



Diel and seasonal vocal activity patterns revealed by passive acoustic monitoring suggest expert recommendations for breeding bird surveys need adjustment

David Singer^{1,2} · Johannes Kamp³ · Hermann Hondong³ · Andreas Schuldt² · Jonas Haggé^{1,2}

Received: 4 September 2024 / Revised: 20 May 2025 / Accepted: 18 June 2025 / Published online: 9 July 2025
© The Author(s) 2025

Abstract

Species identification and recording in breeding bird surveys vastly rely on the registration of avian calls and songs. Despite comprehensive expert knowledge on species-specific activity patterns, data-based analyses of vocal activity patterns are lacking. Recent advances in passive acoustic monitoring allow the direct measurement of bird vocal activity at very high temporal resolution. We conducted a comprehensive survey, recording 25,000 h of audio data at 256 forest sites in Lower Saxony, Germany, to investigate vocal activity patterns of the European forest bird community. Our results reveal a high degree of inter-specific variability in seasonal and diel vocal activity patterns, including strong circular patterns along the day–night cycle and a significant seasonal component. Comparing acoustic detectability to species-specific survey recommendations revealed critical temporal discrepancies for 64.2% of species, and standard protocols (sunrise to 4 h after sunrise) showed discrepancies for 41.5% of species. This highlights the potential for temporal survey optimization to reduce imperfect detection and increase accuracy and precision. Emphasis should be given to the hours before and after sunrise and also sunset for sampling less detectable species. Combining observer-based surveys with passive acoustic monitoring might leverage the strengths of both methods. Our results also emphasize the potential of continuous recording schedules in passive acoustic monitoring to capture diverse temporal patterns. This study provides a baseline for future research on vocal activity patterns across habitats, throughout the year, and regarding anthropogenic impacts. Our findings may raise awareness among ornithologists about the sources of variation in acoustic detectability and its implications for breeding bird surveys, highlighting potential for methodological adjustments in survey timing and consequences for careful interpretation of bird surveys.

Keywords Passive acoustic monitoring · AudioMoth · BirdNET · Imperfect detection · Detection probability · Phenology

Zusammenfassung

Tageszeitliche und saisonale Muster der Gesangs- und Rufaktivität mitteleuropäischer Waldvogelarten, erfasst durch passives akustisches Monitoring, deuten auf Anpassungsbedarf zeitlicher Expertenempfehlungen für Brutvogelerfassungen hin.

Brutvogelerfassungen basieren maßgeblich auf der Registrierung von Vogelrufen und -gesängen. Trotz umfassendem Expertenwissen über artspezifische Aktivitätsmuster sind datenbasierte Analysen akustischer Aktivitätsmuster bislang nur selten durchgeführt worden. Fortschritte im Bereich des passiven akustischen Monitorings (PAM) ermöglichen inzwischen

Communicated by T. S. Osiejuk.

✉ David Singer
d.singer@posteo.de

¹ Department of Forest Nature Conservation, Northwest German Forest Research Institute, Göttingen, Germany

² Department of Forest Nature Conservation, University of Göttingen, Göttingen, Germany

³ Department of Conservation Biology, University of Göttingen, Göttingen, Germany

jedoch die direkte Messung der Gesangs- und Rufaktivität von Vogelgemeinschaften mit hoher zeitlicher Auflösung. In einer umfassenden Untersuchung haben wir 25.000 Stunden Audiomaterial an 256 Waldstandorten in Niedersachsen (Deutschland) aufgezeichnet und mittels BirdNET ausgewertet, um die akustischen Aktivitätsmuster mitteleuropäischer Waldvogelarten zu untersuchen. Unsere Ergebnisse zeigen ein hohes Maß an interspezifischer Variabilität in saisonalen und tageszeitlichen Aktivitätsmustern. Ein Vergleich der akustischen Nachweisbarkeit durch PAM mit artspezifischen Expertenempfehlungen offenbarte kritische zeitliche Diskrepanzen bei 64,2% der Arten; bei den Empfehlungen für standardisierte Erfassungen ganzer Brutvogelgemeinschaften (Sonnenaufgang bis vier Stunden danach) traten Diskrepanzen bei 41,5% der Arten mit der akustischen Nachweisbarkeit mittels PAM auf. Insbesondere artspezifische Erfassungen können somit zeitlich optimiert werden, um Erfassungsgrad und Genauigkeit von Brutvogelerfassungen zu erhöhen. Ein besonderes Augenmerk sollte auf die Stunde vor sowie eine Stunde nach Sonnenaufgang sowie auf den Zeitraum um den Sonnenuntergang gelegt werden, um zu diesen Zeitpunkten schwerpunktmäßig aktive Arten besser zu erfassen. Die Kombination von beobachterbasierten Erhebungen mit passivem akustischem Monitoring könnte die Stärken beider Methoden vereinen. Unsere Ergebnisse zeigen zudem das Potenzial kontinuierlicher Aufnahmeschemata im passiven akustischen Monitoring um die Vielfalt zeitlicher Aktivitätsmuster im Tages- und Nachtverlauf optimal zu erfassen. Diese Studie liefert eine Grundlage für zukünftige Forschung zu akustischen Aktivitätsmustern in verschiedenen Lebensräumen, über das gesamte Jahr hinweg oder im Hinblick auf anthropogene Einflüsse. Unsere Erkenntnisse können das Bewusstsein für die (tages)zeitliche Variabilität in der akustischen Nachweisbarkeit – insbesondere auch von häufigen Arten – und die Notwendigkeit einer kritischen Interpretation der Vollständigkeit von Brutvogelerfassungen schärfen sowie Hinweise für eine Optimierung zeitlicher Vorgaben für Brutvogelerfassungen geben.

Introduction

Acoustic communication plays a pivotal role in the ecology of animals, including birds (Rosenthal and Ryan 2000). Spatio-temporal patterns of animal vocalizations provide detailed information on site occupancy and behaviour (Kershenbaum et al. 2016; Gibb et al. 2019). Birds sing to attract mates and defend their territories (Catchpole and Slater 2008) and use calls to communicate with conspecifics and also other species (Hollén and Radford 2009; Gill and Bierema 2013). In bird surveys, the spatio-temporal distribution of species songs and calls are used to infer presence and abundance and to delineate territories of breeding birds (Bibby et al. 1992; Südbeck et al. 2005). Particularly in ecosystems with dense vegetation, bird observations by humans predominantly result from the detection of auditory cues, while bird sightings are a less important source of observations (Brewster and Simons 2009). Hence, most bird surveys vastly rely on the assumption that birds vocalize regularly during a survey so that their presence and abundance can be inferred by the observer. Survey protocols of bird monitoring programmes set standards concerning seasonality, daytime and weather conditions (Bibby et al. 1992; Greenwood et al. 1994; Jiguet et al. 2012; Sauer et al. 2017). Germany is a country with a long tradition of breeding bird surveys, especially using the territory mapping method (Südbeck et al. 2005). Survey protocols are well established and have been widely applied for breeding bird surveys since the 1960s (Flade 1994). Territory mapping is the preferred method in conservation, impact assessment and environmental planning since the 1990s. However, most

survey recommendations regarding phenological recommendations are based on expert knowledge (Südbeck et al. 2005), as observational studies quantifying diel and seasonal activity patterns are scarce (but see Robbins 1981; Morelli et al. 2022). Although recommendations for the phenological aspects of bird surveys can be based on standardized data (e.g. Strebel et al. 2014), changes in seasonal activity due to climate change have rendered some older recommendations outdated, as earlier arrival of migratory species or earlier egg laying of resident species has effects on vocal activity patterns because many species show highest singing activity around egg laying (Rubolini et al. 2007; Bates et al. 2023; Romano et al. 2023).

As already Zimmer (1919) recognized, detailed studies on temporal activity patterns conducted by human observers are inherently limited in terms of covered species, sites, seasonal period and time of day and is complicated by uncertainties arising from the varying expertise of human observers. Recent advancements in passive acoustic monitoring (PAM) now make it possible to directly measure vocal activity of entire bird assemblages in high temporal resolution over extended periods, with simultaneously surveying multiple sampling sites without human observer bias (Lellouch et al. 2014; Krause and Farina 2016; Thompson et al. 2017; Roark and Gaul 2021). With the combination of energy-efficient autonomous recording units (Hill et al. 2018) and powerful species detection algorithms (Kahl et al. 2021) that are capable of identifying avian vocalizations of entire species assemblages with high precision (Funosas et al. 2024; Singer et al. 2024), it is even possible to acquire data on fine-scale diel activity patterns. Beyond enhancing our understanding

of bird ecology, such detailed insights into species-specific vocal activity patterns may have practical implications for the improvement of survey protocols, particularly in the context of phenological shifts under climate change (Balantic and Donovan 2019). Species-specific knowledge on (acoustic) detectability may also improve the understanding of variability, and the assessment of uncertainty, in breeding bird surveys and long-term bird monitoring (Strebel et al. 2014; Balantic and Donovan 2019). Better quantification of temporal activity patterns could inform species conservation (Day et al. 2015; Mariton et al. 2023).

In this study, we present high-resolution diel and seasonal vocal activity patterns of European forest bird species at the landscape scale, using PAM across 256 study sites, covering an area of over 45,000 km². We aim to address three key research objectives:

- (1) To quantify the diel and seasonal diversity of relative vocal activity patterns in European forest birds at 10-min intervals.
- (2) To compare these patterns to those used in breeding bird survey recommendations based on expert knowledge to identify mismatches between data-driven and expert knowledge-based phenologies.
- (3) To illustrate, how recommendations for breeding birds could be improved by PAM.

Materials and methods

Data collection and pre-processing

We recorded audio data at 256 forest sites in Lower Saxony, Germany (Fig. S1). The study region covers parts of the Atlantic and continental biogeographic regions. Sites covered a broad range of forest habitats, including old-growth deciduous stands left unmanaged for more than 50 years, and managed deciduous, mixed and coniferous forest stands of various age. All study sites were randomly chosen within forest areas of the Lower Saxony State Forests, using the *st_sample* function from the simple features *sf* R package (Pebesma 2018) with a minimum of at least 250 m distance between two sites (for details see Singer et al. 2025). Regarding mean annual temperature and precipitation of the period from 1991 to 2020 (DWD 2025), the study sites were representative for the climatic conditions of German forests expect for the alpine region (Fig. S2). Elevation of the study sites ranges between 0 and 660 m asl.

We studied 256 sites in total, but due to logistical limitations we randomly split them into two yearly cohorts, hence 128 sites were studied in spring 2022, and the other 128 sites in spring 2023. Due to battery failures at 24 sites in 2022/2023, these sites were sampled again in spring 2024

to obtain complete time series for all 256 sites. The inclusion of data from three different years helped to avoid strong signals of year-specific weather conditions in the resulting vocal activity patterns. To record audio data autonomously, one AudioMoth (Hill et al. 2018) (versions 1.0.0/1.1.0 that are technically equal) per site was attached to a tree trunk in waterproof IPX7 cases at ca. 1.8 m height. Devices were programmed to record at a sampling rate of 32 kHz for 30 s every 10 min from 1st March to 21st May in each year, covering the main part of the breeding period of most Central European forest birds (Südbeck et al. 2005). This sampling scheme ensured the highest possible temporal coverage and resolution in accordance with the given limitations regarding battery runtime and our logistic abilities to exchange batteries across the study area. We analysed 97 h of audio data per plot, totalling up to 2.9 years (25,190 h) of audio data. All audio data were analysed using the artificial neural network BirdNET Analyzer 2.2 (Kahl et al. 2021), with default settings (*min_conf*=0.1, *sensitivity*=1, *spp*=1, *overlap*=0). BirdNET uses a 3-s window for signal detection and attributes a confidence score to each detection, going from 0.1 to 1. We deactivated the use of eBird species distribution data (Sullivan et al. 2009) within the BirdNET analysis, as most bird watchers in Germany contribute their observations to the platform ‘ornitho.de’ instead of eBird (Hertzog et al. 2021); hence, the eBird-data may be less complete regarding species coverage.

To minimize false-positive species detections in the raw BirdNET classifications before analysing species-specific vocal activity patterns, we first applied the species-specific thresholding approach of Singer et al. (2024). This approach makes use of aggregated time series features (e.g. the mean confidence score of adjacent acoustic samples) to improve the differentiation of true- and false-positive detections in automated species classification data. The first author validated 225 BirdNET detections per species by listening to all audio files across the confidence score range. Based on that validated sample, we used conditional inference trees to derive species-specific threshold rules. These threshold rules allowed to filter the BirdNET detections according to their confidence scores and additional contextual information from the time series of BirdNET detections. This approach effectively reduces false-positive detections in the BirdNET data (Singer et al. 2024).

Furthermore, to investigate potential biases in the performance of BirdNET regarding times of the day or parts of the season, we randomly selected 50 audio files (30 s) per month and four daytime aspects (sunrise: 1 h before sunrise until 1 h after sunrise, day: between 1 h after sunrise and 1 h before sunset, sunset: 1 h before sunset until 1 h after sunset, night: between 1 h after sunset and 1 h before sunrise), totalling up to 600 files (5 h of audio data). We listened to these files while also checking the sonograms in Audacity visually.

We listed all species identifiable to an experienced observer (D. Singer) per file. Finally, we compared this species list to the species identified by BirdNET after applying the species-specific thresholding approach within the same audio file and analysed the resulting false-negative rates (Fig. S3).

Analysis of activity time series

We included only time series of a minimum of 5 days with at least two detections of a species, aiming to exclude recordings including potentially false-positive BirdNET detections. We transformed the remaining time series of raw BirdNET detections into binary activity data (1 for activity, 0 for no activity) per 30-s file and calculated the moving average including five time steps (5 time steps of 10 min = 50 min) of these time series as a robust measure of detection probability. Finally, we averaged the detection probabilities across sites per species to receive averaged time series across the study region (Fig. 1). Hence, relative acoustic detectability—hereafter referred in the text as detectability—reaches a value of one at the time when a species is detected at the highest number of sites simultaneously. Compared to simply summing species detections across sites per time step, this measure of detection probability accounts for spatial variation in the absolute number of detections to prevent activity patterns from being dominated by single bird individuals at certain sites. Consequently, the resulting relative activity patterns are a robust measure of spatial synchrony in detectability of the species at landscape level. Due to the species-specific scaling, it is not possible to infer the absolute numbers of vocalizations from the relative activity patterns. Only species with time series from at least five sites were included. We visualized the resulting time series of relative detectability as ‘diel–seasonal heatmaps’, where the x-axis represents the day of the year, and the y-axis represents the

time of the day (Fig. 2). Compared to classical two-dimensional time series visualizations, this approach is well suited for illustrating the diel circularity of species activity, capturing the day-and-night patterns in the temperate zone. All times throughout the manuscript are given in the Central European Time (UTC + 1) time zone, ignoring the daylight-saving time change (CEST) within the breeding season.

To infer similarity in diel–seasonal activity pattern between species, we calculated the Pearson’ correlation coefficients of the relative detectability time series (81 days with 10 min time steps) comparing all species and conducted an agglomerative hierarchical cluster analysis on the correlation matrix, using the ‘ward.D2’ method. This method minimizes the total within-cluster variance at each step of the clustering process (Warren Liao 2005). Visualizations were done with the R packages *corrplot* (Wei and Simko 2021) and *ggplot2* (Wickham 2016).

Comparison to expert knowledge survey recommendations

We aimed to assess the additional information content of PAM-derived phenological data when compared to (a) expert-derived species-specific recommendations provided in the survey manual for Germany of Südbeck et al. (2005) and (b) the standard protocol for community-scale breeding bird surveys in the temperate zone, which comprises the time from sunrise to 4 h after sunrise (Jiguet et al. 2012; Kamp et al. 2021). The comparison to species-specific recommendations may help to improve the temporal design of studies or monitoring programmes focussing on single (or small set of) species, e.g. monitoring programmes of woodpecker or owl species, but also species-specific research studies. The comparison to the standard protocols for community-scale

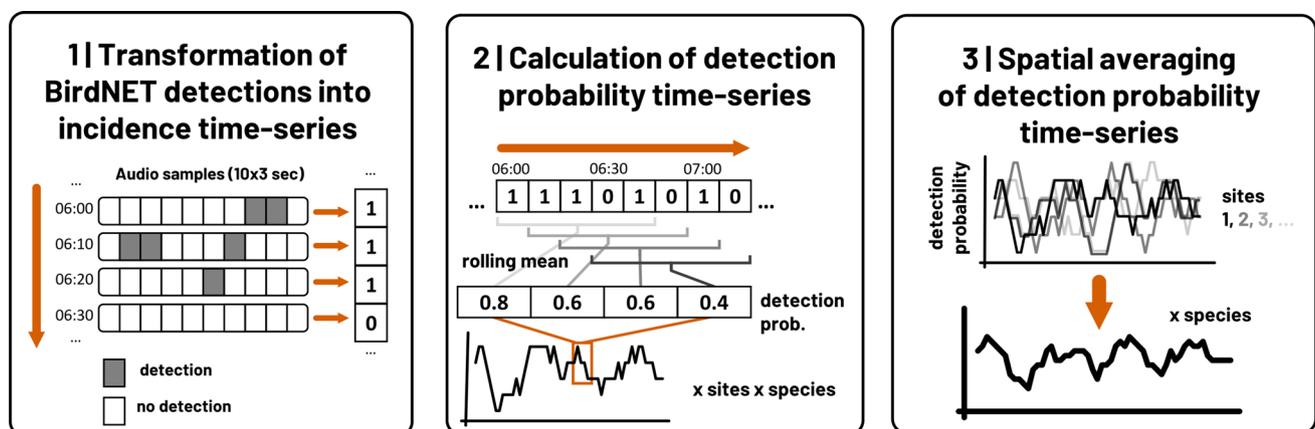


Fig. 1 Data preparation scheme from the BirdNET detections of all sample sites to one averaged detectability time series per bird species

breeding bird surveys may help to evaluate the temporal design, e.g. of common breeding bird monitoring schemes.

Südbeck et al. (2005) divide the breeding season into thirds of months and suggest favourable seasonal survey periods for all species, based on consultation of species experts (Südbeck et al. 2005). Species-specific recommendations from Südbeck et al. (2005) also contain suggestions of the favourable daytime to survey a given species. We translated this expert knowledge on species-specific seasonal and diel favourable survey periods into a machine-readable dataset. Semi-quantitative estimates of best survey time were translated into four categories: early morning sunrise until 9:00 CET, morning: sunrise until 10:00 CET, late morning sunrise until 11:00 CET, noon: sunrise until 12:00 CET. Dawn and dusk were defined as civil dawn/dusk and calculated using the *sunalc* R package (Thieurmél and Elmarhraoui 2022) for the centroid of all study sites (Fig. S1). To compare the species-specific, relative acoustic detectability from the PAM data to the expert knowledge-based survey recommendations, we averaged the diel activity time series within the thirds of months and visualized the resulting distribution of relative detectability per third of month.

We compare the maxima of acoustic detectability from the PAM to those based on expert knowledge in the (a) species-specific survey recommendations and the (b) standard protocol for community-scale breeding bird surveys (Fig. 3). We calculated the ‘temporal completeness’ as the proportion of high acoustic detectability (≥ 0.5) covered by the survey recommendations and the ‘temporal specificity’ as the proportion of survey recommendation time period covering periods of actually high acoustic detectability. We also evaluated the temporal alignment between species-specific high acoustic detectability and the community-scale standard survey methodology for breeding bird surveys in the temperate zone, which comprises the time from sunrise to 4 h after sunrise (Jiguet et al. 2012; Kamp et al. 2021). We categorized the temporal alignment of survey recommendations and species detectability according to the risk of imperfect detection due to sampling at periods of low detectability (Fig. 3).

To evaluate the usefulness of the standard survey protocol at community level, we further analysed hourly detectability of all species relative to sunrise, using the moving average as introduced above. Specifically, we calculated the hourly percentage of species with high detectability (≥ 0.5) for each third of months. Species with short detectability peaks (≤ 2 h) were outlined additionally (Fig. 4). Furthermore, we assessed the hourly dissimilarity in the set of species with high detectability, distinguishing ‘turn-over’ (species exchange) and ‘nestedness’ (gain/loss of species) components of temporal beta-diversity following

Baselga (2010) using the R package *betapart* (Baselga and Orme 2012).

Results

Species-specific vocal activity patterns

Our high-resolution data from PAM revealed distinct diel–seasonal activity patterns of 53 European forest bird species (Fig. 2). Species occupancy, i.e. the presence of a species detected by PAM, ranged from 5 (which was our minimum criterion) to 256 sites. After applying the species-specific thresholds, the number of detections per species ranged from 885 (grey-headed woodpecker *Picus canus*) to 1,029,028 (European Robin *Erithacus rubecula*; Fig. S4). The hierarchical clustering of activity time series revealed four clearly distinct activity types, initially separating a diverse group of diurnal species with peak activity in March/April from three others with very distinct activity patterns, including nocturnal, crepuscular and migratory (diurnal) species (Fig. 5). The first large group of diurnal species could further be separated into species with early spring and mid-spring activity; however, dissimilarity was comparably low here (average linkage height of diurnal species cluster: 0.497, average linkage height of nocturnal, crepuscular and migratory [diurnal peak May] cluster: 0.660, average linkage height of all species: 0.603).

Comparison to expert knowledge-based survey recommendations

Diel activity patterns varied markedly between species, encompassing bimodal, unimodal and uniform distributions with different skewness and kurtosis. Diel patterns changed over the season in many species (species examples in Fig. 6, for figures of all 53 forest bird species see Fig. S5).

Temporal completeness and specificity of the species-specific survey recommendations varied widely across species, encompassing all possible combinations of high and low completeness and specificity (Fig. 7a). The same applied to the standard protocol for breeding bird surveys; however, temporal specificity was generally higher compared to species-specific survey recommendations, except for species with nocturnal and crepuscular activity species which are not covered with by the standard protocol at all (Fig. 7b).

Species-specific survey recommendations demonstrated a critical temporal discrepancy (categories C1 or C2) for

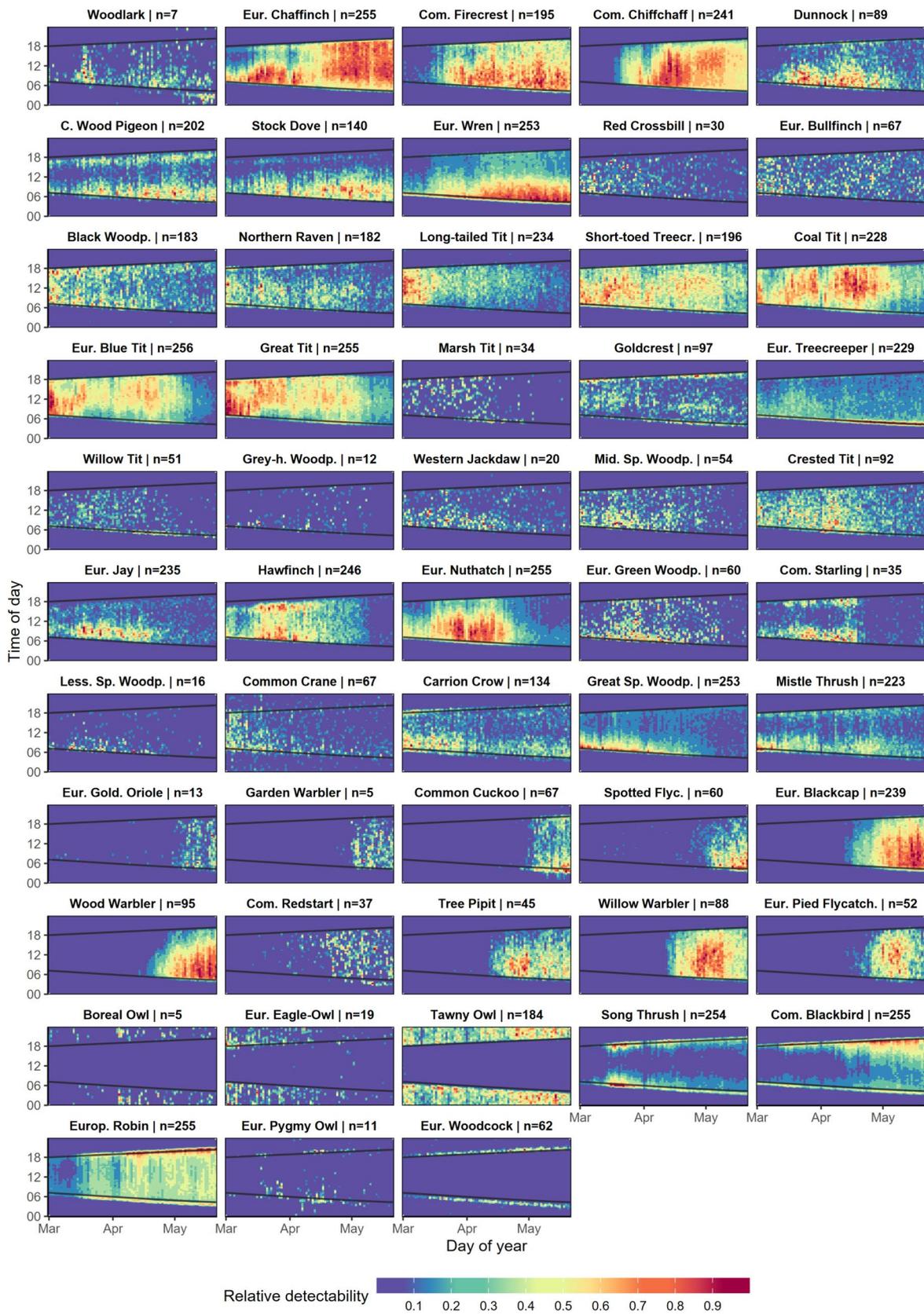


Fig. 2 Diel–seasonal heatmaps of relative acoustic detectability of 53 European forest bird species, sorted according to similarity of activity patterns, revealed by hierarchical clustering (Fig. 5). Relative detectability derived with a moving average approach (cf. methods section) is scaled per species, meaning that relative detectability is 1 at the time when the species was detected at the maximum number of sites simultaneously. Black lines show sunrise and sunset times. n indicates the number of sites included for each species. Time of the day refers to Central European Time (UTC + 1)

64.2% of the species. For 26.4% of the species, species-specific survey recommendations only covered less than 50% of the period of high detectability but were specific (category B), while species-specific survey recommendations were adequately aligned with species detectability for 9.4% of the species (category A). Temporal alignment was generally less critical for the standard protocols with critical discrepancy (categories C1 or C2) for 41.5% of the species. For 32.1% of the species, standard protocols did not reach high completeness but high specificity (category B), while standard protocols were adequately aligned for 26.4% of the species (category A).

The analysis of hourly detectability across species revealed a seasonal pattern. While in the first half of the study period (1st March until 20th April) the percentage of species with high detectability was at maximum in the first 2 h after sunrise and decreased afterwards, the pattern was more constant from end of April onwards (21st April to 20th May) and did not decline strongly beyond 4 h after sunrise (Fig. 4). Hourly dissimilarity also followed a clear pattern with a distinct peak of turnover at sunrise and maximum nestedness before sunrise, here representing a gain of species with high detectability during the dawn phase (Fig. 4).

Regarding the performance of BirdNET throughout the daily cycle, our comparison of BirdNET to a human listener revealed false-negative rates of around 40% for daytime, but close to zero for nighttime on average across species. False-negative rates did not show a seasonal bias (Fig. S3).

Discussion

Our study provides detailed information on vocal activity for 53 European forest bird species, extending our understanding of their diel and seasonal phenology fundamentally. We found a high inter-specific variability of seasonal and diel vocal activity patterns and identified distinct species clusters of vocal activity patterns (i.e. diurnal, nocturnal and crepuscular species) within a European forest bird community. Further, our results provide detailed insights into the acoustic detectability of birds in temperate forests relevant for breeding bird surveys and bird monitoring in general. Our analysis of the temporal alignment between periods of high acoustic detectability and existing expert knowledge-based

survey recommendations revealed temporal mismatches for 64.2% of the species for species-specific recommendation (Südbeck et al. 2005) and 41.5% of the species for standard protocols of breeding bird community surveys (sunrise to 4 h after sunrise), suggesting survey methods for observer-based breeding bird surveys might benefit from adjustment.

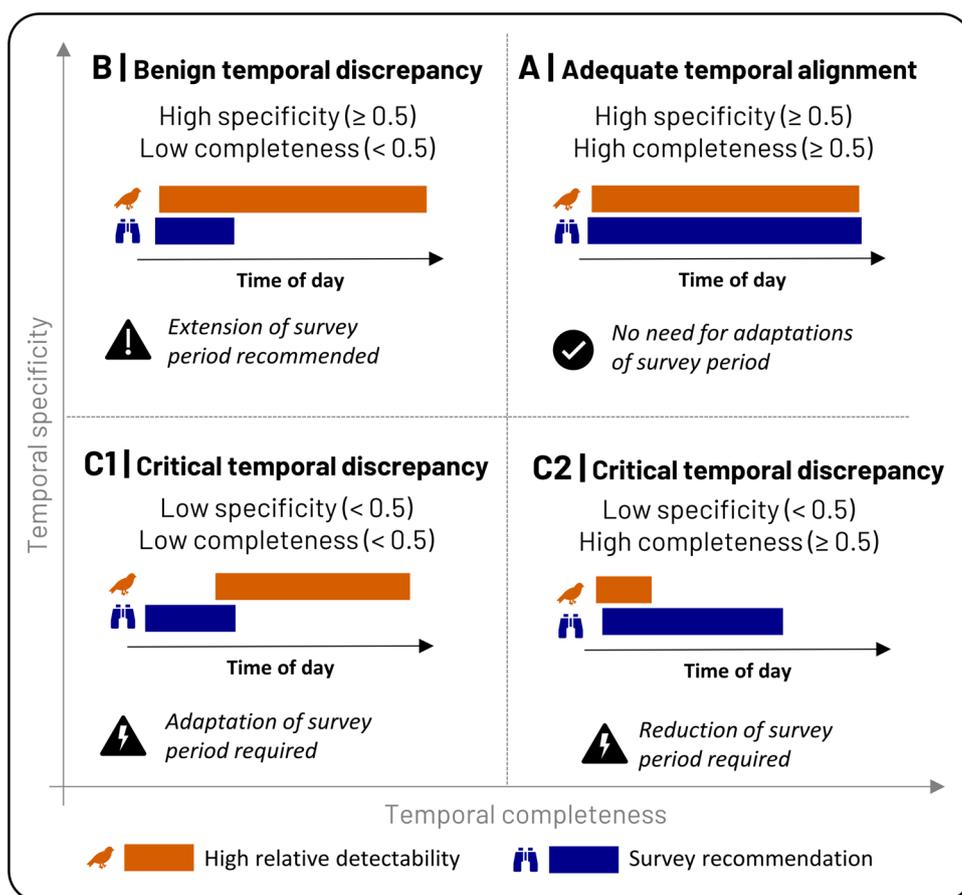
Two-dimensional temporal partitioning of vocal activity

We found strong circular patterns of vocal activity within the European forest bird community along the day–night cycle, encompassing nocturnal, diurnal and crepuscular vocal activity patterns. While the ‘dawn chorus’—a phase of high vocal activity around sunrise—has received much attention in previous studies (Bruni et al. 2014; Gil and Llusia 2020; Puswal et al. 2022), complete diel activity patterns remain poorly studied. Hence, our results provide basic ecological knowledge on diel activity patterns of 53 European forest bird species in the temperate zone and may serve as a valuable baseline for future studies (e.g. studying temporal shifts of activity due to climate change, urbanization or habitat alteration). Even though diel circularity of bird vocal activity is long known (Allen 1913; Robbins 1981; Morelli et al. 2022), our study quantifies fine-scale differences in species acoustic detectability throughout the diel cycle for a comprehensive set of bird species at very high temporal resolution.

Some diel activity patterns might come as a surprise to the experienced bird surveyor. For example, common blackbirds (*Turdus merula*) revealed a distinctly higher activity around dusk compared to dawn, while song thrushes (*Turdus philomelos*) were similarly active in the morning and evening, suggesting that standard surveys focussing on the early-morning hours yield abundance estimates biased low for common blackbirds. Some species like the common cuckoo (*Cuculus canorus*) and woodlark (*Lullula arborea*) revealed partial nocturnality, while tawny owl (*Strix aluco*) demonstrated rather continuous activity throughout the night. Species like common chiffchaff (*Phylloscopus collybita*), Eurasian blue tit (*Cyanistes caeruleus*) or short-toed treecreeper (*Certhia brachydactyla*) were constantly active throughout the day.

We also found a strong seasonal component in the vocal activity patterns during the breeding season. All species within the cluster ‘diurnal–peak May’ (Fig. 5) are mid- to long-distance migratory species and show a negative correlation with detectability of most of the other diurnal species. However, also the other diurnal species reveal a gradual seasonality, with many of the tit species, both treecreeper species and the black woodpecker (*Dryocopus martius*) revealing high detectability at the very beginning of March, while other species like Eurasian chaffinch

Fig. 3 Conceptual visualization of four cases of temporal alignment between high relative detectability of species (as revealed by passive acoustic monitoring) and expert knowledge-based survey recommendations as measured by *temporal specificity* and *temporal completeness* of the survey recommendations



(*Fringilla coelebs*), dunnock (*Prunella modularis*) or the other woodpecker species revealed maximum detectability at the end of March/beginning of April. Such seasonal differentiation of acoustic bird communities is generally well documented (Thompson et al. 2017; Vokurková et al. 2018; Puswal et al. 2022; Wu et al. 2023) and especially driven by seasonal migration (Mason 1995; Krishnan 2019).

The temporal niche partitioning illustrated here is known from activity studies of mammals (Bennie et al. 2014) and is seen as a mechanism that facilitates the coexistence of sympatric species (Frey et al. 2017). Mammals alter their temporal activity patterns to reduce predation risk (Veldhuis et al. 2020). This strategy may also explain the observed crepuscular activity pattern of the Eurasian pygmy owl (*Glaucidium passerinum*), regarded as a strategy to avoid predators such as the larger owl species. However, vocal activity of birds is not a comprehensive measure of all activities that birds do throughout the day (or night), and thus only partly explains overall detectability in surveys. Common blackbirds showed a strong crepuscular pattern in vocal activity (Fig. 2), but diurnal activity can be high and constant as revealed by camera trapping (Schlindwein et al. 2024). Hence, concepts that

may explain temporal activity partitioning of species in camera trapping studies are not directly applicable to vocal activity.

Implications for bird surveys

The analysis of the temporal alignment between periods of high acoustic detectability and species-specific survey recommendations (Südbeck et al. 2005) revealed critical temporal discrepancy for a majority of the studied species. Regarding standard protocols (sampling for 4 h after sunrise), temporal alignment was also critical in many species (41.5%). Even though the resulting imperfect detection is accounted for statistically in a growing number of studies (Kéry and Schmidt 2008; Kellner and Swihart 2014; Strebel et al. 2014), to our knowledge this is rarely done in the context of environmental planning or conservation programmes. Hence, temporal survey optimization through data-based, regularly updated knowledge on temporal patterns of detectability has the potential to increase the accuracy and precision of surveys (Serrurier et al. 2024). Species-specific surveys should be pinpointed to periods with constant high detectability (category A,

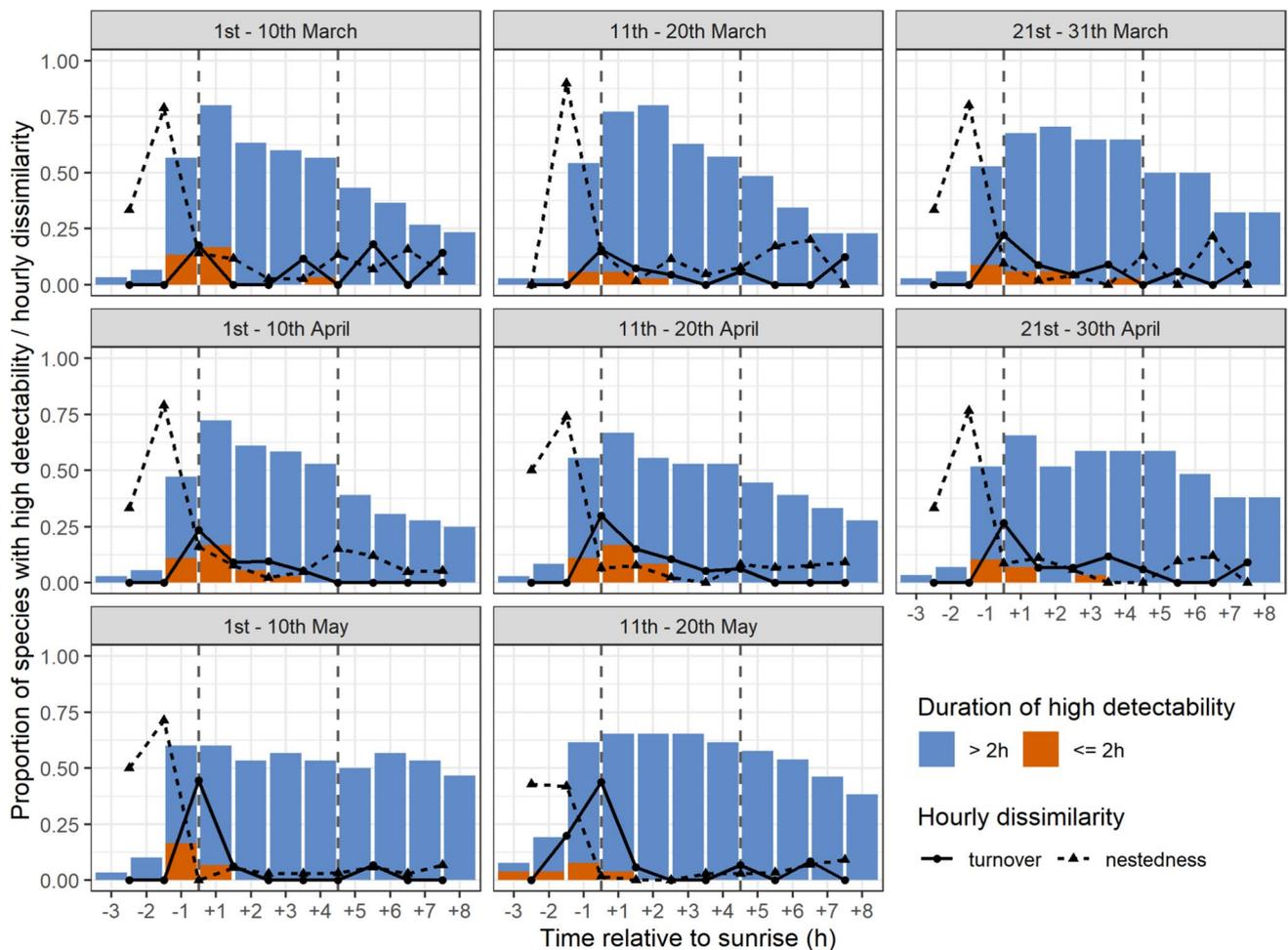


Fig. 4 Percentage of species with high detectability and hourly dissimilarity of the set of species with high detectability, decomposed into turnover (exchange of species) and nestedness (gain/loss of species) (Baselga 2010), in relation to sunrise throughout the breeding season. Panels show month thirds. Percentages of species are calculated in relation to the total number of species per month third.

Dashed vertical lines mark the 4 h after sunrise, which is the standard recommendation for breeding bird monitoring programmes in Europe (Jiguet et al. 2012; Kamp et al. 2021). Species are separated according to the duration of high detectability, outlining species with short period of high detectability in orange and others in blue

Fig. 3), as surveys with low temporal specificity may underestimate absolute population sizes (Tomiałojć and Lontkowski 1989). Even though effects of low specificity on the estimation of relative population trends may be less critical (as the bias is systematic), surveys at periods of low detectability might fail to detect small population change (Wood et al. 2019). Thus, for the 64.2% of species revealing critical discrepancies (categories C1 and C2), we recommend adapting the species-specific survey recommendations to the periods of high detectability. Low temporal completeness, but high specificity (category B) may not critically affect estimations of population sizes or trends for species that are well detectable throughout the whole day; however for species with high detectability limited to short time periods like crepuscular species (e.g. common blackbird, song thrush, Eurasian robin), survey

recommendations should not only be temporally specific, but also temporally complete. For the species of category B an extension of the recommended survey periods to the periods of high detectability would also increase the economic efficiency of field surveys, as observers may stay longer in the field per day and consequently need less survey days to cover a study area.

Optimization of survey timing is feasible in studies or monitoring programmes focussing on single bird species; nevertheless when sampling complete species assemblages, timing of surveys has to be a compromise to cover as many as possible species, or species of interest. It is therefore promising that temporal specificity was generally higher for standard protocols (4 h after sunrise) compared to the species-specific recommendations from Südbeck et al. (2005). However, we still identified a number of rather common species whose detectability

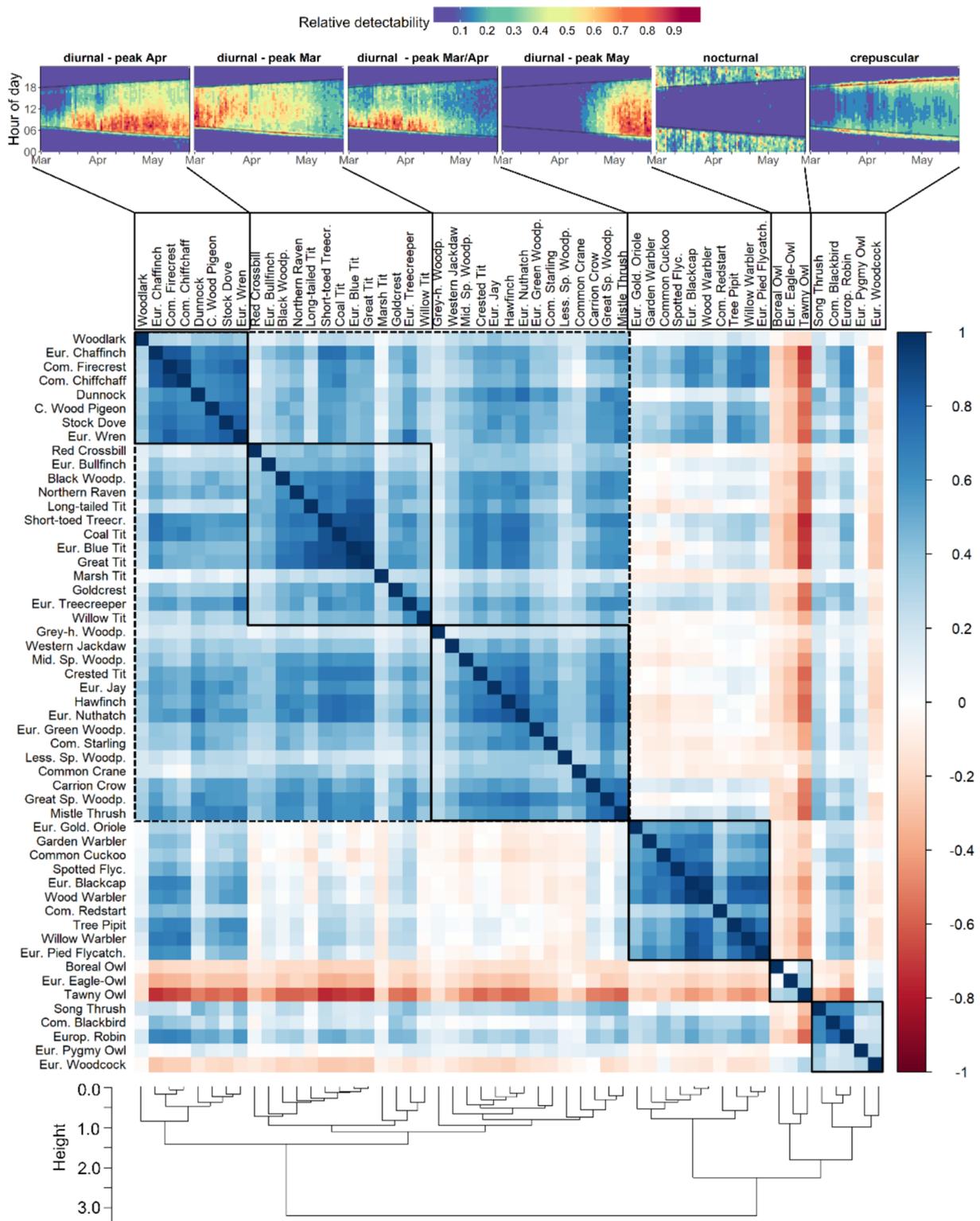


Fig. 5 Time-series correlations (Pearson correlations of the time series shown in Fig. 2) between the relative detectability of species. Rectangles show six clusters of species with similar activity patterns.

Top panels show averaged diel-seasonal vocal activity heatmaps (cf. Fig. 2) per cluster, bottom dendrogram shows the results of the agglomerative hierarchical clustering (see Methods for details)

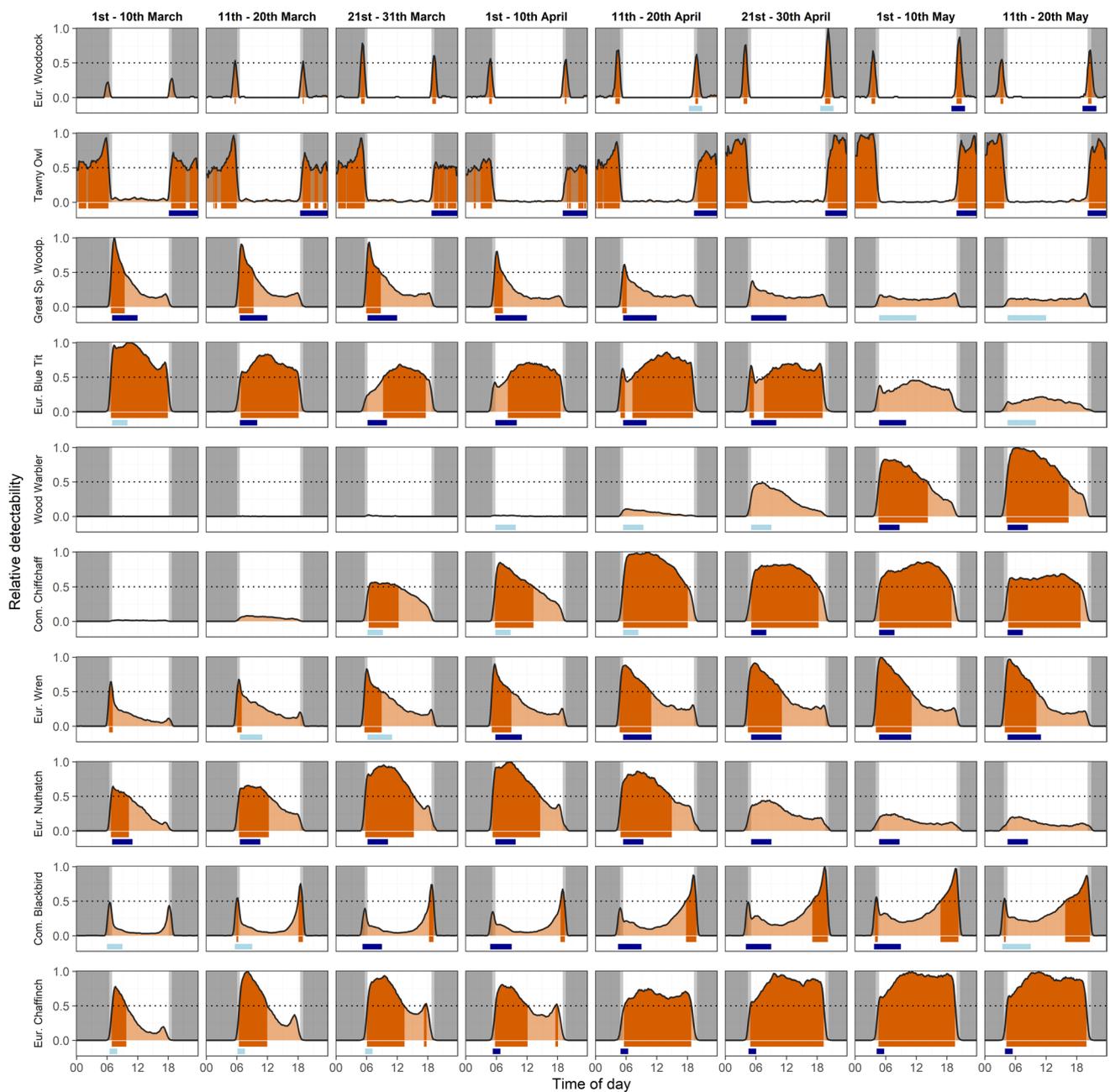


Fig. 6 Diel activity patterns of selected bird species per third of month including at least one example species per cluster (Fig. 5). Activity was standardized to one per species; hence a value of 1 means that a species was detected at the maximum number of sites simultaneously at that time. Figures for all 53 species can be found in the Appendix (Fig. S5). Dark blue bars mark the expert knowledge-based temporal survey recommendations from Südbeck et al. (2005),

while light blue bars mark their extended survey recommendations. The dashed line marks a relative detectability of 0.5, a threshold that defines high detectability. Times of the day with high detectability are marked in dark orange, and times of the day with low detectability are marked in light orange. Nighttimes are marked in grey, and the time between civil dawn and sunset/civil dusk and sunset with a lighter grey. Time of the day refers to Central European Time (UTC + 1)

revealed a critical mismatch with the standard protocol used in monitoring programmes of common breeding birds. As the peak of turnover in the set of species with high detectability at sunrise demonstrates (Fig. 4), sunrise is a critical turning point regarding the detectability of species. Also the detectability of

the species with a short phase of high detectability accumulates around sunrise (Fig. 4), demonstrating crucial importance of the 2 h around sunrise for sampling critical species at high detectability. It is common sense to conduct extra surveys for nocturnal species in territory mapping (Südbeck et al. 2005);

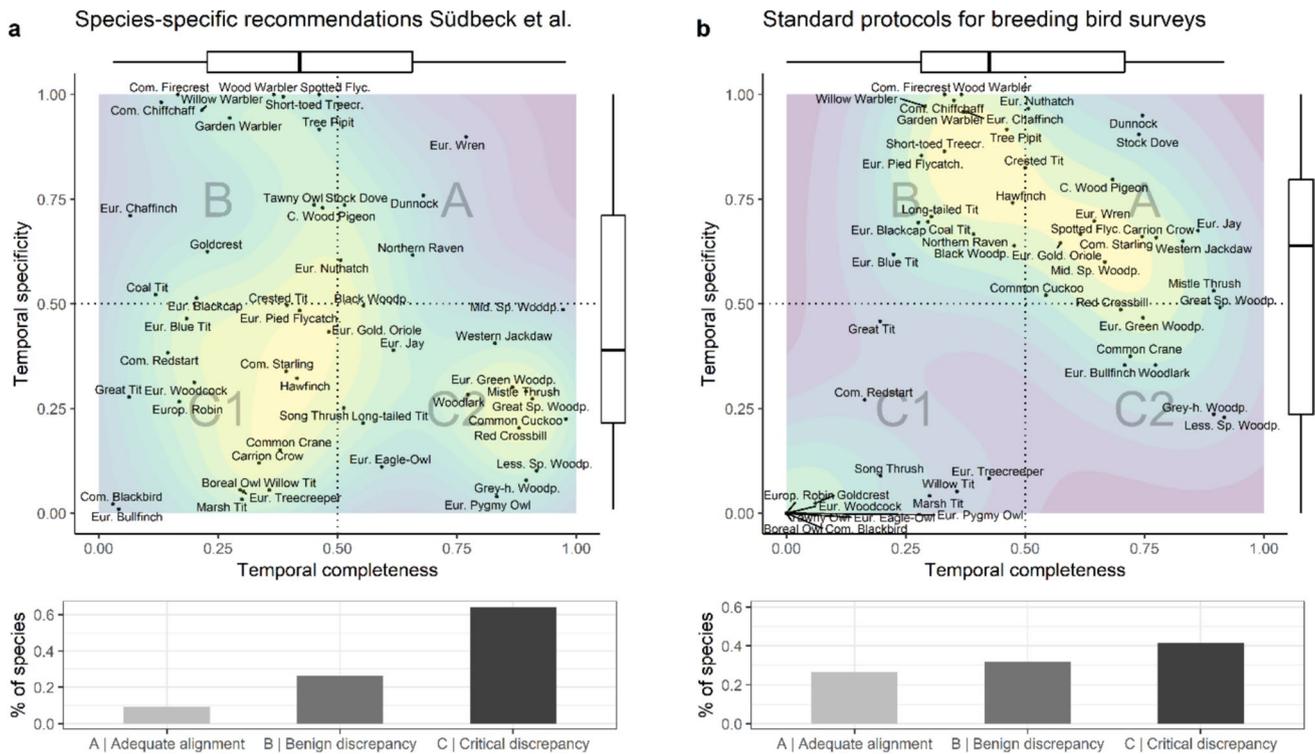


Fig. 7 Temporal alignment of **a** species-specific survey recommendations (Südbeck et al. 2005) and **b** standard protocols for breeding bird surveys in Europe (first 4 h after sunrise; e.g. Jiguet et al. 2012; Kamp et al. 2021) with time periods of high relative species detectability (≥ 0.5) as indicated by passive acoustic monitoring, expressed as temporal specificity and completeness between the survey recommendations/standard protocol and species activity measured by PAM.

A: Adequate temporal alignment, B: benign temporal alignment, C1: critical temporal alignment with low specificity and completeness, C2: critical temporal alignment with low specificity but high completeness (see also Fig. 3). Background colour scale outlines the density of species. Detailed values for all species are given in Table S1 and a summary in Table S2

however, the magnitude of changes in detectability of species with high detectability around sunrise has not been considered in the standard protocols yet (Jiguet et al. 2012; Kamp et al. 2021). Regarding our results, standard protocols for common breeding bird monitoring should optimally include an extra sampling with focus on a limited set of species (e.g. common blackbird, European robin, goldcrest *Regulus regulus*, lesser spotted woodpecker *Dryobates minor*, Eurasian treecreeper *Certhia familiaris*, willow tit *Poecile montanus*) starting 1 h before sunrise. As the species set with high detectability remains rather constant throughout the morning (Fig. 4), the standard round of sampling may follow, starting 1 h after sunrise. Contrary to our expectation, the detectability of species declined more pronounced throughout the day in March and April, but stayed rather constant throughout the day at the end of April and May (Fig. 4). Hence surveys in temporal forests

may be extended beyond 4 h after sunrise from end of April onwards. Optimally common blackbirds, as one of the most common bird species, would be surveyed in a specific sampling in the evening shortly before sunset.

Synergies of acoustic and observer-based surveys

Species-specific surveys as well as standard survey protocols should be designed in a way that suggests surveying in periods of the highest high acoustic detectability of species. Nevertheless, adaptations face logistical restrictions in observer-based real-world surveys. Therefore, combining observer-based surveys with PAM can leverage the strengths of both methods. Substantial synergistic

potential lies in the targeted use of PAM at certain locations within a study area in addition to territory mapping, to increase the detectability of rare species or species of low detectability, and to gauge diel and seasonal detectability that might vary with region and year (Baroni et al. 2023; Gaylord et al. 2023). PAM is particularly beneficial for sampling forest bird species with short phases of high detectability (e.g. Eurasian woodcock *Scolopax rusticola*, common blackbird, Eurasian treecreeper, willow tit, Eurasian pygmy owl) as well as crepuscular species in other habitats (e.g. grey partridge *Perdix perdix* in agricultural landscapes). Furthermore, observer-based playback surveys are the proposed method to survey e.g. woodpeckers or owls due to their low spontaneous vocalization rates (Südbeck et al. 2005). However, playback of songs or even alarm calls can induce unnecessary stress for birds and may lead to an overestimation of population size due to the attraction effects; hence, using PAM to study species with low vocalization rates should be preferred over playback surveys whenever feasible.

Implications for schedules of PAM

As our results demonstrated, temporal patterns within temperate acoustic bird communities are diverse and encompass distinct seasonal and diel activity peaks. Hence, in PAM continuous recording schedules without limitation to certain times of the day are worth the effort, as the periods of highest detectability of all occurring species are included. As our results recorded with a schedule of 5% temporal coverage—recording for 30 s every 10 min—demonstrate, this does not imply a necessity for continuous full-time recordings, but rather suggests that audio samples should be evenly distributed across the 24-h cycle to optimally capture all species present. Studying activity patterns of 12 subtropical montane forest bird species, Wu et al. (2023) also found that short, but regularly distributed recordings closely resembled the activity patterns observed in continuous recordings. Similar findings were made for a tropical bird community, where species richness accumulated more rapidly with short audio samples recorded at high temporal resolution (Metcalf et al. 2022). However, previous PAM studies focussing on birds often used unevenly distributed recording schedules, often focussing on the dawn period (Sugai et al. 2019). Generally, terrestrial soundscape studies were found to have the lowest coverage of the complete diel cycle compared to aquatic or marine studies (Darras et al. 2025). With recent technological developments, it

becomes achievable to record audio data at high temporal resolution schedules or even with constant recoding, as autonomous recording units are energy efficient (Hill et al. 2018) and species classification algorithms are fast (Kahl et al. 2021).

Limitations and future perspectives

Despite the advantages of PAM to study vocal activity patterns, there are still methodological limitations and questions to address in future studies: do species detection algorithms perform constantly throughout the daily cycle or is there e.g. a reduced detectability of certain species within acoustically complex soundscapes during the dawn chorus? How do weather conditions shape vocal activity patterns? How pronounced is inter-annual variability of vocal activity patterns? Furthermore, BirdNET currently does not differentiate between calls and songs. However, as different types of vocalizations have different ecological functions (Gill and Bierema 2013; Gil and Llusia 2020), they might also vary over the day, e.g. depending on the activity patterns of predators. Recent developments of BirdNET and other algorithms will allow to differentiate songs and calls soon (McGinn et al. 2023). More broadly, research on PAM should focus on understanding how species-specific activity patterns relate to habitat use. For example, determining which activity patterns indicate breeding activity in different species.

Regarding the performance of BirdNET, our comparison of BirdNET to a human listener demonstrated rather high false-negative rates of BirdNET during daytime, but low false-negative rates at night (Fig. S3). We conclude that neither daytime nor season significantly biases the performance of BirdNET, making the vocal activity patterns derived from BirdNET ecologically meaningful. As the majority of species is either diurnal or nocturnal, the difference in false-negative rate between day and night should not bias the activity patterns within a single species. Regarding crepuscular species, our results showed that false-negative rates within the hour before sunrise are comparable to daytime while false-negative rates are lower in the hour after sunset. Hence, the vocal activity of some species after sunrise may be slightly overestimated compared to their daytime activity (Fig. S3). Nevertheless, more research is needed to better understand the performance of BirdNET under spatially and temporarily varying composition of acoustic bird assemblages. Our study was limited to forest sites; however, vocal activity patterns may differ between different habitat types. Thus, future work should gather comparable high-resolution acoustic

data in other habitat types, e.g. urban or agricultural areas. Species-specific activity patterns may also differ with habitat. Also for some of the rare forest species, our data is still limited as only a few of the study sites were occupied. Hence, targeted sampling for species like boreal owl (*Aegolius funereus*), Eurasian pygmy owl or grey-headed woodpecker would improve the reliability of the described vocal activity patterns.

Furthermore, our study was limited to the months March to May; however, the breeding season of some species extends beyond this period. Vocal activity peaks of some early species may have been missed as we did not cover February. Also vocal activity peaks of some late migratory species may not have been covered by our study period, so peaks of vocal detectability may not represent the full year activity peak for some species. However, as our results reveal, the study period fitted well to the vocal activity peaks of the majority of the studied species.

Year-specific weather conditions may also influence relative vocal activity patterns. Our data spans three different years, averaging out some of these effects. However, in our primary study years, 2022 and 2023, temperatures tended to be above average in the second half of March but below average at the beginning of April (Fig. S6). Since bird vocal activity can be influenced by temperature to some extent (Strauß et al. 2020; Pérez-Granados et al. 2021), the observed vocal activity patterns may deviate from long-term averages. Therefore, we recommend including additional study years in future studies to better account for year-specific variations.

Sampling the complete annual cycle would reveal further interesting vocal activity patterns throughout the year, even before and after the breeding season. Hence, future work could even dive deeper into temporal patterns of song and call behaviour of bird species assemblages across habitats and throughout the year. Large potential lies within global cooperation of soundscape ecologists for future meta-analyses (Darras et al. 2025).

Apart from identifying temporal variation in vocal activity, anthropogenic impacts on diel-seasonal acoustic activity patterns including noise pollution, artificial light at night and climate change could be studied in future PAM studies. Anthropogenic noise and artificial light at night are both known to interfere with bird vocal activity (Fuller et al. 2007; Kempenaers et al. 2010; Dominoni et al. 2016; Cretois et al. 2024), while climate change can cause phenological shifts of vocal activity. However, cumulative effects and interactions of anthropogenic impacts on vocal activity patterns throughout the year remain unknown. PAM has proven to serve as a valuable tool for such studies (Balantic and Donovan 2019; Roark and Gaul 2021).

Conclusions

We were able to gain fundamental insights into the diverse vocal activity patterns within the European forest bird community. Our comparison of these patterns to the expert-based survey recommendations and standard protocols for breeding bird surveys revealed a critical temporal mismatch between high vocal activity and the recommended survey timing for a large proportion of species. Species-specific survey recommendations and possibly also the standard protocols should be re-evaluated to enhance the accuracy and precision of bird surveys. Beyond adjustments to survey timing, it is crucial to raise awareness among ornithologists about the variability of acoustic detectability across temporal bird communities and the implications for the interpretations of breeding bird surveys.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-025-02307-y>.

Acknowledgements We thank the team from the Forest Nature Conservation Department of the Northwest German Forest Research Institute for conducting the fieldwork: G. Brauer, O. Henning, A. König, A. Lindner, K. Lorenz, N. Mosel, J. Milch, A. Nehrkorn, S. Nitzschke, C. Rachow, J. Wellhäuser, K. Werner and S. Wiehemeyer. We thank the Lower Saxony Ministry of Food, Agriculture and Consumer Protection for the financial support (Stadt.Land.ZUKUNFT) and the Niedersächsische Landesforsten for supporting the study within their forests. We also thank three reviewers and the subject editor for their valuable and constructive comments on an earlier version of this paper. We acknowledge support by the Open Access Publication Funds/transformation agreements of the Northwest German Forest Research Institute.

Author contributions David Singer: conceptualization, data curation, methodology, formal analysis, writing—original draft, project administration; Johannes Kamp: writing—review and editing, supervision; Hermann Hondong: writing—review and editing; Andreas Schuldt: writing—review and editing, supervision; Jonas Hagge: conceptualization, writing—review and editing, project administration.

Funding Open Access funding enabled and organized by Projekt DEAL.

Data availability Data are available on email request to the corresponding author.

Declarations

Conflict of interest The authors declare no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not

permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Allen FH (1913) More notes on the morning awakening. *Auk* 30:229–235. <https://doi.org/10.2307/4071548>
- Balantic C, Donovan T (2019) Temporally adaptive acoustic sampling to maximize detection across a suite of focal wildlife species. *Ecol Evol* 9:10582–10600. <https://doi.org/10.1002/ece3.5579>
- Baroni D, Hanzelka J, Raimondi T et al (2023) Passive acoustic survey reveals the abundance of a low-density predator and its dependency on mature forests. *Landscape Ecol* 38:1939–1954. <https://doi.org/10.1007/s10980-023-01667-1>
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Glob Ecol Biogeogr* 19:134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga A, Orme CDL (2012) betapart: an R package for the study of beta diversity. *Methods Ecol Evol* 3:808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Bates JM, Fidino M, Nowak-Boyd L et al (2023) Climate change affects bird nesting phenology: comparing contemporary field and historical museum nesting records. *J Anim Ecol* 92:263–272. <https://doi.org/10.1111/1365-2656.13683>
- Bennie JJ, Duffy JP, Inger R, Gaston KJ (2014) Biogeography of time partitioning in mammals. *Proc Natl Acad Sci* 111:13727–13732. <https://doi.org/10.1073/pnas.1216063110>
- Bibby CJ, Burgess ND, Hill DA (1992) *Bird census techniques*. San Diego Academic Press, London
- Brewster JP, Simons TR (2009) Testing the importance of auditory detections in avian point counts. *J Field Ornithol* 80:178–182. <https://doi.org/10.1111/j.1557-9263.2009.00220.x>
- Bruni A, Mennill DJ, Foote JR (2014) Dawn chorus start time variation in a temperate bird community: relationships with seasonality, weather, and ambient light. *J Ornithol* 155:877–890. <https://doi.org/10.1007/s10336-014-1071-7>
- Catchpole C, Slater PJB (2008) *Bird song: biological themes and variations*, 2nd edn. Cambridge University Press, Cambridge, New York
- Cretois B, Bick IA, Balantic C et al (2024) Snowmobile noise alters bird vocalization patterns during winter and pre-breeding season. *J Appl Ecol* 61:340–350. <https://doi.org/10.1111/1365-2664.14564>
- Darras KFA, Rountree RA, Van Wilgenburg SL et al (2025) Worldwide soundscapes: a synthesis of passive acoustic monitoring across realms. *Glob Ecol Biogeogr* 34:e70021. <https://doi.org/10.1111/geb.70021>
- Day J, Baker J, Schofield H et al (2015) Part-night lighting: implications for bat conservation: part-night lighting and bats. *Anim Conserv* 18:512–516. <https://doi.org/10.1111/acv.12200>
- Dominoni DM, Greif S, Nemeth E, Brumm H (2016) Airport noise predicts song timing of European birds. *Ecol Evol* 6:6151–6159. <https://doi.org/10.1002/ece3.2357>
- DWD (2025) Climate observation data. Open Data Server
- Flade M (1994) *Die Brutvogelgemeinschaften Mittel- und Norddeutschlands: Grundlagen für den Gebrauch vogelkundlicher Daten in der Landschaftsplanung*. IHW-Verlag, Eching
- Frey S, Fisher JT, Burton AC, Volpe JP (2017) Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sens Ecol Conservation* 3:123–132. <https://doi.org/10.1002/rse2.60>
- Fuller RA, Warren PH, Gaston KJ (2007) Daytime noise predicts nocturnal singing in urban robins. *Biol Lett* 3:368–370. <https://doi.org/10.1098/rsbl.2007.0134>
- Funosas D, Barbaro L, Schillé L et al (2024) Assessing the potential of BirdNET to infer European bird communities from large-scale ecoacoustic data. *Ecol Ind* 164:112146. <https://doi.org/10.1016/j.ecolind.2024.112146>
- Gaylord M, Duarte A, McComb B, Ratliff J (2023) Passive acoustic recorders increase White-headed Woodpecker detectability in the Blue Mountains. *J Field Ornithol* 94:art1. <https://doi.org/10.5751/JFO-00330-940401>
- Gibb R, Browning E, Glover-Kapfer P, Jones KE (2019) Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods Ecol Evol* 10:169–185. <https://doi.org/10.1111/2041-210X.13101>
- Gil D, Llusia D (2020) The bird dawn chorus revisited. In: Aubin T, Mathevon N (eds) *Coding strategies in vertebrate acoustic communication*. Springer International Publishing, Cham, pp 45–90
- Gill SA, Bierema AM-K (2013) On the meaning of alarm calls: a review of functional reference in avian alarm calling. *Ethology* 119:449–461. <https://doi.org/10.1111/eth.12097>
- Greenwood JJD, Baillie SR, Gregory RD et al (1994) Some new approaches to conservation monitoring of British breeding birds. *Ibis* 137:S16–S28. <https://doi.org/10.1111/j.1474-919X.1995.tb08437.x>
- Hertzog LR, Frank C, Klimek S et al (2021) Model-based integration of citizen science data from disparate sources increases the precision of bird population trends. *Diversity Distributions* 27:1106–1119. <https://doi.org/10.1111/ddi.13259>
- Hill AP, Prince P, Piña Covarrubias E et al (2018) AudioMoth: evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods Ecol Evol* 9:1199–1211. <https://doi.org/10.1111/2041-210X.12955>
- Hollén LI, Radford AN (2009) The development of alarm call behaviour in mammals and birds. *Anim Behav* 78:791–800. <https://doi.org/10.1016/j.anbehav.2009.07.021>
- Jiguet F, Devictor V, Julliard R, Couvet D (2012) French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. *Acta Oecologica* 44:58–66. <https://doi.org/10.1016/j.actao.2011.05.003>
- Kahl S, Wood CM, Eibl M, Klinck H (2021) BirdNET: a deep learning solution for avian diversity monitoring. *Eco Inform* 61:101236. <https://doi.org/10.1016/j.ecoinf.2021.101236>
- Kamp J, Frank C, Trautmann S et al (2021) Population trends of common breeding birds in Germany 1990–2018. *J Ornithol* 162:1–15. <https://doi.org/10.1007/s10336-020-01830-4>
- Kellner KF, Swihart RK (2014) Accounting for imperfect detection in ecology: a quantitative review. *PLOS ONE* 9:e111436. <https://doi.org/10.1371/journal.pone.0111436>
- Kempnaers B, Borgström P, Loës P et al (2010) Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Curr Biol* 20:1735–1739. <https://doi.org/10.1016/j.cub.2010.08.028>
- Kershenbaum A, Blumstein DT, Roch MA et al (2016) Acoustic sequences in non-human animals: a tutorial review and prospectus. *Biol Rev* 91:13–52. <https://doi.org/10.1111/brv.12160>
- Kéry M, Schmidt B (2008) Imperfect detection and its consequences for monitoring for conservation. *Community Ecol* 9:207–216. <https://doi.org/10.1556/ComEc.9.2008.2.10>
- Krause B, Farina A (2016) Using ecoacoustic methods to survey the impacts of climate change on biodiversity. *Biol Cons* 195:245–254. <https://doi.org/10.1016/j.biocon.2016.01.013>

- Krishnan A (2019) Acoustic community structure and seasonal turnover in tropical South Asian birds. *Behav Ecol* 30:1364–1374. <https://doi.org/10.1093/beheco/arz087>
- Lellouch L, Pavoine S, Jiguet F et al (2014) Monitoring temporal change of bird communities with dissimilarity acoustic indices. *Methods Ecol Evol* 5:495–505. <https://doi.org/10.1111/2041-210X.12178>
- Mariton L, Le Viol I, Bas Y, Kerbiriou C (2023) Characterising diel activity patterns to design conservation measures: case study of European bat species. *Biol Cons* 277:109852. <https://doi.org/10.1016/j.biocon.2022.109852>
- Mason CF (1995) Long-term trends in the arrival dates of spring migrants. *Bird Study* 42:182–189. <https://doi.org/10.1080/00063659509477167>
- McGinn K, Kahl S, Peery MZ et al (2023) Feature embeddings from the BirdNET algorithm provide insights into avian ecology. *Eco Inform* 74:101995. <https://doi.org/10.1016/j.ecoinf.2023.101995>
- Metcalf OC, Barlow J, Marsden S, et al (2022) Optimizing tropical forest bird surveys using passive acoustic monitoring and high temporal resolution sampling. *Remote Sens Ecol Conserv* 8:45–56. <https://doi.org/10.1002/rse2.227>
- Morelli F, Brlík V, Benedetti Y et al (2022) Detection rate of bird species and what it depends on: tips for field surveys. *Front Ecol Evol* 9:671492. <https://doi.org/10.3389/fevo.2021.671492>
- Pérez-Granados C, Schuchmann K-L, Marques MI (2021) Vocal activity of the Ferruginous Pygmy-owl (*Glaucidium brasilianum*) is strongly correlated with moon phase and nocturnal temperature. *Ethol Ecol Evol* 33:62–72. <https://doi.org/10.1080/03949370.2020.1820582>
- Pebesma E (2018) Simple features for R: standardized support for spatial vector data. *The R J* 10:439. <https://doi.org/10.32614/RJ-2018-009>
- Puswal SM, Mei J, Wang M, Liu F (2022) Daily and seasonal patterns in the singing activity of birds in East China. *Ardea* 110. <https://doi.org/10.5253/arde.v110i1.a4>
- Roark E, Gaul W (2021) Monitoring migration timing in remote habitats: assessing the value of extended duration audio recording. *Avian Conserv Ecol* 16:21. <https://doi.org/10.5751/ACE-01885-160121>
- Robbins CS (1981) Effect of time of day on bird activity. *Stud Avian Biol* 6:275–286
- Romano A, Garamszegi LZ, Rubolini D, Ambrosini R (2023) Temporal shifts in avian phenology across the circannual cycle in a rapidly changing climate: a global meta-analysis. *Ecol Monogr* 93:e1552. <https://doi.org/10.1002/ecm.1552>
- Rosenthal GG, Ryan MJ (2000) Visual and acoustic communication in non-human animals: a comparison. *J Biosci* 25:285–290. <https://doi.org/10.1007/BF02703937>
- Rubolini D, Møller AP, Rainio K, Lehikoinen E (2007) Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Climate Res* 35:135–146. <https://doi.org/10.3354/cr00720>
- Sauer JR, Pardieck KL, Ziolkowski DJ et al (2017) The first 50 years of the North American Breeding Bird Survey. *The Condor* 119:576–593. <https://doi.org/10.1650/CONDOR-17-83.1>
- Sch lindwein X, Randler C, Kalb N et al (2024) Seasonal variation in the diurnal activity pattern of Eurasian Blackbirds (*Turdus merula*) in the forest. *J Ornithol* 165:137–146. <https://doi.org/10.1007/s10336-023-02096-2>
- Serrurier A, Zdroik P, Isler R et al (2024) Mountain is calling – decrypting the vocal phenology of an alpine bird species using passive acoustic monitoring. *Ibis* 166:1338–1353. <https://doi.org/10.1111/ibi.13314>
- Singer D, Hagge J, Kamp J et al (2024) Aggregated time-series features boost species-specific differentiation of true and false positives in passive acoustic monitoring of bird assemblages. *Remote Sens Ecol Conserv* 10:517–530. <https://doi.org/10.1002/rse2.385>
- Singer D, Hagge J, Engel F et al (2025) Biodiversitätsmonitoring in Wäldern mit natürlicher Entwicklung – Monitoringkonzept für den Landeswald in Niedersachsen. Hessen, Sachsen-Anhalt und Schleswig-Holstein. <https://doi.org/10.5281/zenodo.14535159>
- Strauß AFT, Hutfluss A, Dingemanse NJ (2020) Great Tits responding to territorial intrusions sing less but alarm more on colder days. *Ethology* 126:445–454. <https://doi.org/10.1111/eth.12989>
- Strebel N, Kéry M, Schaub M, Schmid H (2014) Studying phenology by flexible modelling of seasonal detectability peaks. *Methods Ecol Evol* 5:483–490. <https://doi.org/10.1111/2041-210X.12175>
- Südbeck P, Andretzke S, Fischer S et al (2005) Methodenstandards zur Erfassung der Brutvögel Deutschlands, 1st edn. Mugler, Radolfzell
- Sugai LSM, Silva TSF, Ribeiro JW, Llusia D (2019) Terrestrial passive acoustic monitoring: review and perspectives. *Bioscience* 69:15–25. <https://doi.org/10.1093/biosci/biy147>
- Sullivan BL, Wood CL, Iliff MJ et al (2009) eBird: a citizen-based bird observation network in the biological sciences. *Biol Cons* 142:2282–2292. <https://doi.org/10.1016/j.biocon.2009.05.006>
- Thieurmel B, Elmarhraoui A (2022) sunalc: compute sun position, sunlight phases, moon position and lunar phase. R package version 0.5.1. <https://CRAN.R-project.org/package=suncalc>
- Thompson SJ, Handel CM, Mcnew LB (2017) Autonomous acoustic recorders reveal complex patterns in avian detection probability. *J Wildl Manag* 81:1228–1241. <https://doi.org/10.1002/jwmg.21285>
- Tomiałojć L, Lontkowski J (1989) A technique for censusing territorial song thrushes *Turdus philomelos*. *Ann Zool Fenn* 26:235–244
- Veldhuis MP, Hofmeester TR, Balme G et al (2020) Predation risk constrains herbivores' adaptive capacity to warming. *Nat Ecol Evol* 4:1069–1074. <https://doi.org/10.1038/s41559-020-1218-2>
- Vokurková J, Motombi FN, Ferenc M et al (2018) Seasonality of vocal activity of a bird community in an Afrotropical lowland rain forest. *J Trop Ecol* 34:53–64. <https://doi.org/10.1017/S0266467418000056>
- Warren Liao T (2005) Clustering of time series data—a survey. *Pattern Recogn* 38:1857–1874. <https://doi.org/10.1016/j.patcog.2005.01.025>
- Wei T, Simko V (2021) R package “corrplot”: Visualization of a correlation matrix. R package version 0.95. <https://github.com/taiyun/corrplot>
- Wickham H (2016) ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York
- Wood CM, Popescu VD, Klinck H et al (2019) Detecting small changes in populations at landscape scales: a bioacoustic site-occupancy framework. *Ecol Ind* 98:492–507. <https://doi.org/10.1016/j.ecoli.2018.11.018>
- Wu S-H, Ko JC-J, Lin R-S et al (2023) Evaluating community-wide temporal sampling in passive acoustic monitoring: a comprehensive study of avian vocal patterns in subtropical montane forests. *F1000Research* 12:1299. <https://doi.org/10.12688/f1000research.141951.1>
- Zimmer C (1919) Der Beginn des Vogelgesanges in der Frühdämmerung. *Verhandlungen der Ornithologischen Gesellschaft in Bayern* 14:152–180

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.