DOI 10.15407/zoo2025.06.589 UDC 598.2:574.4:502.74(477.42)

COMPARATIVE ANALYSIS OF THE AVIFAUNA OF RURAL SETTLEMENTS IN THE PODILSKE POBUZHZHIA REGION

V. V. Novak^{1, *}, A. O. Markova²

- ¹ Municipal Institution of Higher Education "Bar Humanities and Pedagogical College named after Mykhailo Hrushevsky", maidan Hrushevskoho, 1, Bar, Vinnytsia Region, 23000 Ukraine
- ² Schmalhausen Institute of Zoology NAS of Ukraine, vul. B. Khmelnytskogo, 15, Kyiv, 01054 Ukraine
- * Corresponding author

E-mail: vovabiolog@gmail.com

V. V. Novak (https://orcid.org/0000-0002-5291-9364)

A. O. Markova (https://orcid.org/0000-0002-5549-3848)

urn:lsid:zoobank.org:pub:F6E0D0B6-29A6-4184-9D1E-6018F7B9AA23

Comparative Analysis of the Avifauna of Rural Settlements in the Podilske Pobuzhzhia **Region. Novak, V. V., Markova, A. O.** — This article presents an analysis of the results of bird population studies conducted in rural settlements (RS) of the Khmelnytskyi District, Khmelnytskyi region, and the Zhmerynka and Tulchyn Districts of Vinnytsia region during 2014–2016. Research at each monitoring site was carried out in three categories of villages, which differed in population size, degree of urbanization, and other parameters. Over the course of these studies, a total of 174 bird species were recorded on monitoring sites of the Podilske Pobuzhzhia region. Of these, 145 species were noted in Category I RS, 162 species in Category II RS, and 158 species in Category III RS. The highest number of limnophilous species was recorded in Category I RS, campophilous and sclerophilous species were most prevalent in Category II RS, while dendrophilous species dominated in Category III RS. The highest similarity between the ornithofauna of rural settlements and some biotopes was observed in the winter period, while the lowest similarity occurred during the breeding season. Among typical biotopes outside rural settlements, the greatest resemblance to the RS ornithofauna was noted in the Southern Bug River valley in almost all seasons, as well as in pond habitats during the spring migration and breeding periods. The avifauna of RS during the spring migration and breeding season showed a high degree of similarity. During autumn migration, RS of Categories II and III were more similar to each other, while in winter,

[©] Publisher Publishing House "Akademperiodyka" of the NAS of Ukraine, 2025. The article is published under an open access license CC BY-NC-ND (https://creativecommons.org/licenses/by-nc-nd/4.0/)

RS of Categories I and II were more alike than either was to Category III. Bird density was highest in Category III RS in all seasons except winter, where it was lowest in Category I RS. However, in winter, this trend reversed, with Category I RS showing the highest bird density. According to the Shannon diversity index, avifaunal diversity was highest in Category III RS in all seasons except winter, and lowest in Category I RS. In winter, however, the highest diversity was recorded in Category I RS.

Key words: birds, rural settlements, breeding season, migration, wintering, Podilske Pobuzhzhia, Ukraine.

Introduction

Since its inclusion in the Polish–Lithuanian Commonwealth and subsequently the Russian Empire, Podillia has been one of the most densely populated regions. Thanks to the efforts of local peasants, the region became a leader in horticulture, poultry farming and the cultivation of hemp and cereal crops (Yesiunin, 2012). The characteristics of rural settlements in Podillia, such as building architecture, location (near bodies of water, on hilly terrain or within forested areas), agricultural practices (specific crops, cultivation techniques and domestic animals) and landscaping (large areas of orchards and parks), have created favourable conditions for various bird species to inhabit the area.

Today, distinct bird habitats exist within rural settlements, including: individual housing; administrative buildings (schools, kindergartens, cultural centers, etc.); utility infrastructure (tractor and vehicle yards, livestock and poultry farms); parks and squares; cemeteries; wetlands (ponds, rivers, marshy areas); kitchen gardens; and vacant lots (Novak, 2021 a). Each of these habitats hosts a characteristic assemblage of bird species.

Taking into account the socio-economic and demographic indicators of the RS, we were able to classify them into three categories. Each category is characterized by a specific species composition and quantitative structure of the bird population. The aim of this publication is to determine how similar or different bird communities are across villages of these three categories during various periods of the annual avian cycle. For clarity, the bird population indicators in rural settlements were compared with those from bird habitats outside the settlements: the floodplains of the Southern Bug River, various ponds, deciduous forests, and agrocenoses.

Material and Methods

The research was conducted in rural settlements of the Khmelnytskyi District, Khmelnytskyi Region, and the Zhmerynka and Tulchyn Districts of Vinnytsia Region. The study of the qualitative and quantitative composition of the ornithofauna in these rural settlements was carried out in this region from 2014 to 2016.

To determine the species composition and abundance of birds in different types of rural settlements, four monitoring sites were established in 2014, with distances between them ranging from 50 to 70 km. These sites included: "Chornyi Ostriv" (Khmelnytskyi District: villages of Maryanivka, Zakharivtsi, Vovcha Hora, Lanok,



Fig. 1. Monitoring plots within the Podilske Pobuzhzhya region

Lyapyntsi), "Medzhybizh" (Khmelnytskyi District: villages of Trebukhivtsi, Holoskiv, Stavnytsia, Rusanivtsi, Volosivtsi), "Bar" (Zhmerynka District: villages of Balky, Luka Barska, Vasyutyntsi, Chemerysy Barski), "Shpykiv" (Tulchyn District: villages of Rakhnivtsi Lisovi, Levkivtsi, Vynokurnia) (Fig. 1). In each of the 17 villages included in these monitoring sites, census routes were established.

The general criteria by which we classified the rural settlements into three categories were as follows:

Category I Rural Settlements: These villages have a permanent population ranging from 1,000 to 3,500 residents. Most buildings are single-story, with relatively dense development for a rural area and very few uninhabited houses or households. A small number of two-story residential and administrative buildings are present, along with occasional three- or four-story structures. Small parks, public squares, or orchards are typically located near educational institutions. Streets generally have a low level of greenery, and the area of vegetable gardens between streets is minimal.

Category II Rural Settlements: These villages typically have a permanent population of 500 to 1,000 residents. Most buildings are single-story, but there are several two-story public buildings such as schools, cultural centers, and office spaces for agricultural enterprises. Each street contains a few uninhabited houses, around which shrubs and weeds tend to overgrow. Some of these properties are purchased by city dwellers as "dachas" (country homes), where they plant dwarf and semi-dwarf fruit trees, rows of thuja, raspberry, gooseberry, currant, and lawn grass. These villages may have small parks, and the streets generally have a medium level of greenery, with many old fruit and non-fruit trees. Between streets, there are often large areas of vegetable garden plots.

Category III Rural Settlements (formerly referred to as "non-promising" during the Soviet era): These villages have a permanent population of up to 500 people, most commonly between 150 and 350. Nearly all buildings are single-story, with a relatively high number of uninhabited houses — some of which are unfit for living — surrounded by overgrown trees, shrubs, and tall herbaceous vegetation. There is an abundance of old fruit and non-fruit trees, as well as shrubs, and a significant portion of the household gardens is no longer cultivated, becoming overgrown with weeds. Fences are often absent between properties; instead, boundaries are marked by stacked cut tree branches or hedgerows. Streets exhibit a high degree of greenery. A defining feature of this category is the high percentage of land occupied by vegetable gardens — up to 42% of the total village area, which exceeds that of Category I RS (20%) and Category II RS (30%).

All types of rural settlements contain wetland habitats, including ponds, rivers, marshy floodplains, and drainage canals. Surrounding these water bodies are areas of meadow-marsh vegetation, willow thickets, and patches or rows of black alder, white willow, or black poplar.

To conduct the research within the monitoring sites, 21 survey routes with a total length of 40 km were established. The length of individual routes ranged from 1.5 to 3 km, depending on the type of village. Bird counts were carried out using the line transect method, with subsequent recalculation of abundance per $1 \, \mathrm{km^2}$ (Ravkin, 1967). The fixed width of the survey belts varied depending on the size of the bird species and was set at 0–50, 0–100, 0–300, and 0–1000 meters.

Breeding evidence was assessed according to the criteria recommended by the European Bird Census Council (EBCC) (Hagemeijer & Blair, 1997; Keller et al., 2020).

Species names of birds are given according to "Clements checklist of birds of the world" (Clements et. al., 2023).

The classification of the ornithofauna of rural settlements by ecological groups follows the system proposed by V. P. Belik (1992).

Bird population density (individuals/km²) for each species was calculated using a commonly accepted formula:

$$F (density) = (N_i \times K_i) / L_i$$

where N_i is the number of individuals of a given species recorded within the respective survey belt (with widths of 0–50 m, 0–100 m, 0–300 m, and 0–1000 m); for the smallest birds (House Sparrow, European Greenfinch, Common Chiffchaff and others) a survey belt of 0–50 m was used, for small birds (European Starling, Great Spotted Woodpecker, Fieldfare and others) — 0–100 m, for medium-sized birds (Common Wood-Pigeon, Eurasian Jay, Rook and others) — 0–300 m, and for large birds (Common Raven, Common Buzzard, White Stork and others) — 0–1000 m;

 K_i are coefficients (20, 10, 3.3, and 1 respectively) used to scale the survey belt to a standardized area of 1 km²;

L is the length of the transect (in kilometers).

Taxonomic diversity (Shannon index) was calculated using the formula (MacArthur, 1955): N

 $H = \sum_{i=1}^{N} p_{i} \log_{2} p_{i}$

where p_i is the proportion of taxa of the *i*-th rank, and N is the number of ranks (e. g., species, genus, ... order, etc.).

The analysis was performed using the statistical software R 4.2.2 (RStudio 2023.06.1 Build 524) and PAST 4.17. Species richness was calculated based on the principle that if a bird species was recorded even once over the three-year study period, it was included in the species list.

To analyze the similarity in bird species composition among the three categories of rural settlements and four typical biotopes outside rural settlements (the Southern Bug River valley, ponds outside settlements, deciduous forest, and fields), the Sorensen-Czekanowski similarity index (also known as the Czekanowski-Dice-Sørensen index) was used and marked as "Dice index" (Czekanowski, 1932; Dice, 1945; Sørensen, 1948). Calculations and dendrogram construction were carried out using the software PAST 4.17. This index can be used for both qualitative and quantitative data (in this case, the formula is adapted, in our case, by using the arithmetic mean bird species density).

In R 4.2.2, the clustering quality was assessed using cophenetic correlation (Mantel test, "vegan" package) to evaluate the overall clustering tendency of the dataset. As a result, the average linkage method was used to build the clusters — its equivalent in the PAST software is UPGMA (W Mantel = 0.966, P = 0.001). Bootstrap analysis (N = 10,000) was applied to the clusters to estimate standard deviations and compute confidence intervals for statistical functionals. Clustering analysis was based on both species composition and bird species density data across the studied areas. The dendrograms constructed using density data closely resembled those based on species richness. To confirm the similarity in spatial distribution patterns based on both richness and density, cophenetic correlation and Baker's Gamma correlation coefficient were used. The optimal number of clusters was determined using the "res" function from the "NbClust" package. The validity of seasonal variation in species richness was tested using one-way ANOVA in PAST 4.17.

Results

During the study period from 2014 to 2016, a total of 174 bird species were recorded on monitoring sites of the Podilske Pobuzhzhia region, representing 69% of the region's overall avifauna (Matviichuk, 2015; Novak & Novak, 2015). Of these, 145 species were recorded in Category I RS, 162 in Category II RS, and 158 in Category III RS. The species density were calculated for 142 species (56% of the region's overall avifauna) that were recorded in the rural settlements (Table 1: https://doi.org/10.5281/ zenodo.17612277). For other species, for example, the Great White Pelican, Pelecanus onocrotalus (L., 1758), Rosy Starling, Pastor roseus (L., 1758), Arctic Warbler, Phylloscopus borealis (Blasius, 1858), the calculation of species density was not conducted, as they were recorded only occasionally. Rural settlements combine elements of natural and semi-natural environments, creating a stable habitat for various bird species throughout the year. During the breeding season, rural settlements provide favorable conditions for bird reproduction due to the presence of biotopic diversity, various nesting niches, and trophic resources. During seasonal migrations, rural settlements serve as transit stopovers and provide energy resources for migrating birds. Additionally, the mosaic structure of rural landscapes contributes to their better

conservation. In winter, rural settlements provide milder microclimatic conditions and a richer food base, which is critically important for the survival of many bird species. Thus, rural settlements play a critically important role in supporting avifauna under increasing anthropogenic pressure, climate change, and urbanization.

This distribution of species among the three categories of rural settlements is primarily influenced by the degree of urbanization (a higher degree of urbanization corresponds to a greater density of synanthropic species and sclerophiles), the nature and mosaic structure of bird habitats within the settlements (greater mosaicity leads to a higher number of bird species), and the level of greenery (a higher level of greenery leads to a greater number of dendrophilous species).

Overall, the most favorable combination of various factors — such as degree of urbanization, habitat diversity, food availability, level of disturbance, and the presence of suitable nesting and roosting sites — was characteristic of Category II rural settlements, making them the most supportive environments for avian diversity.

To compare the obtained data across all categories of rural settlements as well as with other habitat types in the region, a cluster analysis was conducted. Using the Czekanowski similarity index, seasonal species similarity was assessed among the three categories of rural settlements and compared with neighboring typical biotopes outside rural settlements.

Spring migration

Rural settlements play a key role in providing favorable conditions for birds during seasonal migrations, when access to resources and safe resting places is critically important. These areas are typically characterized by a mosaic of landscapes — a combination of agrocenoses, shelterbelts, meadows, water bodies, and homestead development. Such a structure creates diverse biotopes that offer a wide range of trophic resources for birds of various ecological groups. Moreover, compared to urbanized city territories, rural settlements have lower levels of noise, light, and overall anthropogenic pressure, which reduces the risks of stress and disruption of natural bird behavior. Another important aspect is that rural landscapes function as migratory corridors, connecting natural habitats that have been fragmented due to urbanization and intensive land use.

During the spring migration period, a total of 130 bird species were recorded across Category I–III rural settlements and the typical biotopes outside rural settlements. These data were best clustered using the UPGMA method, with a Mantel correlation coefficient of W = 0.971, P = 0.003 (Fig. 2).

During the spring migration period, the studied areas could be grouped into three distinct clusters based on species composition. The rural settlements (RS) of all three categories formed one cluster; the Southern Bug River valley, ponds outside settlements, and forests formed a second cluster; while the species composition of the fields was the most distinct in terms of species richness and formed a separate, third cluster. On the dendrogram (Fig. 2, a), the rural settlements are clearly grouped into a single cluster. Among them, Category I and Category III RS are more similar to each other (with 71 and 72 species, respectively) than either is to Category II (76 species). The species richness of wetland habitats — such as the Southern Bug River valley (75 species) and ponds outside settlements (65 species) — shows a

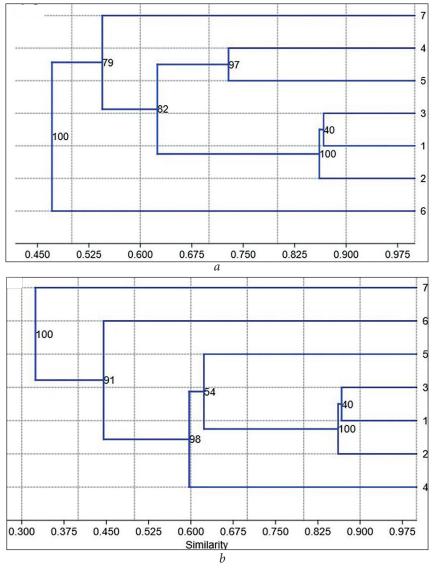


Fig. 2. Similarity of rural settlements and typical biotopes outside rural settlements in spring migration (Dice Similarity index): a — species composition; b — bird species density. 1 — Category I RS, 2 — Category II RS, 3 — Category III RS, 4 — Southern Bug River valley, 5 — Ponds outside rural settlements, 6 — Forest, 7 — Field

strong similarity in species composition. In contrast, the avifauna of the fields (45 species) and forests (54 species) differ the most. The similarity pattern based on species composition closely matches the pattern based on bird population density during the spring migration (Fig. 2, b). This is supported by a very high cophenetic correlation coefficient (R = 0.999) and Baker's Gamma correlation coefficient (R = 1). However, in terms of bird density, typical biotopes outside rural settlements are overall less similar to each other than the rural settlements are.

The similarity of ornithofauna among rural settlements of different categories during spring migration may be attributed to the short-term presence of migrating individuals, during which anthropogenic pressure is minimal. The

slight difference in bird density between the Southern Bug River valley and the ponds outside settlements (Fig. 2, b) may be due to the larger surface area of water in the ponds, which provides more extensive feeding and resting habitats. The typical biotopes outside rural settlements studied are characterized by relatively uniform environmental conditions, which result in a relatively consistent set of bird species. Since the overall area of typical biotopes outside rural settlements exceeds that of their corresponding bird habitats within RS — and birds tend to be more concentrated in RS — this leads to lower bird density in typical biotopes outside rural settlements and, consequently, to differences in cluster analysis. Each typical biotopes outside rural settlements supports a distinct species composition specific to that environment. In contrast, the ornithofauna of RS incorporates species typical of various biotopes outside rural settlements, which results in higher overall species richness in RS. The higher bird density observed in RS compared to typical biotopes outside rural settlements may be due to the greater abundance of synanthropic species and the presence of species from a broader range of ecological groups.

Breeding season

During the breeding season, a total of **131 bird species** were recorded across Category I–III rural settlements and the typical biotopes outside rural settlements. The data were clustered using the **UPGMA method**, resulting in a cophenetic correlation coefficient of $\mathbf{W} = \mathbf{0.752}$, P = 0.001 (Fig. 3).

On the dendrogram based on species richness (Fig. 3, a), a clear cluster separation is not easily distinguishable; however, two main clusters can be identified. The first includes rural settlements of Categories I-III and the Southern Bug River valley and ponds, while the second consists of deciduous forests and agrocenoses. The bird species composition of Category I and Category III RS is more similar to each other (99 and 101 species, respectively) than to Category II RS (102 species). The Southern Bug River valley showed the closest similarity to the rural settlements in terms of species richness, with 78 species recorded. The ponds outside settlements also hosted 78 species, but only 59% of species were shared between these two wetland habitats, indicating distinct species assemblages. Fields (25 species) and deciduous forests (47 species) clearly stand apart and are the most dissimilar in terms of species composition. According to the clustering results, both species composition and bird population density during the breeding season show high similarity (Fig. 3, b), supported by a cophenetic correlation coefficient of R = 0.999 and Baker's Gamma correlation of R = 1. However, the overall degree of similarity is somewhat lower than during spring migration. Bird density in the Southern Bug River valley and ponds differs from their respective species richness values. Ponds are characterized by larger areas of specific nesting habitats and a richer food base, which likely accounts for their differentiation from the river valley in the clustering analysis.

The ecological uniformity of typical biotopes outside rural settlements during the breeding period results in species assemblages that are specific to those habitats, which contributes to their distinctness from the ornithofauna of rural settlements

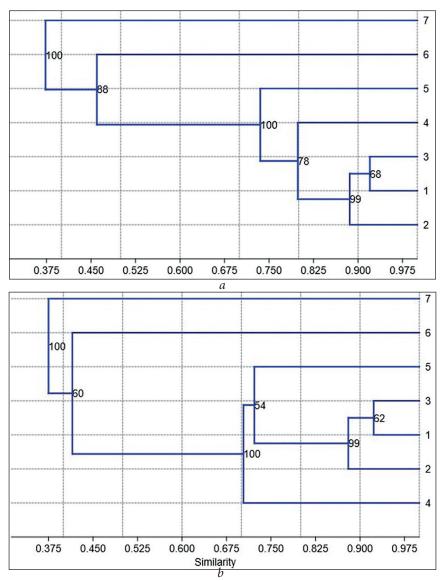


Fig. 3. Similarity of rural settlements and typical biotopes outside rural settlements in breeding season (Dice Similarity index): a— species composition; b— bird species density. 1 — Category I RS, 2 — Category II RS, 3 — Category III RS, 4 — Southern Bug River valley, 5 — Ponds outside rural settlements, 6 — Forest, 7 — Field

(RS). In contrast, RS contain nesting habitats analogous to various typical biotopes outside rural settlements, which increases both their species richness and bird density. A distinguishing feature of Category II RS is the optimal combination of moderate anthropogenic pressure, suitable nesting area coverage, and available food resources for birds. Notably, several species were recorded exclusively in these villages, including the Eurasian Spoonbill *Platalea leucorodia* (L., 1758), Eurasian Hobby *Falco subbuteo* (L., 1758), White-winged Tern *Chlidonias leucopterus* (Temminck, 1815), Tawny Pipit *Anthus campestris* (L., 1758), and River Warbler *Locustella fluviatilis* (Wolf, 1810). These species are considered rare even in the typical biotopes outside rural settlements of the Podillia region.

Differences between Ponds and the Southern Bug River Valley:

Ponds have a significantly larger surface area of open water, which supports a greater number of species and higher concentrations of waterfowl. Extensive reed and cattail thickets provide favorable nesting habitats for wetland birds.

Ponds also contain relatively large areas of marshes and shallow waters, which are ideal feeding grounds for Charadriiformes and other bird species.

Several wetland bird species were recorded exclusively at ponds, including the Great Bittern, *Botaurus stellaris* (L., 1758), Mute Swan, *Cygnus olor* (Gmelin, 1789), Ferruginous Duck, *Aythya nyroca* (Güldenstädt, 1770), Water Rail, *Rallus aquaticus* (L., 1758), Little Ringed Plover, *Charadrius dubius* (Scopoli, 1786), Green Sandpiper, *Tringa ochropus* (L., 1758), Wood Sandpiper, *Tringa glareola* (L., 1758), Common Redshank, *Tringa totanus* (L., 1758), and Common Snipe, *Gallinago gallinago* (L., 1758).

In contrast, river valleys support a higher density and diversity of dendrophilous (tree-dwelling) species due to the extensive tree and shrub vegetation along riverbanks — substantially more than in the areas surrounding ponds.

The overall bird density at ponds is nearly twice as high as in the Southern Bug River valley.

The distinct ecological characteristics of forests and fields account for their comparatively poorer species richness, with dendrophilous species dominating in forests and campophilous species prevailing in fields.

Autumn migration

During the autumn migration period, a total of **118 bird species** were recorded across Category I–III rural settlements and the typical biotopes outside rural settlements. The data were clustered using the **UPGMA method**, resulting in a cophenetic correlation coefficient of $\mathbf{W} = \mathbf{0.809}, P = 0.001$ (Fig. 4).

On the dendrogram based on species richness (Fig. 4, *a*), a clear cluster separation is difficult to define, but three main clusters can still be identified: the first cluster includes rural settlements of Categories I-III; the second groups the Southern Bug River valley and ponds; the third consists of deciduous forests and fields. During the autumn migration, the most similar rural settlements in terms of bird species composition were Category II and Category III (76 and 84 species, respectively), showing greater similarity to each other than either does to Category I (74 species). The Southern Bug River valley, with 54 species, showed the closest similarity to the rural settlements. The ponds outside settlements supported 51 species, but their community structure differed notably from other sites. Once again, fields (26 species) and deciduous forests (32 species) were the most species-poor and taxonomically distinct habitats. According to the cluster analysis, species composition and bird population density during autumn migration showed high statistical similarity (cophenetic correlation coefficient R = 0.997, Baker's Gamma correlation R = 1). However, the position of the ponds shifted noticeably in the cluster dendrogram when comparing species richness versus bird density, highlighting structural differences in their avian communities.

Ultimately, true similarity in species composition can only be confidently stated between rural settlements of Categories I–III, and to some extent between the Southern Bug River valley and Category I RS (Table 2).

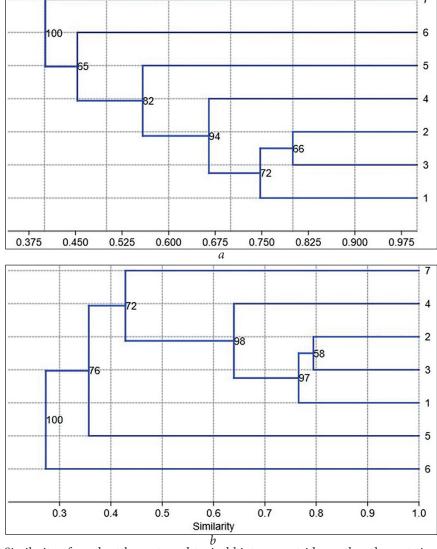


Fig. 4. Similarity of rural settlements and typical biotopes outside rural settlements in autumn migration (Dice Similarity index): a — species composition; b — bird species density. 1 — Category I RS, 2 — Category II RS, 3 — Category III RS, 4 — Southern Bug River valley, 5 — Ponds outside rural settlements, 6 — Forest, 7 — Field

The distinct position of Category I rural settlements in the cluster dendrogram (Fig. 4, b) can be attributed to the mass migration of several highly abundant species.

Notably: European Starling, *Sturnus vulgaris* (L., 1758), showed densities more than 5 times higher than in other RS categories,

Western House-Martin, *Delichon urbicum* (L., 1758), reached densities over 10 times higher,

Common Wood-Pigeon, *Columba palumbus* (L., 1758), had densities 4 times higher,

Large flocks of Eurasian Collared-Dove, *Streptopelia decaocto* (Frivaldszky, 1838), and Rock Pigeon, *Columba livia* (Gmelin, 1789), were observed, with densities more than 9 times higher than in other categories. These elevated densities

| Category | Category I RS | Category II RS | Category III RS | Southern Bug River valley | Ponds | Forest | Field |
|---------------------------|------------------|-------------------|--------------------|---------------------------------|-------|--------|-------|
| Category I RS | 1 | 0.630 | 0.564 | 0.429 | 0.437 | 0.293 | 0.250 |
| Category II RS | _ | 1 | 0.667 | 0.483 | 0.351 | 0.317 | 0.259 |
| Category III RS | _ | - | 1 | 0.591 | 0.392 | 0.349 | 0.236 |
| Southern Bug River valley | - | _ | - | 1 | 0.372 | 0.333 | 0.302 |
| Ponds | _ | _ | _ | - | 1 | 0.186 | 0.283 |
| Forest | _ | _ | _ | _ | _ | 1 | 0.184 |
| Field | - | _ | _ | - | - | - | 1 |

Table 2. Similarity of territories by species richness according to Dice index during autumn migration

are largely explained by the presence and activity of grain storage facilities, which attract large numbers of granivorous and synanthropic birds during the autumn migration.

Despite this high bird density, Category I RS had the lowest species richness (74 species). During the autumn period, birds tend to remain longer in both typical biotopes outside rural settlements and rural settlements compared to spring migration. This is due to the more favorable food base available in autumn, which contributes to the observed differences in both species composition and population density.

Winter period

During the wintering period, a total of **65 bird species** were recorded across Category I–III rural settlements and the typical biotopes outside rural settlements. The data were clustered using the **UPGMA method**, yielding a cophenetic correlation coefficient of $\mathbf{W} = \mathbf{0.964}$, P = 0.002 (Fig. 5).

According to the results obtained using the "res" function from the "NbClust" package, the bird population of the ponds can be clearly separated into a distinct cluster. The remaining areas are grouped into a single cluster, within which deciduous forests and rural settlements (RS) can still be distinguished as separate subgroups. During the wintering period, Category I and Category II RS were the most similar in terms of species richness, with 41 and 47 species, respectively, sharing 8 common species (5%) (Table 3). In Category III RS, 40 species were recorded, representing 76% similarity with Category I and 78% with Category II. Among typical biotopes outside rural settlements, the Southern Bug River valley (37 species) and fields (29 species) were the most similar in species composition. The deciduous forests (29 species) and ponds outside settlements (31 species) showed the greatest distinctiveness and can be considered as entirely separate ornithocomplexes during the winter period.

In rural settlements (RS) of all three categories, both species composition and bird population density (see Tables 3–4, Fig. 5) are significantly similar, in contrast to the more distinct patterns observed in typical biotopes outside rural

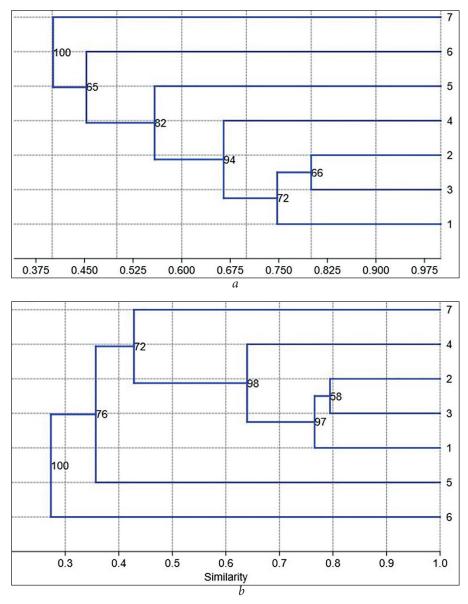


Fig. 5. Similarity of rural settlements and typical biotopes outside rural settlements in winter (Dice Similarity index): a — species composition; b — bird species density. 1 — Category I RS, 2 — Category II RS, 3 — Category III RS, 4 — Southern Bug River valley, 5 — Ponds outside rural settlements, 6 — Forest, 7 — Field

settlements. While the clustering of sites based on species richness and density appears visually similar during the winter period, this similarity is not statistically supported. Specifically, the cophenetic correlation coefficient is R = 0.181, P < 0.05, and Baker's Gamma correlation coefficient is R = 0.065, P < 0.05 — both indicating low agreement between clustering based on species richness and clustering based on density in winter.

During the winter period, a slight distinction is observed between Category III RS and Categories I and II, primarily due to the lower bird density in Catego-

ry III. This difference is mainly due to the limited availability of feeding habitats, such as grain storage facilities, elevators and livestock complexes, which are either absent or minimal in Category III villages. Additionally, there is a scarcity of typical synanthropic species (e.g., Eurasian Collared-Dove, Rock Pigeon, House Sparrow, Passer domesticus (L., 1758)), that contribute significantly to the high bird densities observed in Categories I and II RS. In typical biotopes outside rural settlements, there is a marked discrepancy between dendrograms based on species composition and those based on bird density. For example, similarity in density between deciduous forests and fields arises from contrasting population structures: fields have higher numbers of individuals but fewer species, while forests support fewer individuals but greater species richness. This explains their notable differences in species composition despite similar densities. Furthermore, during winter, a significant portion of ponds becomes ice-covered, rendering large areas of this habitat unsuitable for bird use. As a result, ponds show the lowest bird density among all studied habitats in this season, setting them apart from the rest (Table 4).

Table 3. Similarity of territories by species richness according to Dice index during winter

| Category | Category I RS | Category II RS | Category III RS | Southern Bug River valley | Ponds | Forest | Field |
|---------------------------|------------------|-------------------|--------------------|---------------------------------|-------|--------|-------|
| Category I RS | 1.000 | 0.909 | 0.864 | 0.795 | 0.583 | 0.686 | 0.686 |
| Category II RS | _ | 1.000 | 0.874 | 0.786 | 0.615 | 0.684 | 0.658 |
| Category III RS | - | - | 1.000 | 0.727 | 0.592 | 0.667 | 0.638 |
| Southern Bug River valley | - | _ | _ | 1.000 | 0.618 | 0.667 | 0.727 |
| Ponds | - | - | - | _ | 1.000 | 0.467 | 0.467 |
| Forest | _ | _ | - | _ | _ | 1.000 | 0.552 |
| Field | - | - | - | - | - | - | 1.000 |

Table 4. Similarity of territories by bird density according to Dice index during winter

| Category | Category I RS | Category II RS | Category III RS | Southern Bug River valley | Ponds | Forest | Field |
|---------------------------|------------------|-------------------|--------------------|---------------------------------|-------|--------|-------|
| Category I RS | 1.000 | 0.892 | 0.857 | 0.747 | 0.444 | 0.623 | 0.725 |
| Category II RS | _ | 1.000 | 0.881 | 0.805 | 0.486 | 0.647 | 0.711 |
| Category III RS | _ | _ | 1.000 | 0.789 | 0.438 | 0.645 | 0.714 |
| Southern Bug River valley | _ | _ | _ | 1.000 | 0.484 | 0.567 | 0.765 |
| Ponds | _ | _ | _ | _ | 1.000 | 0.250 | 0.393 |
| Forest | _ | _ | _ | _ | - | 1.000 | 0.556 |
| Field | - | - | - | - | - | - | 1.000 |

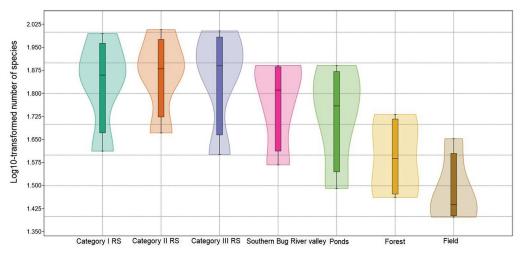


Fig. 6. Number of bird species recorded in rural settlements (RS) of different categories, grouped by ecological affiliation.

Discussion

The presented dendrograms indicate a high degree of similarity among rural settlements (RS) during the spring migration and breeding season. During the autumn migration, Category II and Category III RS become more similar to each other in terms of bird species composition. In the winter season, Category I and Category II RS show greater similarity to each other than either does to Category III RS.

As shown in the dendrograms, the highest similarity between the ornithofauna of rural settlements (RS) and typical biotopes outside rural settlements occurs during the winter period, while the lowest similarity is observed during the breeding season. The increased similarity in winter is primarily due to the lower overall species richness in the region and the movement of many bird species from typical biotopes outside rural settlements into RS in response to deteriorating weather conditions (e. g., decreasing temperatures and increasing snow cover). In contrast, the distinctiveness of RS compared to typical biotopes outside rural settlements during the breeding season is driven by the greater species richness in RS, which results from the presence of a mosaic of nesting habitats and the overlap of ecological features typical of multiple typical biotopes outside rural settlements.

Throughout the year, analysis of the species composition across rural settlements (RS) of different categories revealed distinct differences in the number of species belonging to various ecological groups within each category (Fig. 6). These differences reflect variations in habitat structure, urbanization level, and land-use intensity among RS categories, which influence the suitability of conditions for particular ecological groups (e. g., dendrophiles, limnophiles, campophiles, and synanthropes) across seasons.

In Category I rural settlements, the highest number of limnophilous species was recorded, while species from other ecological groups were less represented compared to Categories II and III. This pattern is primarily due to the characteristics of their wetland habitats (WHs): Category I RS possess the largest wetland areas, along

with a greater number and diversity of nesting sites suitable for limnophilous species, making them especially favorable for water-associated birds.

In Category II rural settlements, the highest number of campophilous and sclerophilous species was recorded. This is primarily due to the presence of actively cultivated garden plots, both between streets and around the perimeter of the settlements. Additionally, the existence of operating livestock farms, grain storage facilities, newly constructed buildings, and abandoned or partially ruined structures creates a diverse range of microhabitats that are favorable for these ecological groups.

In Category III rural settlements, the highest number of dendrophilous species was recorded. This is attributed to the high level of greenery characteristic of these settlements. They contain the largest number of old trees and abandoned homesteads, with surrounding areas becoming overgrown with trees and shrubs. Due to the low population density, tree cutting and pruning are minimal, and many gardens are left uncultivated, allowing shrubs and woody vegetation to thrive — conditions that strongly favor the presence and spread of dendrophilous bird species.

The analysis of seasonal diversity of the ornithofauna in different categories of rural settlements (RS), based on the Shannon index, indicates that in almost all seasons, the highest diversity is observed in Category III RS, while the lowest is recorded in Category I RS (Table 5).

An inverse pattern is seen only in winter, where Category I shows a comparatively higher diversity.

In Category II RS, the Shannon index values are intermediate in all seasons except winter — falling between the higher diversity levels of Category III and the lower levels of Category I. This trend reflects how habitat structure, vegetation cover, and anthropogenic influence shape avian diversity throughout the annual cycle.

Thus, it can be assumed that the higher the degree of urbanization in a rural settlement (RS), the lower the diversity index, while a higher level of greenery and lower disturbance factor tend to result in greater species diversity.

In winter, when the overall number of species is relatively low, and the abundance of certain synanthropic species, such as the House Sparrow, Eurasian Tree Sparrow *Passer montanus* (L., 1758), Rock Pigeon, Eurasian Collared-Dove, and even the Common Raven, *Corvus corax* (L., 1758), which is in the early stages of synanthropization in RS, are particularly abundant, the aforementioned factors (urbanisation, greenery and disturbance) have little influence on the diversity index (Novak, 2021 b). During the winter period, the most critical factors for birds are the availability of food resources and the presence of suitable roosting sites or shelter from adverse weather conditions.

Table 5. Bird diversity (Shannon's index) in rural settlements of different categories

| Category | Spring migration | Breeding season | Autumn migration | Wintering |
|-----------------|---------------------|-----------------|---------------------|-----------------|
| Category I RS | 2.51 ± 0.2 | 2.97 ± 0.14 | 1.74 ± 0.1 | 1.81 ± 0.09 |
| Category II RS | 2.74 ± 0.14 | 2.98 ± 0.08 | 2.12 ± 0.16 | 1.66 ± 0.1 |
| Category III RS | 2.85 ± 0.15 | 3.18 ± 0.15 | 2.54 ± 0.22 | 1.67 ± 0.09 |

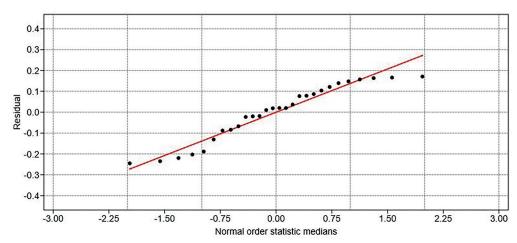


Fig. 7. Bird density in rural settlements (RS) of different categories recorded during various periods of the annual cycle.

Differences among rural settlements (RS) of different categories are evident not only in species composition but also in quantitative structure. When comparing bird density across seasons in each RS type, several patterns emerge. In Category I RS, bird density is generally the lowest throughout most of the year, except during winter. This is likely due to a higher level of human disturbance, a scarcity of green spaces, and a poorer food base compared to Category II and III RS. However, in winter, Category I RS offers a comparatively better food supply for certain overwintering species (Fig. 7). As a result, during the winter season, this category shows the highest abundance of species such as: Rock Pigeon; Eurasian Collared-Dove, which feed at grain storage sites and livestock farms; Fieldfare, *Turdus pilaris* (L., 1758), and Eurasian Bullfinch, *Pyrrhula pyrrhula* (L., 1758), which feed on rowan and viburnum berries, as well as maple seeds; Willow Tit, *Poecile montanus* (Conrad von Baldenstein, 1827), and Eurasian Siskin, *Spinus spinus* (L., 1758), which mostly feed on conifers near administrative buildings (Novak, 2016).

These seasonal shifts illustrate how anthropogenic features such as grain stores, livestock operations, and ornamental plantings in more urbanized RS can create favorable winter conditions for certain species, despite generally lower diversity and density throughout the year.

In Category III rural settlements, bird density is the highest in all seasons except winter (Fig. 9). This pattern is likely driven by the low level of human disturbance, as these villages have fewer residents, allowing migratory birds to stay longer than in more densely populated settlements. This low population density also contributes to the highest bird density during the breeding season among Category III RS.

Additionally, Category III RS has the highest level of greenery, which supports a greater density of dendrophilous species such as: Common Wood Pigeon; Red-Backed Shrike, *Lanius collurio* (L., 1758); Eurasian Jay, *Garrulus glandarius* (L., 1758); Lesser Whitethroat, *Curruca curruca* (L., 1758); Eurasian Blackcap, *Sylvia atricapilla* (L., 1758); Common Chiffchaff, *Phylloscopus collybita* (Vieillot, 1817); Common Blackbird, *Turdus merula* L., 1758; Marsh Tit, *Poecile palustris* (L., 1758); Eurasian Blue Tit, *Cyanistes caeruleus* (L., 1758); Hawfinch, *Coccothraustes coccothraustes* (L., 1758); Yellowhammer, *Emberiza citrinella* (L., 1758), among others.

Notably, the synanthropization of the Wood Pigeon in the Podillia region began in Category III RS, though today its highest breeding density is found in Category I RS (Novak, 2021 c). The presence of overgrown vegetation, including shrubs and herbaceous plants, around abandoned homesteads reduces disturbance levels, enhances the food base, and increases the availability of suitable nesting sites. In winter, however, bird density in Category III RS decreases due to a poorer food base compared to that available in Category I and II RS, where anthropogenic food sources (e.g., grain stores, livestock operations) are more abundant.

In Category II rural settlements, bird density values are consistently at intermediate levels compared to Categories I and III throughout most of the year. However, in winter, this category exhibits the highest bird abundance. This winter peak is primarily due to the better food availability in Category II villages, where residents tend to keep more livestock and poultry than in villages of other categories. In addition, these settlements often have a significant amount of greenery, as well as the presence of grain storage facilities and livestock farms, which serve as important feeding sites for birds during the cold season. Thus, Category II RS combines the favorable features of both Category I (better winter food base) and Category III (abundant vegetation and lower disturbance), offering optimal conditions for birds year-round. This combination likely explains the patterns observed when analyzing the similarity of bird communities across RS categories in different seasons, as measured by the Dice similarity index. Category II often serves as a transitional or "bridge" type, showing high similarity to both the more urbanized and the more natural, green-rich settlements.

The highest similarity in bird density among all categories of rural settlements (RS) is observed during the winter period. This convergence is likely due to the general reduction in species richness and the dominance of a few widespread synanthropic species that concentrate around available food sources. In other seasons, certain specific patterns emerge. During the spring and autumn migration periods, the greatest similarity in density is found between Category I and Category II RS, likely due to the concentration of migratory birds around grain stores and farm infrastructure common to both. While in the breeding season, the highest similarity is observed between Category II and Category III RS, reflecting similar habitat conditions such as the presence of greenery, nesting sites and lower levels of disturbance compared to Category I. These seasonal variations highlight how shifts in bird behavior, habitat use, and resource availability influence the structure and similarity of avian communities in different types of rural settlements throughout the year.

Conclusions

The rural settlements (RS) of the Podilske Pobuzhzhia region play an important role in the conservation of regional avifauna, as 69% of the region's bird species (174 species) have been recorded there. The most favorable conditions for birds are found in Category II RS, where 162 species were recorded. These villages offer a relatively low level of disturbance and a sufficient variety of habitats that support bird presence throughout the year — for breeding, feeding, roosting, and resting.

Each RS category shows distinct ecological characteristics reflected in its bird community structure:

Category I RS host the highest number of limnophilous species, which is due to the largest area of wetlands compared to other categories of rural settlements

Category II RS are richest in campophilous and sclerophilous species

Category III RS support the highest number of dendrophilous species.

These patterns are directly related to the specific environmental conditions and land-use features associated with each settlement type.

The highest similarity between the ornithofauna of rural settlements (RS) and typical biotopes outside rural settlements is observed in the winter period, while the lowest similarity occurs during the breeding season. The winter similarity is primarily due to the lower species richness in the region and the movement of many bird species from typical biotopes outside rural settlements to RS during unfavorable weather conditions—such as decreasing temperatures and increased snow cover.

In contrast, the difference between typical biotopes outside rural settlements and RS in the breeding season is caused by the higher species diversity within RS, which offer a broader variety of habitats.

Among typical biotopes outside rural settlements, the Southern Bug River valley shows the greatest similarity to RS ornithofauna across nearly all seasons, with additional similarity to ponds during the spring migration and breeding period.

The ornithofauna of RS is particularly similar between the spring migration and breeding seasons, reflecting the continuity of habitat use during this part of the annual cycle. During autumn migration, Category II and III RS become more similar to each other, while in winter, Category I and II RS show the highest similarity, more so than either does with Category III RS. These patterns are confirmed by the Czekanowski similarity index.

In terms of bird density, Category III RS consistently show the highest values in all seasons except winter, while Category I RS have the lowest densities. In winter, this trend reverses, with Category I RS showing the highest density.

According to the Shannon diversity index, the highest diversity in all seasons except winter is found in Category III RS, and the lowest in Category I RS. In winter, Category I RS exhibit the highest diversity, likely due to the concentration of wintering synanthropic species.

The reliability of these findings is supported by statistical tests including the Shapiro–Wilk test, Fisher's criterion, permutation test, and Tukey's HSD test.

Acknowledgements. The authors wish to express their sincere appreciation to Dr. Anatolii Poluda, Candidate of Biological Sciences and Senior Research Fellow at the I. I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, for his valuable scientific guidance, critical comments, and continuous support during the preparation of this manuscript. His extensive expertise, professional insights, and careful review significantly contributed to the quality and clarity of the research presented. The authors are deeply grateful for his dedication and constructive input at all stages of this work.

REFERENCES

- Belik, V. P. 1992. Biotopical distribution and ecological classification of animals: Readings to the memory of Professor V. V. Stanchinsky. Smolensk, 13–16 [In Russian].
- Clements, J. F., P. C. Rasmussen, T. S. Schulenberg, M. J. Iliff, T. A. Fredericks, J. A. Gerbracht, D. Lepage, A. Spencer, S. M. Billerman, B. L. Sullivan & Wood, C. L.. 2023. The eBird/Clements checklist of birds of the world: v2023b. https://www.birds.cornell.edu/clementschecklist/download/
- Czekanowski, J. 1932. 'Coefficient of racial likeness' und 'durchschnittliche Differenz', *Anthropologischer Anzeiger*, 9, 227–249.
- Dice, L. R. 1945. Measures of the amount of ecologic association between species. *Ecology*, 26, 297–302.
- Hagemeijer, W. J. M. & Blair, M. J. 1997. *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance*. T. & A.D. Poyser, London, 1–903.
- Keller, V., Herrando, S., Vorisek, P., Franch M., Kipson M., Milanesi P., Marti D., Anton M., Klvanova A., Kalyakin M. V., Bauer H.-G. & Foppen R. P. B. 2020. *European Breeding Bird Atlas 2: Distribution, Abundance and Change*. European Bird Census Council & Lynx Edicions, Barcelona, 1–967.
- MacArthur, R. H. 1955. Fluctuations of animal populations, and measure of community stability. *Ecology*, **36** (7), 353–356.
- Matviichuk, O. A. 2015. Retrospective assessment of the avifauna of the Podilske Pobuzhzhia. *Scientific Bulletin of the L. Ukrainka Eastern European National University. Lutsk*, 2, 61–65 [In Ukrainian].
- Novak, V. V. 2016. Biology and current status of thrushes (Turdus) in the villages of Podilske Pobuzhzhia. *Bulletin of Cherkasy University. Biological Sciences Series*, 2, 80–88 [In Ukrainian].
- Novak, V. V. 2021 a. Spatial distribution of avifauna in the villages of Podilsky Pobuzhzhye. *Ecological Sciences*, **5** (38), 92–98 [In Ukrainian].
- Novak, V. V. 2021 b. Synanthropization of Raven *Corvus corax* in the region Verkhnie Pobuzhzhia. *Ecological Sciences*, 4 (37), 182–187 [In Ukrainian].
- Novak, V. V. 2021 c. Synanthropization of Wood Pigeon (*Columba palumbus*) in Upper Pobuzhia (Ukraine). *Studia Biologica*, 15 (2), 73–80.
- Novak, V. V. & Novak, V. A. 2015. Modern avifauna of the Podilske Pobuzhzhia. *Abstracts XIV International Ornithological Conference of Northern Eurasia*. *Almaty*, 367–368 [In Russian].
- Ravkin, Yu. S. 1967. To the method of recording birds of forest landscapes. The nature of foci of tick-borne encephalitis in Altai. Novosibirsk, Nauka, 66–75 [In Russian].
- Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *Kongelige Danske Videnskabernes Selskab*, **5** (4), 1–34.
- Yesiunin, S. 2012. *Unknown Podillia*. Gorodok, 1–156 [In Ukrainian].

Received 15 April 2025 Accepted 15 December 2025