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# The Long-Lasting Territories of Forest Apex Predators Sustain Diverse Bird Communities throughout the Year

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**Abstract:** Apex predators, such as raptors, are used as surrogates to attain conservation objectives; however, their presence in a particular area does not necessarily mean long-term occurrence. Here we used data on long-lasting (20–40 years) territories of two generalist raptors: the diurnal Northern goshawk and the nocturnal Ural owl in deciduous and coniferous forests of southern Poland to assess their role as hotspots of bird diversity. Species richness and abundance of birds were much higher in the long-lasting territories of both apex predators than in random never-occupied sites and this pattern was common for breeding and wintering periods. These differences were more pronounced in deciduous than coniferous stands. Rare bird species (e.g., annexed in the Bird Directive of the European Parliament and of the Council on the conservation of wild birds such as some woodpeckers and flycatchers) were found to be particularly associated with long-lasting territories of raptors. Long-lasting territories were also characterized by greater forest habitat quality (e.g., higher number of old trees and deadwood) with lower management intensity. These results strongly point to the role of long-lasting territories of raptors as surrogates of biodiversity. Such territories, if known in forests, could be excellent for the designation of protected areas or logging there should at least be reduced to allow for the continuous breeding of apex predators and associated bird assemblages.

**Keywords:** northern goshawk; Ural owl; *Accipiter gentilis*; *Strix uralensis*; surrogates; flagship species; biodiversity hotspots; forest management

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## 1. Introduction

Predatory birds have been proposed as a good indicator of biodiversity [1–3]. Bird communities were found to be more species-rich and numerous within territories of apex predators such as raptors (naming both diurnal and nocturnal species as raptors) [4–6]. Bird assemblages are selected as a proxy of biological diversity due to the high species richness, abundance and association of various bird taxa to the quality of required habitats and their fast response to changes in the environment, both natural and caused by humans [7–9]. The concept of using charismatic species as surrogates for biological diversity was proposed a long time ago, and later either supported by dedicated studies or rejected by other research [10,11]. Raptors (diurnal birds of prey and owls) are particularly valuable as such surrogates due to numerous features making them appropriate "tools" in assessing overall biodiversity (and usually also habitat quality), e.g., relatively large body sizes and characteristic appearance allowing their detection and identification, known habitat requirements often restricted to natural habitats, and acting on the top of food chains, which makes raptors keystones, but also vulnerable to environmental alterations (particularly those caused by humans). Another reason for the use of raptors in conservation biology is that many of these species are icons (flagships) of wildness, e.g., eagles or large owls [8,12,13]. There are exemplary studies on both diurnal raptors and owls testing this conception on bird communities. Among European taxa, several Accipitridae and Strigidae have been examined in this respect. Such studies concerned both relatively rare and large species (such as eagles, *Aquila* spp., or Eurasian eagle owl, *Bubo bubo*), as well as moderately common and medium-size species (e.g., northern goshawks, *Accipiter gentilis*, Ural owls, *Strix uralensis*) [12–14]. However, all these studies considered only contemporary breeding sites identified either shortly before (e.g., a year earlier) overall bird inventory or in the same season of bird inventory. Diurnal raptors and owls could occupy the same site for just a single season but could also be present in some territories for a longer period of time [15,16]. It is probable that long-term territories are mostly localized in areas of permanent conditions (not affected by some serious natural or man-made changes, which prevent constant breeding of raptors) [17]. On the contrary, contemporary breeding sites could be situated in various areas, and some of them do not need to be of the best quality. Therefore, bird communities in long-term and temporary breeding sites of raptors do not need to be similar [18,19]. Usually, it is unknown if raptor territories are only contemporary or long lasting due to missing information from previous years. This could be a serious drawback of studies using raptors as surrogates of biodiversity. Unfortunately, data about the distribution of raptors over longer periods of time are scarce and limited to only some areas being monitored periodically for various purposes (research, conservation, demographic, etc.). The majority of studies on biodiversity in apex predator territories concern only breeding period—mostly diversity of breeding bird communities—whereas knowledge on biodiversity in other periods of the year is scarce (e.g., [20]), and there are no studies dealing with both—breeding and wintering biodiversity. Raptor territories as indicators of biodiversity should show similar patterns over a year [21,22]; therefore, studies on wintering and breeding bird communities could verify that assumption. Another limitation of studies on raptors as surrogates of biodiversity is that they are mostly executed for only one type of habitat (e.g., some type of forest). However, habitat generalists could be considered as good indicators especially if their presence reflects high biodiversity in various types of habitats, which are occupied by these raptors [12]. It is probable that the diversity of birds is high in territories of some raptors only in particular environmental conditions. Studies on raptors as surrogates of biodiversity are usually limited to only selected species, whereas multiple-raptor species studies are infrequent. Even these studies which consider more taxa usually test different raptor species in various environmental conditions or areas, so they really study the utility of each of these species separately [23–25]. Consequently, for some area or habitat they are missing information if more than one raptor species could be a good indicator for biodiversity and if patterns for various diurnal or nocturnal predatory birds are congruent. It could be expected that the simultaneous use of more than one surrogate species should increase the power of biodiversity prediction and consequently be better for determining areas deserving protection [26,27].

Here, we used information about the localization of long-term territories of two medium-size apex predators that are moderately common (diurnal northern goshawk and nocturnal Ural owl) known from two types of forests (deciduous and coniferous), to verify following hypotheses: (i) long-lasting breeding sites of apex predators (e.g., the northern goshawk and Ural owl) are situated in forest stands characterized by a higher quality of habitats and less affected by forest management; (ii) long-term territories of apex predators shelter a higher diversity of birds than random sites in never-occupied forests; (iii) raptor sites over time constantly support a high diversity of birds over a year (during wintering and breeding periods); and (iv) select generalist apex predators are indicators of a high biodiversity of birds regardless of forest habitat type.

## 2. Materials and Methods

### 2.1. Study Area

Forests selected for this study had to be restricted to areas with available former data about the distribution of breeding sites of northern goshawks and Ural owls. Such data were available from the Niepołomice Forest and the surrounding forest complexes in southern Poland. The Niepołomice Forest is a large continuous forest area in the lowland part of Małopolska Voivodeship in southern Poland. It covers approximately 110 km$^2$, with 30% of the area forested by oak-dominated deciduous forests (*Tilio-carpinetum*) and 70% of the area forested by pine-dominated coniferous woods (*Pino-quercetum*) with an admixture of birches. Additionally, data were gathered from environmentally similar oak-dominated deciduous forests in areas surrounding Niepołomice Forest (approx. 30 km$^2$ in total). All these forests are close to each other (nearest distance of only approx. 5 km) and are located in the same climatic and environmental conditions. The joint use of data from the Niepołomice Forest and the surrounding woods was necessary to have substantial and comparable datasets from coniferous and deciduous forests.

### 2.2. Historic and Contemporary Distribution

Northern goshawks and Ural owls have been objects of numerous faunistic, ecological and biological research undertaken on their populations in the Niepołomice Forest and adjacent woods over the last 20–40 years (depending on the forest). Goshawk territories were determined from the previous works of Czuchnowski [28], Bielański [29], Kajtoch [30], and Wiehle et al. [31]. Ural owl territories were taken from the studies of Czuchnowski [32], Kus [33], Kajtoch [34], Matysek et al. [35] and Wiehle and Sobas [36]. Finally, among the dozens of breeding sites determined for these birds over the last few years, 24 sites for goshawks and 22 for Ural owls were determined and selected based on the studies listed above (nearly half in deciduous and coniferous stands). For the analyses, we selected 20 sites for each species (10 in deciduous and 10 in coniferous stands for each), avoiding sites, which are close to forest areas being under wood logging in the year of bird inventory (Table S1, Figures S1 and S2). These numbers could not be larger as there are not many sites where either goshawks or owls are known to breed over longer periods. Many territories were determined only in former years and then were abandoned or were just found in recent years (but were unoccupied previously). These breeding sites were determined using the following criteria: (i) localization was known from a particular area over at least 20 years; (ii) there was no detected break in breeding over that period based on available data; (iii) the territory was confirmed as occupied during the latest inventories in 2019–2021 (authors own data). The problem was that most of the older studies did not provide information about the accurate localization of nests, but instead presented a rough localization of territories (areas of approx. 1 km$^2$ in size). Goshawks build a few nests in the territory used interchangeably, whereas Ural owls utilize either large tree cavities or raptors' nests, depending on their availability [28,32]. Both goshawks and Ural owls are known to occupy various nests in their territories in consecutive breeding periods [28,32]. Considering the above limitations and the breeding biology of these birds, this study focused on the territory, not exact nesting sites. The localization of breeding sites was determined from publications assuming a circle with a 0.56-km radius (an approx. area of 1 km$^2$).

Additionally, 20 sites (also circles 1 km$^2$ in size) were randomly selected in the forest area, where no breeding site of either goshawk or Ural owl was detected over all years of study (10 sites in deciduous and 10 in coniferous woods) (control random sites) (Table S1, Supplementary Materials File S3). That random selection was restricted to only mature forest patches, where at least 80% of the forested area constituted woods of 80 years (in case of pine) or 100 years (in case of oak). To avoid spatial autocorrelation, the external borders of these random sites were situated at a distance of at least 2 km from the borders of the nearest long-term territory and at least 1 km from the nearest other random site.

### 2.3. Bird Survey

The number of wintering and/or breeding birds (depending on time of year) was counted within each goshawk-occupied, owl-occupied, or control site. Bird inventories were made in a non-invasive way (birds were not captured or disturbed); therefore, no special permissions were required.

Wintering birds were counted three times in December 2020 and in January and February 2021 (between the 10th and 20th day of each month). Birds were recorded (species and number of individuals for each species) along 1-km transects, crossing sites longitudinally. Observers counted all birds seen and heard along forest routes to facilitate pace (approx. 2 km/h), and to reduce disturbance and bird movement (which could result in multiple counts of the same individuals or flocks). Birds were counted from one hour after dusk (approx. 8:00 a.m. in December and January, and 7:00 a.m. in February) to one hour before dawn (approx. 3:00 p.m. in December and January, and 4:00 p.m. in February), and only in good weather conditions (no snow, rain, or strong winds) regardless of temperature. For analyses, the maximum number of birds of a particular species observed on the transect was calculated to avoid the multiple use of sedentary birds in forests (e.g., flocks of passerines that are nomadic in winter).

Breeding birds were counted with the point count method [37,38]. At each site, two points were determined approx. 300 m away from the northern and southern sides of the circle, and 500 m from each other (within the circle). Two points were used to increase the detectability of various birds present within a site (approx. 1 km2), since a single point (e.g., designed in the center of site) could not be representative for overall bird assemblage present in that site. More points were not selected due to the time-consuming nature of counts at numerous points (120 points over approx. 140 km$^2$ of forest area were designed already). At each point, birds were recorded within a radius of 100 m by hearing territorial and contact voices (mostly signs of territorial males or drumming, in the case of woodpeckers). All birds seen displaying territorial, mating, or breeding behavior were also recorded. Any moving birds (flying above the trees) were not considered. Moreover, diurnal raptors (Accipitriformes and Falconiformes) and storks (Ciconiformes) were not included, as they have large territories and were mostly observed passing over the point counted. Nocturnal birds (especially other owls, Strigidae, and nightjars, *Caprimulgus europaeus*) were also not considered, as the count methodology did not allow for their proper detection. All other bird species were counted and used in the analyses. Birds were counted three times between 20 March–10 April, 10-20 April, and 20 May–10 June. These dates were settled to cover all species having various breeding activity, including early breeders (mostly sedentary species) and late breeders (long-distance migrants). Counts were performed only in good weather conditions (no rain or wind) between dusk and 4–5 h after dusk (to cover the peak of daily bird activity). For the analyses, the maximum number of territorial birds of a particular species recorded in two points localized within a particular site were calculated (summarized) from data collected during three counts. Consequently, data from single point counts (within a site) were not considered as separate to avoid a spatial autocorrelation of data.

### 2.4. Bird Indices

Two basic measures of bird diversity were adopted, both for wintering and breeding assemblages: (i) species richness (RICHNESS; N), (ii) abundance (number of wintering individuals or breeding males/pairs/territories, depending on the species (ABUNDANCE; N). Additionally, the presence of bird species annexed in the Bird Directive of the European Union was used as a separate metric (NATURA; N), based on the “Bird Directive” of the EU (Directive 2009/147/EC of the European Parliament and of the Council, on the conservation of wild birds). This was added to biodiversity metrics in order to include information about the rarest bird species, which are of special concern in the EU.

### 2.5. Environmental Variables

This work does not aim to analyze details about the habitat requirements of goshawks or Ural owls, as this is the subject of a number of published research studies, including those on the populations examined in the Niepołomice Forest and adjacent woods [28,32,39]. This previous research pointed out that there are no substantial differences in the habitat requirements of these two apex predators: both of them select only mature forests for breeding, which are less affected by contemporary forest management. However, for a proper understanding of the reasons for the observed biodiversity patterns (with respect to overall bird assemblages), several basic environmental features were inventoried. In each long-term territory and random site identified within a circle of 1 $km^2$, a 1-km transect was designed (the same as for wintering birds). Each site was already assigned to two types of woods: deciduous (oak-dominated) vs. coniferous (pine-dominated) (WOOD; 0/1). Along that transect, the following features were quantified: (i) number of veteran trees (OLDTREES; N) (old-growth trees of DBH larger than 80 cm, in the case of pines, birches and alders, or 100 cm, in the case of oaks and other deciduous trees); (ii) number of snags (standing dead trees of DBH larger than 20 cm) and logs (downed, dead trees with a middle diameter larger than 20 cm) (DEADWOOD; N); number of fresh stumps (STUMP; N) left after logging; and (iii) share of clear-cuts (CLEARCUTS; %) within a 100-m patch along the transect. OLDTREES and DEADWOOD were selected to reflect the naturalness of forest patches (presence of old-growth trees and wood of dead trees), whereas STUMPS and CLEARCUTS for an estimation of wood management intensity. The Spearman rank correlation was used to assess collinearity among environmental variables; however, only two pairs of variables were moderately correlated (DEADWOOD and OLDTREES, Rho = 0.41; CLEARCUTS and STUMPS, Rho = 0.51).

### 2.6. Statistical Analyses

To assess the efficiency of bird surveys, species rarefaction curves for all forests and for each group (goshawk, Ural owl and control sites, each independently for wintering and breeding assemblages) were plotted in EstimateS 9.1 [40] using the nonparametric method (Chao 1 estimator) and increasing the empirical sample set by a factor of two. Prior to analyses normality of data (bird diversity metrics) was checked (all analyzed data have a normal distribution, similar variance, and are independent within each analysis). Statistical differences for bird diversity metrics and environmental variables between groups of sites (goshawk or Ural owl or control sites x deciduous or coniferous) were assessed using the Mann–Whitney Z-test. Overall differences of bird diversity metrics and environmental variables among all groups of census points ((goshawk or Ural owl or control sites) x (coniferous and deciduous)) were tested using Analysis of Variance (ANOVA). The importance of environmental variables (described in Section 2.4)) for bird diversity metrics (RICHNESS, ABUNDANCE, NATURA) was assessed with univariate models using Wald statistics. This was performed separately for goshawk and Ural owl plots (each independently for wintering and breeding periods).

Binomial linear regression was used to assess the relation between the presence of raptors (either goshawk or Ural owl) and bird diversity indices; here, basic metrics were used, such as RICHNESS and ABUNDANCE (separately for wintering and breeding assemblages).

Generalized Linear Models (GLMs) explaining selected bird diversity indices (RICHNESS and ABUNDANCE) were only constructed with the presence of raptor species (goshawk and Ural owl) and type of wood (WOOD). GLMs were built for joint data from the goshawk, owl and control random sites. The resulting models were then ranked by increasing AIC values and Akaike weight (w) [41,42]. Only the best models (with $\Delta$AIC < 2) were presented. Separate models were built using RICHNESS and ABUNDANCE and NATURA as the response variables (separately for breeding and wintering birds).

We used canonical correspondence analysis (CCA), a direct ordination technique that seeks to explain variation in avian composition in terms of the measured environmental variables. We used biplot scaling and interspecies distances in the ordination. CCA was implemented to indicate raptor (goshawk and Ural owl) species-specific relations toward the abundance of other birds (expressed as either number of wintering individuals or number of territorial birds during the breeding period) and selected environmental characteristics (listed in Section 2.4)). We used only bird species with at least 5 individuals recorded during the winter period and at least 5 territorial sites recorded during the breeding period.

Analyses were conducted using R 4.2.1 [43] (linear regression, Wald statistics, GLMSs), STATISTICA 12.0 [44] (basic statistics, ANOVA) and PAST 3.06 [45] (CCA).

## 3. Results

### *3.1. Bird Diversity Metrics in Raptor Territories*

During winter counts, 39 bird species were recorded (35 in hawk—deciduous and 23 in hawk—coniferous, 37 in owl—deciduous and 25 in owl—coniferous, 33 in control random—deciduous and 31 in control random—coniferous) (Table S2, Figure 1). A total of 2643 individuals of birds were recorded during wintering counts (633 in hawk—deciduous and 396 in hawk—coniferous, 610 in owl—deciduous and 323 in owl—coniferous, 359 in control random—deciduous and 322 in control random—coniferous) (Table S2, Figure 1).

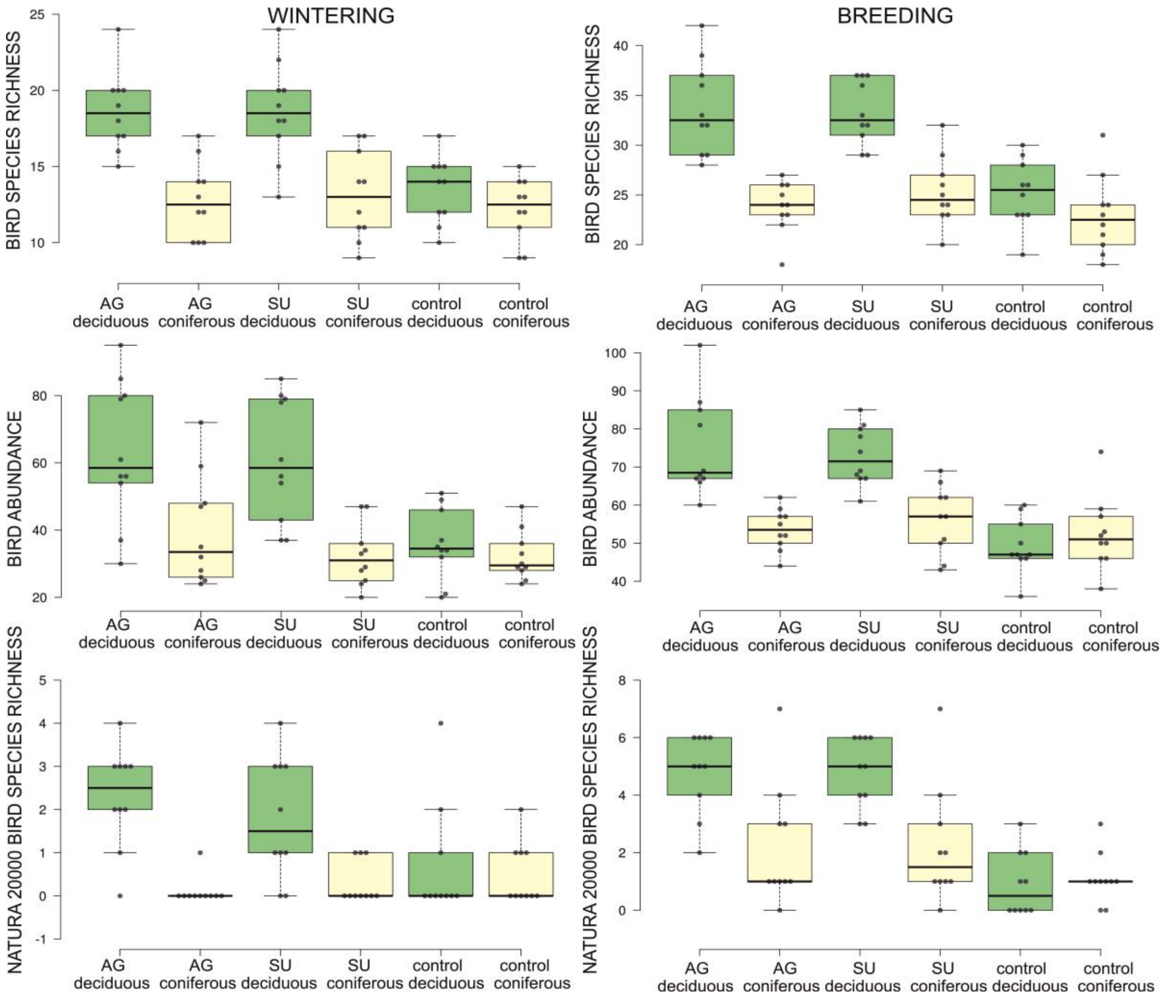


**Figure 1.** Box−plots showing differences in bird diversity metrics (RICHNESS—total species richness, ABUNDANCE—number of wintering individuals or breeding pairs, NATURA—species richness of birds annexed in Bird Directive of UE) in plots localized in long−lasting territories of goshawks (AG), Ural owls (SU) and control random sites. Medians, 95% confidence intervals, and minimum with maximum values are presented. Dots represent samples – their number is equal to number of samples with particular values for selected bird metric.

The breeding community was constituted by 71 taxa (61 in hawk—deciduous and 54 in hawk—coniferous, 59 in owl—deciduous and 56 in owl—coniferous, 50 in control random—deciduous and 43 in control random—coniferous) (Table S2, Figure 1).

In total, 3631 breeding birds were counted at all designed points (752 in hawk—deciduous and 553 in hawk—coniferous, 730 in owl—deciduous and 578 in owl—coniferous, 493 in control random—deciduous and 525 in control random—coniferous) (Table S2, Figure 1).

Four bird species annexed in the Bird Directive were recorded in the winter counts: hazel grouse, *Bonasia bonasia*, middle spotted woodpecker, *Dendrocoptes medius*, black woodpecker, *Dryocopos martius*, and grey-headed woodpecker, *Picus canus*. These species were recorded only in deciduous stands except for the black woodpecker, which was also present in coniferous stands. The majority of observations of these species were recorded in goshawk or Ural owl territories, whereas only single middle spotted and black woodpeckers were found in control sites. Eight bird species annexed in the Bird Directive were found in the breeding period. Except for those listed in the winter counts, there were: white-backed woodpecker, *Dendrocopos leucotos*, red-breasted and collared flycatchers, *Ficedula parva* and *F. albicollis*, and woodlark *Lullula arborea*. These birds were recorded 2–4 times more often in deciduous than coniferous stands, and some were totally absent in coniferous woods. These rare bird species were also found on average 2–2.5 times more often in raptor sites than in random sites (Table S2, Figure 1).

### *3.2. Diverity of Birds in Goshawk and Owl Territories*

Wintering bird assemblages differed significantly in the long-term territories of goshawks and control random sites with respect to RICHNESS and ABUNDANCE; however, the values of NATURA were similar. The same was reported for owl sites (Table 1 and Table S3).

**Table 1.** Results of statistical comparison of bird diversity metrics between groups of plots (occupied vs control by goshawks or Ural owls, separately for two periods: winter and breeding).

| Species | Period | Metric | Z | *p* |
|---|---|---|---|---|
| goshawk | wintering | RICHNESS | 2.46 | 0.014 |
| | | ABUNDANCE | 2.50 | 0.012 |
| | | NATURA | 1.33 | 0.184 |
| | breeding | RICHNESS | 2.47 | 0.014 |
| | | ABUNDANCE | 3.28 | 0.001 |
| | | NATURA | 3.64 | 0.000 |
| Ural owl | wintering | RICHNESS | 2.41 | 0.016 |
| | | ABUNDANCE | 1.91 | 0.056 |
| | | NATURA | 1.27 | 0.204 |
| | breeding | RICHNESS | 3.12 | 0.002 |
| | | ABUNDANCE | 3.45 | 0.001 |
| | | NATURA | 3.78 | 0.000 |

During breeding, all bird diversity indices were significantly different between owl sites and control random sites, and the same for goshawk sites and control random sites (Table 1 and Table S3). ANOVA revealed significant differences for all selected groups, both in the wintering and breeding periods and in all biodiversity metrics except NATURA, measured for the wintering period (Table 2 and Table S3).

Binomial linear regression showed that the occurrence of both goshawks and Ural owls substantially increased RICHNESS and ABUNDANCE of bird species. That effect was observed in both periods, wintering (F = 8.28, $p$ = 0.006 for goshawk vs. bird richness; F = 10.69, $p$ = 0.002 for goshawk vs. bird abundance; F = 8.36, $p$ = 0.006 for Ural owl vs. bird richness; F = 6.34, $p$ = 0.016 for Ural owl vs. bird abundance) and breeding (F = 8.32, $p$ = 0.006 for goshawk vs. bird richness; (F = 12.69, $p$ = 0.001 for goshawk vs bird abundance; F = 13.41, $p$ = 0.000 for Ural owl vs. bird richness; (F = 17.59, $p$ = 0.000 for Ural owl vs. bird abundance), however, it is stronger for breeding bird assemblages (Figure 2).

**Table 2.** Analysis of Variance calculated among all defined groups of plots (goshawk vs. Ural owl vs. control).

| Metric | ANOVA | *p* |
|---|---|---|
| | wintering | |
| RICHNESS | 10.9 | 0.004 |
| ABUNDANCE | 15.5 | 0.004 |
| NATURA | 18.4 | 0.000 |
| | breeding | |
| RICHNESS | 16.2 | 0.000 |
| ABUNDANCE | 7.1 | 0.029 |
| NATURA | 2.3 | 0.323 |

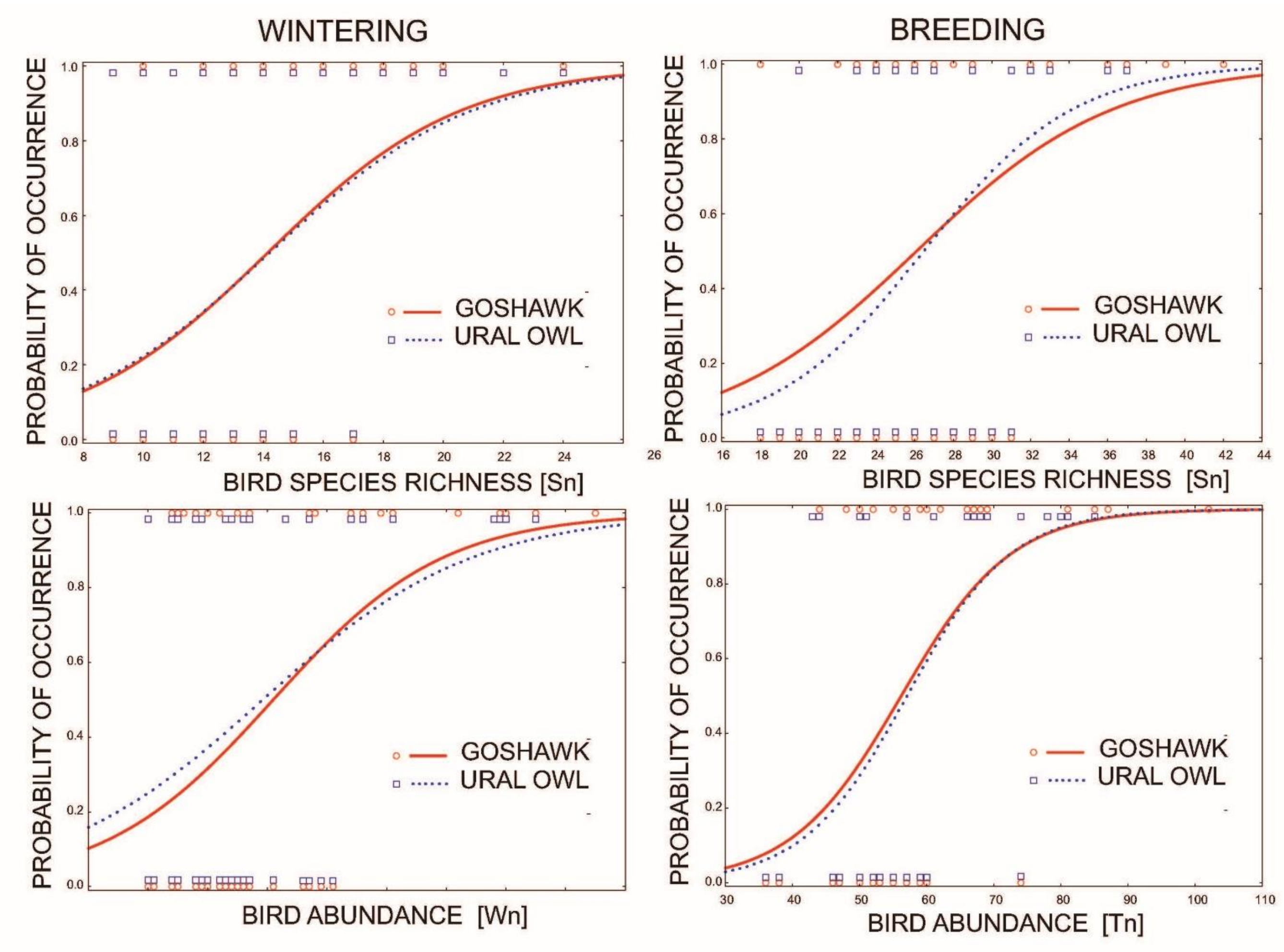


**Figure 2.** Linear regression curves showing dependencies between occurrence of long-lasting territories of goshawks or Ural owls (0—absence, 1—100% certain occurrence) and bird species RICHNESS and ABUNDANCE (both measured for wintering and breeding periods). sN—number of species, wN—number of wintering individuals, tN—number of territorial birds.

*3.3. Environmental Variables in Raptor Territories*

OLDTREES were more numerous in goshawk sites than owl sites (two-fold) and control random sites (nearly three-fold). DEADWOOD was similarly frequent in goshawk and owl sites, whereas in control random sites it was 2.2 times less numerous. CLEARCUTS were almost absent in goshawk and owl sites, whereas in control random sites they covered on average 6%. STUMPS were 1.2 times more frequent in control random sites than in goshawk sites but were two times less frequent in control sites than in Ural owl sites (Tables S3 and S4).

### 3.4. Diverity of Birds in Relation to Environment and Raptor Presence

Bird diversity indices calculated for wintering assemblages were found to be mostly dependent on WOOD. An exception in models constructed for goshawk sites was NATURA, which was also found to be dependent on the presence of goshawks. WOOD was also the only significantly different variable for breeding RICHNESS and NATURA, whereas ABUNDANCE was determined by goshawks (Table 3).

**Table 3.** Statistical significance of univariate models constructed for selected environmental variables and raptor occurrence (goshawks or Ural owls) as explanatory variables for three bird diversity metrics (species RICHNESS, ABUNDANCE, and species annexed in Bird Directive of UE—NATURA).

| | **Wald** | ***p*** | **Wald** | ***p*** | **Wald** | ***p*** |
|---|---|---|---|---|---|---|
| **Diversity Metrics/Variables** | **RICHNESS** | | **ABUNDANCE** | | **NATURA** | |
| goshawk wintering | | | | | | |
| Intercept | 1089.8 | 0.00 | 6291.9 | 0.00 | 2.3 | 0.13 |
| WOOD | 6.8 | 0.01 | 29.6 | 0.00 | 10.3 | 0.00 |
| OLDTREES | 0.3 | 0.56 | 0.0 | 0.88 | 0.1 | 0.72 |
| DEADWOOD | 0.4 | 0.53 | 0.1 | 0.75 | 0.4 | 0.51 |
| STUMPS | 0.1 | 0.73 | 0.2 | 0.68 | 0.3 | 0.56 |
| CLEARCUTS | 0.2 | 0.65 | 1.2 | 0.28 | 0.2 | 0.62 |
| goshawk | 3.3 | 0.07 | 61.9 | 0.00 | 1.3 | 0.26 |
| goshawk breeding | | | | | | |
| Intercept | 3042.3 | 0.00 | 10161.5 | 0.00 | 2.2 | 0.14 |
| WOOD | 5.6 | 0.02 | 1.1 | 0.29 | 5.6 | 0.02 |
| OLDTREES | 0.3 | 0.59 | 3.2 | 0.08 | 1.9 | 0.17 |
| DEADWOOD | 0.0 | 0.88 | 0.1 | 0.74 | 3.4 | 0.07 |
| STUMPS | 0.0 | 0.95 | 0.0 | 0.86 | 0.6 | 0.42 |
| CLEARCUTS | 0.0 | 0.97 | 0.5 | 0.48 | 2.8 | 0.09 |
| goshawk | 3.7 | 0.05 | 11.0 | 0.00 | 17.1 | 0.00 |
| Ural owl wintering | | | | | | |
| Intercept | 10159.1 | 0.00 | 3.7 | 0.06 | 3.7 | 0.06 |
| WOOD | 0.2 | 0.66 | 4.6 | 0.03 | 4.6 | 0.03 |
| OLDTREES | 2.4 | 0.12 | 0.4 | 0.54 | 0.4 | 0.54 |
| DEADWOOD | 0.1 | 0.74 | 0.8 | 0.37 | 0.8 | 0.37 |
| STUMPS | 0.2 | 0.69 | 0.4 | 0.54 | 0.4 | 0.54 |
| CLEARCUTS | 0.2 | 0.65 | 1.0 | 0.33 | 1.0 | 0.33 |
| Ural owl | 17.2 | 0.00 | 15.9 | 0.00 | 15.9 | 0.00 |
| Ural owl breeding | | | | | | |
| Intercept | 3020.2 | 0.00 | 10159.1 | 0.00 | 3.7 | 0.06 |
| WOOD | 4.0 | 0.05 | 0.2 | 0.66 | 4.6 | 0.03 |
| OLDTREES | 0.1 | 0.76 | 2.4 | 0.12 | 0.4 | 0.54 |
| DEADWOOD | 0.1 | 0.79 | 0.1 | 0.74 | 0.8 | 0.37 |
| STUMPS | 0.1 | 0.74 | 0.2 | 0.69 | 0.4 | 0.54 |
| CLEARCUTS | 0.1 | 0.81 | 0.2 | 0.65 | 1.0 | 0.33 |
| Ural owl | 7.8 | 0.01 | 17.2 | 0.00 | 15.9 | 0.00 |

Wintering bird diversity indices were dependent only on WOOD in models constructed for owl sites versus control random sites, and only RICHNESS was determined by owls. In the case of the breeding period, models depended on WOOD and goshawk for all indices (Table 3).

GLMs built on all data (those collected in goshawk, owl, and control random sites) (Table 4) showed that for the winter period, the best models constructed for RICHNESS included: goshawk presence, owl presence, WOOD, OLDTREES, DEADWOOD, and STUMPS, whereas for ABUNDANCE: goshawk presence, owl presence, WOOD, CLEARCUTS, and STUMPS. GLMs built for the breeding period pointed out that the following variables mostly contributed to the explanation of RICHNESS (goshawk presence, owl presence, WOOD, OLDTREES and CLEARCUTS), and ABUNDANCE (goshawk presence, owl presence, OLDTREES and DEADWOOD). The best GLMs constructed for the wintering NATURA metric included: goshawk presence or owl presence, WOOD type, and DEADWOOD, whereas for the breeding NATURA metric: goshawk presence, owl presence, OLDTREES, CLEARCUTS, and STUMPS).

**Table 4.** Sets of Generalized Linear Models explaining bird diversity metrics calculated for wintering and breeding periods based on selected environmental variables and occurrence of apex predators (goshawks and Ural owls). AIC—Akaike Information Criterion, *w*—AIC weight. Only models with ΔAIC < 2 are presented.

| Model | AIC | *w* |
|---|---|---|
| period: wintering explained metric: RICHNESS | | |
| OLDTREES + STUMPS + DEADWOOD + goshawk + Ural owl + WOOD | 302.4 | 0.2 |
| STUMPS + goshawk + Ural owl + WOOD | 302.6 | 0.2 |
| OLDTREES + DEADWOOD + goshawk + Ural owl + WOOD | 303.7 | 0.1 |
| OLDTREES + STUMPS + goshawk + Ural owl + WOOD | 303.8 | 0.1 |
| goshawk + Ural owl + WOOD | 303.9 | 0.1 |
| OLDTREES + CLEARCUTS + DEADWOOD + goshawk + Ural owl + WOOD | 304.2 | 0.1 |
| OLDTREES + STUMPS + CLEARCUTS + DEADWOOD + goshawk + Ural owl | 304.3 | 0.1 |
| Intercept | 383.7 | 0.0 |
| period: wintering metric: ABUNDANCE | | |
| STUMPS + CLEARCUTS + goshawk + Ural + owl | 526.6 | 0.3 |
| STUMPS + goshawk + Ural owl + WOOD | 526.7 | 0.2 |
| OLDTREES + STUMPS + CLEARCUTS + goshawk + Ural owl + WOOD | 527.7 | 0.1 |
| OLDTREES + STUMPS + goshawk + Ural owl + WOOD | 527.8 | 0.1 |
| STUMPS + DEADWOOD + goshawk + Ural owl + WOOD | 528.3 | 0.1 |
| STUMPS + CLEARCUTS + DEADWOOD + goshawk | 528.4 | 0.1 |
| Intercept | 677.8 | 0.0 |
| period: breeding metric: RICHNESS | | |
| OLDTREES + Ural owl + WOOD | 296.1 | 0.3 |
| OLDTREES + goshawk + Ural owl | 297.5 | 0.1 |
| OLDTREES + CLEARCUTS + Ural owl | 297.8 | 0.1 |
| OLDTREES + DEADWOOD + Ural owl | 297.8 | 0.1 |
| DEADWOOD + Ural owl + WOOD | 298.0 | 0.1 |
| OLDTREES + STUMPS + Ural owl + WOOD | 298.1 | 0.1 |
| Intercept | 319.7 | 0.0 |
| period: breeding metric: ABUNDANCE | | |
| OLDTREES + Ural owl | 383.2 | 0.3 |
| OLDTREES + goshawk + Ural owl | 383.7 | 0.2 |
| OLDTREES + DEADWOOD + Ural owl | 384.2 | 0.2 |
| OLDTREES + DEADWOOD + goshawk + Ural owl | 384.2 | 0.2 |
| OLDTREES + Ural owl + WOOD | 384.7 | 0.1 |
| OLDTREES + goshawk + Ural owl + WOOD | 384.8 | 0.1 |
| OLDTREES + CLEARCUTS + Ural owl | 384.9 | 0.1 |
| OLDTREES + STUMPS + Ural owl | 385.1 | 0.1 |
| Intercept | 448.0 | 0.0 |

**Table 4.** *Cont.*

| Model | AIC | *w* |
|---|---|---|
| period: wintering metric: NATURA | | |
| goshawk + WOOD | 118.0 | 0.3 |
| DEADWOOD + goshawk + WOOD | 119.1 | 0.1 |
| goshawk + Ural owl + WOOD | 119.3 | 0.1 |
| OLDTREES + goshawk + WOOD | 119.5 | 0.1 |
| STUMPS + goshawk + WOOD | 119.6 | 0.1 |
| DEADWOOD + WOOD | 119.7 | 0.1 |
| Intercept | 135.9 | 0.0 |
| period: breeding metric: NATURA | | |
| OLDTREES + STUMPS + CLEARCUTS + goshawk + Ural owl | 308.3 | 0.3 |
| OLDTREES + STUMPS + goshawk + Ural owl | 308.7 | 0.2 |
| OLDTREES + STUMPS + goshawk + Ural owl + WOOD | 309.5 | 0.1 |
| OLDTREES + STUMPS + CLEARCUTS + goshawk + Ural owl + WOOD | 309.9 | 0.1 |
| OLDTREES + STUMPS + CLEARCUTS + DEADWOOD + goshawk + Ural owl | 310.3 | 0.1 |
| Intercept | 1136.5 | 0.0 |

According to CCA (Figure 3), the occurrence of goshawks and Ural owls was associated with DEADWOOD and OLDTREES, whereas control random sites tended to be closer to CLEARCUTS and STUMPS. Most wintering bird species tended to be associated with goshawks and Ural owls, including some rare species such as middle spotted, grey-headed and black woodpeckers, whereas some generalists were opposed to these two apex predators. A very similar pattern was found for breeding bird assemblages, where many species associated with old-growth forests and deadwood (rare e.g., woodpeckers and flycatchers, hazel grouse) were associated with goshawks and Ural owls, whereas some generalists and open woodland species (e.g., green woodpecker, *Picus viridis*, pheasant, *Phasianus colchicus*) avoided the proximity of apex predators.

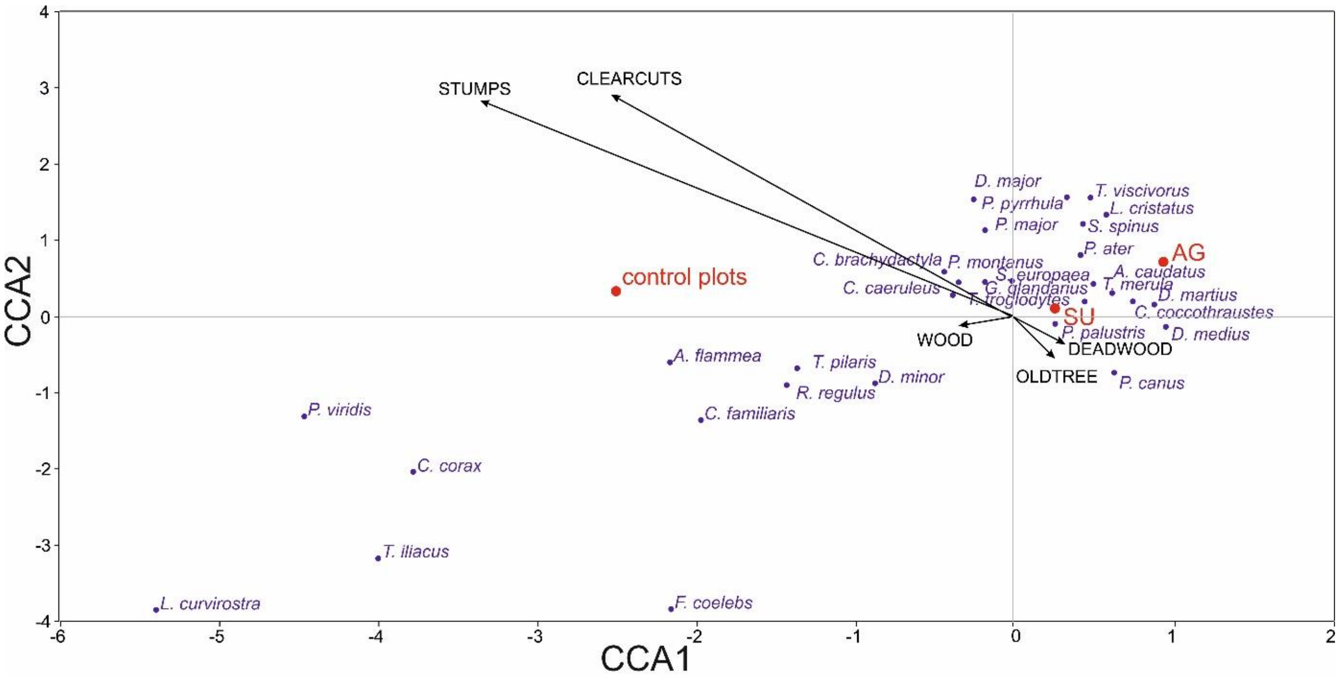


**Figure 3.** *Cont.*

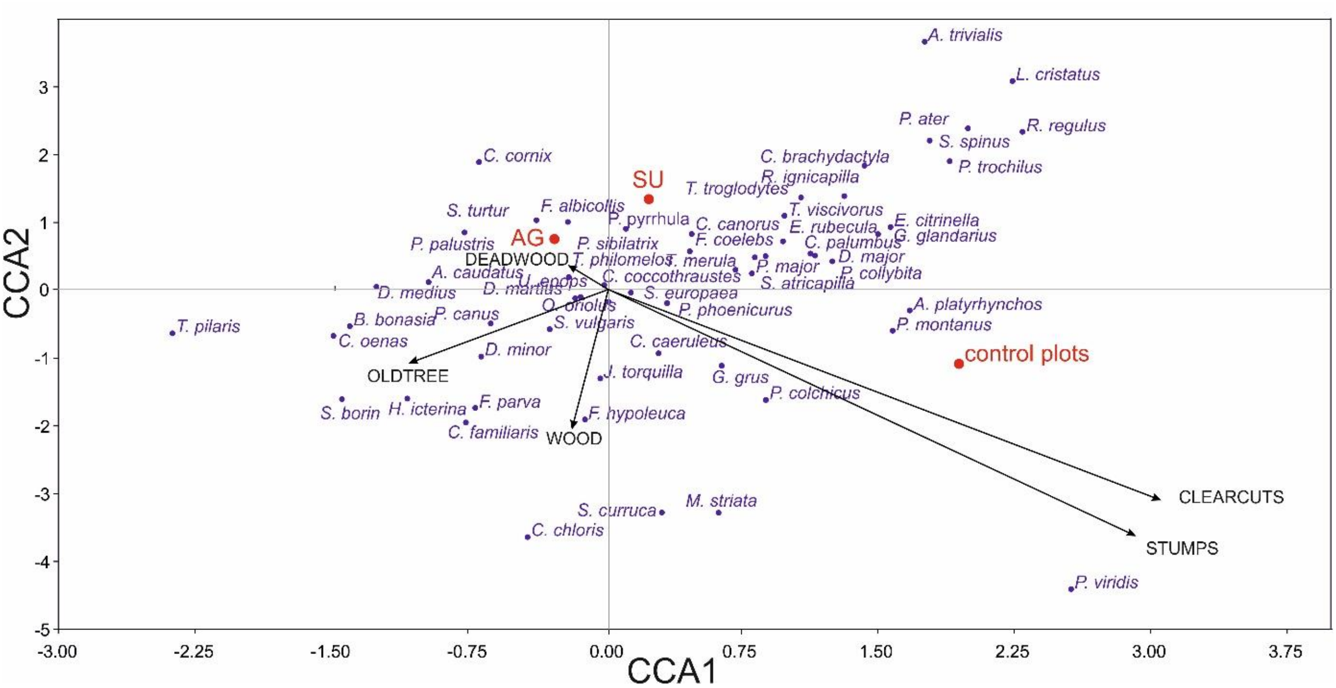


**Figure 3.** Correspondence Canonical Analysis plots showing the ordination of bird species wintering (above) or breeding (below) in examined plots along the first two axes and their correlation with occurrence of goshawks (AG), Ural owls (SU) and control plots, as well as selected environmental variables (WOOD—deciduous vs. coniferous, OLDTREES—number of veteran trees, DEADWOOD—number of large snags and logs, CLEARCUTS—area of clear−cuts and STUMPS—number of fresh stumps). The arrows represent the environmental variables selected, and the dots represent the bird species. The direction of the arrows indicates their correlation with an axis or a particular species. The length of the arrow represents the size of the effect, the longer the arrow the stronger the relationship of that variable with the community.

## 4. Discussion

This study supports the hypothesis that Northern goshawks and Ural owls tend to occupy forest areas characterized by highly diverse bird assemblages over periods of years. It is the first study to examine the long-lasting territories of these apex predators with respect to their association with biodiversity and habitat quality. Indeed, previous research pointed out that either goshawk or Ural owl territories (or nesting sites) are often localized in forests with a high diversity of birds [46,47] or other forest organisms (e.g., arboreal fungi [27]); however, all those previous studies were built on raptor data taken only from a particular period of time, mostly shortly preceding the study on biodiversity. Therefore, these previous studies could not answer the question of whether biodiversity differences observed between raptor-occupied sites and some random or control sites are associated with the presence of raptors breeding there over years, or simply with contemporary conditions of the forest environment or temporary lack of some management actions. It is known that both goshawks and Ural owls are associated with mature stands in temperate or boreal forests [12,39], and that they avoid areas that are heavily logged [48–51]. However, there are also studies showing that these raptors could breed in managed stands (e.g., [52]) but some of these territories are temporary or vanish after logging, or they move to other forest patches. Finally, most of the other studies on habitat requirements and the utility of goshawks or Ural owls as surrogates for biodiversity were made in boreal forests, particularly in Scandinavia [27,46,47,53]. These coniferous forests are far from natural and mostly transformed into spruce-wood production stands [48]. Moreover, boreal assemblages (birds or others) are less diverse than in temperate forests. Therefore, data on goshawks or Ural owls from boreal forests do not need to be universal for all forest types where these two apex predators are distributed [54].

First of all, data collected from various forest stands in southern Poland, where goshawks and Ural owls are relatively widespread but moderately common [55], indicate that both of them are associated with old-growth forest stands. This is partially congruent with the latest environmental study on the distribution of these two predators [39]; however, no strict associations between habitat features and presence of these species were determined in that study. However, Fedyń et al. [39] examined all territory sites regardless of their duration, so many of the sites considered were only contemporary. This study focuses on only long-lasting territories. All of the examined raptor sites were known to be constant over at least 20 years, and some were even in the same forest area since the 1980s. This difference in statistically evaluated patterns strongly supports the statement that most long-lasting territories of raptors are localized in forest stands not being heavily managed, and particularly not being clear-cut over large areas (management focuses on selective logging or abandonment of wood-cutting). With the example of temperate forests in Poland, we concluded that long-lasting territories of both goshawks and Ural owls sustain significantly higher diversities of birds. For the first time, this pattern was tested not only for breeding but also wintering bird assemblages. It is important that long-lasting territories of raptors are characterized by a high diversity of birds, as these organisms are known to be excellent indicators of habitat quality and overall biodiversity [7–9]. However, forest birds are mostly used in this manner for their breeding assemblages, which are much more diverse than during the wintering period. Moreover, most wintering birds are not sedentary; therefore, their distribution and diversity should be more uniform across forests. This study supports that goshawks and Ural owls breed over years in areas that are hotspots not only of breeding birds, but also of wintering birds. These long-lasting territories had to be localized in forests having some features attracting birds throughout the year. Most probably it is some conjunction of greater safety and better food resources. It is known that some species benefit from being in the proximity of predators, which defend their territories against other, subordinate predators ("protective" associates, e.g., [56–58]). Old-growth forests usually are inhabited by more diverse assemblages of animals, which assure various food sources. This could be especially important, as winter is the time when forest management is most intensive. As bird diversity in winter is also greater in long-lasting territories of raptors, it is even more of a reason to avoid intensive logging in such places. Multivariate analyses indicated that metrics describing forest management intensity (clear-cuts and stumps) are also responsible for bird abundance, but not for species richness, and this is consistent over a year. These metrics reflect the presence of gaps in the canopy (either large or local), what is known to be beneficial for some bird taxa—especially these breeding in ecotones, and what could increase number of individuals of some species. Such gaps were more frequent in Ural owl territories than in goshawk sites, and it is simply a consequence of their ecology (Ural owls prefer to hunt along the borders of forest and open lands, whereas goshawks are adapted to hunt in dense woods). Both species are typical for large and continuous forests, however they both are also able to breed in fragmented woods [39,59].

Available data show that the effect of long-lasting territories of raptors is similar in two major types of temperate forests occupied by goshawks and Ural owls in Central European lowlands: deciduous (oak-dominated) and coniferous (pine-dominated) stands [39]. However, spans of differences in bird diversity metrics were much more pronounced for deciduous than coniferous forests. It could simply be an effect of the quality and biodiversity in these two types of forests. The majority of lowlands should be overgrown naturally by deciduous stands [60]; however, centuries of man-made forest management have caused an over-domination of pine-dominated stands, which are mostly planted for wood production. On the contrary, deciduous stands are limited to only some areas, which are mostly naturally regenerated and heterogeneous. Despite these substantial differences in wood structure and history, there are also long-lasting territories of goshawks and Ural owls in coniferous stands, and there are higher diversities of birds, particularly during the breeding period. The coniferous stands in this study are probably comparable to data from boreal populations of apex predators [46,47,53]. However, the novelty of this research is information from deciduous stands being much less widespread but much richer in bird species.

Among the birds present in the examined forests, some species tended to be associated with long-lasting territories of goshawks or Ural owls. This specifically concerns taxa characteristic of old-growth forests such as woodpeckers (middle spotted, grey-headed and black) or flycatchers (pied or collared). It is important to highlight that these are also species being annexed in the Bird Directive, therefore specially protected in the UE. Another part of the examined forest (Niepołomice Forest [61] was designed as an area of special protection for the middle spotted woodpecker and collared flycatcher. Therefore, the maintenance of long-lasting territories of goshawks and Ural owls should be beneficial for conservation of other rare and threatened bird species.

## 5. Conclusions

Goshawks and Ural owls are protected, but their nesting sites are not safe in managed forests. Sustainable forest management is assumed to not be harmful to overall biological diversity if forest management plans consider the needs of nature and species preservation [62]. This is particularly important in the case of Ural owls, as this species is annexed in the Bird Directive and Natura 2000 sites are designed for their protection (including the Niepołomice Forest Special Area for the Protection of Birds: PLB120002). Unfortunately, the content of such management plans is not always supported by a sufficient scientific background, and we do not just mean basic information about species occurrence, but also information on local habitat requirements and associations with other organisms. This study should help to understand the role of the long-lasting territories of apex predators for biodiversity protection.

The major finding of this study, that long-lasting territories of apex predators are hotspots of bird diversity, should be considered in planning management actions in forests. It would be enough to restrict timber logging in core areas (around nests, as has been undertaken for some threatened species [63]), to leave many old trees (which are important for localization of nests [39], but also as shelters and hunting zones since both raptor species hunt from an ambush), and particularly to avoid tree cutting during mating and breeding periods (recommendations already available for Ural owl conservation [64]) and the wintering period (which could have negative impact on raptors even during their absence in the territory [65]). Only some of these core areas with the highest values of bird diversity metrics should be considered as reserves for nature protection. It should be especially acceptable in light of the new 2030 Biodiversity Strategy of the European Union to protect up to 30% of habitats in Europe, including 10% being strictly protected. The long-lasting territories of apex predators could be used as indicators for some of those protected areas. The use of apex predators as surrogates of biodiversity (particularly their long-lasting territories) should be a tool for better management of habitats and conservation of nature.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13122128/s1; Figure S1. Localization of long-term territories of goshawks; Figure S2. Localization of long-term territories of Ural owls; Figure S3. Localization of control sites (unoccupied by goshawks and Ural owls); Table S1: Localization of examined plots with their assignment to the raptor occurrence (AG—goshawk, SU—Ural owl), and forest type (deciduous vs coniferous); Table S2: Diversity of birds detected during wintering and breeding counts on selected plots; Table S3: Basic statistics describing bird diversity metrics and environmental variables for selected plots; Table S4: Values of basic environmental variables collected for selected plots.

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