



**Article**

# **Transformation of hemiboreal ornithocenoses in modern forest management**

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**Abstract.** The ornithocenoses of a sequence of forestry succession stages are studied in different types of hemiboreal forests of the Russian Plain, and the species of birds that determine each of the recognized stages is given. Statistical analysis showed that anthropogenic disturbances and natural succession processes played a significant role in the transformation of ornithocenoses, against a background of less influence from forestry activities (conifer plantations and their maintenance). Dispersion decomposition showed a high proportion of the combined effect of exogenous and endogenous factors, as well as their equivalent contribution to the formation of ornithocenoses, was demonstrated. Various types of logging are shown to facilitate shifts of natural succession of forest ornithocenoses to anthropodynamic successions characterized by specific subclimax stages.

**Keywords:** bird communities, logging, anthropodynamic succession, exogenous and endogenous factors, redundancy analysis, ecological ordination.

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## **Introduction**

Forests are the key terrestrial communities of the temperate climate zone, occupying almost half of the territory of Russia. The forestry industry is one of the oldest sectors of the Russian economy, hence forest communities have been significantly transformed by forestry (Smirnova et al., 2017). An important principle of sustainable forestry is the conservation of biological and landscape diversity with a concomitant increase in the productivity of logging (Schwartz et al., 2020). In forestry management, it is important to take many factors into account, both natural and mediated by technological processes. Understanding the role of factors of different origin and their hierarchy

is important for a deep understanding of ecological gradients in managed forests. With extensive forest exploitation, zonal-subzonal gradients are leveled by successional ones, and only a detailed factorial analysis can reveal their differences (Ravkin, 2013).

Birds, due to their ecological preferences, are a classic indicator group for studying successions in multicomponent forest ecosystems (Johnston and Odum, 1956). Each stage of ecosystem succession is characterized by specific ornithocenoses due to the mobility of birds, their habitat selectivity, and their ecological segregation. The influence of intrapopulation processes on the successional dynamics of bird communities is levelled by the rapid

turnover of generations and the high reproductive potential of most species.

The impact of secondary forest management on ornithocenoses is intensely studied in different climatic zones (DeGraaf and Yamasaki, 2003; Porneluzi et al., 2014; Thorn et al., 2020). An exhaustive meta-analysis of the effect on birds of retention of forestry in boreal and temperate regions (Basile et al., 2019) showed their effectiveness in maintaining the main characteristics of ornithocenoses, except for the abundance of some forest specialist species. At the same time, in each region, specific factors associated with a key indicator, the percentage of forest canopy, were recorded. The effect of specific forestry methods used in Russia (clearcut, gradual harvesting, selective harvest, salvage logging, as well as planting and maintenance) on ornithocenoses requires a comprehensive assessment, but this question is very rarely addressed (Nazarov, 2002).

In this study, we discuss transformations of hemiboreal ornithocenoses caused by forestry management. We considered the issues of (1) the effect of successional factors on the formation of ornithocenoses; (2) ratios between the contribution of endogenous and exogenous factors; (3) variability of successional dynamics depending on the mode of forest management.

## Material and methods

The analysis was based on the data of quantitative counts of birds using the method of absolute mapping of nesting territories on test sites (Gudina, 1999), which is optimal for collecting reliable data on the composition and structure of ornithocenoses and accurately comparing these communities with each other (Tomialojc, 1968).

Bird counts were carried out in the spring and summer seasons of 2006–2010 in secondary hemiboreal forests that had been intensively exploited for a long time. The study area is located in the center of the non-chernozem zone of the Russian Plain between N 56° E 39° and N 58° E 44° in the Vladimir, Ivanovo, Nizhny Novgorod and Kostroma regions of the Russian Federation. We surveyed 38 model plots, reflecting the key stages of anthropodynamic succession shifts in managed forests – spruce forests, pine forests and mixed coniferous-small-leaved deciduous forests.

To track the changes in ornithocenoses in secondary coniferous forests, seven succession stages were considered: recent logging, overgrown clearings, pole-stage stands, young forests, middle-aged forests, maturing and old-growth secondary forests. In mixed communities, five stages were considered, since it is difficult to identify individual stages of the middle-aged and old-growth forests, and after the crown closure, the registration sites were organized only at the maturing forest stage.

After felling, in most cases, the sites are artificially regenerated, and after crown closure in clearings, succession is transformed by various methods of management (thinning and reshaping). In addition to management of forest plantations, the communities under consideration are associated with clearcut, patch, selective and salvage cutting.

Anthropodynamic successions are accompanied by specific dynamics of important characteristics of the nesting biotope, which were assessed for each registration site on a scale from 0 to 4. Some of the characteristics are determined by anthropogenic processes, and some by natural demutation (re-establishment) processes (Table 1). The first group includes the logging area, the burnt area, the waterlogged area, the disturbance of forest canopy, changes in the forest litter, the planting of conifers, the amount of logging remains. The second one is the formation of the edge ecotone at the border of clearing and forest, mosaicity and stratification, as well as key phytocenotic characteristics: the share of open space, projective grass cover, shrub cover, small-deciduous undergrowth, old-growth forest.

The plots included in the successional series were surveyed simultaneously during one nesting season in order to exclude the influence of population and weather factors. Each row (mixed forests, spruce forests, northern pine forests, pyrogenic pine forests) was given a separate survey year. The total area covered by the mapping of model territories was 324 ha, 461 nesting sites of 46 bird species were described. At each model site, bird population density (number of nesting pairs per 1 ha) was determined and 15 topic characteristics were assessed (Online Appendix).

In studying the dependence of the bird population on the structural parameters of nesting biotopes, redundancy analysis was used to build a regression model with a multivariate response (representation of species) and a predictor (site characteristics). It is also a method of limited ordination and allows visualization of the results with the display of positions of accounting areas, projections of species and predictors (Borcard et al., 2018; Schitikov and Rozenberg, 2013). For the constructed model, variance decomposition of variations explained by exogenous and endogenous successional factors was carried out. The calculations were made in the R environment (R Core Team, 2020) using the Vegan community ecology package (Oksanen et al., 2020).

## Results and discussion

During the nesting period, forest areas modified by logging were used by 84 species of birds, of which 73 species were nesting; 46 nesting species were identified directly in the survey sites. All of them are tolerant to anthropogenic factors and are widely distributed (with the exception of *Lullula arborea* L., 1758

**Table 1.** Statistical analysis of the dependence of the structure of hemiboreal ornithocenoses transformed by forest management on endogenous and exogenous factors. Exogenous factors are shaded gray. \*\*\* –  $p < 0.001$ , \*\* –  $p < 0.01$ , \* –  $p < 0.05$ .

	Adjusted proportion of explained variance	The value of the Fisher criterio	<i>p</i> value
<b>Complete redundancy analysis (RDA)</b>	<b>22%</b>	<b>1.7</b>	<b>0.001***</b>
<b>Main axis I</b>	<b>9%</b>	<b>6.8</b>	<b>0.001***</b>
<b>Main axis II</b>	<b>7%</b>	<b>5.5</b>	<b>0.014*</b>
<b>Succession stage</b>	<b>9%</b>	<b>4.42</b>	<b>0.001***</b>
Crown closeness	7%	4.32	0.001***
Scrubland	6%	3.47	0.001***
Waterlogged	6%	3.88	0.001***
Stratification	6%	3.88	0.001***
Projective grass cover	5%	3.21	0.002**
Burnt areas	4%	2.60	0.003**
Openness	4%	2.67	0.004**
Ecotone extent	4%	2.53	0.005**
Deciduous small-leaved undergrowth	4%	2.45	0.005**
Forest floor integrity	4%	2.16	0.006*
Mosaic forest	3%	2.01	0.018*
Old-growth forest	3%	2.08	0.024*
Coniferous undergrowth and planting	3%	1.54	0.053
Felling area	3%	1.67	0.094
Logging residues	0.02%	0.94	0.510

and *Sylvia nisoria* Bechstein, 1795, which are rare because of the population rather than topic factors). The origin of most of the avifauna species of the areas transformed by cutting is European, less often trans-palearctic (Belik, 2006). Birds of the Siberian type of fauna were confined to areas modified by planting of conifers, thinning and fires, using them for invasions into European forests. Forest-steppe bird species, settling in the forest zone, also use cut-down areas in the early stages of succession. The initial stages of succession are characterized by the dominance of open space species, unusual for continuous forested areas; while wader species appear with increased moisture; more advanced succession leads to the spread of forest edge and forest bird species.

The species structure of the studied ornithocenoses is statistically significantly related to the structural parameters of the nesting biotopes. The redundancy analysis model explains 22% of the variability in the structure of forest bird communities (Table 1). When studying forest bird communities using redundancy analysis, relatively low rates of explained data variability within 15–45% are typical (Hanowski

et al., 2003; Jackson et al., 2012; Katoh and Matsuba, 2021; Nikolov, 2013), since the forest is the most complex biogeocenotic system with connections that cannot be comprehensively assessed. At the same time, due to the ability of birds to actively fly, the nesting ornithocenosis is the most mobile and variable component of forest ecosystems, and is updated almost entirely every year.

Despite this, redundancy analysis is very informative. It allows not only to carry out the ecological ordination of the studied ornithocenoses in the space of key factors, but also to trace the relationship between environmental factors and the species that make up the ornithocenoses, as well as the individual contribution to the transformation of the ornithocenosis of each of the evaluated factors and their total contribution.

Figure 1 shows the final triplot of the redundancy analysis model. The trends of successional changes in hemiboreal ornithocenoses are characterized by the proximity of the initial and final stages. For accounting sites of the initial stages of forestry succession, openness, waterlogging, and a developed herbaceous tier are characteristic. The area is dominated by a

few meadow-field species (*Saxicola rubetra* L., 1758; *Emberiza citrinella* L., 1758). In contrast, the counting sites of the late succession stages in secondary forests are characterized by high density, pronounced stratification, the presence of undisturbed forest litter and old-growth trees. In such communities, the diversity of birds is high and there is no pronounced dominant, and in the subdominant core, dendrophilic taxa are recognized, associated with the composition of the canopy-forming trees (*Phylloscopus* Boie, 1826; *Ficedula* Brisson, 1760; *Paridae* Vigors, 1825). These species nest only at the final stages of succession; therefore, they are not represented on the ordination triplot due to their insignificant influence on the final model.

The pyrogenic factor results in the preferential nesting of *Lullula arborea*; *Alauda arvensis* L., 1758 is associated with continuous herbage. Forest mosaic pattern, ecotone effect, and shrub distribution are correlated and are characteristic of succession with replacement of species, leading to coniferous and small-leaved deciduous forests. These factors form communities with codominance of *Acrocephalus dumetorum* Blyth, 1849 and *Sylvia borin* Boddaert, 1783. When ecotones are combined with significant herbaceous vegetation, the communities are dominated by *Carpodacus erythrinus* Pallas, 1770. The growth of small-leaved deciduous undergrowth results in the dominance of *Phylloscopus trochilus* L., 1758. The nesting density of *Erithacus rubecula* L., 1758 is associated with the restoration of forest litter, the dominance of *Fringilla coelebs* L., 1758 in forest communities is connected with pronounced canopy closure, *Turdus viscivorus* L., 1758 and *Anthus trivialis* L., 1758 with the coniferous undergrowth.

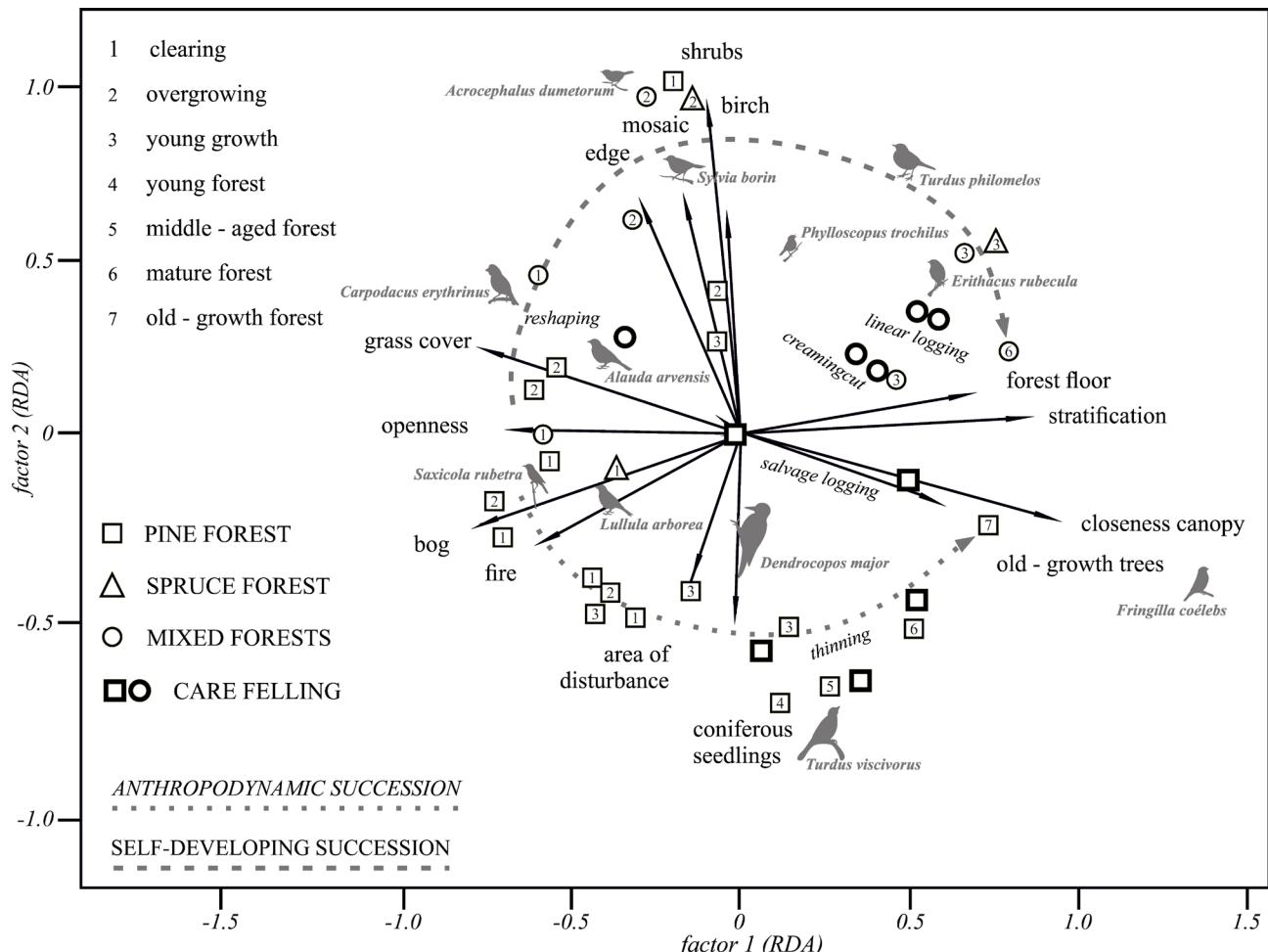
For each species capable of nesting in a cleared area, the conditions of the natural nesting biotope are adequately modeled by forestry succession. Part of the topic characteristics of the felled areas differs from natural nesting habitats (semi-desert, forest-steppe, meadow, tundra, ecotone and pyrogenic). The suboptimality of the nesting biotope results in unstable nesting density even in the dominant widespread bird species, as well as sporadic nesting of other species. Similar conclusions were drawn from the study of clearcut areas in the context of anthropogenic fragmentation of habitats (Matantsev, 2004). We believe that the population dynamics of birds in modern managed forests functions according to the “source-drain” type, since a number of early successional (*Lanius excubitor* L., 1758; *Sylvia nisoria*) and late successional (*Spinus spinus* L., 1758; *Loxia curvirostra* L., 1758; *Fringilla montifringilla* L., 1758) species occupies clearing areas only in breeding seasons with peak numbers. At the same time, some species appear in forest areas precisely on the territories transformed by forest exploitation (*Upupa epops* L., 1758; *Nucifraga caryocatactes* L., 1758; *Oenanthe oenanthe* L., 1758), settling with an increase in numbers in

the surrounding forests or in unforested areas. Similar population dynamics has been traced in changes in the bird population associated with pasture successions (Davis et al., 2016).

These processes have been studied in detail in the managed forests of Fennoscandia based on model bird species (*Ficedula hypoleuca* Pallas, 1764; *Sylvia* sp.; *Troglodytes troglodytes* L., 1758; *Picoides tridactylus* L., 1758), (Artemyev, 2008; Jokimäki and Solonen, 2011; Matantseva and Simonov, 2008; Paakkala et al., 2018). Highly productive habitats in old-growth forests with natural elements of destructive forest mosaic are sources of stable nesting populations. The territories of managed forests can act as absorbing habitats for populations of some species, or they can be a source of population growth and corridors for the restoration of the habitats of others that used extensive elements of the wetland or destruction mosaic formed by megafauna in natural forests of the pre-Anthropocene.

Of the 15 considered factors that affect the population of birds in exploited forests, four have the greatest weight (Table 1). At the same time, the vector of the most significant of the factors, crown density, is unidirectional (strongly positively correlated) with the distribution of old-growth trees. The factors of overgrowth and small-leaved deciduous undergrowth are similarly related. Stratification, in addition to a high level of significance in the constructed model, is recognized because it coincides with the positive values of the main scale. Waterlogging is also shown to be very significant, as it is multidirectional and equidistant from other key factors.

The key natural succession factors that are not supplemented by forestry activities (planting, thinning, reshaping) are the ecotone effect, forestation and waterlogging. The distribution of ornithocenoses in the vector space of these factors is similar to the natural distribution in unexploited forests. Due to the ubiquitous distribution of ecotones and small-leaved deciduous young forests, modern secondary forests are dominated by ornithocenoses composed of species characteristic of these communities. Based on the available data, the factors mediated by forest crop care (maintenance) are either significant at a very low level (disturbance of the forest floor) or not significant (planting, logging areas, logging residues) for ornithocenoses. Such a subtle effect of the ongoing forest management on ornithocenoses has not been recorded in world literature and, apparently, is a feature inherent to Russian forestry. At the same time, it should be emphasized that the vector of the most common of the anthropodynamic succession factors (artificial regeneration of conifers) coincided with the negative values of the second most important main axis; it is clearly opposed to the vector of distribution of small-leaved deciduous undergrowth.



**Fig. 1.** Ordination of ornithocenoses of exploited forests in the space of the main axes of redundancy analysis. Arrows indicate projections of predictors into the ordination space; the lengths of the vectors correspond to the contribution to the successional dynamics. The numbers indicate the stages of succession in each type of forest, the distances between them reflect the similarity of the species structure of the corresponding ornithocenoses. Dashed lines show trends in succession changes in hemiboreal ornithocenoses. The twelve most important bird species are indicated by silhouette pictograms, the degree of contribution of the species to the variability of the structure of the ornithocenoses corresponds to the distance to the origin of coordinates. The horizontal axis reflects the natural successional gradient from open space communities to climax (coniferous-deciduous forests). The vertical axis contrasts successions without planting and maintenance, leading to coniferous and small-leaved deciduous forests (positive values), and successions with planting and staged maintenance, leading to uniform even-aged coniferous stands, predominantly pine forests (negative values).

To compare the contribution of exogenous and endogenous factors with the development of the structure of ornithocenoses, dispersion variance decomposition explained by the corresponding batches of predictors was performed. The decomposition results are presented in the form of a Venn diagram in Fig. 2. The unique influence of each of the groups of factors is statistically significant and comparable (explains approximately 6% of the variability of the species and dominant structure of each of the ornithocenoses). A high proportion of the combined influence of exogenous and endogenous factors is also characteristic, exceeding the unique influence of each of the groups and amounting to almost 10%. The results obtained clearly demonstrate the contribution of anthropodynamic processes to the formation of bird communities in secondary forests. The common approach to the

study of successions, based on their endogenous nature and self-regulation, is not applicable to successions in modern managed forests.

It is very indicative to compare the ornithocenoses formed by different thinning regimes with the stages of demuturation (re-establishment) changes in the bird population after clearcuts when considering correlations with factors reflected in the ordination triplot (Fig. 1).

In the course of succession changes in ornithocenoses of coniferous forests, in the absence of artificial reforestation and maintenance, mixed forest communities are formed, this can be seen in the example of the pine forests of the Volga River left bank and spruce forests located in the upper part of the graph. In mixed forests, with thinning, the effect of reformation logging is noticeable – e.g., the removal of all deciduous species but the preservation of coni-

fers, which makes it possible to redirect successions to the formation of original early successional coniferous communities. Similar results were obtained by two groups of researchers for ornithocenoses in managed boreal forests in Western Canada (Hobson and Bayne, 2000) and mountain forests in Germany (Steverding and Leuschner, 2002).

The remaining care felling slightly changes the structure of the ornithocenoses of secondary coniferous and small-leaved deciduous forests; they are significantly affected by technogenic disturbance of the forest litter. Maintenance loggings form peculiar ornithocenoses, somewhat different from forest ones, despite the preservation of areas of untouched forest stand. Ornithocenoses of mixed forests after selective felling for a long time are close to ornithocenoses at the beginning of crown closure of undergrowth in clearcuts.

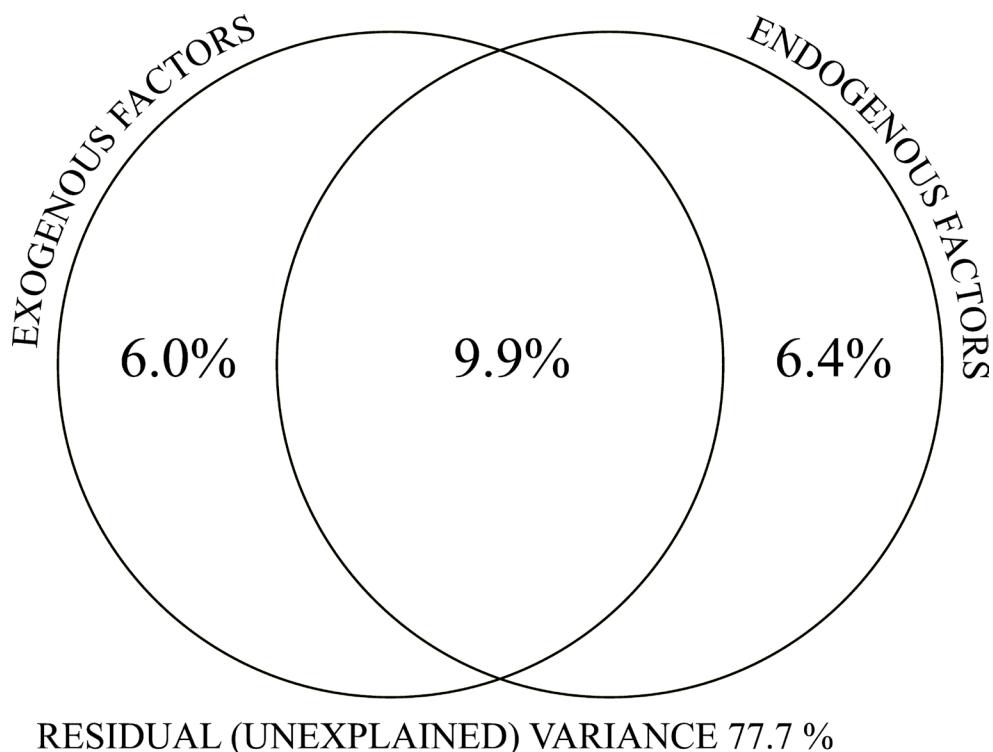
With gradual thinning of pine forests, a return to the previous stages of succession can be observed, i.e., ornithocenosis occupies an intermediate position on the ordination triplot between the initial (before thinning) and an earlier stage of succession. Thinning is a traditional way of caring for forest plantations, similar to the natural processes of windfall and drying out. These processes are not catastrophic for forest ornithocenoses, which have adaptive responses to such processes (Fuller, 2000).

Salvage logging leads to a simplification of the structure of ornithocenoses. Communities are shift-

ed along the distribution vector of old-growth trees to positions very remote from mature pine forests. Due to the maximum removal of organic matter and the destruction of components important for the initiation of succession, they are located on the resulting triplot in the region of the origin of coordinates. This indicates the “primacy” of successional processes. The transition of ornithocenosis to the next stage requires a long time, incomparable with the rate of typical secondary successions after logging. Ornithologists of Central and Eastern Europe came to similar conclusions (Kamp et al., 2020; Źmihorski, 2010), showing that salvage cutting after disturbance slows down demutation processes and has a catastrophic effect on the diversity of forest ornithocenoses, aggravating natural destruction.

## Conclusions

The results of the statistical analysis confirm the generally accepted concept that natural demutation is the key complex dynamic factor that determines the change of ornithocenoses in secondary forests. But it is worth emphasizing that exogenous factors are also important for the formation of the bird population structure in exploited forests. However, in the modern realities of Russian forestry, the influence on ornithocenoses of individual, often locally distributed, anthropodynamic factors (planting and maintenance) remains insignificant. The data obtained on the redi-



**Fig. 2.** Contribution to the formation of ornithocenoses of managed forests by factors of various origins, revealed by the decomposition of dispersion components. The factors are listed in Table 1.

rection of natural successional changes by various logging methods to anthropodynamic changes, with specific subclimax stages, are applicable not just to ornithocenoses. The homogeneity and intrazonation of secondary managed forests affect biodiversity in general, managed shifts lead to oligodominant forest communities with reduced biodiversity, productivity, and sustainability.

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## References

- Artem'ev, A.V., 2008. *Populatsionnaya ekologiya mukholovki-pestrushki v severnoi zone areala* [Population ecology of the pied flycatcher in the northern zone of its area]. Nauka, Moscow, Russia, 266 p. (In Russian).
- Basile, M., Mikusiński, G., Storch, I., 2019. Bird guilds show different responses to tree retention levels. *Global Ecology and Conservation* **18** (1), e00615. <https://doi.org/10.1016/j.gecco.2019.e00615>
- Belik, V.P., 2006. Faunogeneticheskaya struktura avifauny Palearktiki [Faunogenetic structure of the palearctic avifauna]. *Zoologicheskiy zhurnal [Russian Journal of Zoology]* **85** (3), 298–316. (In Russian).
- Borcard, D., Gillet, F., Legendre, P., 2018. *Numerical Ecology with R*. Second Edition. Springer, Berlin – Heidelberg, Germany, 421 p. [https://doi.org/10.1007/978-1-4419-7976-6\\_2](https://doi.org/10.1007/978-1-4419-7976-6_2)
- DeGraaf, R.M., Yamasaki, M., 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *Forest Ecology and Management* **185** (1–2), 179–191. [https://doi.org/10.1016/S0378-1127\(03\)00254-8](https://doi.org/10.1016/S0378-1127(03)00254-8)
- Davis, C., Churchwell, R., Fuhlendorf, S., Engle, D., Hovick, T., 2016. Effect of pyric herbivory on source-sink dynamics in grassland birds. *Journal of Applied Ecology*, **53** (4), 1365–2664. <https://doi.org/10.1111/1365-2664.12641>
- Fuller, R.J., 2000. Influence of treefall gaps on distributions of breeding birds within interior oldgrowth stand in Białowieża Forest, Poland. *Condor* **102**, 267–274. [https://doi.org/10.1650/0010-5422\(2000\)102\[0267:IOTGOD\]2.0.CO;2](https://doi.org/10.1650/0010-5422(2000)102[0267:IOTGOD]2.0.CO;2)
- Gudina, A.N., 1999. *Metody ucheta gnezdiashchikhsia ptits. Kartirovanie territorii* [Methods of accounting for nesting birds. Mapping of territories]. Dikoe pole, Zaporozh'e, Ukraine, 241 p. (In Russian).
- Hanowski, J., Danz, N., Lind, J., Niemi, G., 2003. Breeding bird response to riparian forest harvest and harvest equipment. *Forest Ecology and Management* **174** (1–3), 315–328. [https://doi.org/10.1016/S0378-1127\(02\)00040-3](https://doi.org/10.1016/S0378-1127(02)00040-3)
- Hobson, K.A., Bayne, E., 2000. Breeding bird communities in boreal forest of western Canada: Consequences of “unmixing” the mixedwoods. *Condor* **102**, 759–769. [https://doi.org/10.1650/0010-5422\(2000\)102\[0759:BBCIBF\]2.0.CO;2](https://doi.org/10.1650/0010-5422(2000)102[0759:BBCIBF]2.0.CO;2)
- Jackson, M.M., Turner, M.G., Pearson, S.M., Ives, A.R., 2012. Seeing the forest and the trees: multilevel models reveal both species and community patterns. *Ecosphere* **3** (9), 1–16. <https://doi.org/10.1890/ES12-00116.1>
- Johnston, D.W., Odum, E.P., 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. *Ecology* **37** (1), 50–62.
- Jokimäki, J., Solonen, T., 2011. Habitat associations of old forest bird species in managed boreal forests characterized by forest inventory data. *Ornis Fennica* **88** (2), 57–70.
- Kamp, J., Trappe, J., Duebbers, L., Funke, S., 2020. Impacts of windstorm-induced forest loss and variable reforestation on bird communities. *Forest Ecology and Management* **478**, 118504. <https://doi.org/10.1016/j.foreco.2020.118504>
- Katoh, K., Matsuba, M., 2021. Effectiveness of nature reserves for bird conservation in urban parks in Tokyo. *Journal of Forestry Research*, **32** (5). <https://doi.org/10.1007/s11676-020-01284-7>
- Matancev, V.A., 2004. *Vliyanie fragmentatsii mestoobitanij na strukturu naseleniya i ekologiju ptits* [The impact of habitat fragmentation on the population structure and ecology of birds]. *Vestnik Udmurtskogo universiteta [Bulletin of the Udmurt University]* **1** (10), 3–38. (In Russian).
- Matantseva, M.V., Simonov, S.A., 2008. Ecological and ethological characteristics of Sylvia warbler colonies in patchy habitats on the Courland spit, Baltic Sea. *Russian Journal of Ecology* **39** (5), 373–378.
- Nazarov, A.V., 2002. *Lesovodstvenno-ekologicheskaja otsenka prokhodnykh rubok*

- v el'nikah Karelii [Forestry and ecological assessment of logging in the spruce forests of Karelia] *Agricultural Sciences PhD thesis abstract*. Saint Petersburg, Russia, 19 p. (In Russian).
- Nikolov, S. C., 2013. Bird assemblages in naturally fragmented upland forest in Pirin National Park, Bulgaria. *Acta Zoologica Bulgarica* **65** (4), 493–504.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P. et al., 2020. Vegan: community ecology package. Ordination methods, diversity analysis and other functions for community and vegetation ecologists. Version 2.5-7. Интернет-ресурс. URL: <https://cran.r-project.org/web/packages/vegan/index.html> (accessed: 03.11.2021).
- Pakkala, T., Tiainen, J., Piha, M., Kouki, J., 2018. Three-toed Woodpecker cavities in trees: A keystone structural feature in forests shows decadal persistence but only short-term benefit for secondary cavity-breeders. *Forest Ecology and Management* **413**, 70–75. <https://doi.org/10.1016/j.foreco.2018.01.043>
- Porneluzi, P.A., Brito-Aguilar, R., Clawson, R.L., Faaborg, J., 2014. Long-term dynamics of bird use of clearcuts in post-fledging period. *Wilson Journal of Ornithology* **126**, 623–832. <https://doi.org/10.1676/14-002.1>
- Ravkin, Ju.S., 2013. Jekologija i biogeografija (nekotorye soobrazhenija) [Ecology and biogeography (some considerations)]. *Principle ekologii* [Principles of Ecology] **2** (6), 69–83. (In Russian).
- R Core Team, 2020. R: A language and environment for statistical computing. Интернет-ресурс. URL: <http://www.r-project.org/index.html> (accessed: 10.06.2021).
- Shvarc, E.A., Starikov, I.V., Harlamov, V.S., Jaroshenko, A.Ju., Shmatkov, N.M. et al., 2020. Novyj vzglijad na razvitiye lesnogo kompleksa: Chast' 1. Ustoichivoe razvitiye [A new look at the development of the forest complex: Part 1. Sustainable development]. *Ispol'zovanie i ohrana prirodnnyh resursov v Rossii* [Use and protection of natural resources in Russia] **3** (163), 43–53. (In Russian).
- Shitikov, V.K., Rozenberg, G.S., 2013. Randomizacija i butstrep: statisticheskij analiz v biologii i ekologii s ispol'zovaniem R [Randomization and bootstrap: Statistical analysis in biology and ecology using R]. Cassandra, Tolyatti, Russia, 314 p. (In Russian).
- Smirnova, O.V., Bobrovsky, M.V., Khanina, L.G. (ed.), 2017. European Russian forest: their current state and features of their history. Springer, Dordrecht, Netherlands, 564 p. <https://doi.org/10.1007/978-94-024-1172-0>
- Steverding, M., Leuschner, Ch., 2002. Auswirkungen des Fichtenanbaus auf die Brutvogelgemeinschaften einer submontan-montanen Waldlandschaft (Kaufunger Wald, Nordhessen). *Forstwissenschaftliches Centralblatt* **121** (2), 83–96. (In German). <https://doi.org/10.1046/j.1439-0337.2002.00083.x>
- Thorn, S., Chao, A., Georgiev, K., Müller, J., Bässler, C. et al., 2020. Estimating retention benchmarks for salvage logging to protect biodiversity. *Nature Communications* **11** (1), 4762 (2020). <https://doi.org/10.1038/s41467-020-18612-4>
- Tomialojc, L., 1968. Podstawowe metody badan ilosowych awi fauny legowej obczarow zadrzewionych i osiedli ludzkich. *Notatki Ornitologiczne* **1–2**, 1–20. (In Polish).
- Żmihorski, M., 2010. The effect of windthrow and its management on breeding bird communities in a managed forest. *Biodiversity and Conservation* **19** (7), 1871–1882. <https://doi.org/10.1007/s10531-010-9809-x>