

# The importance of forests along submontane stream valleys for bird conservation: The Carpathian example

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## Summary

The biodiversity and naturalness of forests that cover stream valleys in submontane areas have not been investigated as intensively as riparian forests along large lowland rivers. In this study we compared data on total bird assemblages and on selected indicator species detected in forests along submontane stream valleys ('Vall') with those detected in forests covering submontane slopes and tops in the foothills ('Hill') of the Western Carpathians, considering also environmental characteristics of the studied locations. The aim of this study was to verify the hypothesis that forests along submontane stream valleys harbour significantly richer and more diverse bird communities and that they are an important habitat for rare and threatened species. We found that the species richness, abundance of birds and bird diversity were almost twice as high in 'Vall' than in 'Hill' locations and that indicator species mostly or exclusively inhabit 'Vall' locations. Moreover, species diversity was highly and positively correlated with higher tree species diversity and a higher amount of large trees and dead wood, but negatively correlated with logging intensity. The results of our study confirmed that forested river valleys in submontane areas play an important role as refugia both for rare and endangered bird species as well as for the whole bird assemblage. This study is the first to present an assessment of this type of habitat for birds in the Western Carpathians. Forests along submontane stream valleys, if protected or unmanaged, could be treated as reference areas for nature and biodiversity conservation.

## Introduction

Riparian forests, which are some of the most species-rich environments in Europe, are simultaneously being severely fragmented and depleted due to anthropogenic pressure and the intensive land use of river valleys (Angelstam and Dönn-Breuss 2004, Winter 2012). Riparian forests and their rich plant and animal communities have been the subject of many studies concerning species richness and diversity, ecological interactions, threats, and conservation needs (e.g. Angelstam and Dönn-Breuss 2004, Rodewald and Bakermans 2006). These studies have shown a generally congruent pattern: that riparian forests maintain high biodiversity and their protection is extremely important (Angelstam 1992). Moreover, forests along watercourses can act as buffer strips for riparian and riverine habitats in managed forests (e.g. protecting them from direct impact of wood logging) and also the convers – protecting river banks from erosion by water. The refugial role of buffer strips along watercourses has been proven for birds in boreal forests (Hågvar and Bækken 2005, Kardynal *et al.* 2011). Additionally, the presence of tree-fall gaps and clearings along watercourses may increase the diversity of habitats and may be beneficial for bird communities (Fuller 2000). Finally, the presence of natural habitats in river channels and food resources around

the watercourses (e.g. insects) could be beneficial for the breeding success of forest birds (Strasevicius *et al.* 2013).

In addition to large, lowland river valleys harbouring the majority of riparian forests in Europe (especially in the central and eastern parts of the continent), a network of forested valleys of smaller rivers and streams also exists within submontane and lower mountain areas. There is a lack of thorough scientific knowledge about the forests that cover these valleys due to their sparse distribution (restricted mainly to submontane areas), their relatively small extent (narrow zones along watercourses), and their limited accessibility due to topography – very often steep slopes and wet valley bottoms. So far, few comprehensive studies have been conducted on forests along submontane stream valleys. The results of these studies have demonstrated a high diversity of plant species (Dzwonko and Loster 1989) and the persistence of natural habitats with old forest patches and large amounts of accumulated dead wood due to limited logging (Zielonka *et al.* 2009, Mikuś *et al.* 2013). At the same time, faunistic research in riparian forests along submontane stream valleys is scarce: a few studies have focused on larger mountain valleys crossing forested areas (Knutelski 1988, Wyzga *et al.* 2012, Mikuś 2014). Most ornithological research conducted on mountain and submontane Carpathian forest birds has concentrated on forests located on mountain slopes or mountain tops (Głowaciński 1990, Baláž and Balážová 2012). There is limited information on bird assemblages of forested valleys; instead, the literature has focused on larger valleys within mountains with greater elevations (e.g. Głowaciński 1990, Domokos and Cristea 2014). The North American literature on birds of forested valleys is relatively extensive, but these papers focus on lowland valleys (Keller *et al.* 1993, Hannon *et al.* 2002).

Forests along submontane stream valleys, despite their limited distribution and small areas, are potentially important refugia for many plant and animal species. Insufficient data about their biodiversity prevents effective protection of this important habitat and associated communities of plants and animals. They are rarely protected, and even if so, they are not typically the prime object of the protection. Fortunately, many patches of forests along submontane stream valleys are in a relatively natural state due to the harsh topography, which prevents intensive logging. The important role of these forests in preserving biodiversity should therefore be documented in order to develop strategies for conserving and managing these areas.

Estimating an environment's naturalness and biodiversity is a difficult task, especially for diverse and complex habitats such as forests. Naturalness and biodiversity can be estimated on the basis of inventories of selected keystone species, species guilds, or entire taxonomic groups (Mills *et al.* 1993, Paine 1995). Birds are used as indicators in many types of environments (Gregory and van Strien 2010) including forests (Roberge and Angelstam 2006, Pakkala *et al.* 2014). This group is relatively easy to detect, rich in species, and the populations of many species are abundant, all of which allows for the collection of relatively large data sets. Moreover, within this group some species with narrow habitat and/or food preferences could be used as indicators for particular types of environments, including forests, (e.g. woodpeckers: Mikusiński *et al.* 2001, Roberge *et al.* 2008a; Stachura-Skierczyńska and Kosiński 2016; grouse: Pakkala *et al.* 2003, Åberg *et al.* 2003; other species: Pakkala *et al.* 2014, Kajtoch *et al.* 2014).

In this study we focused on bird assemblages and on selected keystone and/or umbrella species as indicators of biodiversity and naturalness (Mills 1993, Roberge and Angelstam 2006, Gregory and van Strien 2010, Pakkala *et al.* 2014). In the Polish Western Carpathians we compared data on bird assemblages in forests along submontane stream valleys (riparian forests) with forests covering submontane slopes and tops. Our aim was to test the hypothesis that forests along submontane stream valleys harbour significantly richer and more diverse bird communities than forests apart such valleys and that these valleys are refugia for rare and threatened species. The objective was to determine the significance of forests along submontane stream valleys for persistence of bird diversity in lower parts of the Carpathians and to prepare a scientific base for habitat and species conservation and management in these areas.

## Materials and methods

### Study area

Research was conducted in the foothills of the Polish Western Carpathians (Małopolska Province, located south-west and south-east of the city of Kraków, Poland, approximately between  $19^{\circ}31.8'E$  and  $21^{\circ}12.6'E$ ) (supplementary file S1 in the online supplementary material). This area is made up of moderately high hills (300–600 m asl) divided by dense networks of rivers and streams (all within the Vistula drainage). The general landscape of the valleys and foothills is dominated by agriculture (arable land, pastures and meadows), villages, and small towns. Forests cover on average 25% of the land and are located either on the tops of hills or along valleys (mostly along stream valleys, as most larger river valleys are deforested).

The forests covering slopes and tops are mixed with varying proportions of oaks *Quercus* spp., pines *Pinus* spp., beech *Fagus sylvatica*, fir *Abies alba*, hornbeam *Carpinus betulus*, birch *Betula* spp., larch *Larix decidua* and other tree species. Most forests consist of a network of small patches with diverse composition. Foothill forests (outside valleys) are extensively managed but there are no tree plantations consisting of single species. Some patches are semi-natural belonging mainly to the following forest assemblages: oak forests (*Luzulo luzuloidis-Quercetum*), hornbeam forests (*Tilio-Carpinetum*), beech forests (*Dentario glandulosae-Fagetum*, *Luzulo luzuloidis-Fagetum*), fir forests (*Abietetum polonicum*), and pine forests (*Leucobryo-Pinetum*) (Matuszkiewicz 2008).

Narrow riparian forests exist along many watercourses (mainly within forested areas). These forests include willows *Salix* spp., alders *Alnus* spp., poplars *Populus* spp., ash *Fraxinus excelsior*, and spruce *Picea abies*. Forests along watercourses are surrounded by mixed woods on steep slopes with a high share of elms *Ulmus* spp., sycamore *Acer pseudoplatanus*, or fir. Forests along submontane stream valleys are mostly unmanaged or only slightly and locally managed. They belong to riparian and swamp forests (*Alno-Ulmion*), sycamore forests (*Tilio platyphyllis-Acerion pseudoplatani*), fir forests, and locally to other types of forests.

The age of foothill forests is diverse, ranging from young stands to patches approximately 150 years old. Only few small nature reserves exist in the studied area, and some fragments of valleys (channels) are protected as Natura 2000 sites. Foothills have no national parks that protect larger areas. Existing landscape parks (areas protecting landscapes) have only limited importance for nature conservation and protection regimes have a low impact on forestry practices.

### Study design

The distribution and number of submontane valleys located in forests were evaluated prior to plot selection. In the study area, only 18 independent tributaries were found (excluding valleys located outside forested areas and those along which roads and buildings were situated). To avoid pseudoreplication of data (gathering data within the same river tributary), survey points were randomly selected within 18 tributaries ('Vall' points). To randomly select study points, the stream valleys of 18 tributaries were divided into 500 m sections, and a single section in each valley was drawn. A study point was located in the middle of the drawn section and the point included both a narrow zone (usually 10–20 m wide) of riparian forests and the adjacent zones of mixed forest on the slopes (up to 100 m from the stream channel, see next section). In the field it was not possible to assign a clear border between these two types of forests as they constitute natural association with continuously changing microhabitats along a gradient from the valley bottom to the top (surrounded by steep slopes). Additionally, 18 points were randomly selected within the forests in the foothill zone (300–600 m asl) and more than 200 m from the edges of the nearest valley and other points in forests out of valleys ('Hill' points). 'Hill' points were randomly selected within forest plots (2 x 2 km squares) inventoried during a project conducted by

the Polish Society for the Protection of Birds in Polish Carpathians (<http://www.ptakikarpat.pl/>). The points in both categories were at least 150 m from the forests edge to avoid inclusion of species associated with ecotone and open habitats (see Brazaitis *et al.* 2005). Locality of study points is provided as a Google Earth file (supplementary file S1) organized according to Shapiro and Báldi (2012).

### Bird data

Birds were inventoried according to the fixed-radius point count technique (Bibby *et al.* 2000, Gregory *et al.* 2004). For the purposes of this study, only the relative abundance of birds was needed; at each point, birds were counted four times during breeding season (approximately at the beginning of April, end of April, beginning of May, and end of May/beginning of June). About half of 'Vall' and half of 'Hill' points were surveyed in 2012 and the remainder in 2013. Birds were counted within a radius of 100 m from the observation point. All birds were noted during a 15-minute period (including five minutes of "acclimatisation" - a period of silence at the beginning to avoid underestimating the number of pairs of species sensitive to human presence like Hazel Grouse *Tetrastes bonasia*). Voice stimulation was used for some species for which detection probability is known to be low (White-backed Woodpecker *Dendrocopos leucotos*, Three-toed Woodpecker *Picooides tridactylus*, Grey-headed Woodpecker *Picus canus*, and Hazel Grouse; Swenson 1991, Wesolowski *et al.* 2005, Czeszczewik and Walankiewicz 2006). We used play-back recordings of birds (drumming for woodpeckers and male song for grouse) and, with the use of an mp3 player and speaker, we stimulated responses at each point (2 min of stimulation and 1 min of listening, repeated twice) during the two first counts (within periods of high vocal activity of these species). All surveys were performed in the morning and in good weather conditions (without rain and heavy winds). Some species were excluded from the collection of occurrence and abundance data: species strictly dependent on watercourses (not found outside valleys, e.g. Grey Wagtail *Motacilla cinerea*); diurnal raptors and Black Storks *Ciconia nigra* (these species have large territories and survey should rely on nest searches); and owls (due to their nocturnal activity). Only birds exhibiting signs of territoriality, mating, or breeding were counted (we tried to exclude migrating and moving birds). The number of territories/pairs for each species in point counts was assigned to the highest number detected during any of the four surveys.

Four species that are known to be good indicators of the natural state of European forests (known as keystone and/or umbrella species in natural forests), were selected and used in detailed analyses: White-backed Woodpecker (Mikusiński *et al.* 2001, Roberge *et al.* 2008b); Middle-spotted Woodpecker *Dendrocopos medius* (Mikusiński *et al.* 2001, Stachura-Skierczyńska and Kosiński 2016); Hazel Grouse (Åberg *et al.* 2003, Kajtoch *et al.* 2012), and Red-breasted Flycatcher *Ficedula parva* (Pakkala *et al.* 2014).

### Environmental data

A total of 17 environmental and topographic variables were collected for each study point (within a 100-m radius). These variables were: (1) STREAM presence/absence (discriminating the two forest categories), (2) DECIDUOUS (proportion of deciduous tree species), (3) TREE\_DIVER (inverse Simpson diversity of tree species; Simpson 1949), (4) WOOD\_COVER (cover of land by tree canopy), (5) AGE (average age of the larger/higher tree layer), (6) VETERANS (number of larger trees > 80 cm diameter at breast height [DBH]), (7) DEAD (total number of snags and logs > 10 cm DBH), (8) STUMPS (total number of fresh stumps reflecting recent intensity of logging), (9) UNDERSTOREY (number of tree and shrub species in the understorey layer, 1–5 m high), (10) BUSH\_COVER (canopy cover of smaller trees and bushes), (11) BERRIES (presence/absence of *Vaccinium* spp. and/or *Rubus* spp.), (12) ROADS (total length of forest roads within 100-m radius), (13) CLEARINGS (share of clearings and bogs), (14) INCLINATION (average inclination in three categories: flat: 0–5° (1),

moderate: 5–20° (2) and steep: >20° (3)); (15) EXPOSURE (slope aspect in which point was located or exposure of the valley in which point was located – cardinal directions against which slope/valley was located), (16) YEAR (year of count: 2012 or 2013), (17) FOREST\_AREA (area of the forest in which point was located, in km<sup>2</sup>). Factors 1–11 were determined in the field. All of these variables (except 1) were measured along two crossed lines each of 200 m length and oriented N-S and E-W inside a 10-m belt (5 m from both sides of the observer walking along the line). This method was used as it was difficult to count and assign to categories all trees, bushes, stumps etc. within a 100-m radius. Factors 12–15 and 17 were taken from forestry GIS maps (<http://rdlpkrakow.gis-net.pl/>).

### Statistical analyses

Data on bird species richness and relative abundance were used to calculate inverse Simpson diversity indices (1/D; Simpson 1949) using a diversity calculator (Begon *et al.* 2006). Correlations between species richness, abundance, and diversity were assessed using Spearman's rank correlation coefficient. Due to significant and high correlation between these three measures (all  $Rho > 0.9$ ) only the Simpson index of diversity of birds was used in further analyses. Moreover, the Sørensen–Dice coefficient (Dice 1945, Sørensen 1948) was calculated in EstimateS (Colwell 2013) to express similarities of bird assemblages between points located in forests within submontane stream valleys, within submontane slopes and tops, and between points from these two groups (differences tested with Wilcoxon Z-test).

Statistical differences for bird variables between 'Vall' and 'Hill' points were assessed using the Wilcoxon Z-test. To assess the importance of environmental variables on bird diversity, the 17 univariate models were built using Generalized Linear Model (GLM) with log-normal distribution. Their significance was tested using the Wald statistic. Principal Component Analysis was used to check collinearity among the environmental variables (Freckleton 2011). Principal components were extracted for one group of correlated variables (of  $Rho > 0.6$ ): 'naturalness' (TREE\_DIVER, VETERANS, DEAD, BUSH\_COVER, STREAM, STUMPS, ROADS; the five first variables were positively correlated with each other and negatively correlated with the last two). Next, 'Naturalness' component, as well other environmental variables (which were found to be significant according to the Wald statistic in univariate models), and "bird diversity" as response variable, were used to build multivariate models using GLMs. The resulting models were then ranked by increasing QAICc values (modified Akaike Information Criterion adjusted for low sample size and corrected for over-dispersion (for details see Lebreton *et al.* 1992, Burnham and Anderson 2004) and Akaike weight ( $w$ ). The model with the lowest QAICc score and highest weight can be viewed as the most parsimonious, as it explains most of the variance with the fewest parameters. Following Burnham and Anderson (2004), models with  $\Delta QAICc < 2$  compared to the model with the lowest QAICc were assumed to have high strength-of-evidence, while models with  $\Delta QAICc > 10$  have essentially no support. To visualise the most important two effects, the bivariate response surface was plotted in STATISTICA 11.0 software. Individual analyses were performed for four species regarded as good indicators of natural forests: White-backed Woodpecker, Middle-spotted Woodpecker, Hazel Grouse and Red-breasted Flycatcher (see citations in the Introduction). Differences in occurrence of these species in 'Vall' and 'Hill' points were verified using Wald statistics (in GLM). Univariate logistic regression modelling was adopted to build curves showing the relationship between the 'naturalness' component and presence of these four indicator species in studied points. For selected bird species (which were represented in at least 20% of the studied points), the relations with each other and all environmental variables were assessed using Factor Analysis (FA).

Relationships among study points (in respect to bird assemblages and environmental variables) were visualised on dendrogram using Cluster Analysis (CA) (Driver and Kroeber 1932) with Ward's method of hierarchical agglomerative clustering (Ward 1963) and Euclidean distances. All analyses were carried out with STATISTICA 11.0 software (StatSoft Poland).

## Results

### Bird data

In total 60 bird species were detected during the study (Table S1). Similar numbers of species were found in 'Vall' (53) and 'Hill' (49) points; however, the mean value of bird species richness per point was almost twice as high in 'Vall' locations (Table 1, Table S2). Similarly, the mean abundance of birds and mean Simpson diversity indices ( $1/D$ ) were almost twice as high in 'Vall' than in 'Hill' locations (Table 1). The total number of bird pairs/territories was 691 in 'Vall' locations and 377 in 'Hill' locations. Sørensen–Dice coefficients were highest when comparing 'Vall' points (mean 0.62 (0.32–0.91) SD = 0.13), lower when comparing 'Hill' points (mean 0.55 (0.25–0.89) SD = 0.11), and lowest when comparing 'Vall' with 'Hill' points (mean 0.48 (0.19–0.74) SD = 0.10). Differences in Sørensen–Dice coefficients between all of these comparisons were significant ( $P < 0.001$ ). The CA dendrogram (Figure S1) shows that the majority of points within each category ('Vall' or 'Hill') are grouped in separate clusters; however, some exceptions can be observed (three 'Vall' points fall within 'Hill' cluster; two 'Hill' points within 'Vall' cluster).

Among the four indicator species chosen for detailed analyses, one was absent in 'Hill' points (Middle-spotted Woodpecker), two were almost 10 times more frequent in 'Vall' points (Red-breasted Flycatcher and Hazel Grouse), and one was approximately three times more abundant in 'Vall' points (White-backed Woodpecker) (all differences highly significant, Table 2 and Table S1). It is important to note that all these species were also relatively uncommon in 'Vall' points – they were found only in approximately half of 'Vall' points and only as single pairs/territories (with the exception of the Red-breasted Flycatcher, which was found in 1–2 pairs/territories). The occurrence of these species, with the exception of the Middle-spotted Woodpecker, was highly correlated with each other (Table 2).

### Environmental data

The CA dendrogram (Figure S2) showed that the majority of points within each category ('Vall' or 'Hill') are grouped in separate clusters; and again, some exceptions can be observed (two 'Vall' points fall within 'Hill' cluster; two 'Hill' points within 'Vall' cluster).

Most of the environmental variables were found to significantly differentiate bird diversity between 'Vall' and 'Hill' points, with the exception of AGE, UNDERSTOREY, BERRIES, EXPOSURE, YEAR and FOREST\_SIZE (Table 3). The greatest differences with respect to bird diversity were found between 'Vall' and 'Hill' points for the following variables: TREE\_DIVER (2.5 times higher in Vall), VETERANS (almost 10 times higher), DEAD (2.5 times higher), CLEARINGS (8 times higher), STUMPS (6.5 times lower), and ROADS (4 times lower). Some variables were found to be significantly correlated with each other (TREE\_DIVER, VETERANS, DEAD, BUSH\_COVER, STREAM, STUMPS and ROADS). Principal components of these groups of variables were extracted using Principal Component Analysis. The component 'naturalness' explained 63.2% of variation for the variables included.

Table 1. Basic statistics describing bird data used in the study. Z – Wilcoxon test, P – significance of statistical tests. Vall – data from points located in forests along stream valleys, Hill – data from points outside such valleys.

| points<br>variable | Vall |      |      |      | Hill |     |      |     | Statistics  |                  |
|--------------------|------|------|------|------|------|-----|------|-----|-------------|------------------|
|                    | mean | min  | max  | SD   | mean | min | max  | SD  | Z           | P                |
| bird richness      | 27.3 | 18.0 | 37.0 | 5.6  | 14.3 | 6.0 | 27.0 | 5.6 | <b>3.72</b> | <b>&lt;0.001</b> |
| bird abundance     | 38.3 | 23.0 | 55.0 | 10.5 | 20.9 | 7.0 | 36.0 | 7.7 | <b>3.62</b> | <b>&lt;0.001</b> |
| bird diversity     | 23.2 | 16.0 | 31.7 | 4.5  | 11.5 | 5.4 | 22.4 | 4.5 | <b>3.72</b> | <b>&lt;0.001</b> |

Table 2. Spearman rank coefficient (Rho) among four indicator species used in the study and comparison of their frequencies in points located in forests along stream valleys (Vall) and forests out of valleys (Hill), in bold significant results. See Table S1 in online supplementary materials for data about abundance of these species.

| species            | Rho                |                  |                   | Vall vs Hill |              |
|--------------------|--------------------|------------------|-------------------|--------------|--------------|
|                    | <i>D. leucotos</i> | <i>D. medius</i> | <i>T. bonasia</i> | W            | P            |
| <i>D. leucotos</i> | 1.00               |                  |                   | 10.17        | <b>0.001</b> |
| <i>D. medius</i>   | 0.17               | 1.00             |                   | 9.11         | <b>0.003</b> |
| <i>T. bonasia</i>  | <b>0.45</b>        | 0.17             | 1.00              | 9.61         | <b>0.002</b> |
| <i>F. parva</i>    | <b>0.52</b>        | 0.27             | <b>0.40</b>       | 9.52         | <b>0.002</b> |

Combined analysis

GLM analysis of multivariate models showed that the most parsimonious model includes the single component ‘naturalness’ (Table 4). Models which include ‘naturalness’ and WOOD\_COVER similarly explain well the response variable - bird diversity  $\Delta QAIc_c = 0.1$ ), whereas next model - ‘naturalness’ and CLEARINGS has  $\Delta QAIc_c = 1.6$ . Models including more variables were much less fit, the same was true for the intercept model. The bivariate response surface for the ‘naturalness’ component and WOOD\_COVER variable, shows that bird diversity is strongly and positively shaped by forest ‘naturalness’ and coverage of canopy trees (the most preferred were areas of canopy cover at approximately 50% and 80%, Figure 1). Curves showing the relationship between the ‘naturalness’ component and the presence of four indicator species built using logistic regression modelling are presented in Figure 2 (statistical details available in supplementary file S2). The relative relations between environmental variables and selected bird species occurrence in the studied points were visualized using Factor Analysis on Figure 3.

Table 3. Basic statistics describing environmental data used in the study and Wald statistics from univariate Generalized Linear Models in which bird diversity was used as response variable, P – significance of statistical tests. Vall – data from points located in forests along stream valleys, Hill – data from points outside such valleys.

| points<br>variable | Vall   |        |        |       | Hill   |        |        |       | statistics  |                  |
|--------------------|--------|--------|--------|-------|--------|--------|--------|-------|-------------|------------------|
|                    | mean   | min    | max    | SD    | mean   | min    | Max    | SD    | Wald        | P                |
| STREAM             | 1      | 1      | 1      | 0     | 0      | 0      | 0      | 0     | <b>48.7</b> | <b>&lt;0.001</b> |
| DECIDUOUS          | 67.2   | 45     | 85     | 10.5  | 51     | 0      | 90     | 27.2  | <b>18.3</b> | <b>&lt;0.001</b> |
| TREE_DIVER         | 7.5    | 4.8    | 10     | 1.6   | 3      | 1.4    | 6      | 1.4   | <b>59.8</b> | <b>&lt;0.001</b> |
| WOOD_COVER         | 76.1   | 60     | 100    | 13.3  | 76.9   | 60     | 90     | 8.6   | <b>8.1</b>  | <b>0.004</b>     |
| AGE                | 85.3   | 70     | 112    | 12.6  | 78.4   | 44     | 116    | 25.1  | 3.6         | 0.058            |
| VETERANS           | 9.6    | 2      | 30     | 8.6   | 1.1    | 0      | 9      | 2.3   | <b>37.5</b> | <b>&lt;0.001</b> |
| DEAD               | 18.9   | 3      | 42     | 12.5  | 7.8    | 0      | 31     | 8     | <b>27.5</b> | <b>&lt;0.001</b> |
| STUMPS             | 1.4    | 0      | 6      | 2.1   | 9.1    | 0      | 25     | 7.5   | <b>26.2</b> | <b>&lt;0.001</b> |
| UNDERSTORY         | 9.9    | 6      | 13     | 2.1   | 9.4    | 2      | 17     | 4.3   | 1.1         | 0.299            |
| BUSH_COVER         | 46.9   | 25     | 70     | 15.5  | 17.5   | 0      | 50     | 17    | <b>36.7</b> | <b>&lt;0.001</b> |
| BERRIES            | 1      | 1      | 1      | 0     | 0.9    | 0      | 1      | 0.2   | 3.7         | 0.054            |
| ROADS              | 50     | 0      | 150    | 45.2  | 208.3  | 0      | 400    | 103.3 | <b>36.6</b> | <b>&lt;0.001</b> |
| CLEARINGS          | 5      | 0      | 20     | 6.6   | 0.6    | 0      | 5      | 1.6   | <b>27.2</b> | <b>&lt;0.001</b> |
| INCLINATION        | 2.5    | 1      | 3      | 0.6   | 1.6    | 1      | 3      | 0.7   | <b>27.4</b> | <b>&lt;0.001</b> |
| EXPOSURE           | 117.5  | 0      | 315    | 121.7 | 152.5  | 0      | 315    | 104.8 | 2.2         | 0.139            |
| YEAR               | 2012.4 | 2012.0 | 2013.0 | 0.51  | 2012.3 | 2012.0 | 2013.0 | 0.48  | 0.1         | 0.757            |
| FOREST_AREA        | 10.4   | 0.8    | 29.2   | 7.36  | 12.9   | 3.3    | 38.9   | 10.31 | 0.9         | 0.336            |

Table 4. Sets of candidate GLM models (selected among 64 verified models) explaining the diversity of birds in studied forests. Akaike's information criterion for small samples and corrected for overdispersion (QAICc), difference between the given model and the most parsimonious model ( $\Delta$ ) and Akaike weight (w) are reported for each model.

| Model   | k | QAICc | delta | w     |
|---|---|-------|-------|-------|
| NATURALNESS   | 1 | 71.8  | 0.0   | 0.246 |
| NATURALNESS,WOOD_COVER                                | 2 | 71.9  | 0.1   | 0.233 |
| NATURALNESS,CLEARINGS                                 | 2 | 73.4  | 1.6   | 0.109 |
| NATURALNESS,DECIDUOS                                  | 2 | 73.7  | 2.0   | 0.092 |
| NATURALNESS,WOOD_COVER,CLEARINGS                      | 3 | 73.8  | 2.0   | 0.089 |
| NATURALNESS,DECIDUOS,WOOD_COVER                       | 3 | 74.3  | 2.6   | 0.068 |
| NATURALNESS,DECIDUOS,CLEARINGS                        | 3 | 75.7  | 3.9   | 0.035 |
| NATURALNESS,INCLINATION                               | 3 | 76.4  | 4.6   | 0.024 |
| NATURALNESS,DECIDUOS,WOOD_COVER,CLEARINGS             | 4 | 76.5  | 4.7   | 0.023 |
| NATURALNESS,WOOD_COVER,INCLINATION                    | 4 | 76.5  | 4.7   | 0.023 |
| NATURALNESS,CLEARINGS,INCLINATION                     | 4 | 78.5  | 6.7   | 0.009 |
| NATURALNESS,DECIDUOS,INCLINATION                      | 4 | 78.8  | 7.0   | 0.007 |
| NATURALNESS,WOOD_COVER,CLEARINGS,INCLINATION          | 5 | 78.9  | 7.2   | 0.007 |
| NATURALNESS,DECIDUOS,WOOD_COVER,INCLINATION           | 5 | 79.4  | 7.6   | 0.005 |
| CLEARINGS   | 1 | 79.7  | 7.9   | 0.005 |
| DECIDUOS  | 1 | 80.4  | 8.6   | 0.003 |
| DECIDUOS,CLEARINGS                                    | 2 | 80.6  | 8.9   | 0.003 |
| WOOD_COVER,CLEARINGS                                  | 2 | 81.1  | 9.3   | 0.002 |
| NATURALNESS,DECIDUOS,CLEARINGS,INCLINATION            | 5 | 81.2  | 9.4   | 0.002 |
| WOOD_COVER  | 1 | 81.5  | 9.8   | 0.002 |
| INCLINATION   | 2 | 81.6  | 9.8   | 0.002 |
| CLEARINGS,INCLINATION                                 | 3 | 81.7  | 9.9   | 0.002 |
| NATURALNESS,DECIDUOS,WOOD_COVER,CLEARINGS,INCLINATION | 6 | 82.0  | 10.3  | 0.001 |
| DECIDUOS,WOOD_COVER                                   | 2 | 82.1  | 10.3  | 0.001 |
| DECIDUOS,WOOD_COVER,CLEARINGS                         | 3 | 82.5  | 10.7  | 0.001 |
| WOOD_COVER,INCLINATION                                | 3 | 82.7  | 10.9  | 0.001 |
| WOOD_COVER,CLEARINGS,INCLINATION                      | 4 | 82.9  | 11.1  | 0.001 |
| DECIDUOS,INCLINATION                                  | 3 | 83.1  | 11.3  | 0.001 |
| DECIDUOS,CLEARINGS,INCLINATION                        | 4 | 83.8  | 12.1  | 0.001 |
| DECIDUOS,WOOD_COVER,INCLINATION                       | 4 | 84.6  | 12.8  | 0.000 |
| DECIDUOS,WOOD_COVER,CLEARINGS,INCLINATION             | 5 | 85.4  | 13.7  | 0.000 |
| INTERCEPT   |   | 94.3  | 22.5  | 0.000 |
|   |   |       |       | 1.000 |

## Discussion

The results of our study confirmed that forested river valleys in submontane areas (riparian forests and adjacent forests on slopes) play important roles as refugia for both rare and endangered bird species (including natural forests indicator species) as well as for the whole bird assemblage. This research is one of the few existing studies that confirm the high biological values of such habitats (including the Carpathians, but see Domokos and Cristea 2014).

Here we used two levels for estimating naturalness and biodiversity of forests along submontane stream valleys: (i) the entire bird assemblage and (ii) indicator species. The community of forest birds was shown to be significantly richer with respect to species number (1.9 times more species in Valley points compared to Hill points), abundance of breeding pairs/territories (1.8-fold difference), and, as a result, bird diversity as well (1.9-fold difference) (Table 3). These results show that in submontane forests, more birds (defined as species and also number of individuals; the assemblage level) prefer to breed in valleys than outside them. When considering particular species, 13 of 60 (22%) found in the studied area show more or less similar abundance in both



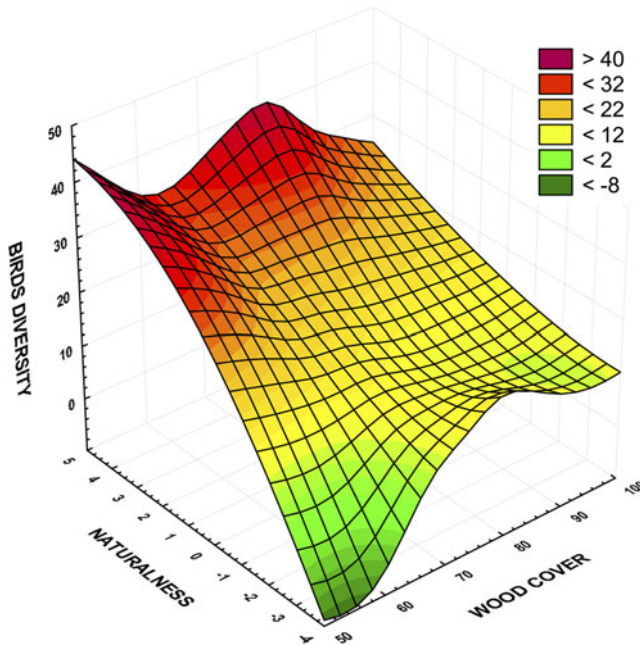


Figure 1. Curve of multivariate logistic regression model presenting influence of two variables: component “naturalness” and WOOD\_COVER on birds diversity in studied forests.

types of forests. These were typically generalist species inhabiting different types of deciduous and coniferous forests, which are similarly frequent in protected and managed stands (Kuczyński and Chylarecki 2013). Nine species (15%) were found to be more abundant in forests covering submontane slopes and tops (Hill sites). This group mainly includes birds associated with forest edges and clear-cuts (Yellowhammer *Emberiza citrinella*, Tree Pipit *Anthus trivialis*, Wood Lark *Lullula arborea*, Common Whitethroat *Sylvia communis*, Green Woodpecker *Picus viridis*, and European Greenfinch *Carduelis chloris*), common forest species (Common Chaffinch *Fringilla coelebs*), and species inhabiting coniferous stands (Coal Tit *Parus ater*). The remaining species (63%) were more common in forests along watercourses. The last group, which contains all indicator species, showed a similar pattern of occurrence probability, which increased with forest naturalness. With the exception of the Middle-spotted Woodpecker, the presence of all other indicator species was found to be significantly correlated with each other; these species seemed to be highly associated with a large amount of older trees, dead wood, and steep slopes (Figure 3). On the other hand, the Middle-spotted Woodpecker is more dependent on high tree species diversity and a significant proportion of deciduous trees (Figure 3). These findings are congruent with the well-known habitat preferences of these species (Mikusiński et al. 2001, Åberg et al. 2003, Roberge et al. 2008b, Kajtoch et al. 2012, Pakkala et al. 2014, Stachura-Skierczyńska and Kosiński 2016). It is also worth noting that among birds associated with old forests having large amounts of dead wood, species such as European Pied Flycatcher *Ficedula hypoleuca*, Grey-headed Woodpecker *Picus canus*, Stock Dove *Columba oenas*, and Black Woodpecker *Dryocopus martius* can also be included, whereas species associated with high tree diversity and a high share of deciduous trees are, e.g. Eurasian Nuthatch *Sitta europaea*, Eurasian Blue Tit *Parus caeruleus*, Spotted Flycatcher *Muscicapa striata*, Eurasian Wren *Troglodytes troglodytes*, Blackbird *Turdus merula*, Willow Tit *Parus montanus*, and Common Chiffchaff *Phylloscopus collybita* (Figure 3). On the other hand, both the Coal Tit and Goldcrest *Regulus regulus* seem to be related mostly

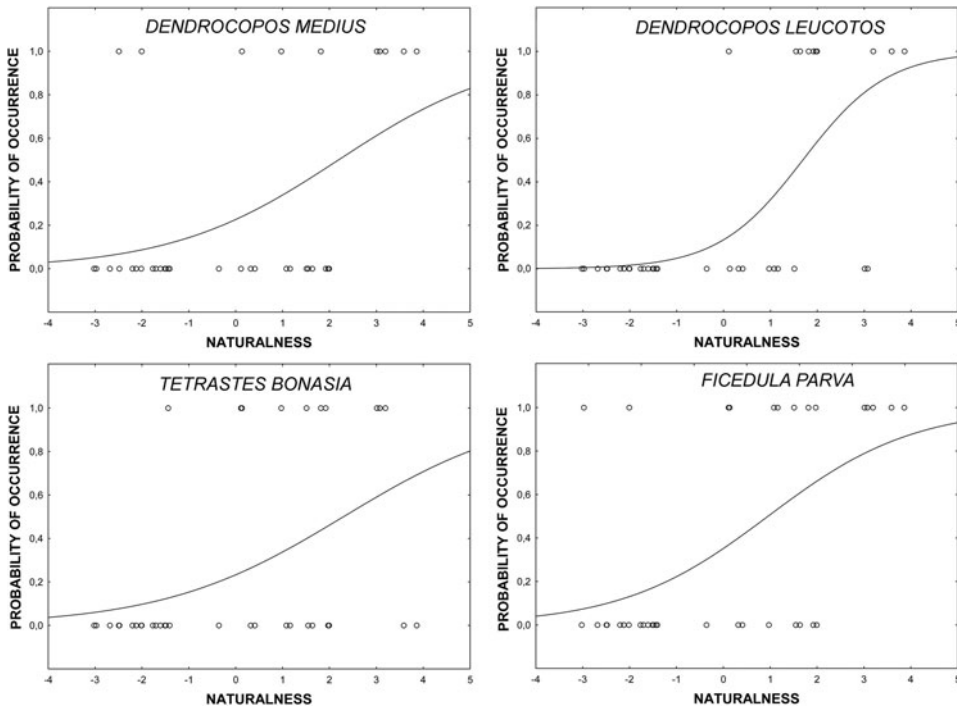


Figure 2. Logistic regression curves showing relationship between occurrence of four indicator bird species and “naturalness” component extracted from variables TREE\_DIVER, VETERANS, DEAD, BUSH\_COVER, STREAM, STUMPS & ROADS.

with managed and coniferous stands. It is important to emphasise that forests along submontane stream valleys may also act as two-way corridors in the expansion and dispersal of lowland and mountain species. Some lowland species may move along these forests into the higher mountains (e.g. Middle-spotted Woodpecker and Black Stork), and some species typical for higher mountains have their lowest localities within these valleys (e.g. single territories of Three-toed Woodpecker *Picoides tridactylus*, Ring Ouzel *Turdus torquatus*, and Pygmy Owl *Glaucidium passerinum*; authors' unpubl. data). The breeding range of these species in the Carpathians mostly covers areas above 700 m in the adjacent Beskidy Mountains, which confirms that the forests along submontane stream valleys may act as dispersal routes for high-mountain species. Therefore, the role of forests along submontane stream valleys as ecological corridors is important, possibly for other groups of animals and plants as well.

Interestingly, bird assemblages of forests both within submontane stream valleys and those covering submontane slopes and tops form distinct clusters (Figure S1). This clustering can be explained as a result of generally higher species richness along watercourses and association of some species, especially rare species and species more dependent on natural, unmanaged types of forest ecosystems. The prominent characteristics of habitats preferred by these species include higher proportions of larger trees and dead wood as well as habitats with greater heterogeneity. On the other hand, bird assemblages in forests far from watercourses consist of more eurytopic species which are simultaneously more numerous. Consequently, these forests sustain a less diverse avifauna.

Differences in bird diversity indices were found to be associated mostly with forest naturalness and logging intensity. In particular, points situated in forests with greater tree diversity,



forests along watercourses) is seemingly also contradictory. However, this is the result of the mosaic structure of these forests, the majority of which consist of dense woods but with local clearings often formed as tree fall gaps or bogs with scattered trees and bushes. Thus, a network of 'internal' forest edges exists in forests along watercourses. Such mosaics favour the presence of many species that either breed or just feed within these small clearings and bogs (Fuller 2000, Shirley 2006). It is worth noticing that the inclination variable also was significant. Forests along submontane stream valleys not only cover narrow strips along watercourses but also steep, often rocky slopes. These slopes prevent intensive logging and at the same time allow for the persistence of larger trees and the accumulation of dead wood (which often fall to the bottom of valleys). Finally, bird diversity was much higher in vicinity of streams than far from the watercourses. It could be related to higher breeding success in vicinity of water in non-regulated channels, with higher availability of natural habitats and greater "production" of food – particularly insects and other invertebrates (Strasevicius *et al.* 2013).

This correlation of high bird diversity with high forest naturalness (and limited logging) is to be expected, as forest species are generally evolutionary adapted to and ecologically associated with natural woods, which covered Europe before human land transformations (Winter 2012). Remnants of these natural forests are still present in some mountain ranges, especially in national parks and nature reserves. This work also shows that some scattered and fragmented old diverse woods in semi-natural state located along watercourses are still present in the western part of the Polish Carpathians. These woods sustain a high diversity of birds and most likely other groups of animals as well. Obviously such forests along small watercourses are not only present in the Polish part of the Carpathians but, as submontane areas (foothills and mountain forelands) also surround the whole Carpathian arc, they are present on other mountain ridges. It would be therefore crucial to study biological importance of this habitat in other parts of Carpathians. Unfortunately, in many areas, these valley forests are being increasingly used for forestry, leading to the elimination of decaying trees considered to be sources of insect pests (mainly beetles from the subfamily *Scolytinae*). These practices may have detrimental effect on forest biodiversity in submontane areas where semi-natural forest patches are heavily scattered and fragmented.

## Conclusions

Woods stretching along watercourses, both at the bottom of stream valleys and on adjacent steep slopes, are potentially important refugia for natural types of forests with high shares of larger trees and dead wood, high tree species diversity, a heterogeneous bush layer, and mosaic structures with presence of natural clearings and bogs. Several reviews that have addressed the importance of maintaining and restoring biodiversity in European forests (Nilsson 1997, Angelstam 1998, Bengtsson *et al.* 2000), including submontane forests (e.g. Schnitzler and Borlea 1998) have pointed out the preservation of unmanaged or only slightly managed forests that are under more natural disturbance regimes (forced by proximity of watercourses and varied topography). Unfortunately, these forests along submontane stream valleys are too scattered and fragmented to be protected as larger units of protection (as national parks or landscape parks due to the complex nature of land ownership along watercourses). However, some of these forests are part of Natura 2000 sites of the EU. Most likely, the most efficient solution would be to prohibit logging in forests along watercourses, leave them unmanaged, and treat them as buffer strips within managed forests, as can be seen in boreal forests of North America, Scandinavia, and recently in Czech Republic (Šálek *et al.* 2013). Such buffer strips protect adjacent forests from water erosion, but more importantly, sustain higher diversity of plants and animals (Lee and Barker 2005), including birds (Hågvar and Bækken 2005, Shirley and Smith 2005, Kardynal *et al.* 2011, Chizinski *et al.* 2011). Consequently, these forests along submontane stream valleys, if protected or unmanaged, could be treated as excellent reference areas for nature and biodiversity conservation, in Poland but also in all Carpathian countries.

## Supplementary material

The online supplementary materials for this article can be found at [journals.cambridge.org/bci](http://journals.cambridge.org/bci)

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