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Elevational distribution of bird assemblages in the Western Carpathians is mainly driven by floristics, climate and productivity

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The Carpathian Mountains have one of the largest remaining primeval and natural forests in the European Union and have been little studied in terms of biogeography. In this paper, we consider the elevational distributions of bird assemblages in the Western Carpathians and the environmental factors that drive them. We used censuses performed by territory mapping methods and explanatory data from 38 study sites (139-year samples) along an elevational gradient from lowland to subalpine zones. We analysed these data matrices with bootstrapped cluster analyses and indirect and direct correspondence analyses (DCA, CCA, CO-CA). Cluster analyses of Euclidean distances from the presence/absence, density, and dominance matrices produced differing numbers of significant clusters (8, 6, 7) corresponding to six, four and five elevational belts. Only three elevational zones—lowland, mountain, and subalpine—were consistent in all classifications. Explanatory variables, *i.e.* floristics, precipitation, temperature and productivity, had the overall highest rank in explaining the variance in canonical correspondence analysis (CCA) ordinations. Floristics and woody plant species dominance were strong predictors of the elevational pattern of bird assemblages in co-correspondence analyses (CO-CA). Our results support the Clementsian concept of significant and discrete assemblages, not tied to fine habitat types, yet rather defined along wide habitat scales.

1. Introduction

According to the United Nations Environmental Programme (UNEP) definition, mountains are characterized as the areas with the minimum of 300 m elevation (Chamberlain *et al*. 2023a). Mountainous areas cover only around a quarter of the Earth's terrestrial surface and support about one-third of terrestrial biodiversity including almost 50% of the recognized biodiversity hotspots (Rahbek *et al*. 2019a, Chamberlain *et al*. 2023a). Some bird species may be restricted to a single mountain, valley or more often to a narrow elevational range. From an evolutionary perspective, a number of interacting ecological factors acting on relatively small geographic scales have led to higher speciation rates on mountains, enhancing high bird diversity and endemism (Rahbek *et al*. 2019a, Chamberlain *et al*. 2023a). Mountain birds are defined as those with a large proportion of their breeding range in mountainous areas (Chamberlain *et al*. 2023a). Mountain environments are often very variable and unpredictable associated with harsh conditions that lead to development of specific adaptation in breeding and resident species. These adaptations cover physiological, life-history and behavioural strategies in high elevation specialists.

Opinions on the relative importance of environmental factors driving distributional patterns and diversity of bird assemblages along the elevational gradients vary among authors (see Chamberlain *et al*. 2023a for review). Temperature has been identified as the most significant factor driving elevation patterns of biodiversity (McCain 2009, Pearce-Higgins & Green 2014, Chamberlain *et al*. 2023a), yet the mechanisms of its effects are not clear (Pearce-Higgins & Green 2014). Among other climatic factors, water availability has also been determined as another important driver (McCain 2009, Pearce-Higgins & Green 2014, Antonelli *et al*. 2018, Chamberlain *et al*. 2023a). Pearce-Higgins & Green (2014) analysed six different predictors of global patterns of bird diversity and showed that potential productive energy (primary productivity) was the most important driver. Vetaas *et al*. (2019) identified the water-energy dynamic model to be in general better predictor of species richness of various taxa than classical primary productivity. Water-energy dynamic model predicts a parabolic response in species richness along an energy gradient because optimal heat provides high level of available liquid water essential for life. Soil erosion rates and diversity also seem to influence elevational species richness patterns of vertebrates (Antonelli *et al*. 2018, Rahbek *et al*. 2019b). Other hypotheses considered, including Rapoport' rule, the species-area relationship, and the Mid-Domain Effect, were less convincing and received lower rankings as the drivers of the elevational patterns of avian diversity (McCain 2009, Chamberlain *et al*. 2023a).

Mountain ranges around the world serve as natural systems for studies of patterns of biological communities and assemblages along the elevational gradients. The decline of environmental factors such as temperature, air pressure, oxygen concentration, and the increase in environmental stochasticity and UV radiation with increasing elevation on a relatively small geographic scale, provide a useful means for examining biological processes. An important impetus in biogeography came from the work of Alexander von Humboldt, who noticed the similarity and worked out general principles between latitudinal and altitudinal zonations of vegetation (Jackson 2009). The Third International Botanical Congress in 1910 attempted to unify the terminology of ecological zonation in latitude and elevation and proposed that 'zone' be used for horizontal (latitudinal) and 'belt' for elevational distribution of vegetation. While zonation can be used to refer to both, the terminology is not closely adhered to in more recent times (Fattorini *et al*. 2019).

A number of biogeographic studies, primarily older, proposed subjective classifications of elevational belts of communities and assemblages (*e.g*. Patterson *et al*. 1998, Shiu & Lee 2003) that sometimes varied among different case studies of the same mountains. For example, several elevational zonation schemes were given for humid mountain forests of the Andes of Bolivia that ranged from two wide to several narrow belts (Bach & Gradstein 2011). More objective statistical divisions of belts are considered. Several statistical procedures can be applied to detect distinct elevational belts of communities and assemblages that were compared and evaluated by Bach & Gradstein (2011). Of these procedures, chronological respectively constrained clustering (Legendre *et al*. 1985), bootstrapped cluster analysis (*e.g*. Pillar 1999) and species turnover peaks (Bach *et al*. 2007) seem to be the most promising.

Some studies did not detect clear elevational zonation and showed rather continuous gradual distribution of plant communities along the elevational gradients, *e.g*. tropical plant communities in Costa Rica (Lieberman *et al*. 1996) and Mexico (Vázquez & Givnish 1998). These studies support the Gleasonian individualistic community concept (Gleason 1917), understanding communities as random aggregations of species that respond to environmental conditions independently. However, none of these studies employed statistical procedures capable of detecting significantly different elevational belts but applied an ordination procedure to visualize gradual community change. Statistically distinct elevational belts based on chronological clustering were described in various communities and assemblages, *e.g*. plants (Hemp 2006, Moradi *et al*. 2017), amphibians and reptiles (Hofer *et al*. 1999), as well as birds (Romdal & Rahbek 2009). In contrast, these studies support the Clementsian community concept (Clements 1916) defining the community as a discrete and integrated unit of taxa repeatable in space and time. Currently, none of the community concepts mentioned thus far is valid. A number of studies, however, support the so-called 'integrated community concept' which proposes that communities reach a range of different dependencies among species or degrees of integration across space and time (Lortie *et al*. 2004).

Bird zonation studies have only been conducted on few mountains around the world, *e.g*. Peru (Patterson *et al*. 1998), Taiwan (Shiu & Lee 2003), Tanzania (Romdal & Rahbek 2009), and Mexico (Medina-Macías *et al*. 2010, Jaime-Escalante *et al*. 2016). In the Carpathian Mts., there is only one ornithogeographic study, which was conducted in Tatra Mts. of Poland, and addressed the diversity, structure, and elevational distribution of bird assemblages (Glowaciński & Profus 1992). This study described bird assemblages of beech-fir forest, spruce forest, dwarf-pine shrubs, alpine meadows and scree along a gradient of 960 to 2233 m a.s.l.

On the basis of the above review, the Carpathian Mts. lack a complete analysis of the distributional patterns (zonation) of the bird assemblages from lowland to subalpine zone. To make such an analysis, we collected published and our own unpublished censuses of primeval and natural forest bird assemblages of the Western Carpathians. In total, data from 38 census plots were subjected to cluster and ordination procedures to test for significant bird assemblage along elevational belts and to identify environmental drivers. We define primeval forests (virgin, old-growth) as forest stands that have never been managed and which contain native plant species. In contrast, we consider natural forests as those that have been cut once, and which consist of naturally regenerated stands containing native plant species and forest structure similar to primeval stands. Most previous studies found different belts of bird assemblages along the elevational gradients in different mountain systems and countries (*e.g*. Patterson *et al*. 1998, Shiu & Lee 2003, Romdal & Rahbek 2009, Medina-Macías *et al*. 2010, Jaime-Escalante *et al*. 2016). Consequently, we expected significant elevational belts driven by similar environmental factors as found in the previous studies. Most previous studies identified climatic factors (temperature and available water (precipitation)) as the primary drivers of elevational pattern of bird species richness so that we assumed that these factors are primarily responsible for the distribution of bird assemblages in the Western Carpathians.

We asked five main research questions:

1. Do breeding bird assemblages of primeval and natural Western Carpathian forests form significant classification patterns in the elevational gradient based on presence/absence, density and dominance matrices?
2. Are classification patterns consistent among different data matrices (presence/absence, density, and dominance) and multivariate techniques (cluster *vs*. ordination analyses)?

3. What are the main environmental factors driving the ordination patterns of the breeding bird assemblages of the primeval and natural forest along the elevational gradient?
4. Are woody plant composition (floristics) and dominance good predictors of bird assemblage composition, density and dominance along the elevational gradient?
5. Do breeding bird assemblages form a continuous gradient along elevation following the Gleasonian (1917) individualistic community concept or are they sharply divided into significant assemblage units following the Clementsian (1916) community unit concept?

2. Materials and methods

2.1. Study area

The Western Carpathians are a mountain range and geomorphological province located in the western part of the Carpathian Mountains in central Europe. The Western Carpathian Mountain belt stretches from the Low Beskids range of the Eastern Carpathians along the border of Poland with Slovakia toward the Moravian region of the Czech Republic and the Austrian Weinviertel. In the south part of the range, the North Hungarian Mountains cover northern Hungary. The Western Carpathians extend for about 400 km from west to east, and cover about 70,000 km². The highest peak is the Gerlachovský štít (2655 m a.s.l.) in the High Tatras, Slovakia. The Carpathians possess certain features of a continental climate, although from the viewpoint of relief they constitute a sort of island amid the surrounding plains, where the climate is much drier. The mean annual temperature ranges from –3.7 to 10.4 °C depending on elevation, while the mean annual precipitation ranges from 500 to 2100 mm (Michaeli 2014).

The study plots were located approximately between longitudes 16°54' and 21°30' E and between latitudes 47°44' and 49°30' N (Fig. 1; Supplement 1, 2), ranging in elevation from 116 to 1720 m a.s.l. We tried to capture the full range of forest types from lowlands to subalpine dwarf-pine habitats. Most of the sites are situated in nature reserves (Supplement 1).

2.1.1. Classification of forest groups

The 38 study plots were classified into eight forest type categories as follows: 18 mixed stands (47.4%, abbreviation MF), 6 floodplain and wet lowland forests (15.8%, FF), 3 oak forests (7.9%, OF), 3 mixed (admixture of other deciduous genera) oak forests (7.9%, MOF), 3 dwarf-pine communities (7.9%, DP), 2 beech forests (5.3%, BF), 2 spruce forests (5.3%, SF) and 1 upper forest line stand (2.6%, TL) (Supplement 1).

2.2. Bird censusing

We selected historical studies conducted by the territory mapping method (Williams 1936) and its versions (International Standard — IBCC 1969, combined version — Tomiałojć 1980) beginning in 1967 (Głowaciński 1978) and ending in 2013 (Bohuš 2013) in the forests of the Western Carpathians and its foothills spreading into Slovakia, the Czech Republic and Poland. Mapping methods are considered as one of the most accurate and complete census techniques capable of estimating the population abundances of several territorial bird species close to absolute numbers (*e.g.* Tomiałojć 1980, Tiainen & Bastian 1983). We only selected studies in which observers carried out at least five valid census visits to the study plot during each breeding season and when the census plot was 8.5 ha or larger. In total, we analysed data from 38 census plots (139 census year samples), in which censuses lasted from one to thirteen years (n = 38, mean = 3.7 years/plot, standard deviation (SD) = 3.2 year/plot). Mean plot size was 17.1 ha with range 8.5–37.5 ha (n = 38, SD = 7.3 ha). Twenty-eight census plots were located in 23 reserves which ranged in size from about 18–855 ha (mean = 267.4 ha, SD = 264.4 ha). The remaining ten plots were in patches of old natural forests. All details regarding characteristics of the census plots are given in Supplement 1.

2.3. Data analyses

2.3.1. Data matrix preparation

For the bird data matrices, we used the same binary, density and dominance (relative abundance) matrices of 139-year census samples in the bootstrapped cluster analyses, canonical correspondence analysis (hereafter CCA), and co-correspondence analysis (hereafter CO-CA). These three matrices are referred to as complete data matrices. From the complete data matrices consisting of 1–13-year series of repeated samples of the same census plots, we randomly selected one year sample from 38 plots using the R function *sample* for random sampling without replacement. Each census sample was treated as equal in time series. These three matrices with only single year samples from 38 census plots are referred as reduced data matrices and were used only in CCA.

The environmental data matrix consisted of 14 variables: census year, nature reserve size, latitude, longitude, wood increment, dendromass, four temperature and four precipitation variables (see Supplement 3 for further information). Four temperature and precipitation variables were defined as follows: mean annual temperature and precipitation 1961–2010, mean temperature and precipitation during breeding months (April–July) 1961–2010, annual temperature and precipitation in census years and temperature and precipitation during breeding months (April–July) in census years. We reduced climatic variables into three (temperature 1, precipitation 1 and 4) due to strong correlations among them. In order to include variables on the composition of woody vegetation species, we subjected the binary data matrix of 44 species × 139 samples to detrended correspondence analysis (hereafter DCA) and took case scores along the first and second ordination axes as two independent

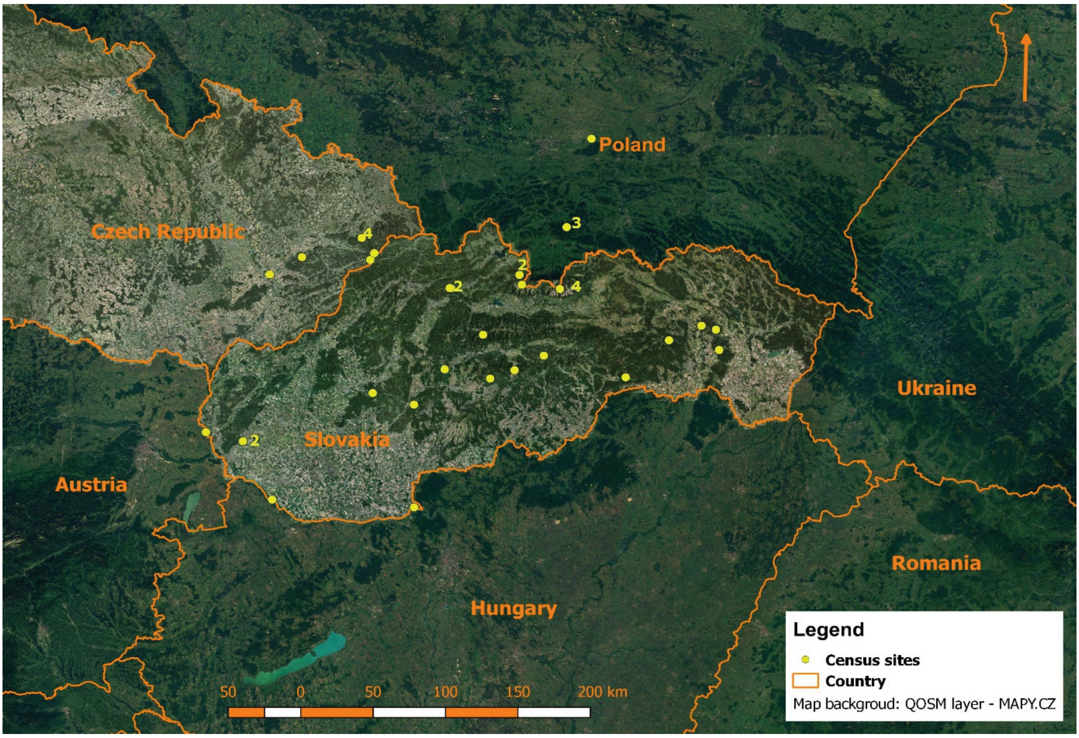


Fig. 1. Geographic distribution of 38 bird census plots in the Western Carpathian Mountains of Slovakia, Czechia and Poland, from which abundance data were used in the study. Points with numbers indicate the number of census plots on this site. Additional information on each plot is given in Supplement 1.

variables that describe the patterns of composition of woody plant species. After this environmental variable selection procedure, we obtained the complete and reduced data matrices of 11 environmental variables × 139 samples and 11 environmental variables × 38 samples. Environmental variables were visualized and normalized by seven tests and normalized if it improved normality. We performed normality tests and correlation matrix analyses in the statistical software NCSS 11 (NCSS 11 Statistical Software 2016).

For the vegetation data matrices, we prepared a presence/absence data matrix of 44 woody plant species detected in the 38 census plots based on our, published and forestry database (National Forest Centre in Zvolen) information (Supplements 1, 2). We also constructed the dominance data matrix of 44 woody plant species from these data, but dominance data were available only for 30 census plots totalling. Thus, we set two data matrices (44 plant species presence/absence × 139 samples and 44 plant species dominance × 123 samples) that were subjected to CO-CAs.

2.3.2. Statistical analyses

We employed multivariate clustering and ordination procedures to test the hypotheses and research questions presented in the introduction. Firstly, we determined significant elevational belts of bird assemblages by the bootstrapped cluster analysis suitable for testing significant groups of assemblages following the recommendation of Bach & Gradstein (2011) (Objective 1). Secondly, based on revealed dendrograms of presence/absence, density and dominance matrices of bird assemblages, we compared and summarized consistency of classification patterns and compared dendrograms by the cophenetic Pearson's correlation coefficient (Objective 2). Thirdly, we tested ranks of eleven environmental factors by the explained variances on species composition, density and dominance of bird assemblages by CCA (Objective 3). Fourthly, we analysed consistency of CCA ordination patterns among three types of bird data matrices by comparisons of axe significance and ranks of environmental factors by the explained variance (Objective 2). Fifthly, we applied CO-CA to predict species composition, density and dominance of bird assemblages by species composition and dominance of woody plant assemblages along the elevational gradient (Objective 4). Sixthly, based on the classification and ordination patterns of three bird data matrices, we analysed whether the bird assemblages form fuzzy or sharp (significant) groups forming elevational belts supporting Gleasonian or Clementsian community concept (Objective 5). We explain these statistical procedures in more detail below.

Bootstrapped cluster analysis

Information on the preparation of data matrices is given in Supplement 3. Subjectivity in interpretation of a standard cluster analysis output, a dendrogram, based on cut off levels set by an analyst can be overcome by testing for statistically significant clusters. Statistical groups (clusters) of species or communities can be understood as existing entities in nature at certain level of probability α. In our case, we applied this procedure to objectively define statistical groups of bird assemblages distributed along the elevational gradient formed by ecological factors. We subjected the presence/absence (binary), density and dominance data matrices to a bootstrapped cluster analysis (UPGMA) in the program MULTIV 3.85b (Pillar 2006). MULTIV is designed to offer an option of bootstrap resampling to generate empirical confidence limits useful in estimation to evaluate group partition sharpness in cluster analysis (Pillar 1999).

We selected six commonly used metrics in community ecology: Pearson's correlation coefficient, Euclidean distances, chord distances for all matrices, Bray-Curtis index for density and dominance matrices, and Jaccard and Sørensen indices for binary matrix. Using three types of datasets and six resemblance measures, we tested the stability and generality of the assemblage classification scenarios. We used 10,000 iterations in all computations and the critical threshold level α = 0.05. Each computation was started with a number randomly generated by the program. To construct dendrograms, we extracted distance matrices from the Multiv output file "Prinda.txt", and exported them to the program R version 4.4.1 (R Core Team 2024) and prepared the dendrograms with application of package "cluster" (Maechler *et al*. 2025) using the function *hclust*. We selected a distance metrics from the applied metrics that gave the best ecological and logical classification pattern of bird assemblages (merging similar forest habitats) based on our knowledge of presence/absence, density and dominance data.

We used the cophenetic Pearson's correlation coefficient to evaluate the similarity of the Euclidean dendrogram classifications based on binary, density and dominance matrices. We used the R function *cophenetic* to compute the cophenetic distances for each hierarchical classification and the function *cor.test* for computing Pearson's correlation coefficients between pairs of cophenetic distances of three hierarchical classifications.

Constrained ordination analyses

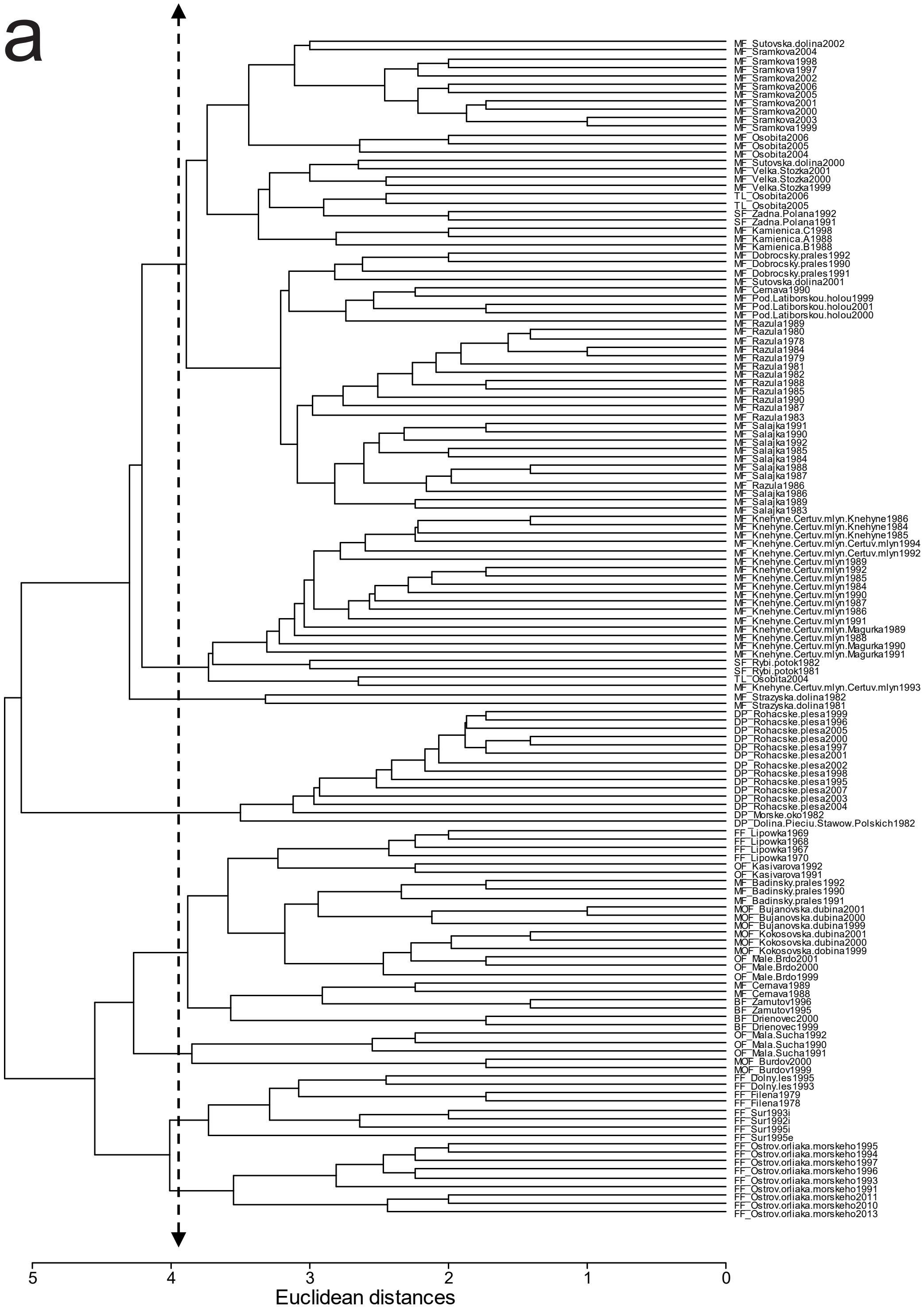
In order to evaluate the effects of floristics and the wide range of environmental variables on bird assemblages, we used two ordination procedures, CCA (ter Braak 1986) and CO-CA (ter Braak & Schaffers 2004). We applied CCA for listing the rank of environmental variables by explained variance indicating their ecological importance and explanation of ordination patterns of bird assemblages by correlation of these factors with canonical axes. This helped to more objectively identify the environmental gradients derived by the canonical ordination axes. We employed CO-CA to predict species composition, density and dominance of bird assemblages along the elevational gradient exhibited by the woody plant assemblages. CO-CA used whole matrices of woody plant assemblages instead of just several environmental factors as the CCA.

Canonical correspondence analysis (CCA)

CCA is the direct (constrained) ordination procedure based on correspondence analysis (CA, reciprocal averaging), efficient when species have bell-shaped response curves or surfaces, the so-called unimodal model to environmental gradients (ter Braak 1986). In indirect ordinations such as CA dominant pattern of community variation along main ordination axes is usually explained intuitively by relating these axes to intuitively selected ecological factors by an analyst. In direct ordinations, the ordination axes are weighted sums of explanatory variables. They are computed by a multiple linear regression of the case scores (CA object scores) on the explanatory variables, taking the fitted values of this regression as new case scores. By this computation, the new case scores are a linear combination of explanatory variables. In direct ordinations such as CCA, the pattern of community variation along ordination axes is explained by the best environmental factors explaining the highest variance of environmental (explanatory) data matrix.

Our complete matrix of 139 samples (objects, cases) consisted of 38 census sites, each of which have 1–13-year bird censuses usually in sequential time series. Due to this wide time series heterogeneity of the data, it was not possible to properly carry out randomization by permutation tests of this data set in program Canoco. Therefore, we conducted the CCA on two data matrices: (1) complete matrix of 139 samples and (2) reduced matrix of 38 samples that were each represented by only one randomly selected census in samples with year series (2–13 years). By carrying out CCAs from two matrices, one with possibly biased permutation test estimates (full matrix) and the other with correct permutation tests (reduced matrix), we were able to directly compare the variable selection procedures and emerged ordination patterns and search for possible dichotomy in results.

In CCA based on full (139 samples) and reduced (38 samples) sample sizes, we used three bird data matrices: presence/absence (binary), population densities and dominance of 84 and 37 bird species and one explanatory matrix of 11 environmental variables. We applied two environmental variable selection procedures with conditional selection (forward selection) and simple effect selection. By these variable selection procedures, we selected 11 variables with the highest weights (variance) and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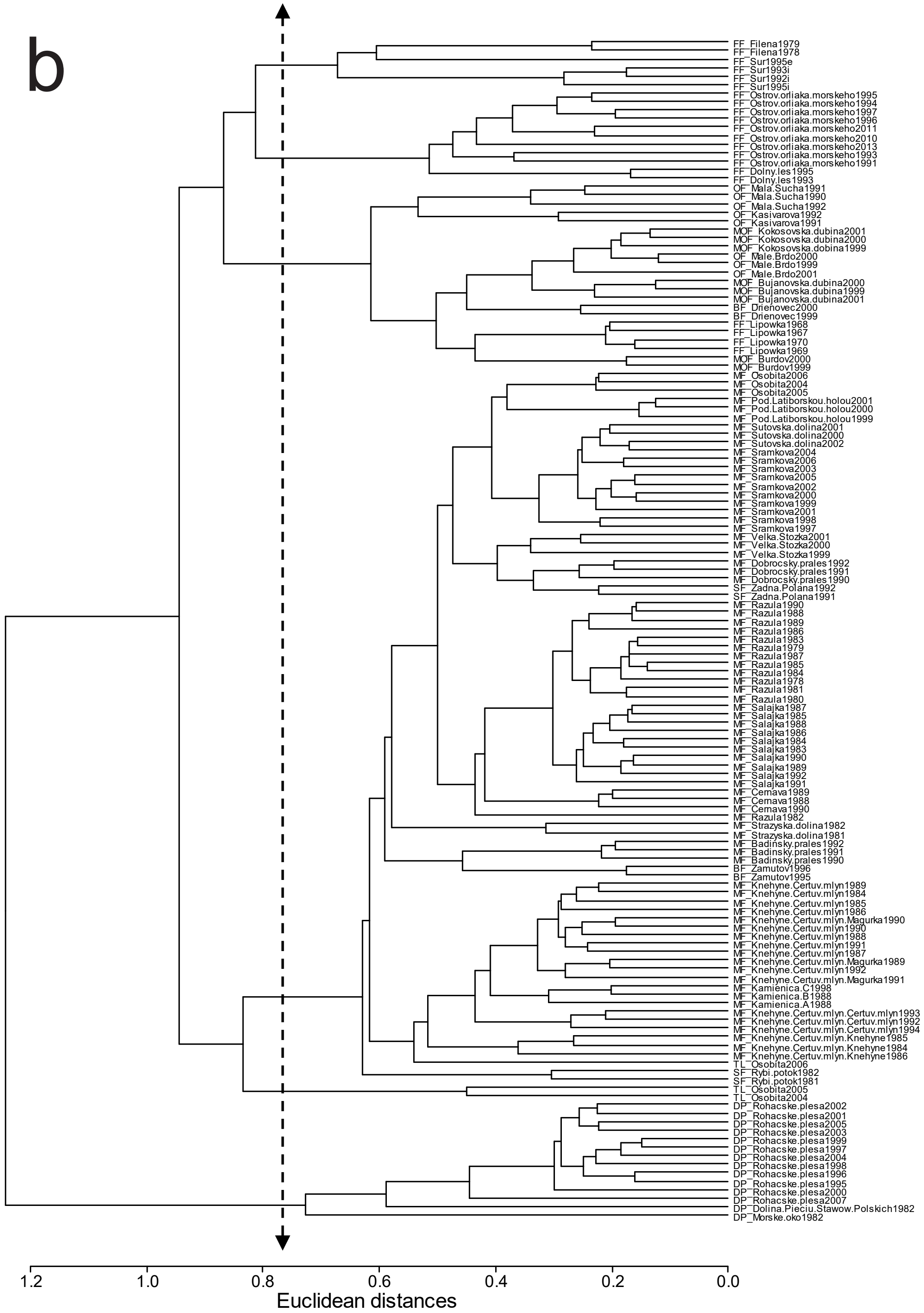
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MF_Razula1988
MF_Razula1989
MF_Razula1986
MF_Razula1983
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Euclidean distances

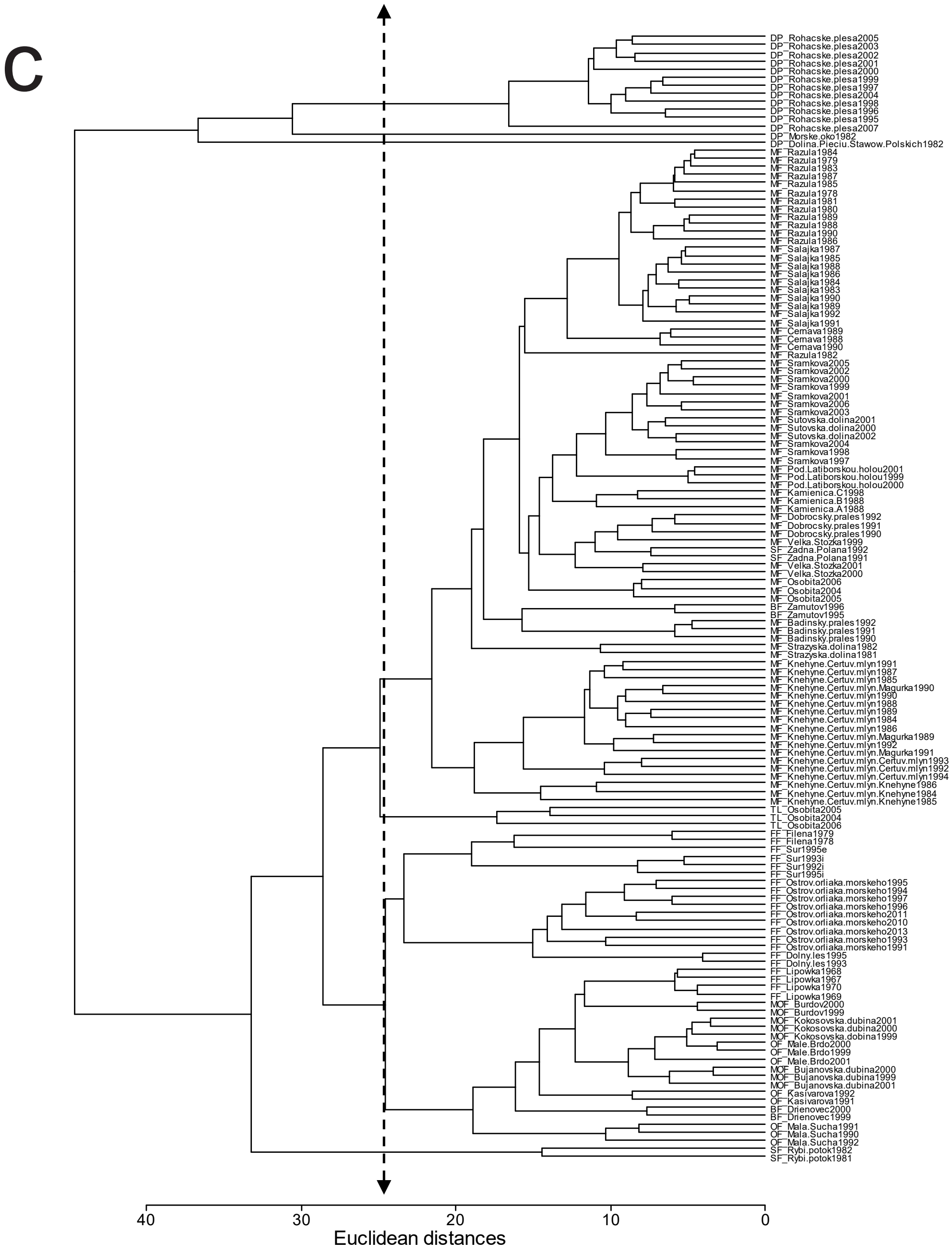

Fig. 2. Classification patterns of breeding bird assemblages of primeval and natural forests in the elevational gradient of the Westerns Carpathians based on presence/absence (a), density (b) and dominance (c) matrices. Significant clusters revealed by bootstrapped resampling at α = 0.05 corresponding the elevational belts of bird assemblages are delineated by dash lines. A name of each sample is composed of a forest type indicated by capital letters, a name of a site and a year of a territory mapping census. Additional information on each site characteristics are given in Supplements 1 and 2. Legend: BF – beech forests, DP – dwarf pine communities, FF – floodplain and wet lowland forests, MF – mixed forests, MOF – mixed oak forests, OF – oak forests, SF – spruce forests and TL – timber line forest.

Table 1. Probabilities $P(G^o \leq G^*)$ and averages of sample attributes generated by 10 000 random iterations of bootstrap resampling of 84 bird presence/absence (binary) × 139-year census sample, 84 bird density × 139-year census sample and 84 bird dominance × 139-year census sample data matrices at different partition levels. The initializer of the pseudo-random number generator was set in automatic mode. In the first data matrix, classification was sharp at the levels of eight groups, in the second matrix at the levels of six groups, and in the third matrix at the levels of seven groups, indicating the numbers of different bird assemblage belts and single sites along the elevational gradient of the Western Carpathians at the critical value $\alpha = 0.05$. The numbers of significantly different clusters revealed by bootstrapped cluster analyses (UPGMA) of Euclidean distances in the three classifications are indicated by bold letters.

Matrix type	Number of groups (clusters)								
	2	3	4	5	6	7	8	9	10
Binary matrix									
$P(G^o \leq G^*)$	**0.1543**	**0.2551**	**0.1834**	**0.0822**	**0.0503**	**0.0735**	**0.0520**	0.0142	0.0090
Average of sample attribute	0.9662	0.9897	0.9853	0.9809	0.9735	0.9826	0.9817	0.9751	0.9749
Density matrix									
$P(G^o \leq G^*)$	**0.3038**	**0.1824**	**0.2744**	**0.167**	**0.1665**	0.0366	0.019	0.0543	0.0435
Average of sample attribute	0.9869	0.9830	0.9879	0.9797	0.9800	0.9708	0.9646	0.9674	0.9531
Dominance matrix									
$P(G^o \leq G^*)$	**0.4998**	**0.314**	**0.177**	**0.1038**	**0.1179**	**0.0551**	0.0418	0.0567	0.0565
Average of sample attribute	0.9978	0.9870	0.9749	0.9637	0.9796	0.9697	0.9745	0.9778	0.9775

significant scores. We used unrestricted permutation tests for evaluation of the statistical significance of the ordination axes. In all computations, we used 9999 iterations. We also used false discovery rate corrections of probability values (*P*) in the environmental variable selection procedure.

Co-correspondence analysis (CO-CA)

CO-CA is the constrained ordination method for relating one community data set to another in order to predict one biological community from another (ter Braak & Schaffers 2004). In this way, we used woody plant assemblages in census sites as a predictor data matrix and bird assemblages as a response data matrix. Unrestricted permutation tests (9999 iterations) were used to test the statistical significance of predictive CO-CA axes. Correlation coefficients between bird-derived and woody plant-derived scores were used to evaluate the ordination fit of the first ten CO-CA axes. We applied this ordination technique for analyses of three data matrices: 84 bird binary and 44 woody plant binary × 139 samples, 84 bird density and 44 woody plant dominance × 123 samples, and 84 bird dominance and 44 woody plant dominance × 123 samples. We performed all ordination analyses in this study in the Canoco 5.11 ordination package (ter Braak & Šmilauer 2018).

3. Results

3.1. Classification and zonation of bird assemblages

To answer the first and second objectives of the study focused on the determination of bird assemblage elevational belts and analyses of differences in elevational belt patterns produced by different data type matrices, we subjected bird presence/absence, density, and dominance data matrices to the bootstrapped cluster analyses. After evaluation the results of these statistical analyses, we aimed to answer the fifth objective whether or not the bird assemblage form statistically distinct groups corresponding to elevational belts supporting Clementsian or Gleasonian community concept. Bootstrapped cluster analyses from three types of data matrices and six resemblance measures produced varying numbers of significant groups of bird assemblage samples corresponding to different elevation belts in the gradient of the Western Carpathians (Supplements 4, 5, 11, 12). We selected metrics of Euclidean distances as a universal measure capable of distinguishing binary, density and dominance data matrices that produced reasonable and the most logical classification patterns.

3.1.1. Presence/absence (binary) classification

The classification of the binary matrix revealed eight significant clusters at α = 0.05 that roughly corresponded to the six distinct elevation belts of the bird assemblage that come from the elevation ranges of the census plots (Fig. 2a, Supplement 5, Table 1). We characterized distinct bird assemblage belts as follows: (1) softwood floodplain forests (116–118 m a.s.l.), (2) hardwood floodplain forests (128–189 m a.s.l.), (3) dry oak forests (130–483 m a.s.l.), (4) oak, oak-beech, beech and mixed forests (199–830 m a.s.l.), (5) mixed and spruce forests (545–1506 m a.s.l.), and (6) dwarf-pine shrubs (1370–1720 m a.s.l.). The mixed and spruce forests formed three significant clusters of overlapping elevational ranges (545–1506, 925–1506, 960–1100 m a.s.l.), thus we merged them into one elevational belt of mixed and spruce forests.

3.1.2. Density classification

The bootstrap analysis of the density matrix revealed six significant clusters at α = 0.05, roughly corresponding to four distinct elevation belts of the bird assemblage that come from the elevation range of the census plots (Fig. 2b, Supplement 5, Table 1). We characterized these four different bird assemblage belts as follows: (1) floodplain forests (116–189 m a.s.l.), (2) oak, oak-beech, and beech forests (130–804 m a.s.l.), (3) mixed and spruce forests (545–1506 m a.s.l.), and (4) dwarf-pine shrubs (1370–1720 m a.s.l.). The floodplain forests formed two distinct clusters with mixed samples of softwood and hardwood sites with partly overlapping elevational ranges (116–142 and 128–189 m a.s.l.); consequently, these could not be logically divided into two distinct belts and were merged into one elevational belt of floodplain forests. Clusters of mixed and spruce forests and timber line forest totally overlapped in elevational ranges because one sample (TL_Osobita_2006) from the timber line forest joined the cluster of mixed and spruce forests; therefore, we merged these two clusters into one elevational belt of mixed and spruce forests.

3.1.3. Dominance classification

Cluster analysis based on the dominance matrix revealed seven significant clusters at α = 0.05 roughly corresponding to five distinct elevation belts of bird assemblages coming from the elevational range of census plots and habitat physiognomy (Fig. 2c, Supplement 5, Table 1). We characterized these distinct five belts of bird assemblages as follows: (1) floodplain, oak, oak-beech and beech forests (116–804 m a.s.l.), (2) mixed and spruce forests (545–1345 m a.s.l.), (3) spruce forest (1300–1400 m a.s.l.), (4) timber line forest (1330–1506 m a.s.l.), and (5) dwarf-pine shrubs (1370–1720 m a.s.l.). Two spruce sites clustered differently. One joined the mixed and spruce forest group, whereas the other formed a separate significant cluster; therefore, the objectivity of this belt is questionable, but we decided to divide it as a separate elevational belt due to distinct habitat physiognomy. The dwarf-pine sites were divided into three significant branches of the dendrogram, but their elevational ranges overlapped, and thus were merged into a single elevation belt of dwarf-pine shrubs.

3.1.4. Comparisons of classifications

In order to analyse differences among dendrograms based on the Euclidean distances from presence/absence, density, and dominance

Table 2. Eigenvalues, explained cumulative variation, pseudo-canonical correlation and explained fitted cumulative variation for the first ten axes of canonical correspondence analysis employed for analyses of 84 bird species binary (presence/ absence) and 11 environmental variables × 139 census samples, 84 bird species density and 11 environmental variables × 139 census samples and 84 bird species dominance and 11 environmental variables × 139 census samples. Census samples represent bird assemblages of primeval and natural Western Carpathian forests in elevational gradient from lowlands to subalpine zone (dwarf-pine communities).

Matrix type and ordination results	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10
84 bird species binary vs. 11 environmental variables × 139 sample matrix										
Eigenvalues	0.3732	0.2466	0.0680	0.0647	0.0530	0.0378	0.0365	0.0253	0.0185	0.0119
Explained cumulative variation	18.58	30.86	34.25	37.47	40.11	41.99	43.80	45.06	45.98	46.58
Pseudo-canonical correlation	0.9758	0.9133	0.7876	0.8992	0.8125	0.7774	0.7402	0.7443	0.6041	0.5903
Explained fitted cumulative variation	39.49	65.57	72.77	79.61	85.22	89.22	93.07	95.75	97.71	98.97
84 bird species density vs. 11 environmental variables × 139 sample matrix										
Eigenvalues	0.3608	0.1948	0.0841	0.0636	0.0437	0.0405	0.0262	0.0169	0.0114	0.0065
Explained cumulative variation	23.73	36.54	42.07	46.26	49.13	51.79	53.52	54.63	55.38	55.80
Pseudo-canonical correlation	0.9599	0.8553	0.7051	0.8661	0.6785	0.7704	0.8424	0.6978	0.7757	0.7028
Explained fitted cumulative variation	42.27	65.09	74.94	82.39	87.51	92.26	95.33	97.31	98.64	99.40
84 bird species dominance vs. 11 environmental variables × 139 sample matrix										
Eigenvalues	0.4856	0.2155	0.0941	0.0541	0.0472	0.0299	0.0236	0.0154	0.0116	0.0069
Explained cumulative variation	29.88	43.14	48.93	52.26	55.16	57.01	58.46	59.41	60.12	60.54
Pseudo-canonical correlation	0.9727	0.8410	0.8146	0.8204	0.7390	0.7420	0.7815	0.7385	0.7647	0.6678
Explained fitted cumulative variation	49.12	70.92	80.43	85.90	90.68	93.70	96.10	97.65	98.82	99.52

matrices, we applied the pairwise cophenetic Pearson's correlations for this purpose. The pairwise cophenetic Pearson's correlations of binary, density and dominance dendrograms were significantly similar at α = 0.0001, yet three data sets were not statistically independent because they originated from one source of sampling (derivations of abundance data) so that significance tests were not valid. The cophenetic Pearson's correlation coefficient between the binary and density dendrogram was 0.76, between the binary and dominance dendrograms 0.68 and between the density and dominance dendrograms 0.95.

3.2. Environmental drivers of bird assemblages

3.2.1 Canonical correspondence analysis (CCA)

To answer the third objective of this study, we employed CCA to analyse the explanatory power of environmental factors by their explained variance of the elevational ordination patterns of bird assemblages. We ran CCA from two types of matrices from the presence/absence, density, and dominance bird data, complete and reduced matrices, to analyse the effects of year sample correlations in time series of 2–13 years on revealed rank of environmental factors. Complete matrices represented all 139-year samples including complete time series, while reduced matrices consisted only of one randomly selected year sample from time series having only 38-year samples corresponding to the number of analysed sites.

3.2.1.1. Complete data matrices

The CCA results supported classifications based on cluster analyses for all data matrices (Fig. 3a–c, Supplement 8a–c) and produced spatially distinct belts in ordination space. The explained cumulative variation of the first two CCA axes was 30.9–43.1% (Table 2). The unrestricted permutation test on all axes, as well as on the separate first axis, was significant for all three data matrices. Based on explained variance, mean annual temperature 1961–2010 was selected as the best explanatory variable by both the simple and conditional effect with strong significance in all tests (Supplement 10a–f). Taking into account the cumulative rank in explained variance of remaining factors based on simple and conditional term effect testing, the eleven environmental factors were ranked as follows: 2. mean annual precipitation 1961–2010, 3. the first DCA axis of woody plant species composition, 4.–5. wood increment, 4.–5. the second DCA axis of woody plant species composition, 6. latitude, 7. reserve size, 8. precipitation during breeding months (April–July) in census years, 9. dendromass, 10.–11. census year and longitude. Two factors in the fourth and fifth positions and the tenth and eleventh positions reached the same scores. All factors in all tests were significant (Supplement 10a–f).

3.2.1.2. Reduced-data matrices

The first two CCA axes explained together 41.1–46.7% of variation (Supplement 6, 7a–c) that is more explained variation than in case of complete matrices. Permutation tests on all axes and separately on the first axis were highly significant in all cases. Based on environmental factor ranking from explained variance in both simple and conditional effect tests of all types of matrices, the factor of the first DCA axis of woody plant species composition was ranked in the first place four times and the factor of the mean annual precipitation 1961–2010 twice (Supplement 10g–l). According to the summation score of the rankings in all tests, the factors were ranked as follows: 1. the first DCA axis of woody plant species composition, 2. mean annual precipitation 1961–2010, 3. wood increment, 4. mean annual temperature 1961–2010, 5. reserve size, 6.–7. latitude, and the second DCA axis of woody plant species composition, 8. dendromass, 9. longitude, 10. precipitation during breeding months (April–July) in census years and 11. census year. The factors of latitude and the second DCA axis of woody plant composition reached the same score and occupied the sixth and seventh positions. Only the first three factors in all tests had significant scores (Supplement 10g–l).

Table 3. Correlation coefficients, eigenvalues and cumulative explained variation for the first ten axes of co-correspondence analysis employed for analyses of 84 bird species binary (presence/ absence) and 44 woody plant species binary (presence/ absence) × 139 census samples, 84 bird species density and 44 woody plant species dominance × 123 census samples and 84 bird species dominance and 44 woody plant species dominance × 123 census samples. Census samples represent bird assemblages of primeval and natural Western Carpathian forests in elevational gradient from lowlands to subalpine zone (dwarf-pine communities).

Matrix type and ordination results	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10
84 bird binary vs. 44 woody plant binary × 139 sample matrices										
Correlation coefficients	+0.9578	+0.8552	+0.8569	+0.8615	+0.7624	+0.7950	+0.8059	+0.7596	+0.7992	+0.7548
Eigenvalues	0.3096	0.1536	0.1154	0.0527	0.0377	0.0346	0.0207	0.0161	0.0148	0.0099
Cumulative explained variation	38.95	58.28	72.79	79.42	84.17	88.52	91.12	93.15	95.02	96.27
84 bird density vs. 44 woody plant dominance × 123 sample matrices										
Correlation coefficients	+0.9534	+0.9300	+0.8686	+0.7069	+0.6613	+0.9129	+0.8536	+0.6673	+0.6608	+0.7084
Eigenvalues	0.6048	0.2145	0.1977	0.0988	0.0663	0.0287	0.0185	0.0134	0.0128	0.0030
Cumulative explained variation	47.77	64.71	80.33	88.13	93.37	95.64	97.11	98.17	99.18	99.42
84 bird dominance vs. 44 woody plant dominance × 123 sample matrices										
Correlation coefficients	+0.9660	+0.9448	+0.9102	+0.9443	+0.9280	+0.7702	+0.7153	+0.9007	+0.7584	+0.6828
Eigenvalues	0.4198	0.2919	0.1257	0.0701	0.0354	0.0180	0.0170	0.0076	0.0053	0.0042
Cumulative explained variation	41.80	70.87	83.39	90.38	93.90	95.70	97.39	98.15	98.67	99.09

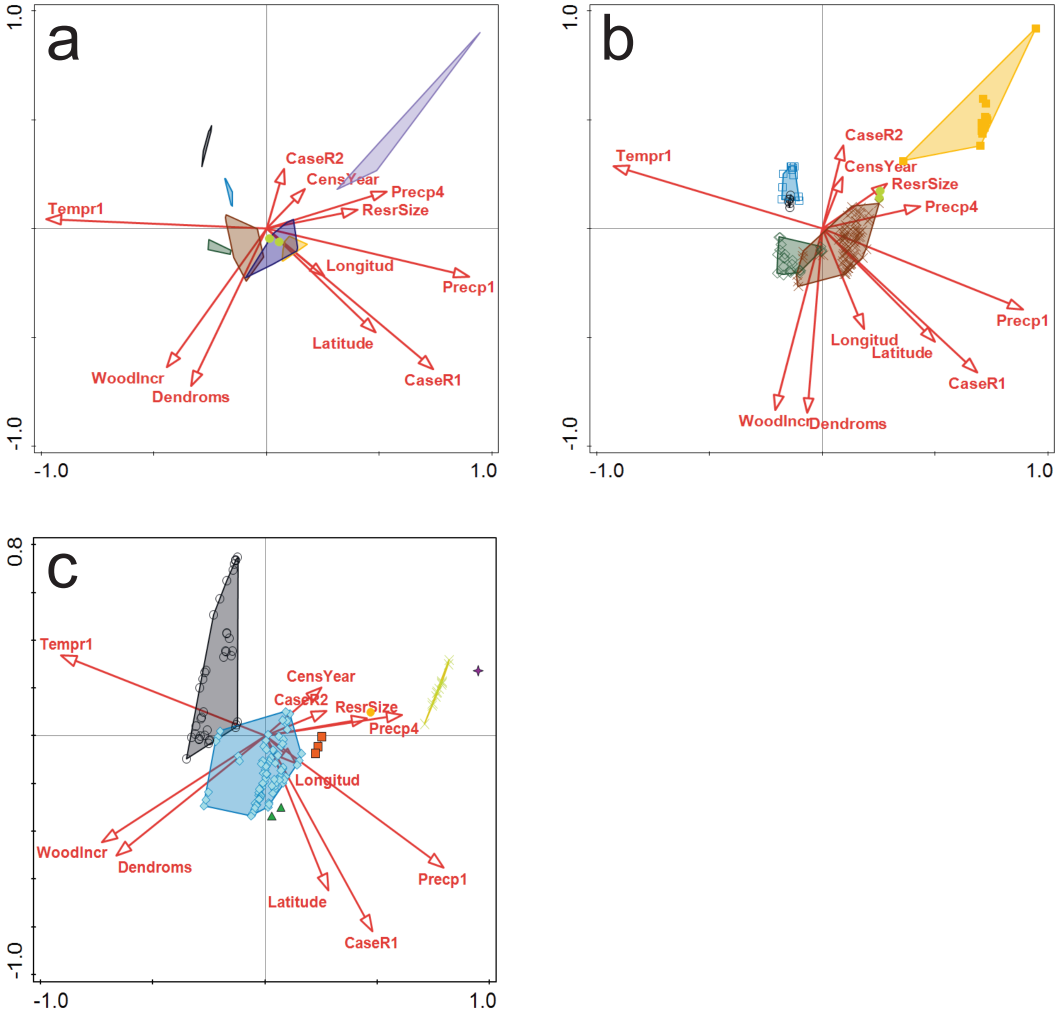

Fig. 3. Biplots of canonical correspondence analysis (CCA) based matrices of 84 bird species presence/absence (binary) vs. 11 environmental variables × 139 samples (a), 84 bird species density vs. 11 environmental variables × 139 samples (b) and 84 bird species dominance vs. 11 environmental variables × 139 samples (c) of breeding bird assemblages of primeval and natural forests in the Western Carpathians. The ordination diagram shows a clear distinction between significant elevational belts of bird assemblages revealed by the bootstrapped cluster analysis of Euclidean distances of the same bird matrices. Legend: graph a: blue and black = two types of floodplain and lowland forests (softwood and hardwoods), green = dry oak forests, brown = oak, mixed oak and beech forests, pale green points = single mixed forest site, yellow and purple = two groups of mixed and spruce forests, pale pink = dwarf-pine communities (subalpine zone); graph b: open black circles and open blue squares = two groups of floodplain and lowland forests, open green diamonds = oak, mixed oak and beech forests, brown × mark = beech, mixed and spruce forests, filled green circle = upper timber line forest and filled orange squares = dwarf-pine communities (subalpine zone); graph c: open black circle = floodplain, lowland, oak, mixed oak and beech forests, blue diamond = beech, mixed and spruce forests, green triangle = single spruce forest, red square = single upper timber line forest, green × mark and filled orange circle and filled purple star = three significantly different dwarf-pine communities (subalpine zone); Environmental variables: CaseR.1 – the first DCA ordination axis of the woody species composition matrix (floristics 1), CaseR.2 – the second DCA ordination axis of the woody species composition matrix (floristics 2), CensYear – census year, Dendroms – dendromass, Longitud – longitude, Precp1 – mean annual precipitation 1961–2010, Precp4 – precipitation during breeding months (April–July) in census years, ResrSize – reserve size, Tempr1 – mean annual temperature 1961–2010, WoodIncr – wood increment.

3.2.2. Co-correspondence analysis (CO-CA)

To answer the fourth objective focused on predicting species composition, density and dominance of bird assemblages by species composition and dominance of woody plant assemblages in the elevational gradient, we applied CO-CA for this task. The woody plant assemblages of primeval and natural forests showed a strong predictive power of the variation of the breeding bird assemblages along the elevational gradient of the Western Carpathians. The first CO-CA ordination axis of bird and plant presence/absence (binary), bird density and plant dominance and bird and plant dominance matrices explained 39.0, 47.8 and 41.8% of explained variation with correlation coefficients 0.96, 0.95 and 0.97, respectively (Table 3, Supplement 9). Only the first axis in binary analysis, the first two axes in density and dominance analysis, and the first five axes in dominance analysis showed higher correlation coefficients than 0.9 indicating a strong predictive power of plant assemblages. In summary, the first two axes of CO-CA explained cumulative variation of 58.3, 64.7, and 70.9% of bird and plant presence/absence, bird density and plant dominance and bird and plant dominance matrices.

4. Discussion

The main conclusions of this study can be summarized as follows, corresponding to the five main objectives set in the Introduction:

1. Bootstrapped cluster analyses of Euclidean distances from the presence/absence, density and dominance matrices produced differing numbers of significant clusters (8, 6, 7) corresponding to six, four and five elevational belts of bird assemblages. The numbers of these significant clusters should be understood as the maximum values when considering the potentially high statistical error type II (Supplement 12). Nonetheless, only three elevational zones were consistent in all classifications: lowland, mountain and subalpine (dwarf-pine) bird assemblage belts. These three groups were divided into subgroups depending on data type and metrics used.
2. Different data type matrices produced different numbers of significant groups of bird assemblages. Similarly, different metrics used in cluster analysis produced different numbers of significant groups of bird assemblages. Classification patterns of cluster analyses approximately corresponded to revealed CCA ordination patterns.
3. CCA of full and reduced data matrices did not produce the same ranking of factor importance, yet climate, floristics and productivity were the most important with rank depending on matrix collinearity, data type and matrix size. When evaluating the weight ranks of environmental variables by cumulative point values, the best predictors were woody plant species composition, mean annual precipitation 1961–2010, productivity (wood increment) and mean annual temperature 1961–2010. The first axis in all CCA ordination analyses (complete matrix) was identified as the elevation gradient that was related to a continuous decline in temperature that affected plant community composition and productivity that drove changes in species composition and structure of bird assemblages reflected in the different elevational belts.
4. CO-CA yielded a very strong predictive power of woody plant assemblage for bird assemblage of all bird data matrices, thus supporting the results of CCA.
5. Patterns of species composition and structure (density, dominance) of the bird assemblages were characterized by the significant and very wide habitat groups representing several plant associations that supported Clementsian community concept. However, bird assemblages did not respond to fine-scale woody plant species composition and dominance patterns coming from the specific forest classification units. In summary, using phyto-sociological units of commonly used systems such as the Braun-Blanquet system for bird assemblage types does not properly reflect their true significant groups in nature.

4.1. The patterns of animal assemblage zonations

Patterns of animal assemblage zonations in mountains on a global scale have been shown to vary widely. Some studies showed clear zonation patterns using various community dis/similarity metrics and numerical analysis approaches (*e.g.* Patterson *et al*. 1998, Nor 2001, Shiu & Lee 2003, Romdal & Rahbek 2009); however, only few of these studies were based on statistical methods dividing elevational gradient into significant assemblage belts. On the other hand, some animal assemblages formed no zonation patterns (*e.g.* Olson 1994).

In the next section, we will focus on studies on vertebrates on global scale that have found more or less clear elevational zonation patterns. The elevational zonation of amphibians and reptiles was analysed in the work of Hofer *et al*. (1999) on Mount Kupe, Cameroon, in tropical West Africa. Chronological clustering of five data matrices of reptiles and amphibians determined two and in one case three elevational belts. The zonation of amphibian and reptile assemblages is similar to other analysed vertebrate groups (summarized below) showing usually two or three zones reflecting gradual changes in habitat along the elevational gradients.

Patterson *et al*. (1998) examined bird, bat and mouse zonation patterns within Manu National Park and Biosphere Reserve in the Andean Cordillera, Peru. The authors used the standard cluster analyses (UPGMA) of presence/absence data and identified three distinct clusters (lowland, intermediate and highland assemblages) and similarly described differences in species composition between lowland and highland faunas. The divisions of elevational gradient (cutoff points) varied among groups. In a broader sense, high rates of species turnover in the three assemblages were not associated with the transition of main vegetation types along the gradient. Other studies of bird zonations from Taiwan (Shiu & Lee 2003) and Mexico (Medina-Macías *et al*. 2010, Jaime-Escalante *et al*. 2016) using similar multivariate numerical procedures also identified three elevational belts corresponded to low-, middle- and high elevation bird assemblages. However, Nor (2001) on Mount Kinabalu (4095 m a.s.l.) in Malaysia found only two wider mouse assemblage belts reflecting changes between vegetation zones of lower montane forest and upper montane forest and subalpine communities.

Romdal & Rahbek (2009) performed chronological clustering of abundance and binary-based metrics for analyses of zonation using the mapping method data of breeding bird assemblages along the elevational natural forest gradient in the Udzungwa Mts., Tanzania. The chronological clustering divided lowland and montane bird assemblages. This procedure of binary matrices delineated six elevational belts. The authors identified two distinct groups of species (36 lowland and 40 montane) approximately similar in species numbers and allocating lowland and montane belts, thus forming two different bird assemblages.

Viterbi *et al*. (2013) used CA for ordination of animal assemblages (spiders, carabids, staphilinids, butterflies and birds) on an *a priori* defined vegetation zones in the Italian Alps and found a clear distinction between montane and alpine belts with an intermediate position of subalpine belt. Although a statistical test of CA ordination scores identified a clear zonation of animal assemblages, the ordination pattern identified a gradual change of the studied assemblages along the elevational gradient.

In summary, published studies of bird assemblages have determined mostly only two (Romdal & Rahbek 2009) or three (Patterson *et al*. 1998, Shiu & Lee 2003, Medina-Macías *et al*. 2010, Viterbi *et al*. 2013, Jaime-Escalante *et al*. 2016) elevational belts, usually dividing low, mid and high elevation faunas. In our study, the bootstrapped cluster analysis of Jacckard and Sorensen dissimilarity indices also produced three significant belts of lowland, mountain, and subalpine bird assemblages roughly corresponding to major transitions of plant physiognomy types. When we applied the same procedure of Euclidean distances using the binary matrix, we identified eight significant groups with statistical error risk that corresponded to six bird elevational belts. Density and dominance matrices identified six and seven significant elevational belts with risk of statistical errors corresponding to four and five bird elevational belts. These classifications have to be understood as the theoretical maximum number of bird zones. In common, we determined three distinct bird elevational belts as in the above-described patterns from these three classifications based on presence/absence, density, and dominance matrices. The cited studies and our results lead to the conclusion that bird assemblages form only very wide significant groups in relation to habitat types and corresponding primarily to major transitions of vegetation physiognomy types along elevational gradients. These conclusions support the Clementsian community concept, but only on very broad habitat scales.

4.2. Environmental drivers of vertebrate assemblages in elevational gradients

In a classical study of the elevational distribution of birds in the Eastern Andes of Peru, Terborgh (1971) concluded that ecotones accounted for less than 20%, competitive exclusion for about one-third, and gradually changing conditions along the gradient for about half of the observed distributional limits. In a later revised study, Terborgh & Weske (1975) deemphasized the importance of gradually changing habitat conditions and proposed that interspecific competition (direct and diffuse) was more important. Using these hypotheses and modern statistical design, Elsen *et al*. (2017) showed in the temperate Himalaya Mts. that temperature was a primary abiotic driver, followed by habitat and interspecific competition. Global meta-analysis of elevational patterns of bird species richness detected temperature and precipitation as main drivers (McCain 2009). Viterbi *et al*. (2013) also identified temperature as the primary factor shaping animal assemblages especially of invertebrates in the Italian Alps, but vegetation variables also seemed important for birds and butterflies. Based on the results of CCA of the complete data matrices in our study, temperature was the best explanatory variable in all analyses. Yet, it was ranked fourth based on the results of CCA of reduced data matrices. In the overall rank of all CCA analyses, temperature stayed in the third position after the floristics and precipitation, thus our study supports the idea that biotic factors are main drivers followed by climatic factors shaping the bird assemblages in the Western Carpathians. Several hypotheses of temperature effects on species richness have been proposed; however, direct evidence for those is relatively weak and the relative importance of the various plausible mechanism is unclear (Pearce-Higgins & Green 2014). Current reviews of bird species richness driving factors underline climate as the main determinant, nonetheless, hypothesis of productive energy linked to abundance of resources such as solar energy, water, plant productivity or prey was generally better ranked than simple predictors (temperature, precipitation, topography, habitat heterogeneity) and were followed by historical constraint (Pearce-Higgins & Green 2014, Pearce-Higgins & Martin 2023). Solar radiation seems to effect elevational distribution of bird assemblages in European mountains and birds respond by higher elevational shifts on sites receiving higher radiation, especially south-facing slopes (Couet *et al.* 2025). The mechanism is not currently known, yet climate change through increasing temperatures and land use changes might be the main drivers. For birds, relative high importance of habitat elevational gradient and ecotones and low significance of interspecific competition were detected in several temperate and subtropical mountain studies (*e.g*. Able & Noon 1976, Navarro 1992, Elsen *et al*. 2017), while competitive interactions seem to be more and ecotone minor important in tropical regions (Terborgh 1971, Terborgh & Weske 1975, Patterson *et al*. 1998).

Long-lasting debate (see Wiens 1989 for review) on relative importance of floristic (*e.g*. Rotenberry 1985, Adams & Matthews 2019), structural (*e.g*. MacArthur & MacArthur 1961, James & Wamer 1982, Müller *et al*. 2010) or synergy effects of both (*e.g*. Hewson *et al*. 2011) vegetation parameters of habitats on bird assemblages has also been considered in studies of bird biogeography (*e.g*. Jankowski *et al*. 2013). Jankowski *et al*. (2013) identified tree species composition, elevation and vegetation structure as the most significant predictors of bird species composition along the elevational gradient in the Peruvian Andes. Tree floristics was always included in best predictive models for all birds and foraging guilds in multiple regressions. Their results underlined a strong correspondence between bird and plant assemblages, as was revealed in our study based on CO-CA and CCA in the Western Carpathians. The primary importance of floristics in animal assemblages was also described in arthropods (Schaffers *et al*. 2008). The effects of tree species composition on bird foraging patterns related to tree-specific diet and physiognomy were identified at several forest sites (Holmes & Robinson 1981, Robinson & Holmes 1982, Holmes & Schultz 1988, Recher *et al*. 1996, Gabbe *et al*. 2002, Korňan & Adamík 2017). It is impossible to separate effects of floristics and habitat physiognomy because each tree species has certain genetically predetermined physiognomy that affects the efficiency of bird foraging techniques (Robinson & Holmes 1982). In addition, chemical composition of foliage, particularly nutritional (crude protein, minerals, non-structural carbohydrates) and digestion-inhibiting (structural carbohydrates, total phenolics, condensed tannins) compound content affects its palatability for arthropods. Plant species with higher foliage palatability can support more arthropods that led to a notion of so-called foliage palatability hypothesis (Greenberg & Bichier 2005). Arthropod assemblages, in result, influence species composition and abundance of dietary resources for birds (Recher *et al*. 1996, Beltrán & Wunderle 2013). In summary, the effects of floristic and structural variables on bird assemblages are impossible to clearly separate because they act in a synergistic way.

Most mountain systems are severely affected by human activities, the impact of which usually declines with elevation (Nogués-Bravo *et al*. 2008). This has major effect on structure and dynamics of ecological communities mainly seen in prevalence of generalist species and reduction of specialists. Due to this fact, most of 461 studies conducted on elevational gradient include disturbed lowlands violating diversity patterns (Nogués-Bravo *et al*. 2008). A total of 203 single elevational transects include disturbed lowlands, whereas only twelve of these studies were conducted on complete and natural gradients. Our study using bird censuses at many sites within primeval and natural forests offers a unique reconstruction of historic bird assemblages on the European continent severely impacted by human activity (Sabatini *et al*. 2018).

Understanding factors shaping mountain patterns of biodiversity has a high priority in biogeography, especially in times of climate change, because they are inhabited by large numbers of endemic and range restricted species that are or can be threatened (Chamberlain *et al*. 2023b). The ornithogeography of the Western Carpathians has not previously been well studied, and our work here is the first to analyse factors driving the regional pattern of bird assemblages in this mountainous area. Understanding the biology and ecology of these species and their assemblages and developing reasonable conservation management plans for them should be our priority to protect this remarkable biodiversity for future generations.

Lintuyhteisöjen korkeussuuntaista levinneisyyttä Länsi-Karpaattien vuoristossa säätelevät pääasiassa floristiikka, ilmasto ja tuottavuus

Karpaateilla on yksi Euroopan unionin suurimmista jäljellä olevista vanhoista ja luonnontilaisista metsistä, ja niiden biogeografiaa on tutkittu vain vähän. Tässä artikkelissa tarkastelemme Länsi-Karpaattien lintuyhteisöjen korkeussuuntaista levinneisyyttä ja sitä sääteleviä ympäristötekijöitä. Käytimme reviirikartoituksiin perustuvaa laskenta-aineistoa sekä tietoja selittävistä ympäristötekijöistä 38 tutkimusalueelta (139 vuoden otokset) korkeusgradientilla alangolta subalpiiniselle vyöhykkeelle. Analysoimme näitä datamatriiseja uusio-otantaklusterianalyyseillä sekä epäsuorilla ja suorilla korrespondenssianalyyseillä (DCA, CCA, CO-CA). Euklidisten etäisyyksien klusterianalyysit esiintymis- tai poissaolo-, tiheys- ja dominanssimatriiseista tuottivat eri määrät merkittäviä klustereita (8, 6, 7), jotka vastasivat kuutta, neljää ja viittä korkeusvyöhykettä. Vain kolme korkeusvyöhykettä – alanko, vuoristo ja subalpiininen – olivat yhdenmukaisia kaikissa luokitteluissa. Selittävät muuttujat, eli floristiikka, sademäärä, lämpötila ja tuottavuus, selittivät

parhaiten kanonisen vastaavuusanalyysin (CCA) ordinaatioiden varianssia. Floristiikka ja puuvartisten kasvilajien hallitsevuus ennustivat yhteiskorrespondenssianalyyseissä (CO-CA) voimakkaasti lintuyhteisöjen korkeusjakaumaa. Tuloksemme tukevat Clementsin käsitystä merkittävistä ja erillisistä yhteisöistä, jotka eivät ole sidoksissa elinympäristöjen hienojakoiseen vaihteluun vaan jotka pikemmin määrittyvät elinympäristöjen laajoilla mittakaavoilla.

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Online supplementary material

Supplementary materials available in the online version of the article includes two PDFs and two spreadsheets.