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Publisher Contact – Julkaisijan yhteystiedot – Utgivarens kontaktinformation
BirdLife Suomi ry / BirdLife Finland
Annankatu 29 A, FI-00100 Helsinki, Finland
Phone: +358 9 413 533 00
E-mail: office@birdlife.fi
Sähköposti – E-post: toimisto@birdlife.fi
www.birdlife.fi

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Rise of the Eagle Owl population due to rat-rich refuse dump sites and fall when closing them: a large-scale long-term "supplementary feeding experiment"

Risto Tornberg*, Kauko Huhtala, Heimo Mikkola, Jere Tolvanen, Jari Valkama & Erkki Korpimäki

R. Tornberg, Department of Ecology and Genetics, University of Oulu, FI-90014 Oulu, Finland
K. Huhtala, Rajavainiontie 11 as. 1, FI-85310 Sievi as., Finland
H. Mikkola, Department of Biology, University of Eastern Finland, P.O.Box 1627, FI-70211 Kuopio, Finland
J. Tolvanen, Sirnäsintie 66, FI-25830 Västanfjärd, Finland
J. Valkama, Finnish Museum of Natural History, FI-00014 University of Helsinki
E. Korpimäki, Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland
** Corresponding author's email: ristotorn@gmail.com*

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Food-supplementation experiments conducted on terrestrial vertebrates have usually shown the importance of food as an agent in increasing reproductive success. However, to date, the number of large-scale food supplementation experiments carried out on top predators has been limited. The Eurasian Eagle Owl (*Bubo bubo*) is the largest nocturnal avian predator in the boreal and temperate regions of Eurasia. Here, we study the diet composition and breeding success of this top predator in relation to the location and distance to rubbish dumps, which sustain large numbers of brown rats *Rattus norvegicus*, one of the main prey items for owls. The number of these rubbish dumps (hereafter dumps) increased in Finland during the period between the 1960s and the 1990s, whereafter their number was steeply reduced, leading to a remarkable decline in rat populations. A similar trend in the Eagle Owl population largely followed this development, raising the question of whether this country-wide "supplementary feeding experiment" was behind this phenomenon. The proportion of rats in the diet of the owls was high, on average, 70% of prey items near the dumps decreasing to around 10–15% at a 6–7 km distance from the dumps. Correspondingly, the number of 3–4-week-old offspring declined in relation to the distance from the dump, so that 0.5 less chicks were recorded at a distance of 10 km from the dump. During the study, the overall density of nests near the dumps was 2.7 times higher than those recorded further away. The availability of extra food material within the dumps (and rats therein) probably induced an increase in the Finnish Eagle Owl population, which saw a decline after dumps were closed.

1. Introduction

Food-supplementation experiments conducted in terrestrial vertebrates have usually shown the importance of food as an agent to advance a breeding season, increase clutch or litter size and improve reproductive success (Boutin 1990, Ruffino *et al*. 2014). The positive effect of food supplements was usually highest during the seasonal scarcity of food resources and showed that many animal populations were food-limited (Boutin 1990, Newton 1998, 2002, Ruffino *et al*. 2014). However, a vast majority of food-supplementation experiments have been conducted with small mammals, herbivorous and insectivorous birds as well as with small or medium-sized predators, while food-addition experiments, showing food limitation in populations of top predators, have remained scarce (but see Ward & Kennedy 1996, Kennedy & Ward 2003, McKinnon *et al*. 2024).

The Eurasian Eagle Owl *Bubo bubo* (hereafter Eagle Owl) is the largest nocturnal avian predator in boreal and temperate areas of Eurasia. Eagle Owls are top predators that have been documented to prey on many medium-sized and even large avian and mammalian predators including, for example, red foxes *Vulpes vulpes*, pine martens *Martes martes*, Ospreys *Pandion haliaetus* and Goshawks *Accipiter gentilis* (Mikkola 1983, Korpimäki & Norrdahl 1989). Large owls and diurnal raptors have suffered from pollution and persecution throughout the world during the 20th century, making them endangered, and in some local cases, near to the point of extinction. In Finland, Eagle Owls suffered from high degrees of persecution due to a perceived threat to small game, however, subsequent studies into the owl's diet soon dismissed the scale of this perceived threat (Sulkava 1966, Mikkola 1970, Huhtala *et al*. 1976, Korpimäki *et al*. 1990). After WWII, Eagle Owl numbers declined throughout the entire European distribution range, which gradually led to the species becoming protected in the whole of Europe. In Finland, the Eagle Owl was partially protected in 1968, leading to full protection in 1983 (Valkama & Saurola 2005). Although this protected status has proved to be a major factor in the growth of its population since the 1970s (Valkama & Saurola 2005), the appearance of a new and abundant food niche may have also contributed to this growth as the owls soon learned to feed on the rapidly increasing brown rat *Rattus norvegicus* populations found in the dumps in southern and central Finland; the major distribution area of Eagle Owls in the country.

Brown rats belong to the typical food base of Eagle Owls in Finland and elsewhere (Sulkava 1966, Sulkava *et al.* 2008, Mikkola 1970, 1983, Huhtala *et al*. 1976, Korpimäki *et al*. 1990, review in Penteriani & Delgado 2019). In the breeding season, their proportion as prey items before the 1970s within the hinterlands was 5–10%, describing a "normal" background level of rats within a countryside landscape (Sulkava 1966, Sulkava *et al.* 2008, Korpimäki *et al*. 1990). The main prey items for the Eagle Owls are water vole *Arvicola terrestris* and *Microtus* voles (the field vole *M. agrestis* and the sibling vole *M. rossiaemeridionalis*), whereas hares (*Lepus* spp.) and forest grouse (Tetraonidae spp.) were the most utilized alternative prey for Eagle Owls breeding in the hinterlands far from villages and rubbish dumps (Sulkava 1966, Korpimäki *et al*. 1990). Whereas, in southwestern Europe, rabbits *Oryctolagus cuniculus* are the most important prey for Eagle Owls (Lourenço *et al*. 2015, Penteriani & Delgado 2019).

Since the 1960s the rise in the standard of living yielded more household waste and led to the establishment of municipal dumps, and more local garbage sites were started in larger villages. Since more edible wastes were carried to these garbage sites, rats learned to utilize these extra food sources, causing their noticeable increase (see Newsome *et al*. 2015). It is little wonder that nocturnal Eagle Owls near villages and towns quickly took advantage of the sudden abundance of these rats (see Marchesi *et al*. 2002), which are ideal-sized prey (mean body mass 400 g) as an alternative to their typical prey species, the water vole (mean body mass 170 g).

This paper studies the diet composition of Eagle Owls at varying distances from the dumps, focusing on the proportions of rat numbers. Data is also presented on the breeding success and breeding density of Eagle Owls in relation to their distance from the dumps, where it can be estimated whether breeding success improved

Fig. 1. Development of number of dump sites in Central Ostrobothnia western Finland from 1955 to 2020.

due to the extra availability of food (rats) and whether it had a role behind the recovery and remarkable growth of the Finnish Eagle Owl population since the beginning of the 1970s, but also in its gradual decline since the early 1990s, which coincided with the closing of the dumps and the inevitable decline in the availability of rats as an easy source of food for the Eagle Owls.

2. Materials and methods

2.1. Study area

The study was conducted in the border area of counties of Central and North Ostrobothnia totaling roughly 12000 km², in western Finland (63°54'N, 24°30'E) during 1966–2021. Mapping of Eagle Owl territories and nest searches were mainly conducted by Kauko Huhtala and his co-workers in the mid and late 1960s. The first nests were discovered by inquiries from locals who knew many traditional nesting sites (*e.g.* rocky areas), where Eagle Owls had traditionally nested earlier. Later, territories were also found by listening to the call of males in early spring (January to March) (*e.g.* Bergerhausen & Willems 1988, Olsson 1997). Searches of nests were initiated in early June each year in areas where hooting Eagle Owls were observed. Fresh droppings, feathers, downs and pellets below the roosting sites helped to locate the core of the territory, and careful searches of the nests were concentrated in these core areas. The Eagle Owl territories were mapped in the central study area, Sievi and its neighbouring municipalities in the late 1960s. Thus, the location of territories and nests were mostly known when the long-term study was initiated in 1970. All known territories and nest sites were inspected annually between 1970 and 2020, and new territories were actively searched. Generally, nests are in the river valleys near settlements and agricultural fields.

Food remains of the Eagle Owl were collected from nest cups and pellets found below roosting sites were used to study the diet composition. Collections were made one to several times for each nesting site. Bird ringers did the main part of the collection when ringing the owlets at the age of 3–4 weeks. Kauko Huhtala did a more detailed search of food remains.

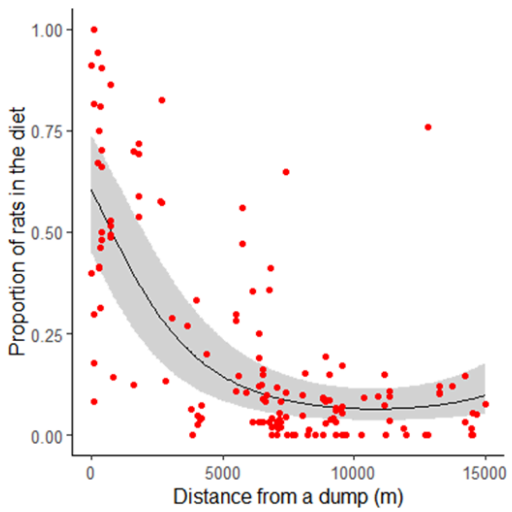

Fig. 2. Proportion of brown rats (*Rattus norvegicus*) in the diet of the Eagle Owl (*Bubo bubo*) as a function of distance to the nearest dump site. Black line represents the model predictions based on the final model (see text for details) with the grey areas representing the 95% confidence interval. Red dots are the data points. Pooled data from 1966-2015.

Identification of prey items was done by comparing bones, nails, hairs and feathers found with reference material of known species in the Zoological Museum, University of Oulu, Finland. Food material consisted of 10551 identified prey individuals collected from 167 nest sites. However, 14 nest sites were removed from the analyses due to the lack of geographic coordinates. One nest was left out as less than 10 identified prey individuals were found. The final data set consisted of 152 nesting sites and 9630 prey individuals from 1966–2015.

Brood size data consisted of 731 nestlings from 294 broods ringed at the age of 3–4 weeks during 1974–2021 as available from the Ringing Center of the Natural History Museum in Helsinki.

The location of all study area dumps, as well as the length of existence (when founded and when closed), were obtained from the Finnish Environment Institute. Distances from the Eagle Owl nests were measured from the nearest two or three dumps, while also considering the levels of activity of the site. Some minor errors may have occurred by the accuracy of nest coordinates since a part (42%) of them were announced by 1000 m accuracy while others by 100 m accuracy.

2.2. History of dumps

Sites for community waste were first necessary in the big municipalities. Later, they were found even in proximity of middle-sized and small villages. Their number started to increase from the beginning of the 1960s, culminating at the beginning of the 1990s and afterwards declined steeply (Fig. 1). Those remaining are not dumps anymore but recycling and packing stations for burning the waste that cannot be recycled. This has meant the depletion of available prey animals like rats, gulls and corvids for their predators. At large and poorly managed dumps, the rat densities can be very high: in one study conducted in southwestern Finland in 1994, the highest density was 950 individuals / hectare (Mikkonen *et al*. 2005).

2.3. Statistical analysis

We analyzed the proportion of rats in the Eagle Owl diet by fitting generalized linear mixed models (GLMM) with binomial error distribution and logit link function. The brood size was analyzed using generalized linear mixed models with Poisson error distribution and log link function. There were only 5 diet data sets and 14 brood size observations that were longer than 15 km distance from the closest dump. These observations were removed from the GLMMs because the regression lines would have been unreliable for these distances. As a result, we had 147 nests for diet analysis and 280 nests for brood size analysis. For both analyses, we fitted as explanatory variables the distance from the closest dump (standardized to facilitate numerical stability) both as a linear and a quadratic term. To account for potential annual and spatial variation we also included the year and the latitudinal coordinate as random intercept terms (assuming a normal distribution with zero mean and variance to be estimated). We did not include the longitudinal coordinate in the models, because the latitudinal and longitudinal

Table 1. Estimates for the parameters in the final models for the proportion of rats in the diet and brood size of the eagle owl. 95% CI refers to the 95% confidence interval of the estimate, sd is standard deviation, *β* denotes the estimation of regression for the curve

Response variable	Parameter	Estimate	
Proportion of rats in the diet	***Fixed terms***	***β***	***95% CI***
	Intercept	-2.19	-2.83, -1.56
	Distance to a landfill site	-0.93	-1.02, -0.85
	Distance to a landfill site^2	0.46	0.38, 0.53
	Random terms	***sd***	***95% CI***
	Year	0.94	0.73, 1.24
	Latitudinal group	0.90	0.58, 1.48
Brood size	***Fixed terms***	***β***	***95% CI***
	Intercept	0.92	0.84, 0.99
	Distance to a landfill site	-0.07	-0.15, 0.003
	Random terms	***sd***	***95% CI***
	Year	0.00	0.00, 0.10
	Latitudinal group	0.00	0.00, 0.12

coordinates were strongly positively correlated for both data sets (diet data: Pearson $\rho = 0.67$; brood data: Pearson $\rho = 0.67$). To facilitate the analysis the latitudinal coordinate (metric coordinate) was transformed into 10 km groups that resulted in 13 latitudinal groups for the diet analysis (from one to 32 nests per group) and 19 latitudinal groups for the brood size analysis (from one to 40 broods per group). The diet analysis included 41 years (from one to 15 nests per year) and the brood size analysis 38 years (from one to 26 broods per year).

We also fitted for both analyses, a model excluding the quadratic term for the distance to the closest dump and chose the model with a lower Akaike information criterion (AIC) value as the final model. All models were fitted using program R 4.4.1. (R Core Team 2024) and R package lme4 (Bates *et al*. 2015). Model validation for the final models was done using the package DHARMa (Hartig *et al*. 2024). Model validation results were acceptable, although for both analyses the data was somewhat under-dispersed compared to the assumed binomial and Poisson distributions. This was probably due to most observations being relatively close to the zero boundary where there is less room for variation compared to higher values.

In addition, based on the above GLMM analysis for the proportion of rats in the Eagle Owl diet, we defined a threshold of distance to the closest dump for nests located within the influence of a dump versus the Eagle Owl nests outside of it. This distance threshold was set at 6 km (see Results). We then divided the nests according to this 6 km threshold and described the diet of the Eagle Owl inside *versus* outside the 6 km distance from a dump. Finally, we defined three distance groups (0–6 km, 6–12 km and 12–18 km from a dump) and calculated mean Eagle Owl nest and brood densities for each distance group over the whole study period.

3. Results

3.1. Eagle Owl's diet related to the distance to dump

For the proportion of rats in the Eagle Owl diet, both the linear and quadratic terms for the distance to the closest dump were statistically significant (Table 1). The model predicted a steep decline in the proportion of rats in the diet from close to a dump (model prediction at 100 m from a dump site, mean [95% confidence interval (CI)]: 0.59 [0.44, 0.73] to about 6000 m (0.11 [0.06, 0.19]) where after the proportion of rats remained relatively stable (prediction at 12 000 m: 0.07 [0.04, 0.12]) (Fig. 2).

Rats were the most abundant prey in the nests closer than 6 km from the dump while water vole took the first position in nests further than 6 km away (Table 2). Yet, water voles were important prey also near the dumps. Large prey like hares (*Lepus timidus*, *L. europaeus*) and muskrats (*Ondatra zibethicus*) also compensated for rats in nests farther than 6 km from the dumps. 80 per cent of hares were juveniles. The percentage of field voles was relatively high, 10–20% of prey items being, by far higher, more than 6 km from the dumps. No differences were found among other prey groups between these distances. Data on home range and territory sizes of the Finnish Eagle Owls is scarce, but satellite-tracking of breeding males has revealed that during the breeding season they mainly hunt within 5–6 km from their nest (J. Valkama, unpubl. data).

3.2. Nest density and breeding success related to the distance to dumps

In total, 178 Eagle Owl nests were within 6 km of a dump, 131 nests within 6–12 km and 40 nests within 12–18 km. This resulted in the total nest number/km² for the whole study period of 1.04 (0–6 km), 0.39 (6–12 km) and 0.07 (12–18 km) nests per km². For the number of chicks produced within these distance groups, the corresponding figures were 2.81, 0.93 and 0.16 chicks per square km. Adjusting these figures annually to 100 km² gives mean densities outside the effect of dumps from 0.2–0.8 nests per 100 km², which is close to that found in earlier studies for South Finland (Table 3, References). The closest group had 2.7 times more nests and 3.0 times more chicks/km² than the next one, while the furthest group had only 6–7% of those of the closest group (Fig. 3).

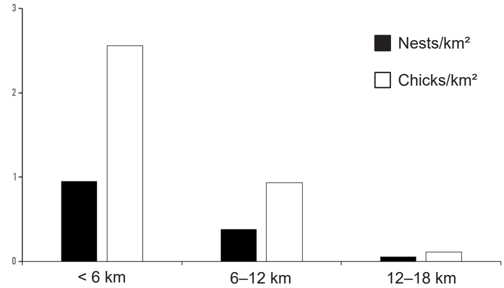

Fig. 3. The total density of discovered eagle owl's nests (nests/km²) and owlets (chicks/km²) within three distance groups from dumps during the years 1974-2014.

For the brood size (*i.e.* number of 3–4-week-old offspring), GLMMs the quadratic term for the distance from the closest dump, was not supported, therefore the final model included only the linear distance term. The final model predicted a slight linear decrease in the brood size from 2.79 [2.44, 3.20] owlets at 100 m from a dump to 2.52 [2.33, 2.71] owlets at 6000 m and 2.26 [1.98, 2.59] owlets at 12 000 m (Fig. 4). However, the linear term for the distance to the closest dump was not quite statistically significant (Table 1). The standard deviations for the random terms were both estimated at zero (Table 1). This again suggests that variation in the brood data is relatively low (*cf.* the model validation results). The zero boundary fits for the random intercept terms essentially means that the model reduces to the regular generalized linear model excluding the random terms. For this type of model that only includes the linear distance term the parameter estimates for the distance term were identical to the final model.

4. Discussion

We found that the proportion of rats in the diet of Eagle Owls during the breeding season declined as the distance from the dump increased: the

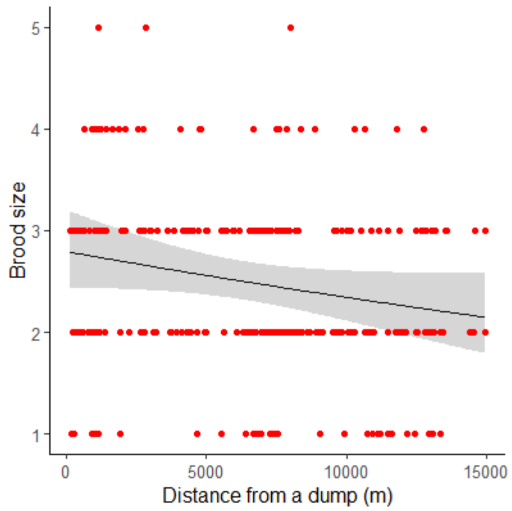

Fig. 4. The brood size of the eagle owl in relation to the distance from the closest dump site. Black line represents the model predictions based on the final model (see text for details) with the grey areas representing the 95% confidence interval. Red dots are the data points. Pooled data from 1974-2001.

proportion of rats in the diet near the dump was close to 70% of all prey items but <10% of prey items >6 km from the dump. At the distance of >6 km from the dump, water voles were the main prey, field voles being the second and rats the third most important by number. The Eagle Owls raised large broods near the dumps, with their breeding success being 2.7 times and breeding density 2.5 times higher near (<6 km) the dumps than further away from them. These results showed that large-scale "supplementary feeding" (rich rat food resources produced by dumps during the 1960s to early 1990s) notably increased the offspring production and breeding density of the Eagle Owl population. There is also historical evidence how the arrival of a dump (*i.e.* the initiation of "supplementary feeding") changed the diet in one Eagle Owl territory in Kuopio, eastern Finland: in 1890 the Eagle Owl diet contained 50% of water vole and only 15% of rats, while in the 1970s, when the active Kuopio city dump was less than 3 km from that territory, the proportion of rats in the diet was as high as 73% but that of water vole only 12% (Mikkola 1974).

There was a clear difference in the proportion of brown rats and water vole between dump nests (<6 km) and those pairs that nested in the next zone (>6–12 km from the dump site). Rat numbers dominate in the nests close to dumps while water voles dominate in hinterland nests. Rats formed almost the whole diet of Eagle Owls during the nesting period, while they usually

Table 2. Diet of the eagle owl in relation to distance to the dump site in Central Ostrobothnia western Finland in 1971-2016. The percentages refer to the proportions of the specified taxa out of the total number of identified prey specimens (N) within each distance group.

Distance from the rubbish landfill site		< 6 km	> 6 km
		%	%
Hares	*Lepus timidus, L. europaeus*	5.5	6.0
Muskrat	*Ondatra zibethica*	0.6	2.2
Water vole	*Arvicola terrestris*	30.9	46.6
Field vole	*Microtus agrestis*	15.4	19.1
Birds	*Birds total*	5.0	6.2
Brown rat	*Rattus norvegicus*	40.7	8.3
Frogs	*Rana sp., Bufo bufo*	1.9	3.5
Other prey	*Mammalia, Reptilia, Pisces*	7.9	5.8
Number of prey items		2855	7696

Table 3. Numbers and mean annual densities of nests and chicks within spherical discs (annuluses) around the dumpsites in 1974-2021.

Distance classes (km)	0–3	6–12	12–18
Spherical areas (km²)	113	452	1017
Partial areas (annuluses)	113	339	678
Number of nests	118	131	40
Number of chicks	318	314	88
Number of nests/km²	1.0	0.4	0.1
Number of chicks/km²	2.8	0.9	0.2
Mean annual number of nests/100 km²	2.2	0.8	0.2
Mean annual number of chicks/100 km²	6.0	2.0	0.3

account for less than 70%, on average. Generally, rats are the second most common prey after water vole, but due to their larger size, rats are equally as important in terms of biomass. Based on stomach analyses, male Eagle Owls consumed twice as many rats as females (Mikkola & Tornberg 2014), which may suggest that males have hunted more frequently at dumps than females. In addition, male Eagle Owls are mainly responsible for hunting and on prey deliveries to the nest in the breeding season, and thus more used to take benefit from rat-rich waste dumps than females that stay in the vicinity of the nest during courtship feeding, egg-laying, incubation and brooding periods. Compared to other regions, rats are valuable prey close to human settlements and less so in other geographical areas (Marchesi *et al*. 2002, Penteriani & Delgado 2019).

During winter, rats are much more available than water vole, which occupy below-ground nests protected by deep snow layers. The much smaller field voles have a high share in the diet by number, likely due to their abundance, especially in peak years of the 3–4-year population cycle of field voles. In South Ostrobothnia (approx. 150 km south of our study area), Korpimäki *et al*. (1990) showed that the proportion of two *Microtus* voles (the field vole and the sibling vole) in the diet of breeding Eagle Owls was, by prey numbers, positively correlated with the abundance indices of these voles in the field, although their average proportion by number was 25% and by weight only 4%, while those of brown rats 30% and 44%, respectively. This data indicates that even in peak years of voles when their densities can rise to 100–200 individuals per ha in grassy habitats (Korpimäki *et al*. 2005), rats were more profitable prey for Eagle Owls than small voles (mean body mass 25 g).

We found that breeding success of Eagle Owls was 2.7 times higher in the vicinity (<6 km) of the dumps than further away from them. This was because, in dumps, the rats formed an extremely dense and easily available food niche. Thus, the parent owls within "dump territories" were apparently in better physical condition, thereby being able to produce more eggs. In contrast, Eagle Owl pairs breeding farther away from dumps probably suffered more frequently from food shortage, resulting in smaller clutch sizes. Corresponding effects have been found among mammalian predators utilizing waste food provided by dumps (Newsome *et al*. 2015). Similarly, starvation amongst the brood was more likely in more distant territories than those next to dumps. Some Eagle Owl parents probably returned hunting even farther than 6 km to these dense rat patches, as can be deduced from our analysis (Fig. 2), because the energy consumption of searching for rat prey occupying dumps is relatively low. Rats, as prey items, are also twice as large as water voles and 16 times larger than *Microtus* voles. Therefore, they probably are far more profitable prey for Eagle Owls than water vole and small voles close to the nests, although transportation costs up to 6 km from the nests can be relatively high. The difference in the brood size between close *vs*. distant sites was, however, not that significant, while the chick production was higher due to more nests in the vicinity of dumps *vs*. hinterlands. There were also broods with only 1–2 chicks in the vicinity of dumps, remarkably lowering the mean. Disturbances in the dumps and close by may have caused breeding failures. So, some females could have made new nesting attempts explaining the below average number of chicks or that some young ones have already left the nest before ringing. It is a well-known fact that high-level nutrition advances laying date at least in other birds of prey (*e.g*. Korpimäki & Hakkarainen 1991, Aparicio 1994, Korpimäki & Wiehn 1998).

In addition, that owl pairs living near dumps had larger broods, their nestling survival was also better than in pairs living on a typical food base. Broods raised near the dumps and tracked after leaving the nest until independence did not lose owlets, while Eagle Owl broods found within forested hinterland areas tended to lose, on average, one offspring up to the post-fledging period (Kauko Huhtala, unpubl. data).

The number of nests found during the study years was 2.5 times larger in the surroundings of dumps than further away from them (>6 km). This is the first time "experimental food supplementation" is increasing the country-wide breeding density of a top predator. In our study area, approx. 40% of the Eagle Owl nests were within the 6 km range *i.e.* under the influence of the dumps. Valkama & Saurola (2005) estimated that at least 1000 Eagle owl pairs (approximately one-third) were nesting under the influence of the dumps and their high population of rats during the 1980s–1990s. The shift of the Eagle Owl population from the hinterland to the proximity of dumps and villages occurred from the 1960s to the 1980s (Helppi & Kalinainen 1984).

We suggest that the rise of the Eagle Owl population has been mainly due to an expanded dump network throughout the country. New dumps were often established several times in a municipality after the old one was filled up or there was no space to enlarge it due to, for example, the spreading of the settlement areas close to them. This was typical in large cities that attracted people from the countryside. As more attention started to be paid to the environment, the sprawling of the dumps was seen as detrimental. Besides, dumping of the possible raw materials was not considered wise any longer and more attention was paid to recycling. Therefore, the number of dumps started to decline in the 1990s, which induced a decline in rat populations within the dumps. This led to a notable decline in breeding success and breeding density of the Eagle Owl population in Finland from the 1990s to 2000s (Valkama & Saurola 2005). From the 2010s onwards, wastes have been treated in large provincial waste stations, recycled and/or burnt. This remarkably reduced the living space of rats, their food and thus reproduction possibilities. Therefore, rat-rich patches for hunting Eagle Owls have drastically declined. In addition, in the 2000s peak densities of vole cycles have also diminished (Korpela *et al*. 2013) and populations of hares and forest grouse have substantially declined, too (Tornberg 2021). These declines of important prey species and groups have induced a severe decline in the Eagle Owl population. According to the monitoring, and earlier more or less accurate estimates of the Eagle Owl population in Finland likely reached its peak density, over 3000 pairs in the early 1990s (Valkama *et al*. 2014), whereas it has steadily declined by a 3% annual rate (Honkala *et al*. 2023). In 2019–2024 the population estimate for Eagle Owls in Finland was 830 pairs (Lehikoinen *et al*. 2025). The Eagle Owl was red listed as a highly endangered species in Finland in the late 2010s (Hyvärinen *et al*. 2019).

It is concluded that the rise and fall of dumps formed an important countrywide "food-supplementation experiment" because, near the dumps, Eagle Owls subsisted almost exclusively on brown rats. This rat-food addition notably increased the offspring production of Eagle Owls, and induced clustering of Eagle Owls close to the dumps and increasing breeding density. Similar effects have been found in many other birds having access to anthropogenic food subsidies (Oro *et al*. 2013). In this sense, our results are consistent with the similar results obtained for Eagle Owls using rabbits in southwestern Spain. When young rabbits were available in the home range, egg-laying started earlier, and offspring production improved. When rabbits were less available, Eagle Owls increased their home range size to obtain alternative prey, adding their dietary diversity, which may also require higher movement speed (Lourenço *et al*. 2015). Compared to unfed control pairs fed pairs usually advanced their initiation of egg-laying, clutch size and breeding success in the earlier food supplementation experiments (Boutin 1990, Ruffino *et al*. 2014). However, notable effects on breeding density remained unknown.

This “food-addition experiment” with Eagle Owls was unique in at least two ways. First, the semi-natural experiment was performed on a large spatial and temporal scale covering thousands of square km and including at least two decades, while in other experiments food was supplemented for some, usually 10 to 20 randomly selected nests during less than five breeding seasons. Second, Eagle Owls still needed to hunt and kill free-running rats which had anti-predatory behaviours and deliver rats to their nests. In other food-supplementation experiments with avian predators, extra food (dead specimens like laboratory mice, chickens, quail or pigeons) was usually provided by experimenters directly to the nest (*e.g.* Korpimäki 1989, Aparicio 1994, Korpimäki & Wiehn 1998, Hörnfeldt *et al*. 2000, Ward & Kennedy 1996, Kennedy & Ward 2003, McKinnon *et al*. 2024). Therefore, Eagle Owls still carried the searching, killing and transportation costs of food items from dump to their nests at a distance. Compared to other studies concerning the anthropogenic food subsidies where mainly immobile (dead) food was provided in dumps (*e.g.* Oro *et al.* 2013, Newsome *et al.* 2015, Oppel *et al.* 2025), effects on the target populations were, however, fairly like we found, namely increased productivity and thereby population growth. Oro *et al.* (2013) stressed accordingly that wide, long-lasting “food-supplementation experiments” with a sudden cessation offer much more reliable results than sporadic, local planned experiments can do.

The Eagle Owl population has undoubtedly collapsed in Finland, but we do not know yet whether it is purely due to declined productivity by vanishing high productive breeding areas such as dumps. Therefore, we need more data on the over-winter survival of Eagle Owls hatched near dumps and forested hinterlands.

Huuhkajakannan nousu lisääntyneiden rottakantoja ylläpitävien kaatopaikkojen vuoksi ja hupeneminen niiden sulkemisen myötä. Laaja-alainen, pitkäkestoinen "ruokintakoe"

Ravinnon on osoitettu tavallisesti olevan tärkeä parantuneen lisääntymismenestyksen tekijä selkärankaisilla eläinlajeilla tehdyissä lisäruokintakokeissa. Huippupedoilla tehdyt laaja-alaiset lisäruokintakokeet ovat olleet kuitenkin harvinaisia. Huuhkaja (*Bubo bubo*) on Euraasian lauhkean vyöhykkeen suurin yöaktiivinen lintupeto. Tutkimme tämän huippupedon ravintovalikoimaa ja lisääntymismenestystä suhteessa etäisyyteen kaatopaikoista, jotka ylläpitävät suuria rottamääriä (*Rattus norvegicus*), erästä huuhkajan merkittävimmistä saalislajeista. Kaatopaikat lisääntyivät Suomessa 1960-luvulta 1990-luvulle, jonka jälkeen niiden määrä jyrkästi väheni johtaen samalla rottapopulaatioiden vähenemiseen. Samanlainen huuhkajamäärien kehitys seurasi tätä ilmiötä. Rottien osuus huuhkajan ravinnossa oli kaatopaikkojen lähellä korkea, keskimäärin 70 % väheten 10-15 % 6-7 km päässä kaatopaikoista. Vastaavasti 3-4-viikkoisten huuhkajan poikasten lukumäärä väheni suhteessa etäisyyteen kaatopaikasta siten, että niitä oli 0,5 poikasta vähemmän 10 km päässä kaatopaikasta. Tutkimuksen aikana kaikkien löydettyjen pesien lukumäärä oli kaatopaikkojen lähellä 2,7 kertaa suurempi kuin kauempana. Ylimääräisen ravinnon saatavuus kaatopaikkojen lähellä (siellä elävät rotat) aikaansaivat luultavasti huuhkajapopulaation kasvun ja kaatopaikkojen sulkemisten jälkeisen vähenemisen.

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Author contributions. RT wrote the main text, KH was responsible for collecting the diet data, EK modified the text, JT ran the statistical tests, HM was responsible for right proofing and JV, as well as others made useful comments on the manuscript.

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Assessing abundance and habitat preferences of Goldcrest *Regulus regulus* and Firecrest *Regulus ignicapilla* using passive acoustic monitoring and point-count surveys in temperate forest ecosystem in Poland

Karol Kustusch*, Dawid Cząstkiewicz & Andrzej Wuczyński

K. Kustusch, Polish Roadkill Observation System, ul. L. Waryńskiego 153, 86-300 Grudziądz, Poland.
D. Cząstkiewicz, Kociołki 34, 19-504, Dubeninki, Poland.
A. Wuczyński, Institute of Nature Conservation Polish Academy of Sciences, al. A. Mickiewicza 33, 31-120 Kraków, Poland.
** Corresponding author's email: karol.kustusch@gmail.com*

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Passive acoustic monitoring (PAM) provides new opportunities for assessing bird abundance and habitat preferences, yet its performance relative to traditional point-count surveys (PCO) remains insufficiently tested, especially for quiet and inconspicuous forest passerines. We compared the vocal activity and habitat associations of the Goldcrest *Regulus regulus* and Firecrest *Regulus ignicapilla* in a temperate forest ecosystem using PAM-derived and PCO-based indices. Across 30 monitoring points in the Romincka Forest (Poland), PAM yielded >33,000 recorded songs and revealed strong spatial variation in both species. Vocal activity measures obtained from PAM correlated positively with PCO detections and territories, confirming the reliability of PAM as a complementary abundance indicator. Goldcrest vocal activity showed a strong positive association with the proportion of coniferous trees—especially spruce—and with local tree-species richness, reflecting the species' affinity for structurally diverse conifer-dominated stands. In contrast, Firecrest abundance was unrelated to forest structure in PAM data, while PCO detections indicated avoidance of pine and lower activity in species-rich stands. No significant relationship with stand age was observed for either species. The weak interspecific correlations in activity parameters highlight their distinct ecological niches despite overlapping ranges. Based on PCO Goldcrests proved to be more abundant, with a territorial ratio of 3:2 compared to Firecrests. Our study demonstrates that PAM effectively captures variation in abundance and habitat selectivity of both *Regulus* species and provides a scalable, efficient complement to traditional surveys in temperate forest ecosystems.

1. Introduction

Regular or periodic monitoring of the population size and community composition of selected animal groups, including birds, is a fundamental aspect of nature conservation. Numerous methods are available for studying birds' abundance (Bibby *et al*. 1992). Among these, the transect method (Lõhmus & Kaasik 2025) and the point-count method are frequently used (Klvaňová & Voříšek 2007). They require an observer to record the number of individuals of a given species heard or seen. An alternative and increasingly common approach involves passive acoustic monitoring (PAM) with autonomous recording units documenting environmental sounds onto digital media without active observer participation (Shonfield & Bayne 2017, Gibb *et al*. 2019).

Autonomous recorders offer numerous advantages for monitoring bird populations and other wildlife. One key benefit is their ability to collect data over extended periods without the need for continuous observer presence, significantly reducing labour costs and human disturbance (Winiarska *et al*. 2024). PAM enable researchers to capture vocal activity during specific times, such as dawn choruses or nocturnal periods, which are often challenging to survey manually (Mirski 2017). Moreover, they provide permanent, high-quality audio records that can be revisited for additional analyses or validation of species identifications. This scalability allows recording units to be deployed across multiple locations simultaneously, improving spatial and temporal data coverage (Baroni *et al*. 2023). PAM is particularly effective in remote or logistically difficult areas, where traditional methods may be impractical (Soanes *et al*. 2023). Their non-invasive nature also makes them ideal for studying cryptic or sensitive species. It also enables to go beyond data scarcity by providing extensive material for statistical analyses (Shonfield & Bayne 2017, Hoefer *et al*. 2023).

While numerous studies have demonstrated the utility of PAM in various ecological contexts (*e.g*. Gibb *et al*. 2019, Penar *et al*. 2020, Szymański *et al*. 2021, Hoefer *et al*. 2023, Scarpelli *et al*. 2023, Van Doren *et al*. 2023, Biffi *et al*. 2024), the integration of PAM and traditional field surveys to validate abundance metrics in birds' species has been tested much less frequently and remains under investigation (Venier *et al*. 2012, Borker *et al*. 2014, Bombaci & Pejchar 2019, Pérez-Granados *et al*. 2019, Hensel *et al*. 2022, Doser *et al*. 2021, Baroni *et al*. 2023). Estimating abundance can be applied using a variety of different approaches. Determining absolute bird abundance based on audio recordings is time-consuming, requires additional equipment and results may still be imprecise (Pérez-Granados & Traba 2021). An alternative, more widely adopted approach, involves using the number of species detections (calls or songs) per time unit as an indicator of birds' abundance (Pérez-Granados *et al*. 2019, Hutschenreiter *et al*. 2024).

The number of detections may be reflected by the abundance of birds near the recorder, as more birds potentially result in a greater number of vocalizations. It may also be a result of individual birds frequently staying near the recorders due to habitat preferences or the use of specific resources, and thus serve more as an indicator of habitat selectivity than abundance. Finally, it may also stem from the specific patterns and vocal habits of individual species (Hutschenreiter *et al*. 2024). Vocal activity can be represented in several ways: the number of calls recorded during the monitoring period; the number of detections, *i.e.*, the number of recordings on which a species was detected per unit of time; or the maximum number of calls recorded on single recordings per unit of time. Each approach yields different results and can illustrate specific ecological and behavioural traits of particular bird species (Pérez-Granados *et al*. 2019, Pérez-Granados & Traba 2021, Hutschenreiter *et al*. 2024).

The Goldcrest *Regulus regulus* and Firecrest *Regulus ignicapilla* are solitary species with relatively close phylogenetic relationships and similar ecological niches, often co-occurring within the boundaries of their overlapping geographic ranges. They have developed a series of adaptations to avoid direct competition for resources, enabling their sympatric existence. These include preferences for different microhabitats and feeding niches, with the Goldcrest typically selecting coniferous stands, while the Firecrest prefers mixed forests (Cramp & Brooks 1992, Kralj *et al.* 2013). For the Goldcrest, the dominance of spruce or fir is key, occasionally pine; for the Firecrest, aside from the presence of the aforementioned conifers, a mix of deciduous trees is generally essential (Mikusek & Dyrcz 2003, Kopij 2007, Staszewski 2010, Szczypiński 2015, Wilniewczyc & Wachecki 2017, Ławicki *et al*. 2020, Mandziak *et al*. 2021, Barczyk *et al*. 2024).

The present study is a comparative analysis involving two wildlife detection methods in two closely related forest bird species. The Goldcrest and the Firecrest occur sympatrically across many European forests; however, despite their phylogenetic relatedness, they exhibit different population trends, ecological requirements and behavioural traits. These characteristics make them an appropriate model for this type of research. The specific aims of the study were to: (i) evaluate bird vocal activity recorded using passive acoustic monitoring and traditional point-count surveys, with particular emphasis on the utility of PAM for detecting relatively quiet and inconspicuous bird species; (ii) compare the vocal activity of the Goldcrest and the Firecrest and assess whether detection rates reflect the relative abundance of the two species; (iii) examine the vocal activity of both species in relation to selected habitat characteristics of the studied forests, assuming that frequent vocal presence at a site reflects habitat attractiveness. To our knowledge, this is the first European study that combines traditional point-count surveys, abundance metrics derived from passive monitoring, and habitat selection analyses in forest-dwelling passerines.

2. Materials and methods

2.1. Study area

The study was conducted in the Polish section of the Romincka Forest (RF), an extensive forest complex (approximately 430 km²) located at the Polish-Russian-Lithuanian border (Fig. 1). Within Poland's borders, the forest covers around 155 km², which constitutes 36% of its total area. It spans latitudinally with a width of approximately 30 km and a length of several kilometers along the north-south axis. The area is located at the southern edge of the hemiboreal forest ecoregion (*sensu* Manton *et al*. 2025), so it is predominantly composed of coniferous forests, with a significant proportion of Norway spruce

Fig. 1. Romincka Forest and the distribution of autonomous recording units.

(*Picea abies*) at 42.1% and a smaller proportion of Scots pine (*Pinus sylvestris*) at 16.4% of the total forest area.

The influence of a continental climate promotes the presence of numerous boreal elements among the flora and plant communities. Forests account for 72% of the area, agricultural land for 24%, while the remaining area consists of water bodies, wetlands, and moist meadows (Natura 2000). The mean annual temperature is 7.1°C, with average annual precipitation ranging from 600 to 700 mm, and snow cover lasting an average of 65 days per year (Grzybek 2014). The area is protected under Natura 2000 as the Special Area of Conservation (SAC) PLH280005 Romincka Forest (147 km²) and as the Romincka Forest Landscape Park (https://pkpr.warmia.mazury.pl/).

2.2. Field procedures

The data used in this study were collected between April and June 2024. All data were collected in 30 monitoring points spread in the entire territory of the Romincka Forest (Fig. 1). The points were selected as to include the boundaries of the main nature reserves, and to reflect the approximate conifer-to-deciduous tree ratio typical of Romincka Forest (60/40% for RF vs. 65/35% for monitoring points).

Two methods of bird census were applied: passive acoustic monitoring (PAM) and point counts conducted by observers (PCO). Audio recordings were obtained in four days: April 15th, May 4th, May 20th, and June 4th, however there is one day gap in the recording dataset for three monitoring points. Recordings were made in 24-hour cycles, for 5 minutes every 10 minutes, producing 144 recording sessions per day. The monitoring was conducted using 30 AudioMoth acoustic recorders, one item per point, (v1.2.0, Hill *et al*. 2018), with a fixed sampling frequency of 48 kHz and a medium gain setting. Each recorder was installed in a point centre on a tree at a height of 2 meters above the ground and oriented in a fixed direction for the entire duration of the monitoring. To protect the devices from adverse weather conditions, they were packed in zip-lock bags before being placed inside protective plastic containers.

Point counts involving observers consisted of six field surveys at each of the 30 monitoring points, totalling 180 counts. The surveys were conducted from sunrise till 10:00 on the following dates: April 10th–15th; April 26th–29th; May 3rd–5th; May 17th–22nd; June 1st–4th; June 17th–21st. Point counts involved 10 minutes long observations of vocal activity of territorial males by observers (KK, DC). The numbers and locations of individual singing males were recorded on a map in two, predefined distance categories: 0–25 m and over 25 m. Both recorder-based observations and point counts were carried out on calm, windless days.

The habitat characteristics around each monitoring point were determined based on direct field measurements. Each tree species (with a minimum height of 5 meters) was identified at 5-meter intervals along transects running in four cardinal directions (north-south and east-west), within a 50-meter radius from each recorder. The closest tree were included, ranging from 0 to several meters distance to the 5 m mark. For dead trees, the nearest neighbouring live tree was recorded. Using this method, a species composition of 40 trees was obtained for most monitoring points. Exceptions included points located near forest clearings and wetlands without trees, where the number of recorded trees was correspondingly lower (29–35 trees; n = 4), depending on the distance of the recorder from the forest edge.

The mean tree cover density (TCD) within individual monitoring points ranged from 38% up to 95% (mean 84%, median 89%). Forest density characteristic was sourced from Copernicus High Resolution Layer Tree Cover Density dataset that provides information on the proportional crown coverage per pixel at 10-meter spatial resolution (ranges from 0% (all non-tree covered areas) to 100%), whereby (TCD) is defined as the "vertical projection of tree crowns to a horizontal earth’s surface“ (Copernicus Land Monitoring Service 2023).

Data on the age of forest stands were obtained from the Forest Data Bank (https://www.bdl.lasy.gov.pl/) for forest compartments within a 50-meter radius of each recorder. For monitoring areas overlapping multiple forest compartments,

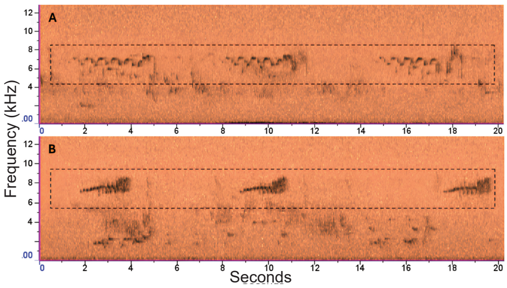

Fig. 2. Sonograms of Goldcrest *Regulus regulus* (A) and Firecrest *Regulus ignicapilla* (B) songs (Raven Pro).

an average age was calculated.

Seven monitoring points were located within nature reserves: Mechacz Wielki, Czarnówko, Boczki, Dziki Kąt, and Struga Żytkiejmska. The study was conducted under a permit issued by the Regional Directorate for Environmental Protection in Olsztyn, Poland (WOPN.6205.1.22.2024.MH).

2.3. Data analysis

Prior to the analysis, each 5-minute recording was divided into 60-second segments to facilitate recording review. This process resulted in a total of 84,240 individual recordings. One minute is sufficient to catch at least one complete song of either species. The song of Goldcrest consists of short wavering units lasting up to several seconds (rarely more than 20). Firecrest's song is simpler and shorter, with less variation in pitch, lasting 1.5–3 seconds (Cramp & Brooks 1992) (Fig. 2). Subsequently, the sonograms of each one-minute recording were manually reviewed using the Raven Pro 1.6 software (K. Lisa Yang Center for Conservation Bioacoustics 2024). During the review, only recordings of courtship songs of the Goldcrest and Firecrest were noted (Fig. 2); other vocalizations made by these species were not included. The following were used for further analysis: a one-minute recording containing at least one phrase (or its fragment) of a species' song, referred to as a detection, and the number of songs recorded during the monitoring period. The total number of detections and songs was then calculated for each monitoring point across all recording days. Since recordings at three points were conducted over only three days (as opposed to four days at the other points), daily average values of detections and songs (*i.e.*, PAM detections/day and PAM songs/day) were used in subsequent analyses.

Detections and territories were also obtained during point counts involving observers. A detection was defined as the activity (song) of each male recorded individually during a single observation at a point. The total number of detections of a species throughout the entire monitoring period (60 minutes) served as an indicator of species activity at a listening point (PCO detections). Territories were defined based on simultaneously singing individuals of a given species, representing the minimal number of male individuals present at the monitoring point (PCO territories).

The statistical analyses aimed, first, to examine the mutual relationships among parameters of vocal activity for each species and between the two species, and second, to assess the environmental factors influencing the occurrence of the Goldcrest and Firecrest. Spearman rank correlations and chi square test for independence were used to test the relationships between activity parameters across 30 monitoring points. General Linear Models (GLMs) were employed to quantify the associations between forest characteristics and bird activity. Species-specific vocal activity parameters (PAM detections/day, PAM songs/day, and PCO detections) served as response variables, assuming a normal distribution. The predictors included species richness of woody vegetation (No of tree species), average age of forest stands (Age of trees), and the ratio of coniferous to deciduous trees (Coniferous/Deciduous). To meet the assumptions of linear modeling, both response and environmental variables (except for the No of tree species) were log-transformed. A variance inflation factor (VIF) test was conducted to assess potential multicollinearity among the predictors. None of the predictors had VIF > 3.3; therefore, all were retained in the model. Given the relatively small sample sizes, the analysis was limited to main effects only. Testing the relationship between forest characteristics and the variable 'PCO territories' was also omitted due to

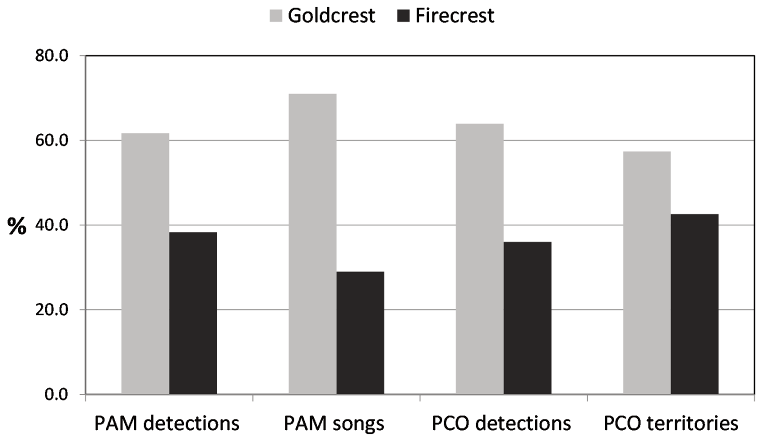

Fig. 3. Differences in the abundance of Goldcrest *R. regulus* and Firecrest *R. ignicapilla* in the Romincka Forest, expressed by activity parameters obtained through passive monitoring (PAM) and point counts (PCO).

the low variability in the number of territories. Partial Eta squared (η_p^2) was reported as a measure of effect size. The overall performance of the models was evaluated using the coefficient of determination. All statistical analyses were performed using Statistica version 13 (Dell Inc., 2016).

3. Results

3.1. Relationships among parameters of bird activity

Passive acoustic monitoring resulted in 7,551 detections (one-minute recordings containing at least one song or its fragment) and a total of 33,692 recorded songs of the Goldcrest and the Firecrest. The detection rates of both species were highly uneven and varied substantially among monitoring points (Table 1). For example, the number of Goldcrest songs recorded at a single point ranged from 0 to 2,424, while for the Firecrest it ranged from 0 to 1,650, indicating considerable spatial variation in the densities of both species in the Romincka Forest. During the point-count surveys, a total of 136 detections and 54 territories of both species were recorded (Table 1).

Vocal activity parameters were approximately twice as high in the Goldcrest compared with the Firecrest (Fig. 3). The number of Goldcrest territories (32) was also higher than that of the Firecrest (23), although the difference was less pronounced than in vocal activity. Although the material collected via acoustic recorders was substantially richer than that obtained from point-count surveys, the proportional results of the two methods were consistent. Specifically, no significant differences were found in interspecific proportions between PAM detections and PCO detections (χ^2 = 0.285, df = 1, p = 0.594), nor between PAM songs and PCO detections (χ^2 = 3.289, df = 1, p = 0.070).

Intraspecifically, a statistically significant positive correlation was found between the vocal activity parameters obtained using both analytical methods. Vocal activity was also correlated with the estimated number of territories in both species (Fig. 4). In contrast, the interspecific comparison showed that the activity and abundance of the Goldcrest and the Firecrest were not correlated for any of the analysed parameters (Table 2), which shows behavioural differences between the two species.

3.2. Associations between forest characteristics and bird activity

The GLM results linking bird activity with forest community characteristics confirmed clear differences between the Goldcrest and the Firecrest (Table 3). In the Goldcrest, both

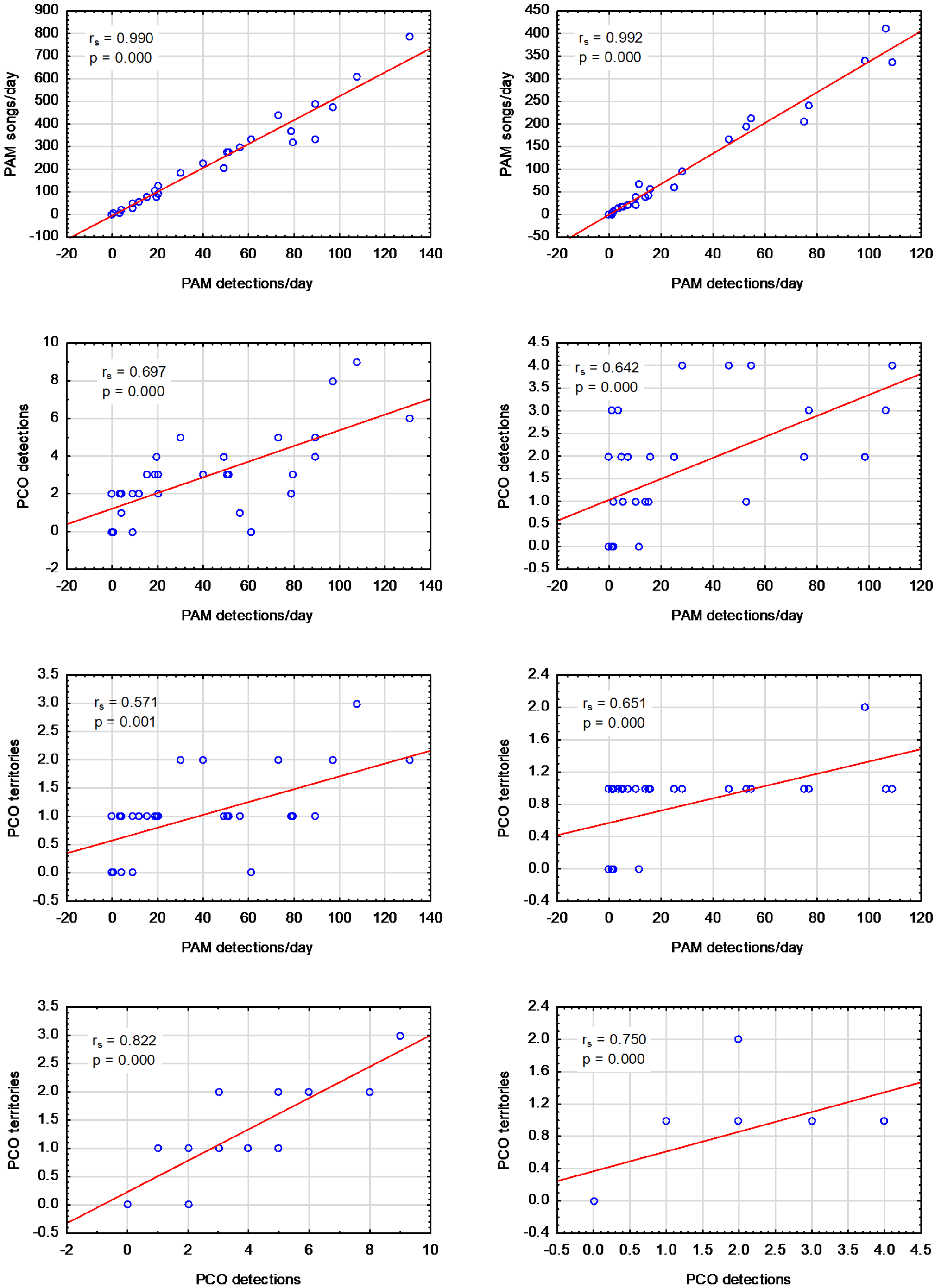

Fig. 4. Spearman rank correlations between activity parameters of Goldcrest *R. regulus* (left panel) and Firecrest *R. ignicapilla* (right panel) at 30 monitoring points, based on audio recordings and point count observations. Due to the strong relationship between the mean number of PAM songs and PAM detections, shown in the two upper plots, subsequent correlations are presented only for PAM detections.

Table 1. Numbers of detections, songs and territories of Goldcrest *Regulus regulus* and Firecrest *Regulus ignicapilla* in the Romincka Forest, and habitat parameters at individual monitoring points.

	Passive monitoring				Point counts by observers				Habitat parameters					
	Detections		Songs		Detections		Territories							
Point no.	Goldcrest	Firecrest	Goldcrest	Firecrest	Goldcrest	Firecrest	Goldcrest	Firecrest	Deciduous trees	Coniferous trees	Spruce	Pine tree	Tree species (total)	Age of trees (mean)
1	77	40	322	90	4	1	1	1	20	10	10	0	5	43
2	315	212	1486	773	2	1	1	1	23	17	17	0	9	137
3	387	4	1899	5	8	0	2	0	1	39	37	2	3	138
4	160	113	916	378	3	4	2	1	0	40	40	0	1	78
5	357	308	1339	959	5	3	1	1	3	37	37	0	4	49
6	37	3	125	9	0	3	0	1	30	10	10	0	2	49
7	36	5	186	9	2	0	1	0	19	21	21	0	5	47
8	0	0	0	0	2	0	1	0	13	27	27	0	4	57
9	0	0	0	0	0	2	0	1	17	23	23	0	3	35
10	13	426	33	1650	2	3	1	1	24	16	16	0	5	83
11	46	218	233	853	2	4	1	1	3	37	36	1	3	77
12	2	0	14	0	0	0	0	0	28	2	1	1	4	37
13	317	45	1262	265	3	0	1	0	0	40	28	12	2	115
14	15	7	93	27	2	1	1	1	13	16	14	2	7	26
15	293	6	1768	23	5	0	2	0	0	40	40	0	1	55
16	204	101	1091	247	3	2	1	1	14	26	26	0	7	57
17	119	0	722	0	5	0	2	0	19	21	20	1	7	65
18	429	63	2424	228	9	2	3	1	11	29	20	9	6	153
19	0	0	0	0	0	0	0	0	0	40	0	40	1	85
20	201	18	1096	68	3	2	1	1	3	37	37	0	3	150
21	82	15	505	51	3	3	1	1	18	22	22	0	6	65
22	81	20	366	71	2	1	1	1	31	9	9	0	5	52
23	16	60	94	171	1	1	1	1	31	9	6	3	7	95
24	195	184	816	668	4	4	1	1	1	39	39	0	2	97
25	75	301	424	817	3	2	1	1	13	27	16	11	4	78
26	225	42	1176	155	1	1	1	1	18	22	22	0	7	57
27	356	55	1949	148	4	1	1	1	22	18	18	0	7	110
28	393	22	2360	61	6	2	2	1	2	2	22	0	3	64
29	184	296	1004	1024	0	2	0	2	18	18	15	0	7	53
30	46	326	232	1007	3	4	1	1	17	17	13	0	4	99
Total	4661	2890	23935	9757	87	49	32	23						

Table 2. Spearman rank correlation matrix among the activity parameters of Goldcrest *R. regulus* and Firecrest *R. ignicapilla*. All correlations were non-significant (p > 0.05).

	Firecrest			
	PAM detections	PAM songs	PCO detections	PCO territories
Goldcrest				
PAM detections	0.334	0.333	0.057	0.169
PAM songs	0.331	0.322	0.044	0.175
PCO detections	0.172	0.135	0.058	-0.102
PCO territories	0.110	0.080	-0.039	-0.164

parameters collected via acoustic recorders (mean PAM detections and songs per day) showed a strong positive association with the ratio of coniferous to deciduous trees, and with tree species richness. Goldcrest activity recorded during point counts (PCO detections) did not show any relationship with the forest variables included in the models. In the Firecrest, the only significant relationship was a negative association between PCO detections and tree species richness. No association was detected between the activity of either species and forest stands age.

Because the GLM models indicated the importance of coniferous trees, we additionally examined correlations between the abundance of the two dominant conifer species and bird activity (Table 4). In the Goldcrest, only spruce abundance was significantly correlated with bird activity, whereas pine showed no significant relationship (all activity parameters and the number of territories were positively associated with spruce). In contrast, in the Firecrest, the only significant negative correlation concerned pine, and only for results obtained from point counts (PCO territories and marginally for PCO detections).

4. Discussion

Using two complementary detection methods, we documented the occurrence of two related passerine species in a lowland boreal forest in northern Poland. We demonstrated clear interspecific differences in vocal activity, habitat preferences, and abundance of the Goldcrest and the Firecrest. Moreover, we compared passive acoustic monitoring (PAM) with point-count surveys (PCO), highlighting the reliability of PAM as a complementary tool to traditional field methods.

In Poland, both species occur sympatrically, with the Goldcrest typically being more numerous and at times outnumbering the Firecrest by as much as fourfold (Mikusek & Dyrcz 2003). However, this ratio often shifts in favour of the Firecrest in deciduous forests (Kopij 2007), with either balanced or reversed proportions reported in some habitats, such as old beech–fir stands (Mandziak *et al*. 2021) or deciduous parts of the Białowieża Forest (Barczyk *et al*. 2024). In the mixed forests of the Eastern Carpathians the ratio of both species was almost equal (Polak 2025). In the Romincka Forest (RF), the Goldcrest proved to be more abundant than the Firecrest, with an approximate ratio of 3:2. Given the boreal character of the forest and the species' association with spruce, this dominance is in line with expectations.

Our data confirmed that PAM is an effective monitoring tool in forest ecosystems. We found positive correlations between parameters of vocal activity obtained through PAM and PCO, as well as between vocal activity and local abundance of both species at individual monitoring points. A particular advantage of PAM was its ability to collect large datasets (>33,000 songs) with relatively low field effort compared to traditional methods. PAM also proved highly effective for Regulus species, despite their reputation as rather quiet and inconspicuous forest birds. The collected material allowed us to detect a markedly uneven distribution of both Goldcrest and Firecrest in the RF, as well as interspecific differences in vocal activity and habitat preferences. Overall, the consistency between PAM and PCO results underscores the potential of PAM in ecological research on birds and other vocally active animal groups.

Our findings confirmed the generally known habitat preferences of both species—clearer in

Table 3. Results of the General Linear Models (GLM) assessing the influence of forest characteristics on the vocal activity of Goldcrest *Regulus regulus* and Firecrest *Regulus ignicapilla* in the Romincka Forest. Three habitat variables were measured in the field around each monitoring point: species richness of woody vegetation (No. tree species), average stand age (Age of trees), and the ratio of coniferous to deciduous trees (Coniferous/Deciduous). All response and environmental variables (except No. tree species) were log-transformed. Partial Eta squared (η_p^2) is reported as a measure of effect size. Coefficient of determination (R^2) for each model is also presented. Positive and negative effects are indicated in the second column.

Variable	Effect	d.f.	η_p^2	F	p
Goldcrest – PAM detections/day (model R^2 = 0.610)					
Intercept			0.020	0.47	0.499
No tree species	+	1, 23	0.271	8.57	**0.008**
Age of trees	+	1, 23	0.070	1.74	0.200
Coniferous/Deciduous	+	1, 23	0.493	22.35	**0.000**
Goldcrest – PAM songs/day (model R^2 = 0.620)					
Intercept			0.005	0.12	0.728
No tree species	+	1, 23	0.318	10.73	**0.003**
Age of trees	+	1, 23	0.050	1.20	0.284
Coniferous/Deciduous	+	1, 23	0.521	25.04	**0.000**
Goldcrest – PCO detections (model R^2 = 0.263)					
Intercept			0.000	0.00	0.988
No tree species	+	1, 21	0.007	0.15	0.699
Age of trees	+	1, 21	0.021	0.46	0.506
Coniferous/Deciduous	+	1, 21	0.116	2.76	0.112
Firecrest – PAM detections/day (model R^2 = 0.116)					
Intercept			0.020	0.43	0.517
No tree species	+	1, 21	0.048	1.06	0.315
Age of trees	+	1, 21	0.053	1.17	0.292
Coniferous/Deciduous	+	1, 21	0.008	0.17	0.682
Firecrest – PAM songs/day (model R^2 = 0.104)					
Intercept			0.004	0.09	0.766
No tree species	+	1, 21	0.044	0.98	0.334
Age of trees	+	1, 21	0.045	1.00	0.329
Coniferous/Deciduous	+	1, 21	0.011	0.24	0.631
Firecrest – PCO detections (model R^2 = 0.543)					
Intercept			0.042	0.79	0.387
No tree species	-	1, 18	-0.314	8.25	**0.010**
Age of trees	+	1, 18	0.030	0.56	0.464
Coniferous/Deciduous	+	1, 18	0.050	0.96	0.341

Table 4. Spearman rank correlations between bird activity and numbers of spruce *Picea abies* and pine *Pinus sylvestris* around 30 monitoring points.

	Goldcrest				Firecrest			
	Spruce		Pine		Spruce		Pine	
Variable	r_s	p	r_s	p	r_s	p	r_s	p
PAM detections/day	**0.456**	**0.011**	-0.109	0.566	0.080	0.674	-0.148	0.436
PAM songs/day	**0.452**	**0.012**	-0.127	0.502	0.097	0.608	-0.136	0.473
PCO detections	**0.505**	**0.004**	-0.001	0.994	0.188	0.321	-0.359	0.051
PCO territories	**0.490**	**0.006**	0.066	0.730	-0.121	0.525	**-0.374**	**0.042**

the case of the Goldcrest and less distinct for the Firecrest. The vocal activity of the Goldcrest in the RF showed a strong positive relationship with the proportion of coniferous trees, which aligns with the species' national-scale habitat preferences (Kosicki *et al*. 2015) and broader European patterns (Cramp & Simmons 2004). Associations with coniferous forests, particularly spruce, have been widely documented in regional studies in Poland (*e.g*., Kopij 2007, Mikusek & Dyrcz 2003, Szczypiński 2015, Polak 2025). Across Europe, Goldcrest occurrence generally mirrors the distribution of spruce and fir forests (Hagemeijer & Blair 1997). Fir is absent in the RF, but spruce is a dominant species and the Goldcrest's strong association with spruce was clearly reflected in our results. PAM data also indicated a preference of this bird for areas with higher tree-species richness. This is noteworthy, as the species is known to tolerate homogeneous coniferous stands, where it may even reach its highest densities (Hagemeijer & Blair 1997). Apparently, the RF—far removed from a plantation-type forest—offers a structurally diverse environment favourable to this species.

For the Firecrest, the results from the RF indicated primarily the avoidance of pines and a surprising negative association with tree-species richness. Data from remote sensing sources suggest that Firecrests indeed avoid pine stands but select species-rich forests in Poland (Kosicki *et al*. 2015). Regional studies have consistently shown the Firecrest to occur in mixed forests, including pine–spruce or fir stands with a deciduous component (Mikusek & Dyrcz 2003, Kopij 2007, Ławicki *et al*. 2020, Mandziak *et al*. 2021, Polak 2025). Throughout Europe, the species displays broader habitat preferences than the Goldcrest, and deciduous forests with even a small admixture of conifers may constitute suitable breeding habitat (Hagemeijer & Blair 1997).

We found no relationship between vocal activity and stand age in either species. Some studies in Poland have shown a preference for mature forests, particularly stands over 75 years old (Szczypiński 2015, Sikora *et al*. 2015). In the Natura 2000 Special Protection Area Puszcza Napiwodzko-Ramucka, Firecrests reached their highest densities (75% of males) in stands aged 80–200 years, with an average stand age of 123 years (Sikora *et al*. 2015). However, in the montane forests of Eastern Carpathians, Goldcrests preferred younger forest stands and Firecrests were more abundant in mature forests (Polak 2025). The lack of any pattern in the RF may result from local environmental factors that render even younger stands attractive for both species, for example habitat or climatic variables influencing food abundance and availability.

Overall, the relationships observed in our study area may stem from habitat specificity of the Romincka Forest, including factors which was not fully captured in our analyses. This forest is not a plantation-type ecosystem but a structurally complex and heterogeneous woodland containing nature reserves and a diverse mosaic of microhabitats that differ in temperature, light, and humidity. Such conditions may enhance food availability for both Regulus species and, consequently, shape their fine-scale spatial distribution.

Hippiäisen (*Regulus regulus*) ja tulipäähippiäisen (*Regulus ignicapilla*) runsautta ja elinympäristö-preferenssejä koskeva arviointi passiivisen akustisen monitoroinnin ja pistelaskennan avulla lauhkean vyöhykkeen metsäekosysteemissä Puolassa

Passiivinen akustinen monitorointi (PAM) tarjoaa uusia mahdollisuuksia lintujen runsauden ja elinympäristö-preferenssien arviointiin, mutta sen toimivuutta perinteisiin pistelaskentoihin verrattuna ei ole vielä riittävästi testattu, erityisesti hiljaisten ja huomaamattomien metsälinnuston varpuslintujen osalta. Vertailimme hippiäisen (*Regulus regulus*) ja tulipäähippiäisen (*Regulus ignicapilla*) ääntelyaktiivisuutta ja sen yhteyttä elinympäristöihin lauhkean vyöhykkeen metsäekosysteemissä PAM- ja pistelaskentaperusteisten indikaattorien avulla. Rominckan metsässä (Puola) sijaitsevilla 30 havaintopisteellä PAM tuotti yli 33 000 äänitettyä laulua ja paljasti voimakasta paikallista vaihtelua molempien lajien välillä. PAM:lla saadut ääniaktiivisuusmittarit korreloivat positiivisesti pistelaskentahavaintojen ja reviirien kanssa, mikä vahvistaa PAM:n luotettavuuden yksilömäärän täydentävänä indikaattorina. Hippiäisen ääniaktiivisuus liittyi voimakkaan positiivisesti havupuiden osuuteen – erityisesti kuuseen – sekä paikalliseen puulajiston monimuotoisuuteen, mikä heijastaa lajin suosivan rakenteellisesti monipuolisia, havupuuvaltaisia metsiköitä. Sen sijaan tulipäähippiäisen yksilömäärä ei PAM-aineiston perusteella liittynyt metsärakenteeseen, kun taas pistelaskentahavainnot viittasivat männyn välttelyyn ja pienempään aktiivisuuteen puulajistoltaan monipuolisissa metsiköissä. Metsikön iällä ei havaittu merkittävää vaikutusta kummankaan lajin osalta. Lajien välisten aktiivisuusparametrien heikot korrelaatiot korostavat niiden erillisiä ekologisia lokeroita, vaikka esiintymisalueet osittain limittyvät. Pistelaskenta-aineiston perusteella hippiäinen osoittautui runsaammaksi lajiksi, reviirisuhteen ollessa noin 3:2 tulipäähippiäiseen verrattuna. Tutkimuksemme osoittaa, että PAM havaitsee tehokkaasti vaihtelua molempien *Regulus*-lajien runsaudessa ja elinympäristövalikoivuudessa ja tarjoaa skaalautuvan, tehokkaan täydennyksen perinteisille laskentamenetelmille lauhkean vyöhykkeen metsäekosysteemeissä.

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Author contributions. AW: Conceptualization, Formal analysis, Visualisation, Writing - original draft, Writing - review & editing. KK: Conceptualization, Investigation, Methodology, Visualisation, Writing - original draft, Writing - review & editing. DC: Investigation, Methodology, Writing - review & editing.

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

Martin Korňan[‡]*, Ľudovít Kocian, Karel Pavelka, Rudolf Kropil, Peter Lešo, Jan Pavelka[†], Katarína Mikulová & Vladimír Šebeň

M. Korňan, R. Kropil, P. Lešo, Department of Applied Zoology and Wildlife Management, Faculty of Forestry, Technical University in Zvolen, T.G. Masaryka 20, SK - 960 01 Zvolen, Slovakia.
Ľ. Kocian, Ipeľská 5, SK - 821 07 Bratislava, Slovakia.
K. Pavelka, Museum of Moravian Wallachia Region, Horní náměstí 2, CZ - 755 01 Vsetín, Czech Republic & Dolní Jasenka 776, CZ - 755 01 Vsetín, Czech Republic.
K. Mikulová, Slovak Hydrometeorological Institute, Department of Climatological Service, Jeséniova 17, SK - 833 15 Bratislava, Slovakia.
V. Šebeň, National Forest Centre, Forest Research Institute, T.G. Masaryka 2175/22, SK - 960 01 Zvolen, Slovakia.
‡Current address: Centre for Ecological Studies, Ústredie 14, SK - 013 62 Veľké Rovné, Slovakia.
†Deceased
** Corresponding author's email: martin.kornan@gmail.com*

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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

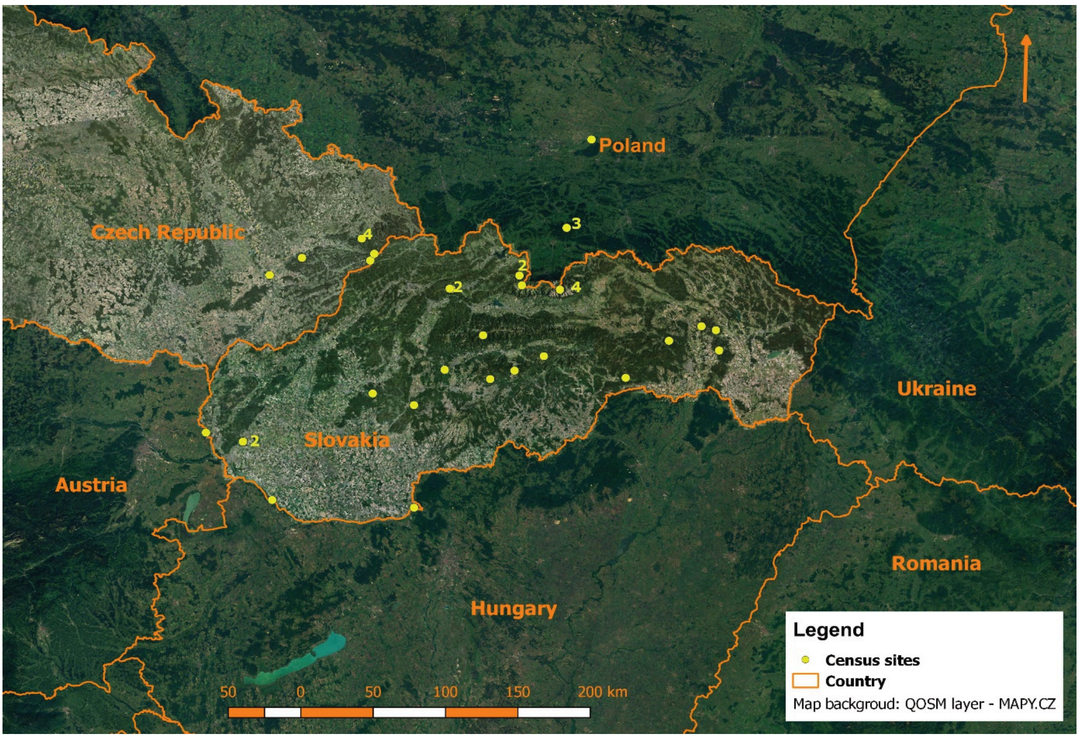


Fig. 1. Geographic distribution of 38 bird census plots in the Western Carpathian Mountains of Slovakia, Czechia and Poland, from which abundance data were used in the study. Points with numbers indicate the number of census plots on this site. Additional information on each plot is given in Supplement 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 $\alpha = 0.05$. 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

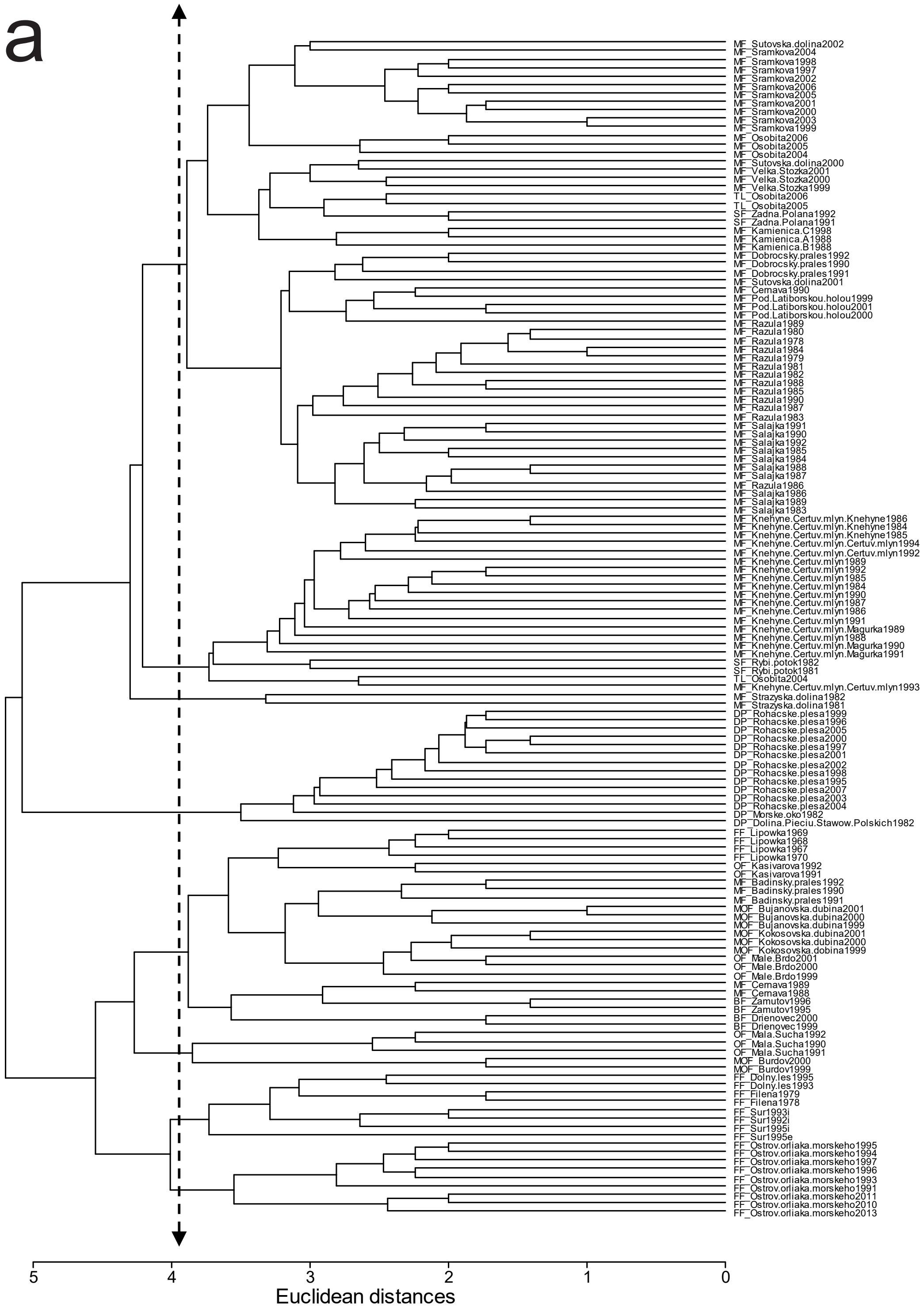
In order to evaluate the effects of floristics and the wide range of environmental variables on bird assemblages, we used two ordination procedures, CCA (ter Braak 1986) and CO-CA (ter Braak & Schaffers 2004). We applied CCA for listing the rank of environmental variables by explained variance indicating 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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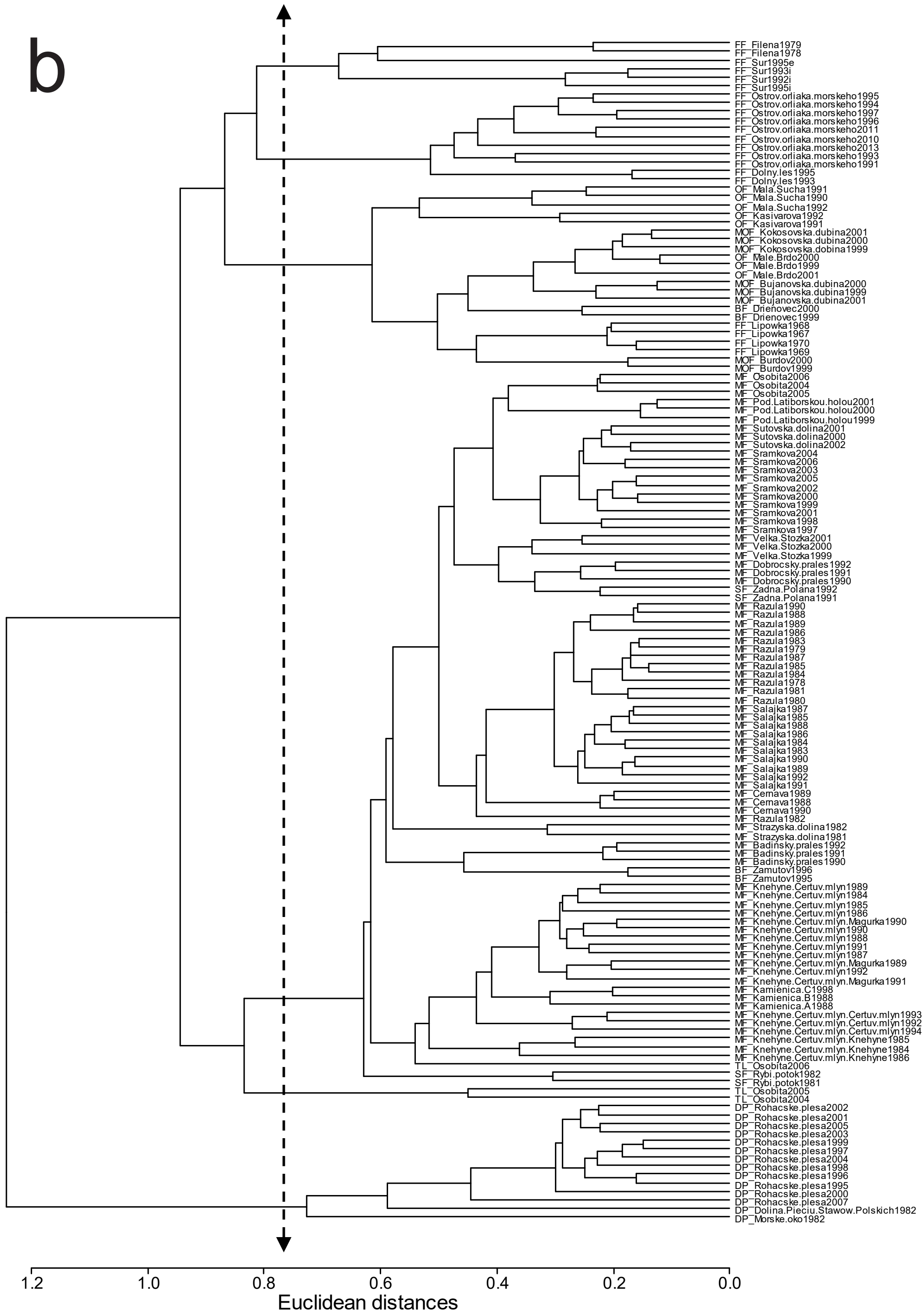
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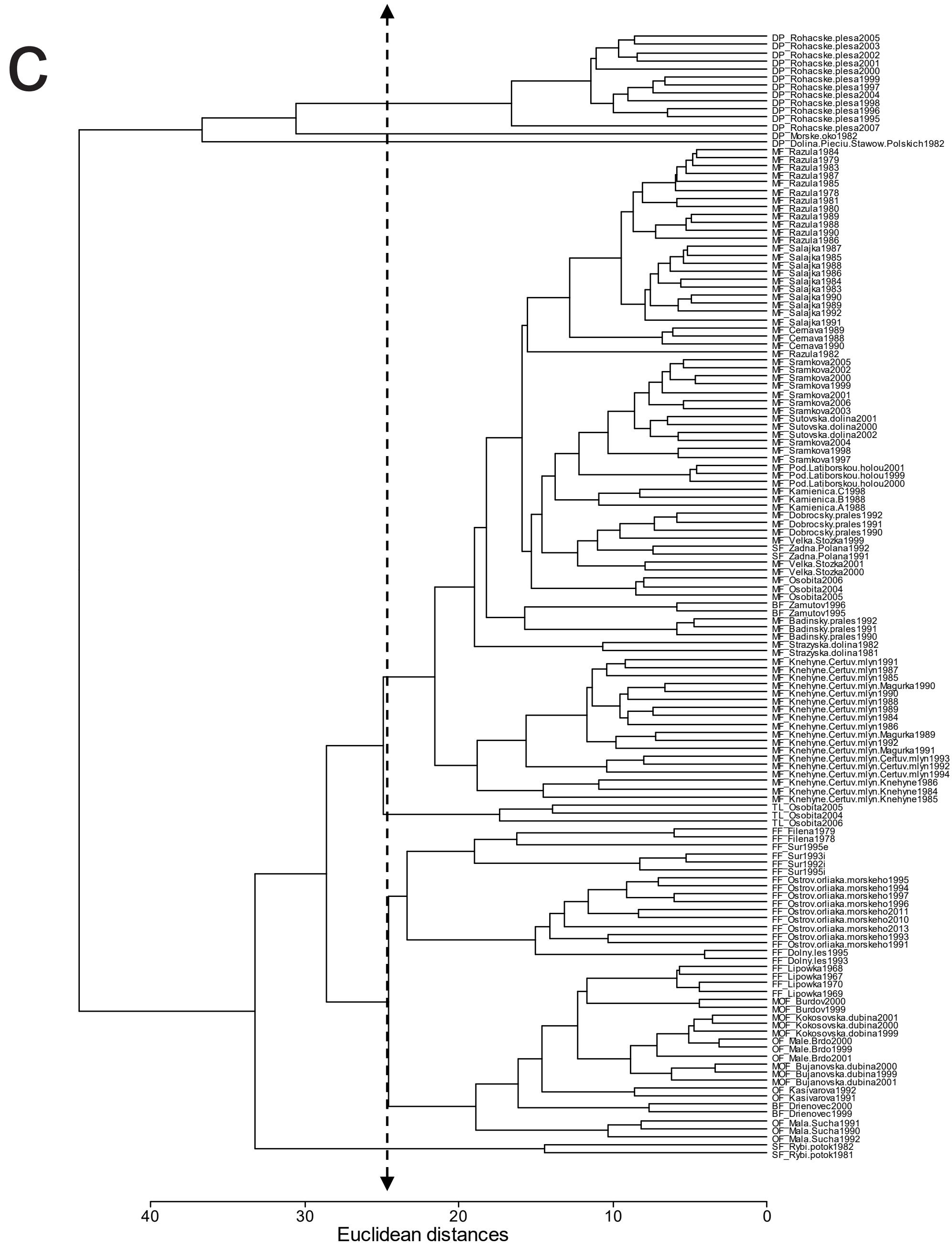

Fig. 2. Classification patterns of breeding bird assemblages of primeval and natural forests in the elevational gradient of the Westerns Carpathians based on presence/absence (a), density (b) and dominance (c) matrices. Significant clusters revealed by bootstrapped resampling at α = 0.05 corresponding 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 α = 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 $\alpha = 0.0001$, 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

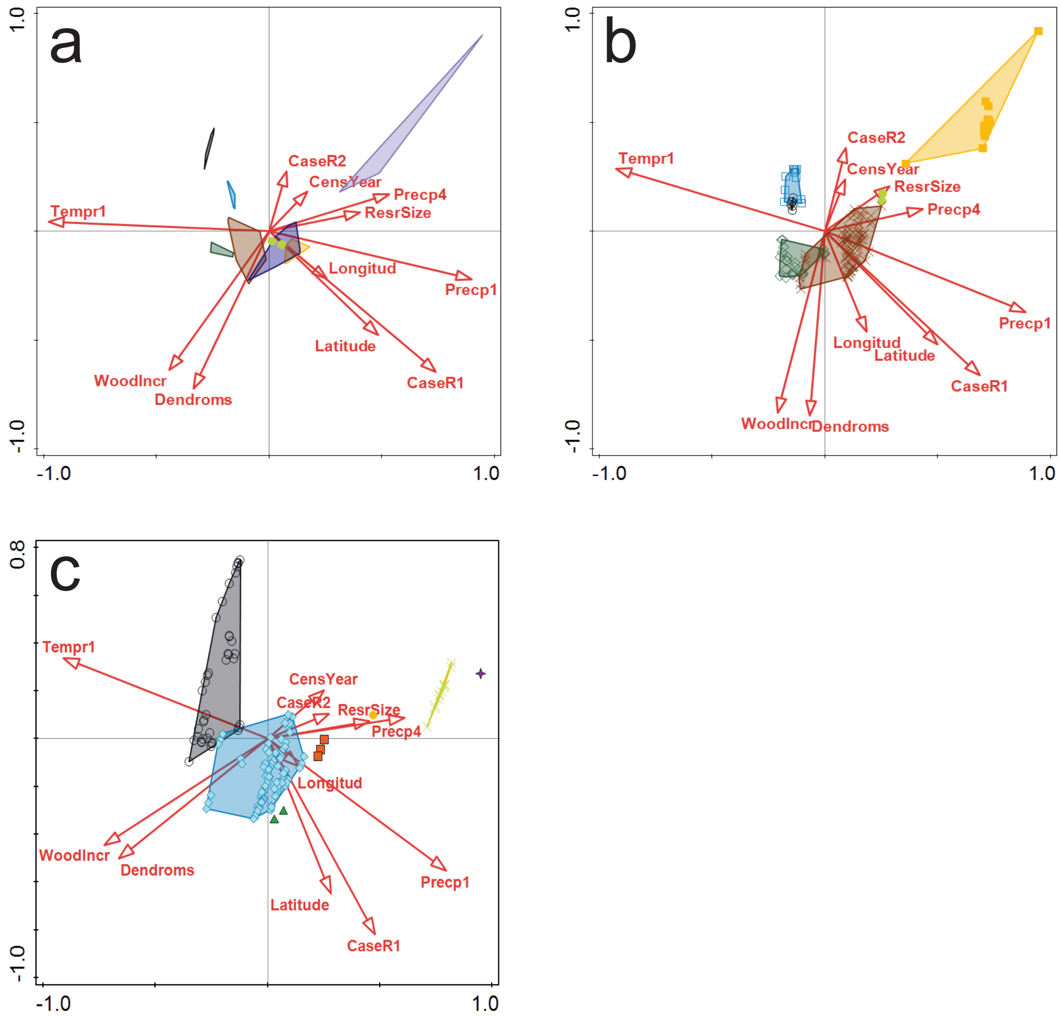

Fig. 3. Biplots of canonical correspondence analysis (CCA) based matrices of 84 bird species presence/absence (binary) vs. 11 environmental variables × 139 samples (a), 84 bird species density vs. 11 environmental variables × 139 samples (b) and 84 bird species dominance vs. 11 environmental variables × 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.