwood *et al.* 2009). Mean values of the between-forest and between-regime similarity indices were compared using the unequal-variance *t*-test on ranked cases (Ruxton 2006). SPSS 13.0 was used for all statistical analyses (SPSS 2004).

3. Results

A total of 6,920 bird individuals were recorded: 1,569 (57 species) in Pisz and 5,351 (74) in Mieszkowice. The RDA revealed that the two disturbance regimes appeared important for many bird species. In Pisz Forest, the majority of the common species (for definition, see above) were more often encountered in the wind-throw than in the undisturbed forests (Fig. 2a). The intact forests supported more individuals of species that breed in dead or live trees, viz. the Crested (*Parus cristatus*) and Coal Tit (*P. ater*), the Wood Warbler (*Phylloscopus sibilatrix*) and Chaffinch (*Fringilla coelebs*). The wind-throw area was particularly preferred over the mature forests by the Great

Spotted Woodpecker (*Dendrocopos major*), Red-backed Shrike, Mistle Thrush (*Turdus viscivorus*), Woodlark (*Lullula arborea*) and Cuckoo (*Cuculus canorus*).

In Mieszkowice Forest, twice as many species preferred clear-cuts ($N = 26$ species) as compared to mature forests ($N = 13$). Woodlark, Yellowhammer, Willow Warbler, Garden Warbler (*Sylvia borin*), Starling (*Sturnus vulgaris*), White-throat and Great Spotted Woodpecker were associated with clear-cuts. On the contrary, Wood Warbler, Robin (*Erithacus rubecula*), Song Thrush (*Turdus philomelos*), Crested Tit, Marsh Tit (*Parus palustris*) and Goldcrest (*Regulus regulus*) showed the opposite tendency, i.e., were more commonly recorded in mature forests (Fig. 2b).

Species-specific responses to the natural disturbance and the anthropogenic clear-cuts were highly significantly positively correlated. Birds preferring the wind-throw in Pisz Forest (e.g. Woodlark) also preferred clear-cuts in Mieszkowice Forest (Fig. 3). Species preferring the undisturbed tree stand (e.g. Wood Warbler) in Pisz Forest also avoided clear-cuts in Mieszkowice Forest.

The approximation of bird community density

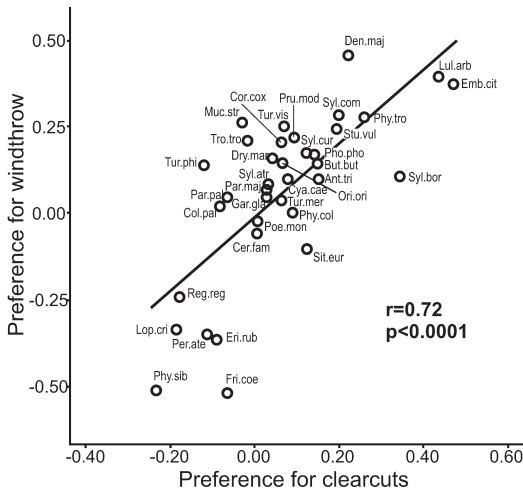


Fig. 3. Correlation between preferences of each species to the anthropogenic and natural disturbances (expressed as species specific scores along the first axis of RDA presented in Figs. 2–3; positive values denote preference and negative values avoidance). For more details, see Fig. 2.

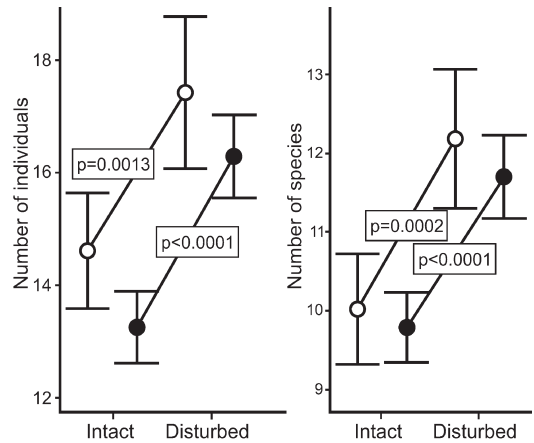


Fig. 4. Mean numbers of bird individuals and species recorded at point counts in disturbed and intact habitats in the Pisz Forest (open dots) and in the Mieszkowice Forest (filled dots). Whiskers denote 95% confidence intervals, and the statistical significance of the differences between disturbed and intact habitat types is given separately for each study area.

expressed as the mean number of individuals per point was significantly higher in the disturbed plots as compared to the intact tree stand, and this pattern was similar for the two disturbance types (Fig. 4). On average, 2–3 more individuals per point were recorded in the disturbed habitat compared to the intact one. The mean number of bird species recorded per point in the disturbed forest was significantly higher compared to the intact tree stands, and this tendency was similar for the

two disturbance types (Fig. 4). On average, two more species per point were noted in the disturbed forest than in the undisturbed habitat.

The diversity of the bird community, expressed as the expected cumulative species' number for a given number of randomly chosen individuals was higher for the disturbed habitats as compared to the undisturbed ones. This pattern held for both disturbance types (natural and anthropogenic) as well as for the pooled material.

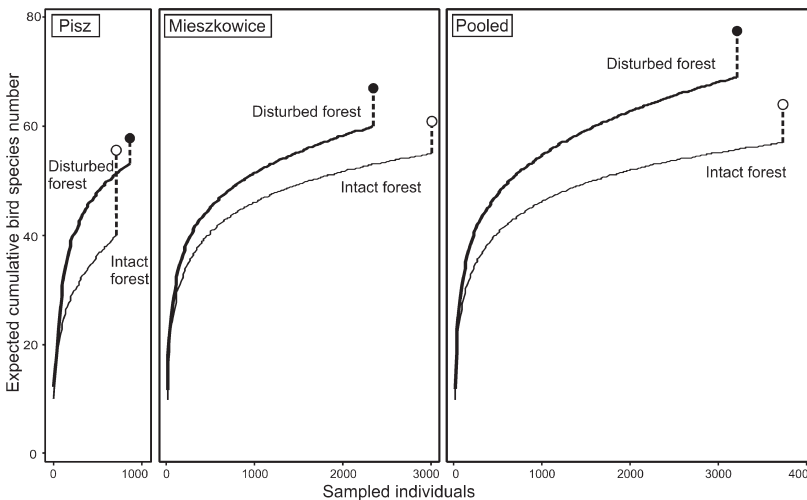


Fig. 5. The expected cumulative number of bird species as a function of the number of sampled individuals in the Pisz Forest and in the Mieszkowice Forest, as well as for the pooled material. Dots denote the estimated species richness corrected for unseen species as assessed by the abundance-based coverage estimator (ACE) in the disturbed forest (filled dots) and intact forest (clear dots).

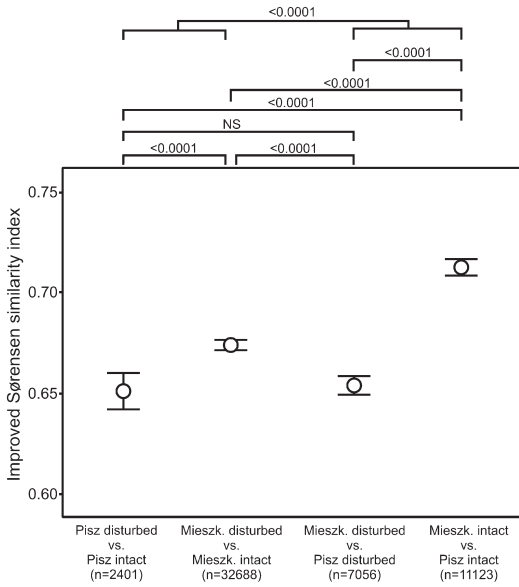


Fig. 6. The average value of the improved Sørensen similarity index, computed for all available point pairs from disturbed and intact forests within each study area, and from the disturbed and intact types of habitat within each study area. ‘Whiskers’ denote 95% confidence intervals; numbers of point pairs for each mean are given in brackets. The statistical significance of the similarity is indicated above the mean values.

The difference seems to be high. For example, in order to see 57 bird species, one had to record 3,723 randomly selected individuals in the intact stands or just 1,242 individuals in the disturbed habitats (Fig. 5). Moreover, estimated species richness, corrected for the species unseen during the counts (ACE), is higher for the disturbed tree stands compared to the undisturbed ones. The abundance-based coverage estimator reached higher values for the disturbed habitat compared to the undisturbed habitat, and this tendency was true for natural and anthropogenic disturbances as well as for the pooled material (Fig. 5).

In general, the similarity of the bird species’ community within a forest but between habitats (disturbed versus intact in Pisz Forest and the same for Mieszkowice Forest) was highly significantly lower compared to the similarity between forests but within habitats (Pisz versus Mieszkowice in the disturbed habitat and the same for the undisturbed habitat) (Fig. 6). The mean value of the improved Sørensen similarity index computed for all

possible point-pairs within each studied forest ($N = 35,089$ point pairs) denoted 0.673 whereas the value for between-forest point pairs ($N = 18,179$) reached 0.690 (values not shown on the chart as a separate symbol) and the difference was highly significant ($p < 0.0001$, Fig. 6). The highest similarity between the compared habitats and forests was noted for bird species recorded in the undisturbed stands of the Pisz and Mieszkowice Forests (Fig. 6).

4. Discussion

The present similarity analysis supports the common view that disturbances play an important role for the bird community, but also that man-made disturbances can, at least to some degree, mimic the effects of natural disturbances on the forest bird community. The avian species composition recorded at points 300 m apart but located in two different habitat types (i.e., disturbed or undisturbed) showed a lower similarity than did the species composition recorded within a given habitat type but located in the two study areas (that were 500 km apart). The importance of disturbances in shaping bird communities has been frequently reported (e.g., Głowaciński 1975, Hansson 1983, Fuller 2000, Greenberg & Lanham 2001, Faccio 2003, Edenius 2010, Žmihorski 2010). However, a more detailed inspection of the similarity analysis suggests that the results are not so straightforward. In particular, the mean value of the similarity index, computed from the data obtained from the two disturbed habitat types (wind-throw in Pisz, clear-cut in Mieszkowice), was not considerably higher than that obtained from the Pisz area (wind-throw versus mature forests) and was even lower than that obtained from the Mieszkowice area (clear-cut vs. mature forests). This may suggest that the nature of disturbance (natural vs. anthropogenic) is crucial and may consequently affect the similarity in species composition between compared habitat types.

Moreover, it is worth noting that the similarity between the wind-throw and the intact mature forests in the Pisz Forest was significantly lower than the similarity between the clear-cuts and intact mature forests in the Mieszkowice Forest. This finding may suggest that clear-cutting transforms the

bird community to a lesser extent than a windstorm (see also Niemelä 1999 and references therein). However, as the data originate from two distinct forest areas (see below), this interpretation should be treated with caution and needs further research.

In both study areas, “winners” and “losers” of the studied disturbances can be pin-pointed, consistent with earlier studies on different taxonomic groups (e.g., Fuller 2000, Greenberg & Lanham 2001, Tomiałojć & Wesolowski 2004, Venier & Pearce 2007, Kolbin 2008, Žmihorski & Durska 2011). The RDA showed that the responses of particular birds to the studied disturbances varied greatly, from strong preference to distinct avoidance, but some species appeared quite unaffected, of which the Chiffchaff (*Phylloscopus collybita*) is a good example: its abundance was similar between the disturbed and undisturbed plots.

The positive response of some species to disturbances can be associated with the recently-created new, suitable habitat of early successional stages, and an increase in dead wood at the windthrow area (Faccio 2003). Woodpeckers, for example, use dead wood on disturbed plots for foraging and nesting (e.g., Koivula & Schmiegelow 2007). Moreover, an increase in arthropod abundance in disturbed stands (Bouget & Duelli 2004) can drive an increase of species richness and abundance of birds (Hansson 1983, Fuller 2000, Venier & Pearce 2007). On the other hand, edge-avoiding species responded negatively to the two studied disturbance forces (e.g., Rosenvald & Lõhmus, 2003), which can be related to higher predation pressure close to forest/open-area edges, habitat loss caused by the reduction of mature-stand sizes, and/or a behavioural response to open ground (Potvin *et al.* 2000, Batary & Baldi 2004, Griesser *et al.* 2007).

The present analysis indicated that disturbances increased species density, species diversity and species richness, consistent with previous studies on birds and other taxa (Greenberg & Lanham 2001, Bouget & Duelli 2004, Loehle *et al.* 2005, Toivanen & Kotiaho 2007b). This finding also supports the intermediate disturbance hypothesis (e.g., Molino & Sabatier 2001). The increase of habitat heterogeneity at disturbed plots may be the main driver of this effect (Greenberg & Lanham 2001, Faccio 2003, Loehle *et al.* 2005). Moreover, the effect of food availability driven by

an increase in insect abundance at the disturbed plots may appear important, at least for insectivores (Jokimäki *et al.* 1998).

The present study detected striking similarities in the response of birds to natural and anthropogenic disturbances, but certain limitations must be acknowledged. Firstly, the study was conducted in managed stands, where certain structural elements characteristic of naturally-regenerating forests are extremely scarce, particularly very large and dead/dying trees (cf. Esseen *et al.* 1997, Kohm & Franklin 1997). Undoubtedly long-term forest management solely driven by needs of timber production leads to strong habitat transformation compared to natural conditions (Wesolowski 2005). Therefore, the present results may not generalize to natural stands or special protected areas. Secondly, the present study aimed at comparing bird faunas associated with two disturbance regimes, which were in two distinct areas.

Hence differences between the two study areas may have affected the results. These differences may be related to geographical location or stand history, and perhaps sampling technique, as in Pisz the points were 300 m but in Mieszkowice they were 500 m apart. However, the similarity analysis indicates these effects to be moderate if not non-existent (Fig. 6). The community-level difference between the two areas was less important than the difference between the compared habitat types (disturbed versus intact). The differences between the two areas may actually increase the reliability of the present results: species-specific responses were significantly correlated *despite* the differences between the two areas. Thirdly, the bird communities recorded in the present study did not contain rare or threatened species, which can be found among European woodpeckers, raptors and galliforms (cf. national Red Lists). The response of such rare birds to the two disturbance regimes may be different from the one reported here.

Natural and anthropogenic disturbances differ in many ways and therefore forestry activities cannot exactly match or substitute fires or windstorms (Bengtsson *et al.* 2000, Kardynal *et al.* 2009, King *et al.* 2009). However, the similarities in the response of birds to natural and anthropogenic disturbances, investigated in this study, were distinctive. Bird species that preferred the natural windthrow also preferred the anthropogenic clear-cuts:

the Yellowhammer and Woodlark may benefit from both disturbance regimes. On the other hand, the Wood Warbler avoided clear-cuts and the wind-throw in a similar way. Moreover, community diversity, the number of individuals and species per point, and the observed and estimated species richness changed in similar ways as a response to the studied, natural and anthropogenic disturbances. These results show that for some groups of bird species inhabiting managed stands, anthropogenic disturbances may act as a substitute for natural disturbances, suppressed in these stands by forest management. Hence, despite obvious differences between anthropogenic and natural disturbances, described above, both disturbances can increase the richness in bird fauna in managed forests, at least as far as the common forest species are concerned.

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Ihmisen aikaansaamien ja luontaisten häiriöiden vaikutukset talousmääntymetsien pesimälintuihin Pohjois-Puolassa

Avohakkuut ovat korvanneet luontaiset häiriöt, kuten metsäpalot ja myrskytuhot, sukkession käynnistäjinä valtaosissa eurooppalaisia metsiä. Metsätalouteen on kuitenkin avohakkuiden negatiivisten ympäristövaikutuksien vuoksi viime aikoina otettu tekniikoita, jotka jäljittelevät luontaisia häiriöitä paremmin. Ihmisen aikaansaamien ja luontaisten häiriöiden samankaltaisuutta on kuitenkin tutkittu melko vähän.

Tässä tutkimuksessa verrattiin myrskytuhoalueen, avohakkuiden ja varttuneen talousmetsän linnustoa Pohjois-Puolassa. Mainittujen häiriöiden johdosta avomaiden ja reunavyöhykkeiden lajisto runsastui (esim. keltasirkku *Emberiza citrinella* ja kangaskiuru *Lullula arborea*), mutta sulkeutuneen metsän specialistit vähenivät (sirittäjä *Phylloscopus sibilatrix*, töyhtötiainen *Parus cristatus* ja hippipiäinen *Regulus regulus*).

Lintuyhteisön yksilötiheys, standardoitu lajirunsaus ja arvioitu lajimäärä olivat korkeampia häirityissä kuin koskemattomissa varttuneissa talousmetsissä. Lajikohtaiset vasteet myrskytuhoon ja avohakkuuseen olivat positiivisesti korreloituneita, eli laji, joka runsastui yhden häiriötekijän seurauksena runsastui myös toisen seurauksena. Tämä havainto viittaa siihen, että ihmisen aiheuttamalla häiriöllä, kuten avohakkuilla, on merkitystä luontaisten häiriöiden korvaajana joillekin lajeille.

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