

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

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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 enables 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, Hoefler *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, Hoefler *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 & Dyrzc 2003, Kopij 2007, Staszewski 2010, Szczypiński 2015, Wilniewicz & 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

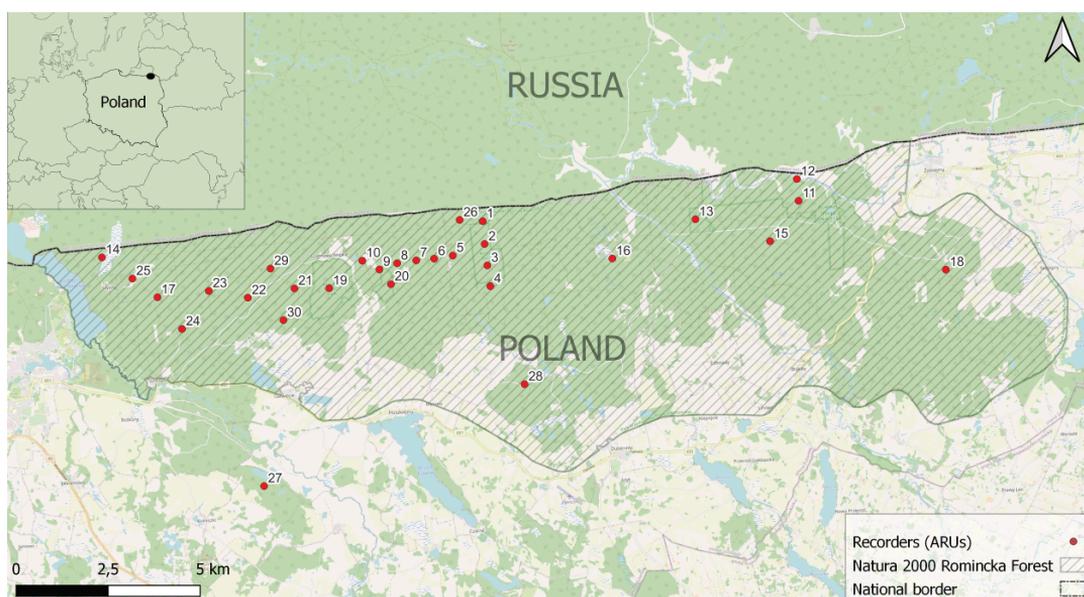


Fig. 1. Romincka Forest and the distribution of autonomous recording units.

(*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,

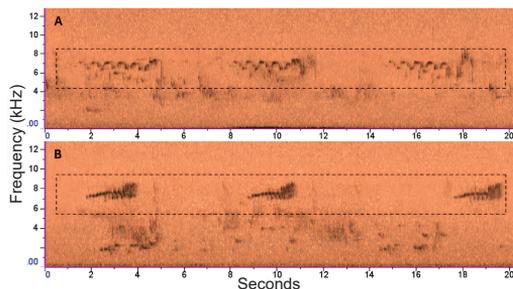


Fig. 2. Sonograms of Goldcrest *Regulus regulus* (A) and Firecrest *Regulus ignicapilla* (B) songs (Raven Pro).

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

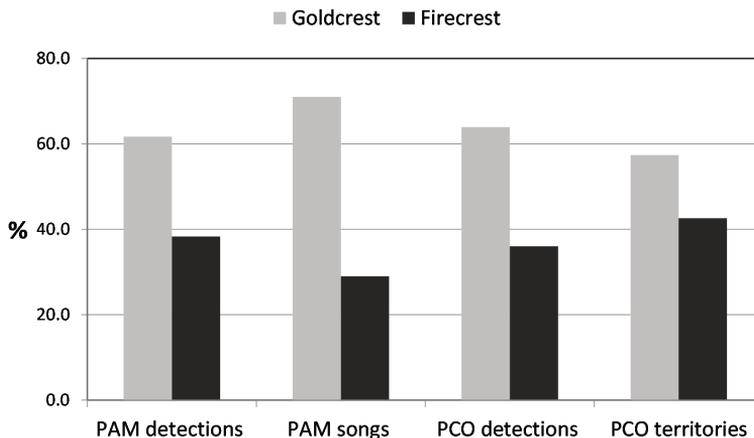


Fig. 3. Differences in the abundance of Goldcrest *R. regulus* and Firecrest *R. ignicapilla* in the Romincka Forest, expressed by activity parameters obtained through passive monitoring (PAM) and point counts (PCO).

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 ($\chi^2 = 0.285$, $df = 1$, $p = 0.594$), nor between PAM songs and PCO detections ($\chi^2 = 3.289$, $df = 1$, $p = 0.070$).

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

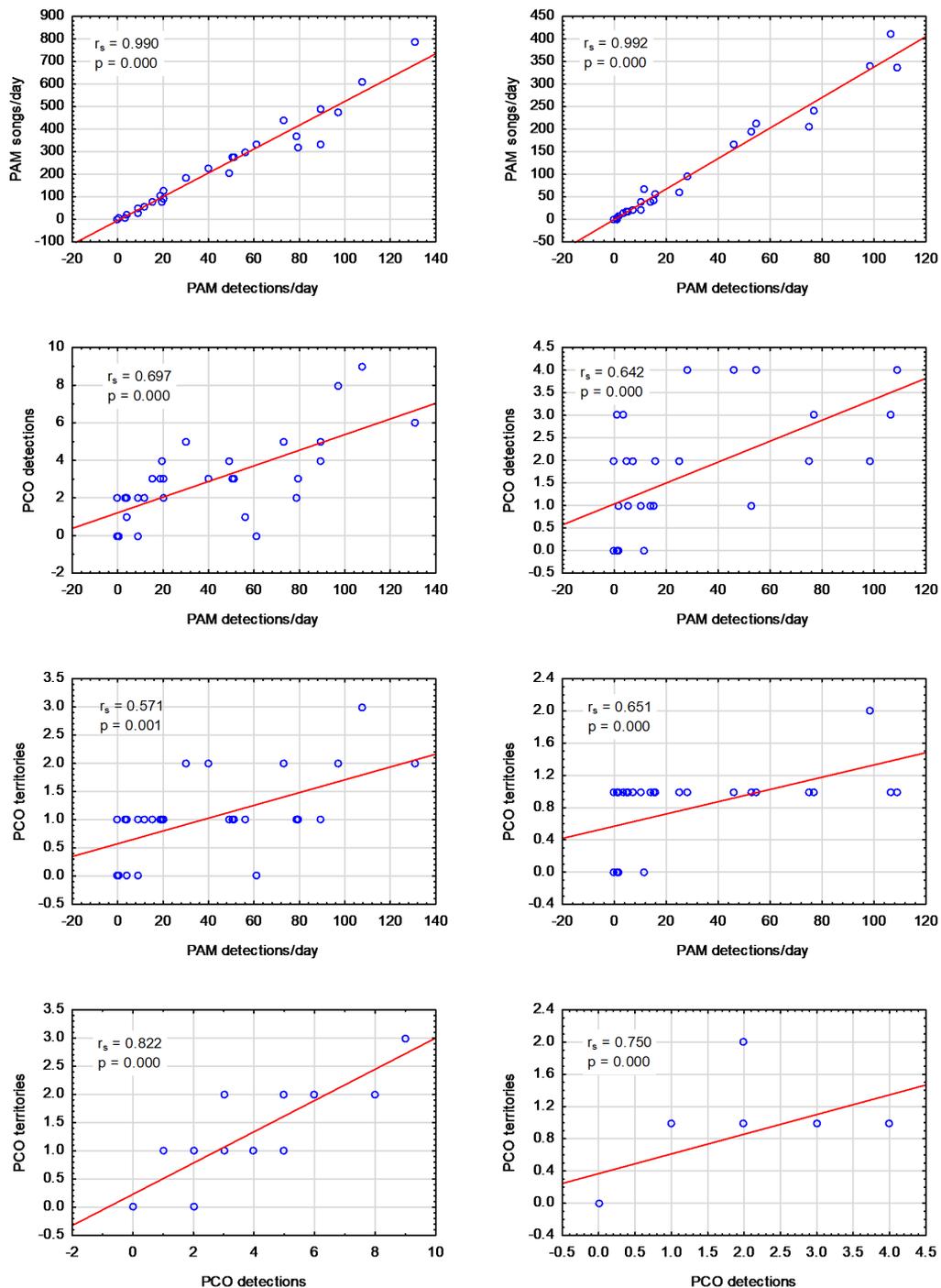


Fig. 4. Spearman rank correlations between activity parameters of Goldcrest *R. regulus* (left panel) and Firecrest *R. ignicapilla* (right panel) at 30 monitoring points, based on audio recordings and point count observations. Due to the strong relationship between the mean number of PAM songs and PAM 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.

| Point no. | Passive monitoring | | | | Point counts by observers | | | | Habitat parameters | | | | | |
|-----------|--------------------|-----------|-----------|-----------|---------------------------|-----------|-------------|-----------|--------------------|------------------|--------|-----------|----------------------|---------------------|
| | Detections | | Songs | | Detections | | Territories | | Deciduous trees | Coniferous trees | Spruce | Pine tree | Tree species (total) | Age of trees (mean) |
| | Goldcrest | Firecrest | Goldcrest | Firecrest | Goldcrest | Firecrest | Goldcrest | Firecrest | | | | | | |
| 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 & Dyrz 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.

| Variable | Goldcrest | | | | Firecrest | | | |
|--------------------|--------------|--------------|--------|-------|-----------|-------|---------------|--------------|
| | Spruce | | Pine | | Spruce | | Pine | |
| | 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 & Dyrz 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 & Dyrz 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 metsäekosysteemeissä 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 metsäekosysteemeissä 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 välisen aktiivisuusparametrien heikot korrelaatiot korostavat niiden erillisiä ekologisia lokeroita, vaikka esiintymisalueet osittain limittyvät. Pistelaskenta-aineiston perusteella hippiäinen osoitautui runsaammaksi lajiksi, reviiirisuhteen 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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