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Acoustic Monitoring Enables Multi-Taxa Conservation Assessment and Prioritisation Over Large Scales and for Rare and Cryptic Species

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ABSTRACT

Aim: To combat the global biodiversity crisis, robust and scalable data are needed to target, monitor and evaluate conservation efforts, particularly in data-poor regions and for cryptic taxa. Passive acoustic monitoring (PAM) has the potential to provide solutions, but real-world examples are still rare. We demonstrate how PAM data can be used to rapidly and effectively map distributions of multiple taxa over large scales, in data-poor regions. We show how these data can be used to assess the importance of existing protected areas and prioritise future conservation efforts, including for rare and cryptic species often neglected in such assessments.

Location: Global with a case study from Polesia, Eastern Europe.

Time Period: Present.

Major Taxa Studied: Bats, Birds, Small mammals and Bush crickets.

Methods: Using machine-learning and manual verification, we identified bats, nocturnally active birds, small mammals and bush crickets from over 34,000 monitoring hours at 506 sites in the Polesia region of Belarus and Ukraine. Using multi-species generalised mixed models in a Bayesian framework, we then predicted occupancy and acoustic activity for these species and their associations with protected areas, over a 151,000 km² project area. We identified areas of high conservation priority as measured by species richness and/or importance for globally or regionally threatened species.

Main Conclusions: Our approach provides a roadmap for collecting and processing large-scale, multi-taxa biodiversity data using passive acoustic monitoring. In our case study region, we show that although existing protected areas contain a relatively large proportion of high conservation priority areas, there are significant gaps in the protected area network. We also show low surrogacy of areas of high conservation priority between taxa at fine scales, but did at larger scales, showing the importance of multi-taxa monitoring to prioritise protected areas that conserve a wide variety of species.

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1 | Introduction

The global biodiversity crisis necessitates effective, scalable and data-driven conservation efforts, which are particularly challenging for difficult-to-monitor or poorly studied taxa, and in regions with limited available data (McCord et al. 2021). Lack of data are especially pertinent for nocturnal, elusive and cryptic species, which can be heavily impacted by anthropogenic change, but where traditional monitoring techniques are difficult to implement effectively, particularly across broad spatial scales. These species are therefore frequently neglected when implementing evidence-based conservation efforts. The same problems occur for the monitoring of threatened and endangered species, which by definition are often rare; thus effective monitoring typically requires huge amounts of survey effort, which is unsustainable for large-scale conservation initiatives.

Methods to collect data on a broad range of taxa, including poorly surveyed species, are needed to properly target or assess conservation efforts, as relationships that hold for single species or species groups often do not extend to wider taxonomies (Yong et al. 2018). However, traditional surveys for multiple taxonomic groups are both logistically and technically challenging, often leading to conservation efforts based on data for a limited set of species. This is particularly so in remote or data-poor regions that do not have large standardised national monitoring schemes and have limited resources to collect data and conduct monitoring. These regions are often of the highest conservation value and vulnerable to damaging environmental pressures including anthropogenic disturbance and harvesting, climate and land cover change (Hochkirch et al. 2021).

Passive acoustic monitoring (PAM) has emerged as a promising tool to collect data on both cryptic and nocturnal species, as well as a wide range of other species across expansive areas (Ross et al. 2023; Sugai et al. 2019). PAM has the ability to detect nocturnal animals such as echolocating bats, nocturnal birds, stridulating insects and small mammals, which are often neglected in large-scale monitoring due to the difficulty and expense in surveying them (Newson et al. 2017; Middleton et al. 2023). PAM also has the potential to provide rapid, systematic data collection over large geographic regions, due to the automated nature of data collection and the ability of non-specialists to collect data. This could address the immediate need for biodiversity data at the onset of conservation and restoration projects, where prioritisation of efforts and project monitoring are critical (Sutherland et al. 2004). An advantage of PAM is the capacity to survey multiple taxonomic groups simultaneously. This multi-taxa approach could be a powerful tool in regions where systematic biodiversity data collection is lacking, offering the potential to prioritise conservation efforts and evaluate their impact across a diverse array of taxonomic groups.

While the potential of acoustic monitoring for multi-taxa surveys has been recognised, to our knowledge, there are currently no published works using large-scale, multi-taxa data sets from PAM to prioritise conservation efforts at landscape scales. Limitations in the use of PAM are perhaps due to the

lack of knowledge of how to collect, process and analyse such datasets and that the development of automated data processing has only recently become sufficiently scalable. This includes the complexities of developing machine learning classifiers for multiple taxonomic groups, the scarcity of labelled training data and the time and expertise required for manual examination of recordings featuring multiple species (Müller et al. 2023). Typically, during targeted PAM for single taxonomic groups, many biological sounds from non-target groups are captured within recordings but are often discarded during analytical pipelines (Newson et al. 2017). This overlooks the opportunity to gather valuable data, particularly in regions where comprehensive survey data for certain species groups is absent or limited.

Multi-taxa analysis has generally been limited to soundscape analyses, where acoustic recordings of biotic, geophonic and anthropogenic sounds are distilled into one or more acoustic indices (Fuller et al. 2015). Acoustic indices have, however, been shown to be seriously limited in their ability to predict species richness or community change (Sethi et al. 2023). Despite these challenges, there is a clear need for species-specific occurrence and abundance data, as well as assessments across taxa, to gain a comprehensive ecological understanding of ecosystems and their conservation status for multiple taxonomic groups. This becomes especially important for directing conservation actions and fulfilling legal requirements for protection (Kotila et al. 2023).

Here, we demonstrate how multi-taxa PAM can be used as a tool to prioritise conservation efforts for cryptic taxa at previously unprecedented scales. We quantify relationships of formerly unsurveyed taxa with the existing protected area network and evaluate protected area coverage for the distributions of four taxonomic groups. This was the first large-scale systematic survey of biodiversity in Polesia, a region spanning 18 million hectares in northern Ukraine and southern Belarus, which contains some of Europe's best preserved natural landscapes. Polesia has a relatively extensive protected area network, but protection is not underpinned by systematically collected data on biodiversity patterns across taxa, and is threatened by fragmentation and degradation due to multiple land-use pressures (Kirkland et al. 2023). In common with many parts of the world, protected area designation is based on partial assessments of biodiversity, focused on the occurrence of particular target species for conservation whose distributions are relatively well known or easy to survey.

To assess the efficacy of Polesia's protected area network, we deployed acoustic recorders at 506 sampling points across the region, collecting 2884 nights of data. We developed separate high and low-frequency (ultrasonic and audible frequency) machine-learning classifiers using random forest and convolutional neural networks (CNNs), and identified recordings of bats, nocturnally active birds, small mammals and bush crickets through machine learning and subsequent manual validation. Using multi-species models generated from the acoustic data, we identified areas of high conservation priority and assessed these against the current protected area network. This study adds to the literature on the potential for surrogacy in conservation planning (Rodrigues and Brooks 2007), but for

the first time does so using large-scale data on cryptic species, mapped using PAM. We therefore illustrate the power of coupling this emerging technology with modern computational power and analytical capabilities that now enable large-scale mapping of species that were previously very difficult to monitor and map at scale.

2 | Methods

2.1 | Study Area

Our study area encompassed the central part of an *eco-region* called Polesia, spanning from Poland, across northern Ukraine and southern Belarus, up into Russia. Polesia is a lowland area, containing some of Europe's best preserved peatland and deciduous forest ecosystems and includes the Chernobyl Exclusion Zone in the east of the region. There has been recent designation of new PAs and expansion of existing PAs within the region, with further designation and expansion planned. A bid for UNESCO World Heritage status is being prepared (<https://wildpolesia.org/our-work/>).

2.2 | Sampling Regime

To survey multi-taxa acoustic biodiversity throughout Polesia, we deployed acoustic recorders at 506 sites across the region from 2019 to 2022 using a stratified, random sampling design. Sampling points were designated by overlaying a 15×15 km grid over the region of interest (22.94, 50.5:51.81, 53.04); 30 cells were designated as sampling sites, as they overlapped areas of conservation interest (existing protected areas, or potential new protected areas) and 30 grid cells were chosen randomly, acting as control sites. Protected area status was split into three categories: (1) protected areas (PAs), (2) Emerald Sites and (3) non-PAs. PAs are designated to protect habitats or biodiversity in the region and limit hunting, forestry and access; they range from IUCN category Ia–VI (Dudley 2008), but are generally in good condition because of their inaccessibility and large size. Many Emerald Sites (a non-EU analogue of Natura 2000 sites) have been identified as important areas for habitat or biodiversity, but do not have legal protection. Non-PAs have no protection (dominated by agriculture and forestry, in the region). Some randomly chosen cells were moved where access was deemed to be difficult or certain land cover types were underrepresented (see Figures S1–S4; Tables S1 and S2) for the sampling locations, the proportions of sampling locations by land cover type and the proportions of land cover across the project region. Within grid cells, 10 points were randomly designated to survey with an acoustic recorder, with a minimum of 1 km distance between sampling points.

Acoustic recorders were placed at each sampling point, once, between the months of April and September, for a minimum period of four consecutive nights. A period of four nights was chosen to adequately sample the acoustic diversity within a point, while maximising the number of sampling locations within the study period, by allowing transfer of acoustic recorders to different locations.

We used Wildlife Acoustics SM4Bat FS which were set to record with a sample rate of 384 kHz, a trigger threshold of 12 dB and to use a high pass filter of 1 kHz (bespoke firmware provided by Wildlife Acoustics) which defined the lower threshold of the frequencies for the triggering mechanism. Recording was set to continue until no trigger is detected for a 2.0 s period up to a maximum of 5 s (Newson et al. 2015). Acoustic recorders had a schedule from 1 h before sunset, to 1 h after sunrise, capturing the main activity periods for nocturnal and crepuscular species.

2.3 | Classification of Acoustic Recordings

Ultrasonic recordings were processed separately to detect and identify species producing ultrasonic sounds (bats, Orthoptera, small mammals and one moth species, *Pseudoips prasinana*) and those producing audible sounds (birds). Ultrasonic recordings were analysed using a supervised Random Forest classifier that we built for the region using the open-source software Tadarida (Bas et al. 2017; Newson et al. 2017), and made available through the BTO Acoustic Pipeline (<http://bto.org/pipeline>). The training data used to build the ultrasonic classifiers for the Acoustic Pipeline comprise over 90,000 known species recordings (4,244,634 labelled sound events), collected or collated by ourselves from over a decade of working on the sound identification of bats and other species groups that are commonly recorded as 'by-catch' during bat surveys (Newson et al. 2017). For bats, the species coverage for the region was complete and included the range of calls that bats can produce (echolocation, feeding buzzes and social calls). However, because of the difficulty in manually distinguishing *M. mystacinus* and *M. brandtii*, and *N. leisleri* and *V. murinus* echolocation calls specifically in the absence of diagnostic social and/or feeding buzzes, we treat results for these together. For bush-crickets, the training data again included all species, with some species identified retrospectively, and built into the classifier, although for small mammals there were some gaps in knowledge, that meant that for some small mammal species, it was not possible to assign an identification to species, and were instead assigned to a higher level (e.g., dormouse, *Apodemus* or shrew species).

For birds we developed a convolutional neural network (CNN) capable of detecting 10 owl species (*Asio flammeus*, *Aegolius funereus*, *Asio otus*, *Athene noctua*, *Bubo bubo*, *Glaucidium passerinum*, *Strix aluco*, *Strix nebulosa*, *Strix uralensis*, *Tyto alba*), two nightjar species (*Caprimulgus europaeus* and *Caprimulgus ruficollis*) and a range of nocturnally active species of interest (*Coturnix coturnix*, *Crex crex*, *Luscinia luscinia*, *Luscinia megarhynchos*, *Grus grus*, *Porzana porzana* and *Scolopax rusticola*). To train the CNN we needed a large labelled audio dataset. We used our own recordings supplemented with recordings from collaborators and the xeno-canto platform to develop a training dataset of c.250,000 labelled sound events for target species, for potential confusion species and a range of ambient and anthropogenic noises. From this audio library we generated training and evaluation datasets containing 4000 and 400 randomly selected samples per species, respectively. During initial testing we found a balanced dataset led to significant numbers of false positive detections. We partially overcame this by increasing the sample of the non-target class 20-fold. At last, to increase the classifier's ability to detect concurrent species vocalisations we

generated multi-species training clips by mixing up to three randomly selected species' clips.

CNNs performance depends heavily on the amount of training data, which is often limiting for scarce species. Two methods are commonly used to overcome this: data augmentation and transfer learning. For species where sample size fell below 4000 samples we used time shifting to make additional training samples. Then during model training we used inline amplitude shifting and mixup. For mixup we used non-target sound clips (background soundscapes of other taxa and ambient sounds) which were randomly mixed with training data. Augmentation helps to reduce overfitting, thereby improving generalisation to new environments. Transfer learning involves taking an existing CNN that has been pre-trained on a large dataset so has learned how to extract features from input data and using this as the backbone of the CNN onto which a custom classification head is added for the task at hand. For our backbone we used the ECA-NFNet-L0 model (Wightman et al. 2023) which is a variant of normalisation-free efficient nets (Brock et al. 2021). These were pretrained on the ImageNet dataset, are fast in training and inference and have shown state-of-the-art performance in image classification (Brock et al. 2021). The main input to the backbone was a Mel-scaled spectrogram (150–10,000 Hz, window length 1024, hop length 256, 128 Mel bins). We added a channel to the model input to contain the Mel bin indices replicated across the time dimension. This step helps to preserve the importance of frequency position in detected features. After extracting features we used L2 pooling, attention weighting and a dropout layer ($p=0.2$) prior to the final classification layer. We did not use a final softmax layer as species can co-occur at clip level. We used an initial learning rate of 0.0001 with a cosine decay, an Adam optimizer and a binary cross entropy loss function. The model was trained on a desktop computer with a NVIDIA GeForce RTX 2060 with a batch size of 32 over 25 epochs. The best model was selected using *F*-score calculated on the withheld evaluation dataset. Using the same dataset, for each species we determined the prediction score at which *F*-score was maximised to identify a score threshold that balanced precision and recall (see Data S1 for classifier metrics). When the model was applied to field recordings we extracted all detections exceeding these score thresholds. A minimum of a 100 detections for each species recorded at each location were manually checked for accuracy. At locations where there were less than 100 detections, all recordings were manually checked.

For the ultrasonic recordings, all recordings at each site were manually checked (up to a maximum of 1000) above a classification probability of 0.5 (see Barré et al. 2019 and Data S1 for classifier metrics).

2.4 | Explanatory Variables and Prediction Surface

We obtained land cover data for Polesia using the code and method from Dowling and de Jong (2021), and used in Kirkland et al. (2023) which assigns 20 m² pixels to one of 13 land cover types. We simplified the 13 land cover types to 11: pine forest, oak forests, wet deciduous forest, birch forest, floodplain meadows, agriculture, raised bog, transition mires, scrub and forest clearings, water and urban.

PA status was obtained, including Emerald Network sites, using spatial data from the World Database of Protected Areas (UNEP-WCMC and IUCN 2022).

Proportional land cover data were extracted at 20 m, and using a 1000 m, and 5000 m buffer around each acoustic sampling point, to test the scale at which species' occupancy and activity distributions are best predicted. PA status was extracted at the sampling point. Note that at the 20 m scale, the proportion of a given land cover was either 0 or 1 since this is the same resolution as that of the land cover data.

Hexagonal prediction surfaces were produced at 1 km and 5 km resolution at which proportional land cover data were extracted using the R package 'exactextractr' at each resolution and PA status was extracted at the centre point of each hexagonal cell. Hexagonal cells reduce sampling bias from edge effects of the grid shape, which is related to high perimeter:area ratios and over large spatial areas, a hexagonal grid suffers less distortion due to curvature than a square grid (Birch et al. 2007). A prediction surface was also produced at the original land cover resolution of 20 m.

2.5 | Statistical Analysis

We used two methods to model species distributions: occupancy and acoustic activity models. Occupancy was modelled for all taxa, whereas activity was only modelled for birds, bats and small mammals. Acoustic activity models use the number of 5-s recordings with positive species identifications per recording night, and so give a measure of relative abundance or site usage for that species (Border et al. 2022). We did not assess activity for birds or bush crickets, due to the behaviour and ecology of these groups. Nocturnal birds in the nesting season, and bush crickets are relatively stationary at breeding sites and the number of calls is likely to relate to season or temperature (bush cricket stridulations) rather than the relative use of a site by multiple individuals (Newson et al. 2017).

2.5.1 | Multi-Species Occupancy Modelling

We used multi-species occupancy models to quantify species-specific habitat associations, assess the effects of protected area status on species habitat use and predict species distributions and species richness across the study area. Multi-species occupancy models are extensions of single-species occupancy models that use detection-nondetection data from multiple species and explicitly account for imperfect detection (i.e., the failure to detect a species at a location when it is truly present; (MacKenzie et al. 2002)) by separately modelling detection probability from occupancy probability. These models estimate species-specific parameters (e.g., intercepts, covariate effects) as random effects arising from a community-level distribution, which enables inferences at multiple scales (i.e., species, community) and leads to greater precision of estimates, particularly for rare species with a limited number of detections (Dorazio et al. 2006). Additionally, by fitting models in a Bayesian framework, we can readily generate species richness estimates (and uncertainty estimates) that are adjusted for imperfect detection of the species in the modelled

community. Here we used recent extensions of multi-species occupancy models (Tobler et al. 2019; Doser et al. 2023) that also incorporate residual correlations between species using a latent factor model.

We fit a separate multi-species occupancy model for the four taxa (bats, birds, bush crickets and small mammals). Let $y_{(i,j,k)}$ denote the detection (1) or nondetection (0) of species i at site j on recording day k generated from the machine learning classification algorithm. False negatives could occur in $y_{(i,j,k)}$ as a result of the species being present at the site but not vocalising during the time period of sampling, or from the acoustic classifier failing to detect and correctly identify the vocalisation in the recording. Also define $z_{(i,j)}$ as the true presence (1) or absence (0) of species i at site j . We model the observed data conditional on the true occupancy status of the species at each site according to

$$y_{(i,j,k)} \sim \text{'Bernoulli'}(p_{(i,j,k)} \times z_{(i,j)})$$

where $p_{(i,j,k)}$ is the probability of detecting species i at site j during sampling day k . We model detection probability $p_{(i,j,k)}$ following

$$\text{'logit'}(p_{(i,j,k)}) = \alpha_{(0,i,\text{YEAR}_i)} + \alpha_{(1,i)} \times \llbracket \text{'DATE'} \rrbracket_{(j,k)} + \alpha_{(2,i)} \times \llbracket \text{'DATE'} \rrbracket_{(j,k)}^2$$

where $\alpha_{(0,i,\text{YEAR}_i)}$ is a year-specific intercept for each species to account for differences in detection probability across the different years when each site was sampled, and $\alpha_{(1,i)}$ and $\alpha_{(2,i)}$ represent species-specific linear and quadratic effects of survey date on detection probability. For the small mammal community, models with a separate intercept by year on detection probability did not converge, and so we modelled detection probability for small mammals with a constant intercept across the 4 years.

We model the true occupancy status $z_{(i,j)}$ using a Bernoulli distribution, such that $z_{(i,j)} \sim \text{'Bernoulli'}(\psi_{(i,j)})$, where $\psi_{(i,j)}$ is the occupancy probability for species i at site j . We model species-specific occupancy probability according to

$$\text{'logit'}(\psi_{(i,j)}) = X_j \beta_i + \text{'w'}_{(i,j)},$$

where X_j is a vector of covariates (including an intercept), β_i is a vector of effects for species i of the covariates in X_j and $\text{'w'}_{(i,j)}$ is the value of a latent variable for species i at site j . The latent variable $\text{'w'}_{(i,j)}$ is estimated using a factor modelling approach (Doser et al. 2023), which explicitly accounts for residual correlations between species within each of the four taxa after accounting for the covariates included in the model. All species-specific occupancy (β_i) and detection ($\alpha_{(0,i,\llbracket \text{'YEAR'} \rrbracket_j)}, \alpha_{(1,i)}, \alpha_{(2,i)}$) parameters were modelled as random effects from a common, community-level normal distribution following Dorazio and Royle (2005), which enabled information sharing across species and increased precision of covariate effects.

We compared a series of models that differed in the specific covariates included in the model of species-specific occupancy

probability to determine: (1) the spatial scale at which land cover is most prominently related to species-specific occupancy probability; (2) how occupancy probability is related to multiple classifications of protection status; and (3) how protection status influences the relationship between land cover and occupancy probability. To assess occupancy relationships with land cover, we included 10 land cover variables: oak/small leaved deciduous forests, birch forests, floodplain meadows, raised bog, fen and transitional mires, scrub, water, urban/developed areas, pine and spruce forests and deciduous swamp forest. We calculated the proportion of each of these land cover variables at three spatial scales for each taxonomic group: 1 km (all four groups), 20 m (insects and mammals) and 5 km (bats and birds). Agriculture was the most dominant land cover class, but we removed this land cover class to avoid land cover proportions summing to 1. We tested model fit by AUC, by swapping agriculture for pine (the second most dominant land cover class) and all models fitted better without the agricultural land cover class. We chose these scales based on the ecology of the groups and at the scales at which they move and forage. We compared models at the two spatial scales for each group to determine which spatial scale was more associated with occupancy probability for each species. To assess the impacts of protected areas on the different species, we compared models with and without a categorical variable indicating the protection status of the given location. For models with protection status included in the model, we also estimated a separate effect of the five major land cover types (oak/deciduous forests, floodplain meadows, raised bogs, fen/transitional mires and wet, deciduous swamp forests) within the different protection statuses. These land cover types were chosen as they are often present in PAs due to their importance for biodiversity and threatened status'. This resulted in a total of six candidate models for each species group. We compared models using the Widely Applicable Information Criterion (WAIC; Watanabe 2010), a fully Bayesian information criterion that is well-suited for comparing complex, hierarchical models such as multi-species occupancy models (Hooten and Hobbs 2015).

We fit all models using the spOccupancy package (Doser, Finley, et al. 2022; Doser, Leuenberger, et al. 2022) in R (R Core Team 2023), which implements multi-species occupancy models in a Bayesian framework using Markov chain Monte Carlo (MCMC). We used the vague, default priors provided by spOccupancy (Doser, Finley, et al. 2022; Doser, Leuenberger, et al. 2022; Doser et al. 2023). We ran all models for three chains of 200,000 iterations with a burn-in period of 100,000 iterations and a thinning rate of 100, resulting in a total of 3000 samples from the posterior distribution. We assessed model convergence using visual assessment of traceplots with the coda (Plummer et al. 2006) and MCMCvis packages (Youngflesh 2018) and the potential scale reduction factor (i.e., Rhat; Brooks and Gelman 1998). Model fit was assessed using posterior predictive checks summarised with a Bayesian p -value (Hooten and Hobbs 2015), which revealed adequate model performance for crickets and mammals. For birds and bats, we found evidence of overdispersion in the data relative to that predicted from the model, which is likely due to unexplained heterogeneity in detection probability. As a result, estimates of occupancy probability for these species are likely conservative.

After fitting the models, we subsequently predicted species-specific occupancy probability across a hexagonal grid at the resolution of the top-performing model for the given group. We then estimated species richness for each group at each grid cell from the predicted species-specific occupancy estimates. By estimating species richness in this manner as a derived quantity arising from the multi-species occupancy model, we were able to generate maps of species richness that accounted for imperfect detection and species correlations, which we could subsequently use to assess differences in richness across protected areas.

2.5.2 | Multi-Species Acoustic Activity Models

Additionally, for three taxonomic groups (birds, bats, small mammals) we used a multi-species generalised linear mixed model to assess how species-specific acoustic activity (as measured by the number of vocalisations per night) was related to land cover and protection status. More specifically, let $v_{(i,j)}$ denote the number of vocalisations detected of species i at site j . We modelled $v_{(i,j)}$ according to

$$v_{(i,j)} \sim \text{NB}(\mu_{(i,j)}, \kappa_i),$$

where NB represents the negative binomial distribution, $\mu_{(i,j)}$ is the average acoustic activity of species i at site j , and κ_i is a species-specific overdispersion parameter to account for large overdispersion in the vocalisation data. We modelled $\mu_{(i,j)}$ according to

$$\log(\mu_{(i,j)}) = X_j \gamma_i$$

where X_j is a vector of covariates (including an intercept) at site j and γ_i is a vector of effects of the covariates for species i . We include the same land cover and protection status covariates as described for the multi-species occupancy models, with the addition of a linear and quadratic effect of the average Julian date of recordings at the given site to account for variation in detection/activity across time, and a log-linear effect of total recording length to account for variation in recording time across sites. Note that here we did not include an additional component to account for residual species correlations as we did in the multi-species occupancy models, as initial fits of such models did not converge. We modelled species-specific covariate effects as random effects from a common community-level distribution, analogous to the multi-species occupancy models, which substantially improved the ability to generate estimates for rare species in the data set.

We compared the same set of candidate models as with the occupancy models. We fit all models in a Bayesian framework using MCMC algorithms implemented in the spAbundance R package (Doser et al. 2024). We used vague normal priors for regression coefficient means, vague inverse-Gamma priors for community-level variance parameters, and independent uniform priors with lower bound 0 and upper bound 100 for the negative binomial overdispersion parameters. We ran all models for three chains of 100,000 iterations with a burn-in period of 50,000 iterations and a thinning rate of 50, resulting

in a total of 3000 samples from the posterior distribution. We assessed convergence using the same tools as described for the multi-species occupancy models. Posterior predictive checks indicated adequate model fit.

We subsequently predicted species-specific abundance across a grid at the resolution of the top performing model for each group of species. To facilitate comparison across species with drastically different acoustic activity levels, we scaled species-specific acoustic activity estimates to relative acoustic activity following the approach of Border et al. (2022).

2.5.3 | Quantifying Taxonomic Surrogacy

We used a correlation matrix approach to test the spatial correlation between different taxonomic groups. We tested the correlation between predicted species richness of bats, birds, small mammals and bush crickets at the 1 km² scale. We also tested spatial correlation separately for groups within PAs and for regionally red-listed species and IUCN red-listed species. We also compared these results to the correlation of species richness of each taxonomic group from the raw, unmodelled data to help verify our findings.

2.5.4 | Mapping Areas of High Conservation Priority

Mapping of areas of high conservation priority was conducted in four ways:

1. Overlaying of the highest 10% quantile predicted species richness from occupancy models for the four taxonomic groups at a 0.1° longitude × 0.05° latitude scale (~61 km²) and mapping these as hotspots of species richness.
2. Mapping the highest activity (bats) or occupancy rate (birds, bush crickets) for all of the nationally red-listed species. As all bat species are red-listed in Ukraine, we just selected species that were red-listed in Belarus and overlaying as in 1.
3. Mapping the highest 10% quantile occupancy rate of the three IUCN red-listed species surveyed in the study: Greater Noctule, Barbastelle and Pond Bat and overlaying this as in 1.
4. Mapping the highest 10% quantile predicted species richness of regionally red-listed birds and overlaying as in 1.

3 | Results

3.1 | Multi-Species Distribution Models

From 2, 884 nights of monitoring, we identified 644, 534 bat vocalisations from 15 species or species pairs, 6, 130 small mammal vocalisations from 6 species or species groups, 17, 153 bush cricket stridulations from 17 species or species pairs and 99, 902 vocalisations from 13 species of nocturnally active birds (Figures S1–S3).

We used multi-species species distribution models modelling occupancy and acoustic activity, predicted by land cover type and protected area status, to assess the spatial coverage and placement of protected areas relative to biodiversity within Polesia.

We tested whether models including no, two (PAs and non-PAs) or three protected area statuses (PAs, Emerald sites and non-PAs) were more informative. Bat occupancy was best predicted at a 5 km² resolution and the model with three PA statuses (PA, unprotected area, Emerald site) was the best fit according to WAIC (Table S4). Bird, small mammal and bush cricket occupancy models fitted best at a 1 km² resolution, also with three PA statuses. The occupancy of bat species is likely to be driven at a larger scale than birds, small mammals and bush crickets due to their generally larger foraging ranges and often long commutes between roost and feeding areas (Nado et al. 2019; Zeale et al. 2012).

For acoustic activity, we developed multi-species abundance models for bats, birds and small mammals, excluding bush crickets as their acoustic activity is relatively fixed spatially, linked to the time of season and temperature (bush cricket stridulations) rather than relative use of a site by multiple individuals

(Newson et al. 2017). The optimal models for acoustic activity of bats, birds and small mammals were at 1 km² resolution, incorporating all three PA statuses (Tables S6–S11) for bats and small mammals, but only two for birds (PA, Non-PA). The spatial distribution of bat species' acoustic activity was driven at smaller scales than for occupancy, indicating this approach's potential for explaining fine-scale drivers of bat biodiversity and therefore conservation planning. Acoustic activity has been shown to be an important predictor of habitat suitability for bats, especially for species that are widely distributed, but have strong ecological associations with certain environmental variables such as land cover type (Border et al. 2022).

3.2 | Distribution and Overlap of Taxonomic Groups

Areas of high species richness of the four taxonomic groups differed in their geographical extent and overlap with protected areas (Figure 1). Correlation matrices revealed a positive, but generally weak correlation in predicted species richness between taxa at the 1 km² scale (Table S12), with small mammals and bush crickets having the strongest correlation (0.53) and bats and bush crickets having the weakest

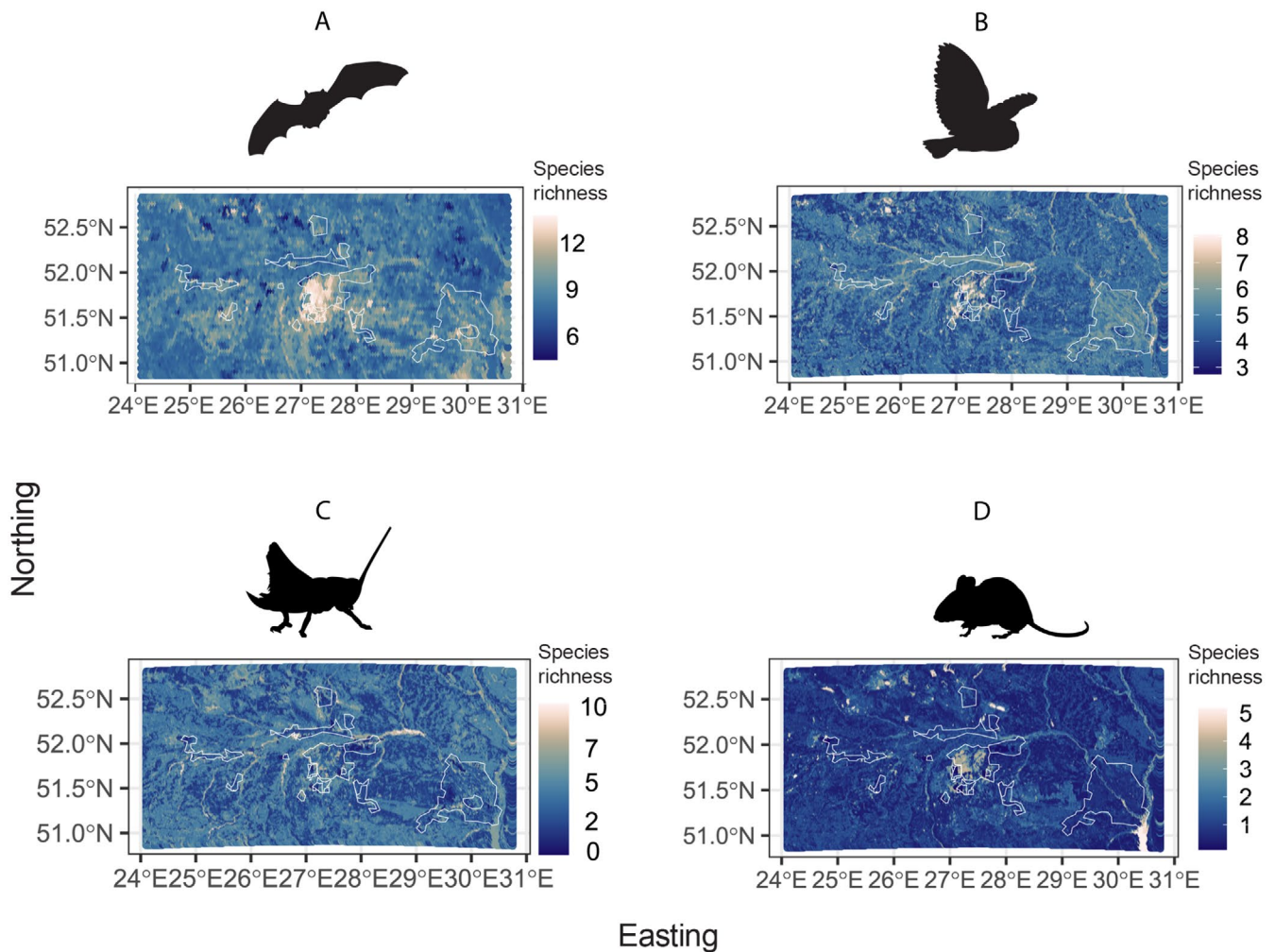


FIGURE 1 | Predicted species richness of bats (A) at 5 km² resolution, and birds (B), small mammals (C) and bush crickets (D) at 1 km² resolution, and their relationship with PAs (white boundaries) in Polesia.

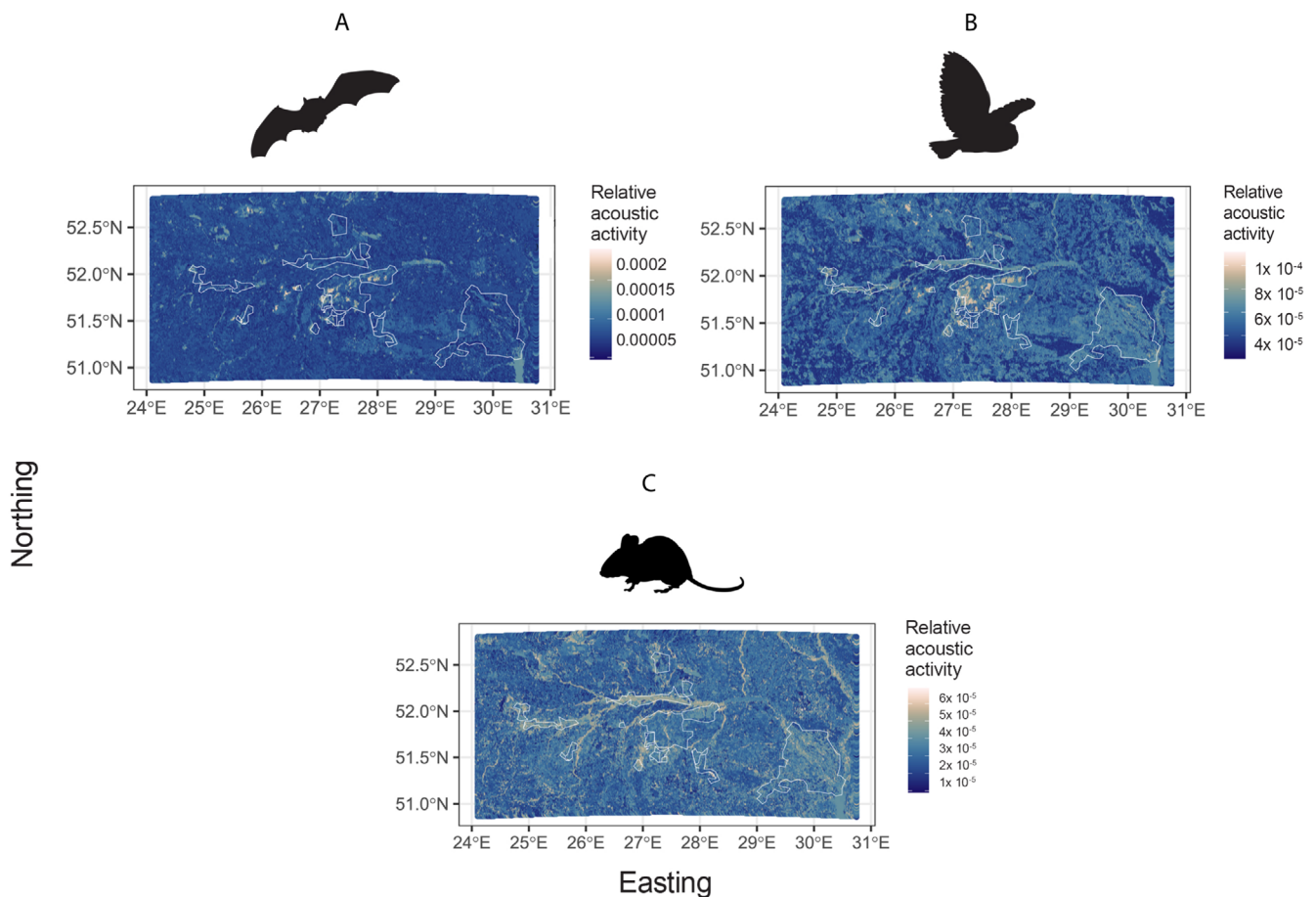


FIGURE 2 | Predicted relative acoustic activity of bats (A), nocturnally active birds (B) and small mammals (C) at 1 km² resolution.

(0.05). This correlation in species richness differed inside PAs (Table S13); however, the correlation between species richness in bats and birds weakened from 0.4 over the total survey area to 0.15 inside PAs, whereas, the correlation between all the other taxa strengthened. Correlation between species richness between taxa was also weak in the raw, unmodelled data (Table S15).

Bat and bird acoustic activity had some overlap, and there was a weak correlation between activity at the grid scale (0.21), but PAs differed in the relative importance for areas of high activity (Table S14, Figure 3) and acoustic activity showed a weaker correlation within PAs (0.18) than overall (0.21). There were large differences in the spatial overlap of predicted bat and small mammal activity (Figure 2), and bat and small mammal activity had no correlation with each other at the grid scale overall (−0.05) or solely within PAs (−0.07). Bat and small mammal activity models showed broadly similar patterns to occupancy, with high activity following rivers and in certain PAs, but there was a weak correlation at the grid scale (0.06, and 0.21, respectively; Table S14).

When validating predictions against survey data, acoustic activity was generally slightly underpredicted, but there were also large, unrealistic predictions due to the overdispersion of the data (Richards 2008). Data are heavily right-skewed and there are very high counts that are difficult to explain with commonly available environmental variables, such as roosting or

swarming sites for bats, or communal nesting or feeding sites for small mammals, where very high numbers of animals can congregate, producing many sound events. We dealt with the issues of accurately predicting activity by binning results into categories from low to high activity, based on realistic activity rates from the raw data. These relative estimates of activity likely give greater ecological meaning than the raw predictions, which may be unrealistic.

3.3 | Mapping Areas of High Conservation Priority

We mapped areas of high conservation priority for all species surveyed and for species of regional and global conservation importance: first, we overlaid the cells with the highest predicted (top 10% quantile) species richness and activity of each taxonomic group (Figure 3); second, we focused on species of conservation concern by mapping high predicted occupancy for regionally red-listed species (Figure 3); and occupancy of the three IUCN red-listed species in the region (Figure 3).

There was very low overlap of the highest predicted species richness cells (top 10%) between all taxa at the 1 km² scale, with only 0.2% of the highest species richness 1 km² cells overlapping. Bats and birds showed a 13.6% overlap, bats and small mammals, 18.3%, bats and bush crickets, 6.3%, birds and small mammals, 19.3%, birds and bush crickets, 15.6% and small mammals and bush crickets, 6.4%. However, at the larger scale (0.1° × 0.05°

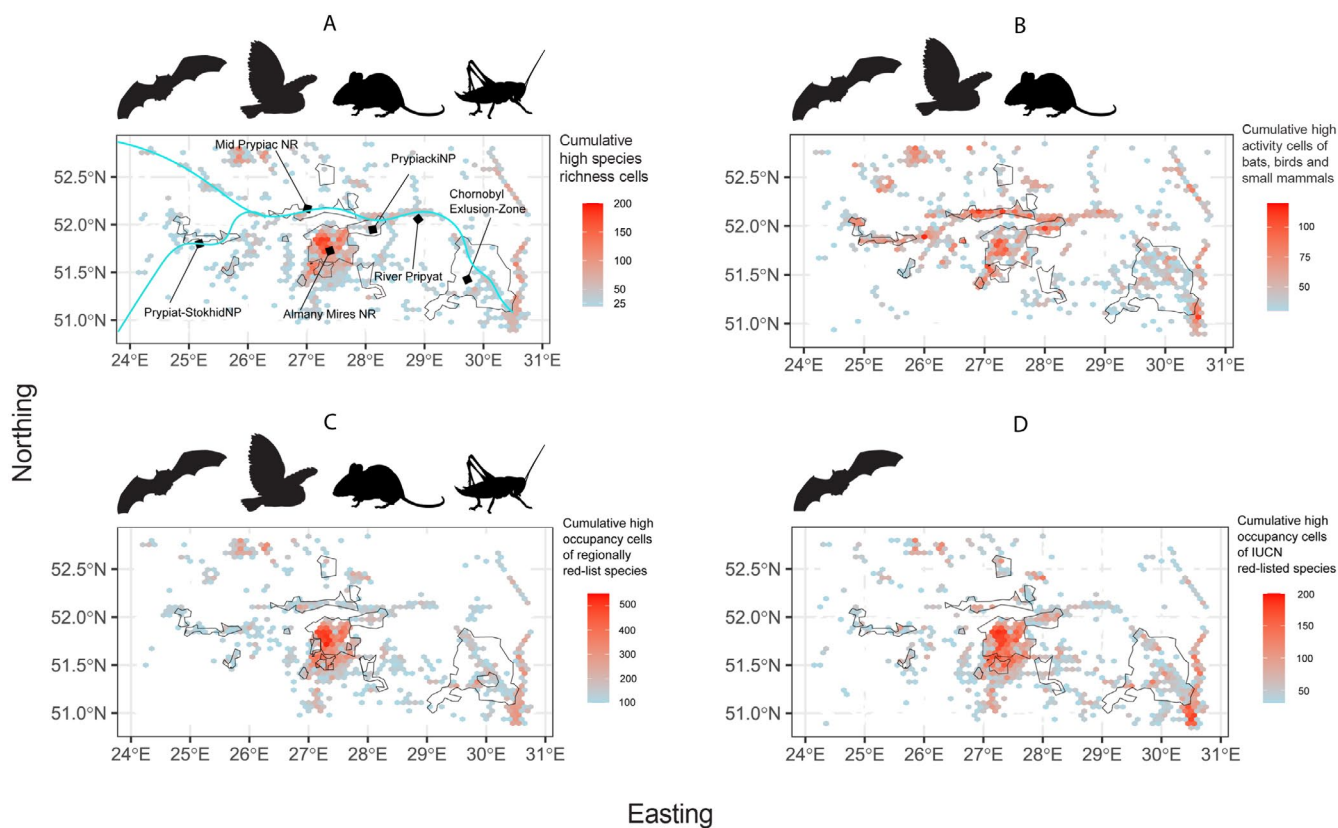


FIGURE 3 | Areas of high conservation priority mapped (from top left to bottom right): Number of cumulative top 10% predicted species richness 1 km cells for all taxonomic groups at a $0.1^{\circ}\text{N} \times 0.05^{\circ}\text{E}$ (A), number of cumulative top 10% relative acoustic activity 1 km^2 cells for bats, nocturnally active birds and small mammals at a $0.1^{\circ}\text{N} \times 0.05^{\circ}\text{E}$ (B), number of cumulative top 10% predicted occupancy 1 km^2 cells of regionally red-listed species for all taxonomic groups at a $0.1^{\circ}\text{N} \times 0.05^{\circ}\text{E}$ (C), number of cumulative top 10% predicted occupancy 1 km^2 cells of IUCN red-listed species at a $0.1^{\circ}\text{N} \times 0.05^{\circ}\text{E}$ (D).

$\sim 61\text{ km}^2$) we saw key areas of overlap, particularly inside, and surrounding Almany Mires NR, where cumulative overlap of the top 10% quantile predicted species richness cells was nearly $10\times$ that of the average (Figure 3, Figures S18–S21). There were other clear relationships of overlap in high predicted species richness at this scale, particularly following riverine areas including the Pripjat and its tributaries.

Overall, overlap at the 1 km^2 scale was low between regionally red-listed species with less than 1% of top 10% quantile cells overlapping, but at the larger scale, there were shared relationships between areas of high predicted occupancy for regionally red-listed bats and bird species (Figure 3). Particularly in PAs such as Almany Mires NR and the Chornobyl Exclusion Zone, which were important for both red-listed bats and birds. There were noticeable disparities, however, with important areas for red-listed bats in the unprotected lower Pripjat region in Belarus and the Rivnenskyi NR in Ukraine, which were less important for birds. In contrast, the Mid-Pripjat NR and Prypiat–Stokhid National Nature Park were of more importance to red-listed birds than bats.

In contrast, IUCN red-listed species (Barbastelle, Greater Noctule and Pond Bat) highly overlapped at the 1 km^2 scale, with 26% of the top 10% quantile cells overlapping and 38% of Pond Bat and Greater Noctule (which prefer more open habitats to Barbastelle) high occupancy cells overlapping. There

were similar patterns of high conservation priority to overlapping areas of high species richness and activity, with the highest occupancy of IUCN red-listed species overlapping in Almany Mire NR the Chornobyl Exclusion Zone, and along river systems.

The lack of overlap of areas of high biodiversity between taxonomic groups at finer scales demonstrates the importance of prioritising conservation and PA placement on data from multiple taxa. Using our multi-taxa acoustic approach, we found shared areas of importance for different taxa at a larger scale where conservation decisions can be made, based on data from a diversity of species with different ecological requirements (Burrascano et al. 2018).

3.4 | Differential Importance of PAs to Taxonomic Groups

PAs were most important for bat diversity, relative to the other taxonomic groups (Figure 4) and mean predicted bat species richness in PAs was on average 9.48 [9.1 – 9.86 89% CI] vs. 7.77 [7.4 – 8.13 89% CI] in Non-PAs and 8.53 [7.97 – 9.14 89% CI] in Emerald sites. Overall, PAs had on average a slightly higher average bird species richness (7.15 [6.69 – 7.6 89% CI]) than in non-PAs (6.52 [6.12 – 6.94 89% CI]), and Emerald sites (4.6 [4.1 – 5.1 89% CI]); however credible intervals overlapped. Bush

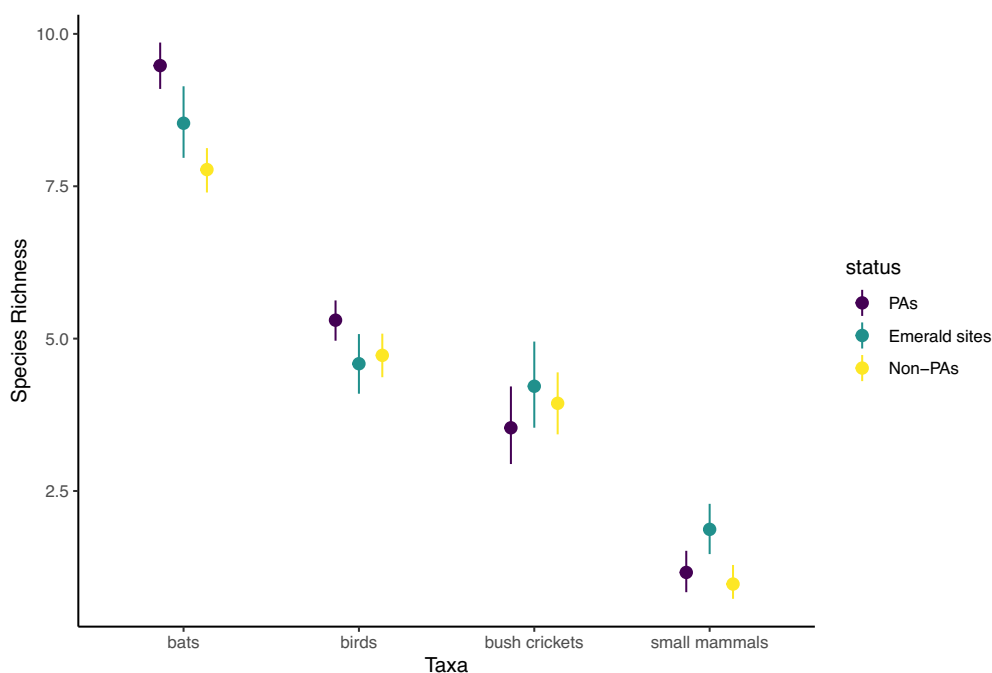


FIGURE 4 | Average predicted species richness of bats, birds, small mammals and bush crickets in protected areas (PAs), Emerald sites and non-PAs.

cricket species richness had no clear relationship with PA status, but had a slightly lower average species richness in PAs (3.6 [3.0–4.25 89% CI]) relative to non-PAs (4.05 [3.53–4.56]), and higher species richness in Emerald sites (4.2 [3.5–4.95 89% CI]), but credible intervals overlapped. Small mammal diversity was also weakly related to PA status with a slightly higher average species richness in PAs (1.17 [0.79–1.61 89% CI]) than in non-PAs (0.98 [0.71–1.39 89% CI]), but the highest average species richness was in Emerald sites (1.9 [1.5–2.3 89% CI]).

We show that the spatial nuance of different taxonomic relationships with PAs is important (i.e., some PAs are more important for bird diversity, others for bats; Figure 1) and that this nuance can be somewhat lost when averaging species richness across PAs (Figure 4). This highlights the importance of assessing PA suitability across multiple taxa.

Five of fifteen species of bat and (Figure S5) four of nine species of birds (Figure S7) had higher occupancy on average in PAs than non-PAs, but no species of small mammal or cricket did (Figures S6 and S8). Emerald sites did not have consistent relationships with bat or bird occupancy, but generally were associated with high predicted occupancy of small mammal and bush cricket species. Emerald sites in Polesia are dominated by floodplain meadows which are likely important for these taxa. 14/15 bat species had higher activity in PAs than non-PAs (Figure S9) and 6/9 bird species, with two species (Common crane and Common quail) having lower activity in PAs than non-PAs (Figure S10). Small mammals had, on average, slightly lower activity between PAs and non-PAs (Figure S11).

PAs contained a much greater proportion of cells with high (top 10%) predicted species richness or acoustic activity for a taxonomic group than Non-PAs, for each of bats, birds, bush

crickets (Table S3). Despite Polesia's relatively extensive PA network, the majority of high species richness and acoustic activity cells (67%–88%) are located outside protected areas. To protect the areas of highest species richness and acoustic activity an additional 14,100–16,400 1 km² of land for each taxonomic group would need to be protected. Our mapping exercise could be used to prioritise areas where these overlap for the most species.

3.5 | Land Cover Relationships With Species Occupancy and Acoustic Activity

PAM allowed us to demonstrate species relationships with land cover type over larger geographic scales than usually possible, particularly for the cryptic, nocturnal and poorly surveyed species we covered in this study. Bats generally had higher occupancy and activity than average in areas with a high proportion of open land covers: meadows, fen and transition mires, raised bog, scrub and near water (Figures S12 and S13). Sites with a high cover of deciduous forest: birch, wet deciduous and oak forests had generally lower occupancy and activity than average, apart from certain species such as Barbastelle, which is generally associated with forest habitats (Russo et al. 2005).

Birds had varying relationships with land cover depending on their ecology. There was generally high occupancy of wetland-associated bird species in fen and transition mires and raised bogs, but low activity, which follows expected relationships of the importance of these habitats for low breeding densities of wetland bird species (Figures S14 and S15) (Silva-Monteiro et al. 2021). Meadows were particularly important for Spotted Crake and Corncrakes with both species having high occupancy and activity in this land cover type and forest land cover types

(particularly wet deciduous, pine and oak) were predictably associated with high occupancy and activity of Tawny owl which is a species strongly associated with lowland, temperate forests (Yatsiuk and Wesołowski 2020).

Meadows were generally associated with high occupancy and activity of shrew spp. and European Water Vole (Figures S17 and S18). Sites with a high proportion of water in the surrounding area were strongly associated with Dormouse spp. and European Water Vole.

Bush cricket species (and one moth species) were relatively species-specific in their associations with land cover, but meadows were strongly associated with high occupancy of several species (Figure S16). We also found strong associations between oak forest cover and the occupancy of the moth, Green Silver-lines (*Pseudoips prasinana*) and the Dark Bush-cricket (*Pholidoptera griseoptera*). Short-winged Cone-heads (*Conocephalus dorsalis*) were strongly associated with wet-deciduous forest.

4 | Discussion

Here, we demonstrate how PAM can be used to provide landscape-scale data on the occurrence and acoustic activity of multiple taxa, thereby contributing to systematic conservation planning (Margules and Pressey 2000), such as PA designation. These data were collected using a single survey method and provided data on four taxonomic groups, including nocturnal and cryptic species for which large-scale datasets are rare (Thompson 2013). Through the use of acoustic monitoring, we assessed protected area coverage for forty-seven species (or species groups) in the data-poor Polesia region (northern Ukraine and southern Belarus), and quantified the spatial surrogacy of these taxonomic groups. This would have been unfeasible using traditional methods, due to the time and expense required.

The study design and analytical techniques we developed are particularly well-suited for prioritising conservation efforts in data-poor regions, allowing for informed decisions based on multi-taxa datasets, including those for cryptic species. Given the recent military conflict and instability in Polesia, which pose significant threats to biodiversity (Russell et al. 2024), our findings are particularly timely. They provide a critical resource for future conservation initiatives in a region where systematic monitoring has become increasingly challenging.

We found protected areas supported a higher species richness of birds and bats than Emerald sites and non-protected areas. In turn, Emerald sites supported a greater richness of bats and small mammals than non-protected sites. There was also greater bat and bird acoustic activity for the majority of species monitored (bats: 14/15, birds: 6/9) in protected areas versus non-protected sites. Similarly, bat (12/15) and small mammal species (2/6) exhibited greater activity in Emerald sites compared to non-protected areas. These findings provide novel evidence that the existing protected area network- established without reference to these previously cryptic or unmonitored species- is also providing much wider benefit for these taxa. This adds to the literature demonstrating positive associations between the

Natura 2000 network and abundance for bat species in Europe (Ancillotto et al. 2023; Kerbiriou et al. 2018), and of SPAs and bird occurrence, abundance and trend (Donald et al. 2007; Barnes et al. 2023).

We are unaware of any similar large-scale studies on small mammals, although there is evidence that habitat protection may benefit shrews (Benedek et al. 2022), which we found associated with Emerald sites, but not legally protected sites. More broadly, small mammals are often associated with fallow agricultural habitats (Janova and Heroldova 2016), in line with our finding of their association with riparian agricultural habitats. The only group without any evidence of association with protected sites was bush crickets, underscoring the fact that insects are rarely considered when establishing protected sites, despite their potentially widespread declines (Chowdhury et al. 2023). These findings demonstrate the important multi-taxa potential of PAM to address important questions of surrogacy and systematic conservation planning in a way that has not been possible until now.

The weak spatial correlation of species richness and acoustic activity across taxa at finer scales (1 km²) contrasted with the emergence of distinct areas of shared high biodiversity at broader scales. This emphasises the importance of basing conservation efforts (such as PA designation), on multiple taxa, and at sufficient scale, a possibility now more readily available with PAM. A large proportion of high conservation priority areas, as measured by our results across taxa, were in PAs, comprising Europe's largest remaining intact transition mires, and one of Europe's last remaining unmodified major river systems. This highlights the importance of wetlands and natural hydrological regimes in driving biodiversity (Rolls et al. 2018). Given that wetlands are among the most threatened habitats globally (Zedler and Kercher 2005), our results show the importance of conserving these habitats in order to achieve multiple biodiversity objectives, in addition to carbon storage, flood mitigation, water storage etc. This is especially pertinent in Europe where historical wetland loss and degradation have been particularly extensive (Fluet-Chouinard et al. 2023).

Although protected areas in the Polesia region overlapped strongly with areas of high conservation priority, there were significant gaps. Notably, wetlands and riverine areas surrounding Almany Mires NR, and along the river Pripyat and its tributaries are not currently protected, but emerged as crucial for biodiversity and species of conservation concern, in our analysis. Whilst some are designated as Emerald sites, they lack legal protection in Ukraine. Our results show Emerald sites were strongly associated with high small mammal and bat diversity and acoustic activity. These should be a focus of future lobbying efforts for protection alongside major gaps in the protected area network that overlap with areas of high conservation priority, particularly as the conservation of such keystone species as small mammals can be critical for the conservation of their predators (Ratajc et al. 2022).

Despite the difficult terrain and poor road access in Polesia, we found that between 5 and 10 recorders were feasible for a field-worker to deploy at the same number of sites per day. Acoustic surveys allowed for over 500 sites to be surveyed for a minimum

of four nights in less than 200 days of fieldwork, including deployment and collection of recorders. In contrast to traditional surveys which are often limited to one taxonomic group, multi-taxa acoustic monitoring shows clear advantages in areas with a lack of resources in funding, time or expertise, but could also offer benefits in carbon efficiency for well-surveyed regions where citizen scientists often use private vehicles to collect data (Gillings and Harris 2022). We estimate that traditional methods would have required over 500 fieldwork days to survey nocturnal birds alone at the same number of sites (averaging two visits per site).

The additional ability of acoustic monitoring to sample cryptic and nocturnal species, offers advantages over other methods (Lambert and McDonald 2014) when these species are of conservation or ecological importance. We show that important data can be collected for multiple taxonomic groups using the same sampling design and recorder. The height and configuration of recorders could easily be altered to maximise detection for a taxonomic group (i.e., lower placement of recorders for small mammal species) (e.g., *Apodemus* species), that produce quiet and/or high frequency calls where the detection distance is low (Middleton et al. 2023) or multiple recorders could be placed at a site, optimised for different species groups. Our small mammal distribution models generally had lower AUC values than for other taxa, which may have led to an underrepresentation of their species richness and acoustic activity throughout the study region. This was potentially due to the lower number of detections of small mammals, and our inability to discriminate between some *Apodemus*, shrew and dormice spp. Our relative inability to identify small mammal species also would have reduced our sensitivity to discriminate between different levels of species richness for this taxa and potentially reduced this taxa's relative contribution to mapping areas of High Conservation Importance through species richness. Future work on the acoustics of these species will improve our capability of mapping small mammal distributions through acoustic surveys.

Acoustic recorder settings were a limitation of our study approach, we used recorders optimised for high-frequency recording, and although modified to trigger with lower frequency sounds (1 kHz), this could have reduced our detectability of audible species, such as nocturnal birds and reduced detectability could have been extrapolated due to our predictive modelling approach. Any detection bias for low frequency vocalising species is likely to be consistent across our sampling sites, however, and we did detect low-frequency vocalising species (e.g., Tawny Owl) at a significant proportion of sites (Figure S2). Acoustic recorders with the capacity to both record at audible and ultrasonic frequencies have since become available and we suggest using those in future multi-taxa studies, using continuous (rather than triggered) recording for audible species.

The multi-taxa acoustic survey approach we present has broader implications beyond species distribution modelling. It can inform site-based conservation, long-term population monitoring, phenology studies, restoration efforts and behavioural ecology (Ross et al. 2023). For instance, we identified probable breeding sites for protected species, such as Great Grey

Owls (*Strix nebulosa*), whose nests are legally protected in both Ukraine and Belarus. Acoustic monitoring can enhance our ability to survey cryptic, rare and protected species across extensive areas (Wood et al. 2023). Notably, the occurrence data generated from our research informed the scientific justification for establishing Pushcha Radzivila National Park and several regional protected areas in Ukraine. We anticipate that our findings on red-listed bats will contribute to the expansion of Rivnenskyi Nature Reserve, enhancing its scientific and conservation value as it represents the most comprehensive study on bats conducted in the region.

The ability for volunteers or non-experts to deploy equipment and the ability to cover large geographic areas can increase the spatial and temporal scale of questions asked through traditional monitoring (Ross et al. 2023). It allows large-scale and long-term data to be collected by more individuals, previously limited to those with taxonomic expertise to undertake extensive surveys. Combining traditional survey methods with acoustic monitoring can yield improved estimates of population abundance (Doser et al. 2021), though further research is necessary to understand the stochasticity of acoustic activity and the spatial-temporal resolutions required for population estimates.

After the devastating effects of the war in Ukraine, and the recent dismantling of the conservation sector in Belarus, systematically collected biodiversity data will be important to prioritise conservation efforts in Polesia. The methodologies, survey techniques and machine-learning classifiers developed in this study provide a foundational platform for low-resource biological monitoring, not only in the region but also globally.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used to produce the analyses in this manuscript will be stored on Zenodo.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** geb70175-sup-0001-AppendixS1.docx. **Appendix S2:** geb70175-sup-0002-AppendixS2.pdf. **Data S1:** geb70175-sup-0003-DataS1.xlsx.