Winter bird communities in a managed mixed oak-pine forest (Niepołomice Forest, southern Poland)

Piotr SKÓRKA and Joanna D. WÓJCIK

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Abstract. Winter bird communities in a managed mixed oak-pine forest (Niepołomice Forest, southern Poland) were studied during winters the 1996/1997, 1998/1999, and 2000/2001 using the line-transect method. The transect (9.5 km long, 100 m wide) was conducted through three habitats: forest edge, mature, and young stands. The authors noted 5,764 individuals within the transect belonging to 33 bird species. The largest number of species was noted in mature stands – 27 (mean density: 34.0 inds/10 ha), then at the forest edge – 24 (19.4 inds/10 ha), and 18 species in young stands (25.2 inds/10 ha). The density of birds varied between winters and decreased during their course. The density of plant-eaters was significantly lower than that of invertebrate-eaters, but the total biomass of these groups did not differ. Plant-eater biomass was significantly higher in mature stands and at the forest edge than in young stands. Invertebrate-eater density was considerably lower at the forest edge, but the biomass of this trophic guild did not differ significantly among habitats. Plant-eater biomass was significantly lower during winter 1998/1999 and it is supposed that this variation in plant-eater density affects the most total variation in bird communities in the Niepołomice Forest. The authors’ results indicate that old stands are probably the most favourable habitat for some small birds in winter.

Key words: winter bird communities, forest management, guilds, habitat, Niepołomice Forest, S Poland.

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I. INTRODUCTION

The general rules in forest management in Poland have led to the existence of a mosaic of stands differing in age. Despite the rules of forest management, permitting only specific areas and minimal age of stands to be cut (BOBEK et al. 1994), considerable parts of large forest complexes are clearcuts or similarly-aged young stands. Forest fragmentation by clearcuts is an important factor in the decline of many bird populations (FAABORG 1995, ROBINSON et al. 1995). A finding associated with the forest fragmentation process is an increase in the proportion of the remaining habitat con-
sisting of forest edge. Forest birds are very sensitive to changes in habitat structure and may be used to
determine the effects of a forest management scheme (McKay & Coulthard 2000, Uliczka &
Angelstam 2000). Many studies have shown that old stands have more species and diversity esti-
mators are higher (MacArthur et al. 1966, Karr & Roth 1971, Glowaciński 1981, Swift et al.
fragments have fewer species typical of forest interior and their abundance is lower (Blake 1987).
However, those studies mainly dealt with breeding birds while surprisingly little attention was di-
rected toward wintering ones. Winter is a critical period for most birds (Graber & Graber 1979,
Spencer 1982) and habitat availability may play an important role in the occurrence of many spe-
cies, as well as their abundance. Therefore, it is possible that the chances of survival until the breed-
ing period may depend on habitat availability (Telleria & Santos 1995, Donald et al. 1997,
Telleria et al. 2001). As different species react differently to habitat type, it is reasonable to con-
sider these species separately. Moreover, grouping a large number of species into functioning guilds
is the most useful way to study many phenomena (Wilson 1999). In the present study the authors
used trophic guild to check the effect of different habitats on wintering bird communities. Consid-
eration of the trophic structure of bird communities provides information on community structure
and organization that simple analyses of species richness, diversity, and density do not (Blake
1983). The trophic structure reflects, at least in part, the importance of various food resources and
the variation in trophic structure among habitats may therefore reflect variation in the availability of
food resources in different habitats.

The southern part of the Niepołomicz Forest is an example of managed mixed oak-pine forest in
Poland and it is one of the best studied forest complexes. Kania (1968) was the first to study bird as-
semblages in the SE part of the Forest, while subsequently extensive studies were made by Glowaciński
studies concerning some species were carried out (Glowaciński 1973, Wasilewski 1990, Czuch-
nowski 1992) but wintering bird communities have been studied only partially there (Kania 1968,
concerning species composition and their density in winter is necessary for a better understanding
of the functioning of the Niepołomicz Forest ecosystem (Glowaciński & Weiner 1975, 1983).

The main aim of this work is to characterise the composition of the wintering bird communities
in three different habitats of the Forest as well as between seasons. The authors also compared di-
versity estimators for these habitats and examined the effects of habitats and seasons on trophic
guilds.

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II. STUDY AREA AND FIELD METHODS

The Niepołomicz Forest (50°01’-50°08’ N and 20°13’-20°27’ E) is situated in the western part
of the Kotlina Sandomierska dale, about 20 km east of Kraków (southern Poland). The Niepołomicz
Forest area (108.5 km²) is divided into two parts: northern (28 km²) dominated by oak-hornbean
forest Tilio-Carpinetum, and southern (about 80 km²) dominated by coniferous trees. The study was
carried out in the southern part where the mixed oak-pine forest Pino-Quercetum predominates
Quercus sp., spruces Picea abies and birches Betula sp. The climate of the studied area is transi-
tional from oceanic to continental (Suliński 1981). Mean annual temperature is 8.2°C (in July:
18.5°C, in January: -3.0°C), annual rainfall is 645 mm, and mean thickness of snow cover 10 cm
(Wiszniecki 1973). The snow cover lies on average from the third week of December to the end
of the second week of March. For a more detailed description of the study area see also GLOWACIŃSKI (1975) and GRODZIŃSKI et al. (1984).

The wintering bird communities were studied during three winters: 1996/1997, 1998/1999, and 2000/2001. A 9.5 km long line transect was established. Birds were counted within a 100 m belt (50 m on each side of walking observer). Mean speed of walking was about 2 km/h and each count began at about 30-60 minutes after sunrise. 8, 6, and 6 controls were made in consecutive winters respectively from 1st December and 27th February. All counts were made during good weather with no heavy falls or strong wind. Difficulty in identification of Treecreepers *Certhia familiaris* and *C. brachydactyla* resulted in their being treated as *Certhia sp.*

The transect was divided into three sectors based on different habitats.

1. Mature stands. In this habitat the transect was 6.6 km long (66 ha) and was conducted in the forest interior. Within this habitat old and tall forest *Pino-Quercetum* predominated but in some parts small patches of younger stands occurred. Pines dominated over oaks and spruces. Age of trees was about 60-80 years.

2. Young stands. The transect length in this habitat was 1.25 km (12.5 ha). It was characterized by a mosaic of young coniferous trees aged from 20-40 years, with a few young oaks and alders *Alnus glutinosa*.

3. Forest edge. The transect length in this habitat was 1.65 km (16.5 ha). Pines dominated over oaks, in wetter parts alders also occurred. There was no wide and transitional ecotone such as young trees and shrubs, but mature forest bordered close with open area (meadows, pastures, and arable land).

**III. DATA ANALYSIS AND STATISTICS**

Birds were divided into two trophic guilds: plant-eaters and invertebrate-eaters according to the work of KUJAWA (1995) (Table I-III). Because of different feeding biology and their small noted number within transect, birds of prey were excluded from this classification. Pheasant *Phasianus colchicus* was also excluded from this classification as a non-native species and because of its too large body size. The division of species cannot be regarded as absolute as some species may change their diet during certain periods (KUJAWA 1995). To calculate the biomass of birds (mean body weight) BUSSE (1990) work was used. Because the transect length differed in different habitats, all data were standarized to density of individuals per 10 ha and density of biomass of birds (gram per 10 ha) before the analysis. The following indices of bird species diversity were calculated according to the work of MOUILLOT & LEPRETRE (1999): Shannon diversity index (*H’*), Simpson dominance index (*C’*), and equitability index (*J’*). To compare winter bird communities in the Niepolomice Forest with communities from other studies the Sørensen similarity index (*QS*) was used according the equation: 

\[
QS = \frac{2c}{a+b} \times 100
\]

where *a* is the number of species in the first community, *b* is the number of species in the second community, and *c* is number of species common to both communities. Also calculated was the Renkonen similarity index (*Re*) which is a simple sum of common percentage of dominance of the species to both compared communities. It was assumed that dominating species are those of at least a 5% fraction of the community.

Two-way ANOVA was used to test the effects of year and habitat type on total bird density. Log-transformed data was used to homogenize the variation and to normalize data distribution. Three-way ANOVA was used to check the food type effect, year, and habitat on density and biomass of birds from two guilds. The analysis was conducted separately for density and biomass. In the case of density log-transformed data was used. Two covariates were included in ANOVA: the temperature and data of census. “A posteriori” comparisons of means were also made using Tukey’s test for unequal samples.
IV. RESULTS

During the three studied winters 5,764 individuals within the transect belonging to 33 species were noted (Tables I-III). Moreover, a further 19 species were noted in the Niepolomice Forest and adjacent areas: Mallard Anas platyrhynchos, Kestrel Falco tinnunculus, Grey Partridge Perdix perdix, Collared Dove Streptopelia decaocto, Ural Owl Strix uralensis, Meadow Pipit Anthus pratensis, Bohemian Waxwing Bombycilla garrulus, Great Grey Shrike Lanius excubitor, Jackdaw Corvus frugilegus, Hooded Crow C. corone cornix, Raven C. corax, House Sparrow Passer domesticus, Tree Sparrow P. montanus, Greenfinch Carduelis chloris, Goldfinch C. carduelis, Linnet C. cannabina, Hawfinch Coccothraustes coccothraustes, and Corn Bunting Miliaria calandra.

Table I

Species composition and density of birds wintering in mature stands. Means and standard deviations (SD) are given for each winter. Trophic guilds: I – invertebrate-eaters, P – plant-eaters. Densities of the dominating species (proportion N 5%) are bolded.
Winter bird communities from southern Poland

The density of birds varied among winters (ANOVA $F_{2,49} = 5.435, p < 0.008$). The highest density was noted during the winter 1996/1997 and the lowest during the winter 1998/1999 ($p < 0.02$). A significant effect of covariates on bird density ($F_{2,49} = 3.861, p < 0.03$) was noted but this explained only a 14% of variance in density. Bird density decreased as winter continued (beta = - 0.36, $t_{49} = -2.58, p <0.02$) but no significant effect of temperature on bird density was found.

Species composition and bird density in different habitats

It was found that habitats were inhabited by different numbers of species. The largest number of species – 27, was noted in the mature stands (Table I) and the lowest – 18 – in the young stands (Table II). Only three species were dominants in three habitats simultaneously: Great Spotted Woodpecker *Dendrocopos major*, Willow Tit *Parus montanus*, and Blue Tit *Parus caeruleus*.

In the mature forest, additional dominating species were Mistle Thrush *Turdus viscivorus*, Golderest *Regulus regulus*, Coal Tit *Parus ater*, and also in some years Great Tit *Parus major* and Siskin *Carduelis spinus* (Table I). The last species occurred in small wet parts where alders were present. The observation of Fieldfare *Turdus pilaris* and Yellowhammer *Emberiza citrinella* were probably accidental because the forest interior is not their typical winter habitat. However, small flocks of Fieldfares were noted during late autumn feeding on mistletoe berries, even in the centre of the Niepo³omice forest.

Only 18 species were noted in the young stands (Table II). The dominating species were similar to those in the mature forest, with the exception of Mistle Thrush and Siskin, which were seen there only occasionally. Moreover, Long-tailed Tit *Aegithalos caudatus* and Nuthatch *Sitta europaea* were dominants during some winters. Observation of the Reed Bunting *Emberiza schoeniclus* (on 30th December 1996) was noteworthy in this habitat.

### Table II

| Species composition and density of birds wintering in young stands. For explanations see Table I |
|---|---|---|---|---|
| | mean SD | % | mean SD | % | mean SD | % | mean SD | % |
| I Dryocopus martius (LINNAEUS, 1758) | – – – | 0.3 0.7 | 1.2 – – – | 0.1 0.3 | | | | |
| I Dendrocopos major (LINNAEUS, 1758) | 1.7 0.9 | 6.2 | 2.5 0.9 | 11.4 | 1.6 1.0 | 6.3 | 1.9 7.6 | |
| I Troglodytes troglodytes (LINNAEUS, 1758) | 0.3 0.6 | 1.1 | – – – | 0.3 0.4 | 1.1 | 0.2 0.8 | | |
| P Turdus viscivorus LINNAEUS, 1758 | 0.1 0.3 | 0.4 | – – – | – – – | – 0.1 | 0.2 | | |
| I Regulus regulus (LINNAEUS, 1758) | 4.1 8.7 | 14.9 | 9.2 5.2 | 41.6 | 11.2 7.5 | 44.2 | 7.8 30.7 | |
| I Aegithalos caudatus (LINNAEUS, 1758) | – – – | – – – | – – – | 2.4 4.2 | 9.5 | 0.7 2.9 | | |
| I Parus palustris LINNAEUS, 1758 | – – – | 0.3 0.7 | 1.2 | 0.7 1.6 | 2.6 | 0.3 1.1 | | |
| I Parus montanus CONRAD VON BALDENSTEIN, 1827 | 7.0 5.7 | 25.5 | 3.5 2.1 | 15.7 | 1.1 1.2 | 4.2 | 4.2 16.5 | |
| I Parus ater LINNAEUS, 1758 | 2.6 2.4 | 9.5 | 1.6 2.8 | 7.2 | 1.2 2.2 | 4.7 | 1.9 7.4 | |
| I Parus caeruleus LINNAEUS, 1758 | 8.8 6.2 | 32.0 | 2.3 4.8 | 10.2 | 4.3 3.3 | 16.8 | 5.5 21.7 | |
| I Parus major LINNAEUS, 1758 | – – – | 0.8 1.3 | 3.6 | 2.1 3.4 | 8.4 | 0.9 3.5 | | |
| I Sitta europaea LINNAEUS, 1758 | 1.0 1.5 | 3.6 | 1.3 1.2 | 6.0 | – – – | – – – | 0.8 3.2 | |
| I Certhia sp. | 0.6 0.7 | 2.2 | – – – | 0.4 0.4 | 1.6 | 0.4 1.4 | | |
| P Emberiza citrinella LINNAEUS, 1758 | 0.1 0.3 | 0.4 | – – – | – – – | – 0.1 | 0.2 | | |
| P Emberiza schoeniclus (LINNAEUS, 1758) | 0.1 0.3 | 0.4 | – – – | – – – | – 0.1 | 0.2 | | |
| P Carduelis spinus (LINNAEUS, 1758) | 1.0 1.5 | 3.6 | – – – | – – – | – 0.4 | 1.6 | | |
| P Pyrrhula pyrrhula (LINNAEUS, 1758) | – – – | 0.4 1.0 | 1.8 | 0.1 0.3 | 0.5 | 0.2 0.6 | | |
| P Garrulus glandarius (LINNAEUS, 1758) | 0.1 0.3 | 0.4 | – – – | – – – | – <0.1 | 0.2 | | |
| Total | 27.5 | 100.0 | 22.1 | 100.0 | 25.3 | 100.0 | 25.2 | 100.0 |
At the forest edge 24 species were noted, 10 of them being dominants (Table III). The presence of field and meadows were responsible for the occurrence of species such as Pheasant, Fieldfare, Magpie *Pica pica*, and Reed Bunting. Despite this fact forest species prevailed.

### Table III

<table>
<thead>
<tr>
<th>Species composition and density of birds wintering at forest edge. For explanations see Table I</th>
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<tr>
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<tr>
<td><strong>– Buteo buteo</strong> (LINNAEUS, 1758)</td>
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<tr>
<td><strong>– Phasianus colchicus</strong> (LINNAEUS, 1758)</td>
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<tr>
<td><strong>I Picus viridis</strong> (LINNAEUS, 1758)</td>
</tr>
<tr>
<td><strong>I Dryocopus martius</strong> (LINNAEUS, 1758)</td>
</tr>
<tr>
<td><strong>I Dendrocopos major</strong> (LINNAEUS, 1758)</td>
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<tr>
<td><strong>P Erithacus rubecula</strong> (LINNAEUS, 1758)</td>
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<td><strong>P Turdus merula</strong> (LINNAEUS, 1758)</td>
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<td><strong>P Turdus pilaris</strong> (LINNAEUS, 1758)</td>
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<td><strong>P Turdus viscivorus</strong> (LINNAEUS, 1758)</td>
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<td><strong>I Regulus regulus</strong> (LINNAEUS, 1758)</td>
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<td><strong>I Parus caeruleus</strong> (LINNAEUS, 1758)</td>
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<tr>
<td><strong>I Sitta europaea</strong> (LINNAEUS, 1758)</td>
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<tr>
<td><strong>I Certhia sp.</strong></td>
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<tr>
<td><strong>P Emberiza citrinella</strong> (LINNAEUS, 1758)</td>
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<tr>
<td><strong>P Emberiza schoeniclus</strong> (LINNAEUS, 1758)</td>
</tr>
<tr>
<td><strong>P Carduelis spinus</strong> (LINNAEUS, 1758)</td>
</tr>
<tr>
<td><strong>P Pyrrhula pyrrhula</strong> (LINNAEUS, 1758)</td>
</tr>
<tr>
<td><strong>P Garrulus glandarius</strong> (LINNAEUS, 1758)</td>
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<tr>
<td><strong>P Pica pica</strong> (LINNAEUS, 1758)</td>
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<tr>
<td><strong>Total</strong></td>
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</table>

Statistically significant differences in bird density were found among habitats (ANOVA $F_{2,49} = 9.54; \ p <0.003$). “A posteriori” comparisons showed that the mean densities at forest edge in 1998/1999 and 2000/2001 were significantly lower than in mature forest in 1996/1997 (p <0.002 and p <0.02, respectively). Indicators of biodiversity had the highest value at the forest edge ($H' = 3.67, J' = 0.80, C = 0.89$) and in mature stands ($H' = 3.35, J' = 0.71, C = 0.85$) and the lowest in the young stands ($H' = 2.91, J' = 0.70, C = 0.82$).

### Comparisons of trophic guilds

The total density of invertebrate-eaters was statistically higher than plant-eaters (ANOVA $F_{1,100} = 219.922, \ p <0.001$), but the total biomass of these two guilds did not differ significantly.

It was found that habitat had a significant effect on difference in density between the guilds (ANOVA $F_{2,100} = 34.261, \ p <0.001$) as well as differences in biomass between the guilds (ANOVA...
Density of plant-eaters at the forest edge was higher than in young stands, but it did not however differ from mature stands (Fig. 1A). The density of plant-eaters in young stands was the lowest of the two guilds. Densities of invertebrate-eaters were generally significantly higher than those of plant-eaters in each habitat, with the exception of forest edge, where densities of the guilds were similar (Fig. 1A). Densities of invertebrate-eaters in mature and young stands did not differ significantly, but were higher than at the forest edge (Fig. 1A).

It was found that the biomass of plant-eaters in mature stands was significantly higher than in young ones, but did not differ from forest edge, nor did it differ from invertebrate-eater biomass in each habitat (Fig. 1B). Biomass of plant-eaters in young stand was statistically the lowest and only invertebrate-eater biomass at forest edge was similar (Fig. 1B). The invertebrate-eater biomass was lower than plant-eater biomass at the forest edge (Fig. 1B).

**Fig. 1.** Comparison of density (A) and biomass (B) of plant-eaters and invertebrate-eaters in consecutive habitats. Arrows indicate statistically significant differences based on Tukey tests. Explanation: * – p<0.5, ** – p<0.01, *** – p<0.001.
No significant differences between density of the guilds in different winter seasons were found—for each year the total invertebrate-eater density noted in the transect was higher than those of plant-eaters (Fig. 2A). Instead, a significant effect of winter on the difference in total biomas were found between the guilds (ANOVA $F_{2,100} = 4.085$, p <0.02). The plant-eater biomass was similar to that of invertebrate-eaters, except during winter 1998/1999, when the plant-eater biomass was lower than for other winters and lower than invertebrate-eater biomass during winter 1996/1997 (Fig. 2B).

Fig. 2. Comparison of density (A) and biomass (B) of plant-eaters and invertebrate-eaters in consecutive winters. In the cause of density arrows were not shown because no interaction was found (all differences among trophic guilds were significant (p<0.001) but none within the guilds). Explanation see: Fig. 1.
V. DISCUSSION

Species composition

Bird communities in mature stands in the Niepolomice Forest were very similar to other communities of wintering birds in forests of Poland according to the Sørensen index (Table IV). The Renkonen index shows that dominating species were also similar, but variation in value of this index \( (Re: 26.7-78.2) \) was higher than in the case of the Sørensen one \( (QS: 50.0-86.3) \). The values of the two indices are significantly correlated \( (r = 0.333, p = 0.03) \). According to these indices winter bird communities in deciduous and beech forests are less similar to bird communities described in the present study. The most similar to communities in the Niepolomice Forest were bird communities in coniferous forests near Przemyśl (SE Poland – Table IV; HORDOWSKI 1996 a). The most characteristic of the mentioned forests was the presence of Middle Spotted Woodpecker \( Dendrocopos medius \) in almost all the sample plots. The similarity was also great with coniferous forests near Legnica and Turew (TOMIAŁOJC 1974, KUJAWA 1995). Wintering bird composition and dominance in deciduous and beech forests generally were less similar to the bird communities in mature stands in the Niepolomice Forest (Table IV). Hawfinch \( Coccothraustes coccothraustes \) was the most characteristic species in these forests (TOMIAŁOJC 1974, HORDOWSKI 1996 a).

### Table IV

Comparison of the Sørensen \( (QS) \) and Renkonen \( (Re) \) indices among winter bird communities in the Niepolomice Forest and winter bird communities studied by other authors in various forests in Poland. Explanations: A, B, C – the mature stands of coniferous forest, the young stands and the forest edge in this study, respectively, D – coniferous forest near Legnica (TOMIAŁOJC 1974), E – coniferous forest near Turew (KUJAWA 1995), F, G, H, I – coniferous forests near Przemyśl (HORDOWSKI 1996 a), J – coniferous (spruce) forest in Śleża Mt. (CEMPULIK 1979), K – deciduous forest near Legnica (TOMIAŁOJC 1974), L – deciduous forest in the Niepolomice Forest (GŁOWACISKI 1975), M, N – deciduous forests near Przemyśl (HORDOWSKI 1996 a), O – beech forest in Śleża Mt. (CEMPULIK 1979), P – beech forest near Przemyśl (HORDOWSKI 1996 a), R – beech forest in Beskid Sądecki Mts (authors’ unpublished data), S – edge of forest near Turew (KUJAWA 1995). # – lack of appropriate data. Means were used during calculation the Renkonen index for studies carried on more than one winter season.

|       | A   | B   | C   | D   | E   | F   | G   | H   | I   | J   | K   | L   | M   | N   | O   | P   | R   | S   |
|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| **QS** |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
|       | 75.6| 74.5| 75.6| 81.6| 78.4| 72.3| 58.5| 77.3| 54.1| 69.6| 69.4| 73.9| 61.9| 57.9| 68.2| 55.0| 86.3|     |
|       | 81.0| 72.2| 75.0| 76.2| 78.9| 68.8| 85.7| 64.3| 54.1| 65.0| 64.9| 66.7| 69.0| 74.3| 58.1| 76.2|     |     |
|       | 66.7| 73.9| 62.5| 72.7| 63.2| 73.2| 52.9| 30.0| 65.2| 60.5| 61.5| 62.9| 63.4| 54.1| 64.6| 66.7|     |     |
| **Re** |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
|       | 78.3| 58.9| 75.2| #   | 78.2| 54.1| 65.1| 50.1| 65.8| 32.9| 38.3| 44.9| 32.5| 29.2| 29.8| 47.5| #   |     |     |
|       | 46.3| 72.1| #   | 74.1| 50.9| 68.2| 56.7| 63.6| 40.9| 39.7| 42.9| 26.7| 24.2| 38.6| 44.9| #   |     |     |     |
|       | 47.5| #   | 58.5| 39.6| 45.3| 56.2| 31.9| 40.0| 50.0| 57.1| 43.5| 38.6| 43.7| 46.2| #   |     |     |     |     |

In any case the value of the Sørensen index was not lower than 50%. As TOMIAŁOJC (1970) argued, the index value of 60% between compared communities indicates a high degree of similarity. In the case of the young stands and the forest edge the Sørensen index also showed high values in comparison with other bird communities of mature forests (Table IV). It suggests that winter bird communities are generally less variable geographically and among habitats than breeding bird communities as far as species composition is concerned.
The most characteristic feature of bird community in the Niepolomice Forest was the domination of Mistle Thrush in the mature stands and at the forest edge. A large number of mistletoe clumps with berries in trees is the main factor affecting density of this species in winter (WALASZ 2000, SKÓRKA & WÓJCик in prep.). Surprisingly, the dominating species was also the Willow Tit but simultaneously Marsh Tit Parus palustris occurred in small numbers. It is interesting because most authors believe that the densities of these tits in winter are similar. However, in the case of Willow Tit individuals from northern areas may invade during some winters (WALASZ 2000) and therefore density of this species may be higher. This seems to be supported by the present authors’ observations, because they often saw flocks of Willow Tit over 15 individuals. The Willow Tit generally live during winter in small flocks consisted of few pairs of adult and young birds (MATTHYSEN 1990) and the mean size of these flocks vary from 2.0 to 5.9 individuals in different geographical regions (HORDOWSKI 1996 b).

Interesting also was occurrence of Blackbirds Turdus merula in the forest. All noted individuals were males, confirming TOMIAŁOJCici’s (1990) and WALASZ’s (2000) claims.

Forest management, biodiversity, and trophic guilds

It was found that the number of birds decreased through the winter. This is probably an effect of mortality, sometimes high during winter (GRABER & GRABER 1979, HOGSTAD 1982, SPENCER 1982). However, winter progression and temperature explain only a small part of the variance in density and other factors may be responsible for density fluctuations. For example, the behaviour of individual birds and/or flock size may vary with temperature, the time of day, an the presence of other species (GRUBB 1975, ALATAO 1982, PETIT 1989, VILA et al. 1996, WINECKI 2000), which may cause changes in real density or detectability of birds. However, including these factors in this study was not possible. Bird density varied also among winters as well as among habitats. It seems that the variation in plant-eater density is the most probable factor responsible for differences in the total density of birds among seasons. The abundance of plant-eaters depends mostly on seeds and fruits availability, whose number varies considerably for different years (SNOW & SNOW 1988). In the present study, the lowest bird density was during winter 1998/1999 when a considerably lower plant-eater density was noted.

The results indicate that forest habitats have important effect on bird density, but this effect also varies among groups of species. The highest value of biodiversity indices was found at the forest edge. As opposed to KUJAWA (1995), the present authors did not find significant differences in bird density between mature stands and the forest edge. However, guild analysis showed that invertebrate-eater density at the forest edge was statistically lower than in other habitats. This effect was also noted by KUJAWA (1995). At the forest edge, temperature variation and wind velocity are higher (GEHLHAUSEN et al. 2000) and as most invertebrate-eaters are foliage gleaning species, these variable conditions may disturb their foraging. Moreover, the predation may be higher at the forest edge (SUAREZ et al. 1997). However, the highest plant-eater density and biomass were observed at the forest edge (Fig. 1). This may be a result of the presence of some species of shrubs with fruits on adjacent meadows and fields. The higher plant-eater density and biomass at the forest edge is characteristic of this habitat (KUJAWA 1995).

The biodiversity indices and species number were also high in the mature stands. The highest invertebrate-eater density was noted there. This finding is typical for mature stands. The upper parts of tall trees are the richest source of food for these species (YAHNER 1986, KRAMS & THIEDE 2000), moreover canopies of coniferous trees provide a more stable and higher temperature (PETIT 1989, JENNI 1991). It is also interesting that the plant-eater density and biomass was similar to that noted at the forest edge. Despite plant-eater density in mature stands was considerably lower than invertebrate-eater density, while biomass of these guilds was similar. It suggests that mature stands may be an important habitat for wintering plant-eating birds.

The lowest values of biodiversity indices and species number were noted in young stands. However, this was an effect of the small number of plant-eaters in this habitat. It may be an effect of
small number of fruiting shrubs, especially mistletoe. In mature stands most plant-eating birds were seen foraging on mistletoe clumps. Surprisingly, the density of invertebrate-eaters did not differ significantly from that of mature stands. Moreover, young stands are less structurally diversified than mature stands. It is known that habitats with more layers (e.g. mature stands) are inhabited by a larger number of species than structurally simplified habitats (MacArthur et al. 1966, Karr & Roth 1971, Glowacki 1975, 1981).

Density, biomass and food resources

The present results suggest that variation in the density of the communities is higher than the variation in biomass. If we focus on ecosystem functioning it may be more fruitful to consider it by using the biomass, as this may reflect total energy flowing through the ecosystem more properly than using only density of individuals (Weiner & Glowacki 1975, Glowacki & Weiner 1977, 1983). If variation in the biomass of birds is a reflection of variation in food resources we may suppose that variation in density may be an artefact in many situations as a result of different body size of species. In some years different species are able to more or less monopolize resources and to compete more or less successfully that which causes variation in density, but not in biomass. It suggests that biomass is a better predictor of variation of food resources than density of individuals or guilds.

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