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Exploring avian bycatch from a nationwide camera-trap monitoring program in Taiwan: Community composition, data completeness, and monitoring potential

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ABSTRACT: Camera-traps are increasingly used for long-term monitoring of terrestrial mammals, yet they also generate extensive avian bycatch data that remain underutilized. Here, we explore the potential of avian bycatch from large-scale, long-term camera-trap monitoring in Taiwan to characterize terrestrial bird community composition, evaluate sampling completeness, and assess its utility for ecological monitoring. Using data collected from 2015 to 2023 across elevational and seasonal gradients, we summarized species occurrence patterns, relative abundance indices, and diversity metrics based on Hill numbers. A total of 102 bird species or species groups were recorded from over 36,000 independent detection events, with species richness varying across elevations but showing relatively limited seasonal differences. Rarefaction and extrapolation analyses indicated that species richness (q = 0) did not reach asymptotes, reflecting incomplete detection of rare, arboreal, and canopy-associated species, whereas diversity estimates emphasizing common and dominant species (q = 1, 2) converged consistently across seasons and elevations, despite uneven sampling effort across elevational zones. As a species-level illustration, Malayan Night-Heron (*Gorsachius melanolophus*) case study demonstrated how camera-trap bycatch can provide valuable spatial, temporal, and behavioral information for cryptic, ground-associated birds that are not consistently detected in conventional forest surveys. Overall, our results show that avian bycatch from a large-scale, fixed-location camera-trap monitoring program offers a complementary data source for understanding terrestrial bird communities, particularly for dominant and ground-dwelling taxa. Given the long-term continuity of this government-operated monitoring program, continued accumulation and integration of avian camera-trap bycatch data hold substantial promise for future ecological research and biodiversity monitoring.

KEY WORDS: Avian camera-trap bycatch, camera trapping, community composition, elevational gradient, long-term monitoring.

INTRODUCTION

Birds are widely recognized as effective indicators of biodiversity and ecosystem condition (Fraixedas *et al.*, 2020), and long-term monitoring of avian communities is essential to ecological research and conservation planning (O'Brien and Kinnaird, 2008; Burton *et al.*, 2015). Patterns of bird species richness and community composition often vary along environmental gradients such as elevation, reflecting changes in season, habitat structure, and resource availability (Herzog *et al.*, 2003; Liang *et al.*, 2021; Hu *et al.*, 2025). Consequently, improving monitoring approaches for underrepresented components of avian communities has become an important issue in biodiversity research and conservation globally. In regions such as Taiwan, with steep elevational gradients, these patterns can occur over relatively short spatial distances, underscoring the need for comprehensive monitoring across space and time. In Taiwan, national-scale avian monitoring has been advanced through long-running programs such as the Taiwan Breeding Bird Survey (BBS) and the Taiwan New Year Bird Count (NYBC), which provide valuable information on avian diversity, distribution, and population status of breeding and wintering bird communities at the island-wide scale, respectively (Lin *et al.*, 2023a,b). Despite their importance, conventional visual- and auditory-based survey methods are less effective for cryptic, ground-dwelling, or forest-interior species, whose detectability is constrained by dense vegetation, low vocal activity, or nocturnal and crepuscular behavior. As a result, certain components of the avian community remain under-represented in existing monitoring frameworks, highlighting the need for complementary approaches.

Camera trapping has become a widely used tool for wildlife monitoring, originally targeting medium- to large-sized mammals (Burton *et al*., 2015; Sollmann, 2018). Because camera traps operate continuously with minimal disturbance, they provide standardized records of animal presence and activity across different spatial and temporal scales (O'Brien *et al.*, 2010). Beyond their original focus on mammals, an increasing number of studies have demonstrated that camera traps can reliably detect terrestrial and understory bird species, particularly those that are ground-dwelling, cryptic, or otherwise difficult to survey using visual or auditory methods (O'Brien and Kinnaird, 2008; Samejima *et al.*, 2012; Murphy *et al.*, 2018; Mere Roncal *et al.*, 2019; Fontúrbel *et al.*, 2020; Nguyen *et al.*, 2025). These studies established the technical

feasibility of using camera traps to document specific subsets of avian communities, especially ground-associated taxa that are often under-represented in traditional bird surveys. However, because most camera-trap systems are originally designed for mammals, the detectability of bird species may vary substantially depending on species ecology and camera placement configuration.

Despite this demonstrated capability, avian records obtained from camera-trap surveys are typically treated as non-target bycatch and are rarely analyzed systematically, particularly at large spatial scales (Burton *et al.*, 2015; Fontúrbel *et al.*, 2021). While several studies have shown that camera-trap bycatch can be used to describe avian assemblages, seasonal activity, and elevational distributions (Murphy *et al.*, 2018), the suitability of these data for different analytical purposes remains poorly understood. In particular, few studies have explicitly evaluated sampling completeness or distinguished between rarely detected species and those that are frequently or consistently recorded within avian bycatch datasets. In addition, because detection probabilities may vary among species depending on body size, behavior, habitat use, and camera placement, the interpretation of avian bycatch data requires careful consideration of methodological limitations. This lack of evaluation limits the effective use of camera-trap bycatch data for avian research and highlights the need for an exploratory assessment that clarifies both the structure and limitations of such data before they are applied to broader ecological questions.

In Taiwan, large-scale, long-term camera-trap monitoring has expanded rapidly since 2015 through the coordinated efforts of government agencies, with cameras deployed at fixed locations across broad geographical and elevational ranges. Although these cameras were primarily established for terrestrial mammals, their standardized deployment, continuous operation, and multi-year accumulation of data provide a unique opportunity to explore avian bycatch at an island-wide scale. The same monitoring system has already supported large-scale ecological analyses of native mammals in Taiwan, including assessments of the impacts of free-roaming dogs on native carnivores (Ho *et al.*, 2025). However, avian bycatch from camera-trap surveys in Taiwan has not been systematically characterized. Questions such as which bird species are most frequently recorded, how detections are distributed across elevation and seasons, and which components of the avian community are sufficiently sampled to support ecological analyses remain unclear. Moreover, because the monitoring protocols were originally optimized for mammals, evaluating the strengths and limitations of these avian bycatch data is necessary before broader ecological applications can be considered.

In this study, we take an exploratory approach to examine avian bycatch data derived from large-scale, long-term camera-trap monitoring in Taiwan. Our objectives are to summarize the taxonomic composition and relative frequency of bird species recorded as bycatch, describe differences in bird communities across elevation zones and seasons, and assess survey completeness using Hill-number-based rarefaction and extrapolation. Because ground-based camera traps preferentially detect terrestrial and ground-associated species, we further use a representative ground-associated bird to illustrate how avian camera-trap bycatch data can be applied beyond community-level descriptions. Specifically, we used the Malayan Night-Heron (*Gorsachius melanolophus*) as a case study to demonstrate how camera-trap bycatch can provide insight into spatial distribution, temporal dynamics, and diel activity patterns of cryptic species that are difficult to consistently detect in forest environments despite increasing observations in urban and suburban areas. Together, these analyses aim to clarify the strengths, limitations, and monitoring potential of avian camera-trap bycatch data as a complement to existing bird monitoring programs in Taiwan.

MATERIALS AND METHODS

Study area

Taiwan is a mountainous island in East Asia with a subtropical climate, characterized by strong elevational and environmental gradients over a relatively short spatial distance. The island covers approximately 36,000 km², and approximately 70% of the island is mountainous, with elevation ranging from sea level to 3,952 m, resulting in distinct variation in temperature, precipitation, and vegetation along elevational gradients. Mean annual precipitation is approximately 2500 mm, and average temperatures range from about 16 °C in winter to 28 °C in summer in lowland areas. In contrast to the largely forested mountainous regions, western Taiwan consists primarily of lowland plains with intensive human development. These geographic and climatic features make Taiwan suitable for examining broad-scale biodiversity patterns using spatially extensive monitoring data.

Camera-trap monitoring and data preparation

Data used in this study were obtained from the government-led project "Optimization of Long-term Wildlife Monitoring System and Data Integration" implemented by the Forestry and Nature Conservation Agency of Taiwan (Weng, 2025). This project was initiated in 2015 in response to the rabies outbreak in Formosan Ferret-badger (*Melogale subaurantiaca*) in 2013, with the primary goal of establishing a long-term camera-trap monitoring program for surveying populations of medium- to large-sized mammals in Taiwan. Over time, the monitoring program expanded in both spatial extent and elevational coverage, resulting in a standardized camera-trap system covering broad elevational and

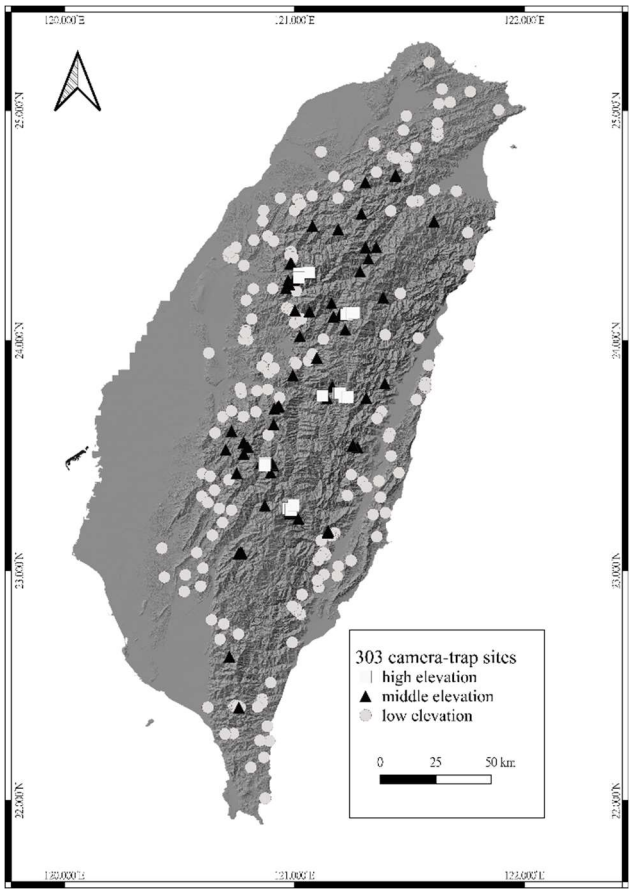

Fig. 1. Spatial distribution of camera traps across Taiwan from March 2015 to February 2023. Elevational categories used in subsequent analyses were defined as low elevation (< 1,500 m), middle elevation (1,500–2,500 m), and high elevation (> 2,500 m).

geographic gradients across Taiwan. By February 2023, 315 camera stations had been deployed across the main island and two offshore islands (Green Island and Orchid Island), spanning elevations from approximately 10 to 3,300 m (Fig. 1). Because camera traps operate continuously and record all mammals and birds passing through the detection zone, the dataset also contains many avian records collected as non-target bycatch.

We used the camera trapping data from March 2015 to February 2023. Camera traps were deployed using a standardized protocol designed primarily for monitoring terrestrial mammals rather than birds. Consequently, camera placement height, angle, and detection settings were optimized for mammals and may influence the detectability of different bird species. The number of active camera stations increased from 60 in 2015 to more than 300 during the study period. Therefore, sampling effort and elevational coverage varied over time as the monitoring program expanded from lowland areas to include mid- and high-elevation regions. For this study, a total of 303 cameras located on the main island of Taiwan were included, while cameras from two offshore islands were excluded. Camera traps operated continuously once deployed, resulting in sampling effort that varied both temporally and spatially through the study period. This uneven distribution of sampling reflects the phased expansion of the monitoring program and was considered when interpreting descriptive patterns in subsequent analyses.

All camera-trap images were screened manually to identify bird records, and only images that could be confidently identified to the species or predefined species-group level were retained for analyses. Less than 1% of bird images could not be reliably identified and were excluded from subsequent analyses (Supplementary Table S1). To maintain consistency and reduce misclassification, morphologically similar species that could not be reliably distinguished in camera-trap images were grouped at higher taxonomic levels. For example, White's Thrush (*Zoothera aurea*) and Scaly Thrush (*Zoothera dauma*) were classified as *Zoothera* sp., and all leaf warblers were categorized as *Phylloscopus* sp. To minimize pseudo-replication caused by repeated detections of the same individual, we defined an independent detection event as consecutive images of the same species at the same camera separated by at least one hour (O'Brien *et al.*, 2003). Independent detection events were treated as the primary sampling unit in subsequent analyses and standardized by camera-days when calculating relative abundance indices. When multiple individuals of the same species appeared in a single image, they were treated as a single detection event. Only independent detection events were used in subsequent analyses. This processing resulted in a standardized dataset of avian bycatch records suitable for descriptive community- and species-level analyses.

Data stratification and analytical approach

To summarize avian bycatch patterns across environmental gradients, detection data were descriptively stratified by elevation and season. We categorized elevation into three broad categories representing major environmental zones: low elevation (< 1,500 m), middle elevation (1,500 to 2,500 m), and high elevation (> 2,500 m). We divided the year into a conventional four-season framework: spring (March to May), summer (June to August), autumn (September to November), and winter (December to February). These stratifications were used only to organize and visualize variation in species composition and detection frequency, rather than to test causal effects of elevation or season. Camera numbers and associated sampling effort within each elevation category were summarized to aid interpretation of descriptive results.

To summarize avian community composition, we calculated Relative Abundance Index (RAI) for each species as the number of independent detection events divided by the total sampling effort (camera-days), multiplied by 100. To reduce the influence of unusually

high detection frequencies at individual camera stations, extreme outlier values exceeding three standard deviations were excluded prior to calculating mean RAI values. RAI is a widely accepted method in camera-trap studies for ranking species prevalence and comparing community structures across habitats (Sollmann *et al.*, 2013). Here, we used RAI as a standardized measure to describe relative detection frequency and to facilitate comparison of community composition across descriptive groupings, rather than as an estimate of absolute abundance. Because detection probabilities may differ among bird species depending on body size, behavior, habitat use, and camera placement configuration, RAI values should be interpreted as relative detection metrics rather than direct measures of population density or abundance. Differences in species composition among seasonal and elevation groups were quantified using the Bray-Curtis dissimilarity index (Oksanen *et al.*, 2025), which emphasizes shared species and their relative abundance while down-weighting joint absences, making it suitable for camera-trap bycatch data with many zero values. Bray-Curtis dissimilarity matrices were used to summarize patterns of community similarity among groups and to support exploratory comparisons of avian assemblages across environmental gradients. Community composition analyses and ordinations were performed using the 'vegan' package (version 2.7-2; Oksanen *et al.*, 2025).

Species diversity and sampling completeness were evaluated using Hill-number-based rarefaction and extrapolation analyses with the iNEXT package, based on abundance data derived from independent detection events. This approach accounts for differences in sampling effort and reduces bias in diversity estimation (Chao *et al.*, 2014; Hsieh *et al.*, 2016). Species diversity indices were quantified using Hill numbers of order $q = 0$ (species richness), $q = 1$ (Shannon diversity), and $q = 2$ (Simpson diversity), which provide a unified mathematical framework for comparing diversity patterns with different sensitivities to species abundance (Chao *et al.*, 2014). Rarefaction and extrapolation curves were generated based on abundance data (independent detection events) to assess whether sampling effort was sufficient to characterize avian diversity within each elevation and seasonal grouping. All diversity estimates were accompanied by 95% confidence intervals derived from 1,000 bootstrap replications (Chao *et al.*, 2014). In this study, Hill-number–based results were used primarily as diagnostic tools to distinguish well-sampled components of the avian community from those dominated by rare or infrequently detected species.

Species-level illustration: Malayan Night-Heron

To illustrate the potential of camera-trap bycatch data for monitoring ground-dwelling birds, the Malayan Night-Heron was selected as a focus species. Although the species is increasingly observed in urban and suburban environments in Taiwan, its occurrence and activity patterns within forest habitats remain comparatively less documented by conventional surveys. Elevational distribution was summarized by calculating mean RAI and naïve occupancy rate (proportion of cameras detecting the species) across elevation bins, with finer elevational intervals (200 m) used to depict distributional patterns. Temporal patterns were further explored by calculating the annual mean RAI and naïve occupancy rate for low-elevation sites (< 1,000 m) from 2016 to 2022. These analyses were intended to provide descriptive examples of potential applications of camera-trap bycatch data rather than formal population trend assessments. We then used non-parametric Kernel Density Estimation (KDE) (Ridout and Linkie, 2009) to visualize the diel activity pattern, providing an example of how camera-trap data can be used to characterize activity patterns of cryptic avian species. Activity pattern analyses and kernel density estimations were conducted using the 'overlap' package (version 0.3.9; Meredith *et al.*, 2024). All statistical analyses were performed in R (version 4.4.2).

RESULTS

From March 2015 to February 2023, the nationwide camera-trap network recorded more than 320,000 images containing birds, collected by 292 of the 303 deployed camera stations. After applying the independence criterion, a total of 36,000 independent avian detection events were retained, representing a total of 102 species groups (hereafter referred to as species). A detailed species-level summary of camera stations recording each species across elevational categories and seasons is provided in Supplementary Table S1. Species detections were broadly comparable across seasons, with 75 species recorded in winter, 72 species in autumn, 69 species in spring, and 65 species in summer (Table 1). In contrast, species richness varied more strongly along the elevational gradient, with 79 species recorded at low elevations, 64 species at middle elevations, and 36 species at high elevations. Sampling effort was uneven across years and elevational categories, reflecting the phased expansion of the monitoring program, with substantially greater camera-trap effort at low elevations and during later years of the project (Fig. 2).

Community composition and relative abundance patterns

Avian community composition based on RAI showed broadly similar patterns across seasons, with a small set of ground-dwelling and forest-associated species dominating detections throughout the year (Fig. 3A). Swinhoe's Pheasant (*Lophura swinhoii*) and Taiwan Partridge (*Arborophila crudigularis*) consistently ranked among the most abundant species in all seasons, while several winter

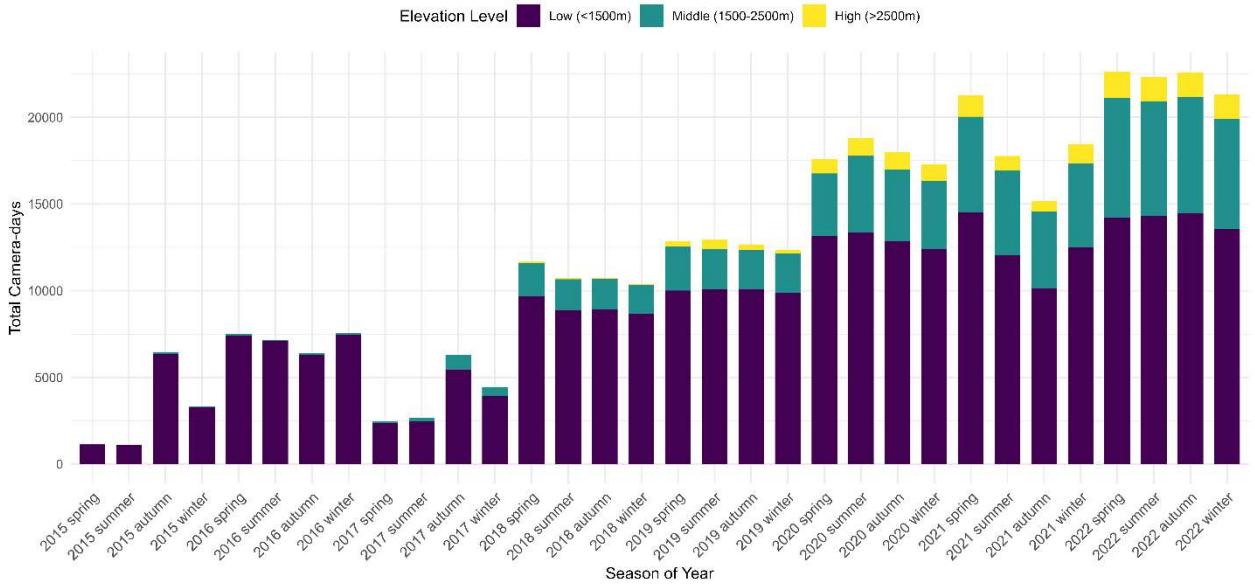

Fig. 2. Temporal and elevational distribution of camera-trap sampling effort from spring 2015 to winter 2022 (from December 2022 to February 2023). Bars represent total camera-trap effort (camera-days) per season and year, partitioned by elevational category (low, middle, and high). Sampling effort increased over time and was unevenly distributed across elevational categories due to the phased expansion of the monitoring program.

Table 1. Summary of avian bycatch observed and estimated avian diversity based on Hill numbers (q = 0, 1, and 2) across **A.** elevational and **B.** seasonal assemblages. For each assemblage, values are shown for observed diversity, extrapolated diversity estimated using iNEXT, and the number of undetected species inferred from extrapolation. Estimates are based on abundance data derived from independent camera-trap detection events.

A. Elevational assemblages

Assemblage	Metric	q = 0	q = 1	q = 2
All	Observed	102	9.84	4.68
	Extrapolation	116.38	9.85	4.68
	Undetected	14	0	0
Low	Observed	79	8.7	4.86
	Extrapolation	91.84	8.71	4.86
	Undetected	11	0	0
Middle	Observed	64	6.1	3.07
	Extrapolation	78.16	6.12	3.07
	Undetected	14	0	0
High	Observed	36	9.65	5.9
	Extrapolation	38.59	9.74	5.91
	Undetected	2	0	0

B. Seasonal assemblages

Assemblage	Metric	q = 0	q = 1	q = 2
Spring	Observed	69	8.53	4.28
	Extrapolation	76.58	8.55	4.28
	Undetected	7	0	0
Summer	Observed	65	9.7	4.95
	Extrapolation	77.59	9.73	4.95
	Undetected	12	0	0
Autumn	Observed	72	8.91	4.2
	Extrapolation	85.81	8.95	4.2
	Undetected	13	0	0
Winter	Observed	75	10.26	5.09
	Extrapolation	88.56	10.29	5.09
	Undetected	13	0	0

visitors, including *Zoothera* sp., Pale Thrush (*Turdus pallidus*), and Brown-headed Thrush (*Turdus chrysolaus*), showed higher relative contributions during winter. Despite these seasonal shifts in individual species, the overall community composition patterns remained relatively stable across seasons, which was further reflected by low Bray-Curtis dissimilarity values between seasonal assemblages (all pairwise dissimilarities < 0.3; Fig. 4A).

In contrast, the variation in RAI rankings along the elevational gradient were more pronounced (Fig. 3B). Low- and middle-elevation assemblages were dominated by similar core species, including Swinhoe's Pheasant and Taiwan Partridge, whereas high-elevation assemblages were characterized by a distinct set of species and reduced contribution from lowland dominants. Several elevation-associated species, such as Malayan Night-Heron, contributed more strongly at low elevation, while Taiwan Liocichla (*Liocichla steerii*) and White-tailed Robin (*Myiomela leucura*) contributed more strongly at middle elevations. Overall composition at high elevations differed substantially from that at the lower elevations. Consistent with these patterns, Bray-Curtis dissimilarity values indicated strong compositional turnover between high and lower elevation assemblages (Fig. 4B), whereas low and middle elevation community composition exhibited greater similarity to each other.

Species diversity and sampling completeness

Rarefaction and extrapolation analyses based on Hill numbers revealed contrasting patterns of sampling completeness depending on the order of diversity

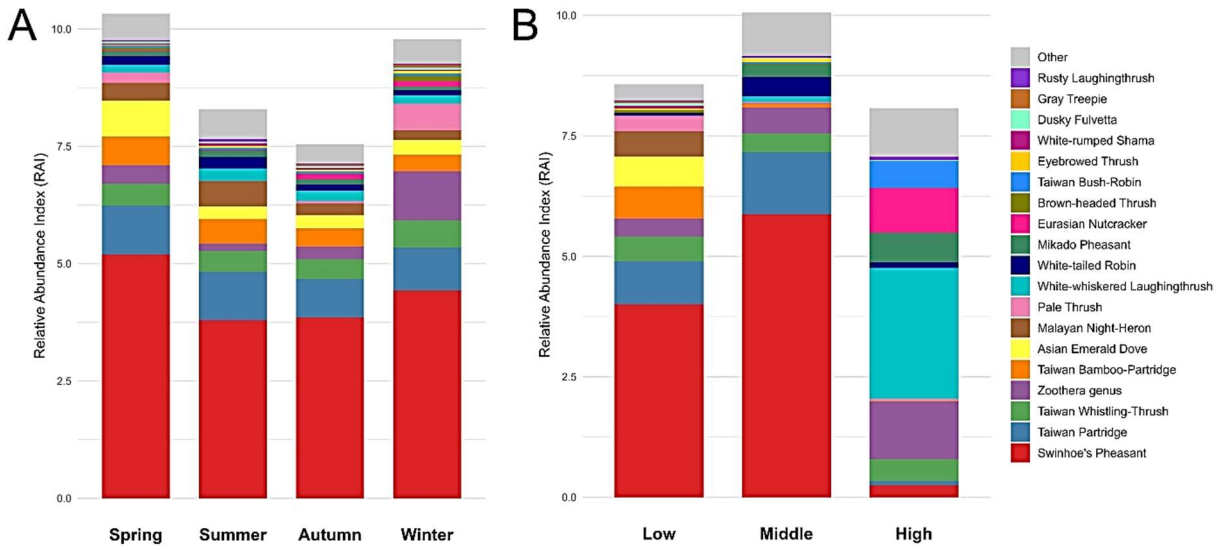

Fig. 3. Relative abundance composition of bird communities recorded by camera traps across **A.** seasons and **B.** elevational categories in Taiwan from March 2015 to February 2023. Bars represent relative abundance indices (RAI) for the most frequently recorded species, illustrating dominant species and changes in community composition across temporal and spatial gradients. RAI values were calculated after excluding extreme outliers exceeding three standard deviations. Elevational categories were defined as low elevation (< 1,500 m), middle elevation (1,500–2,500 m), and high elevation (> 2,500 m).

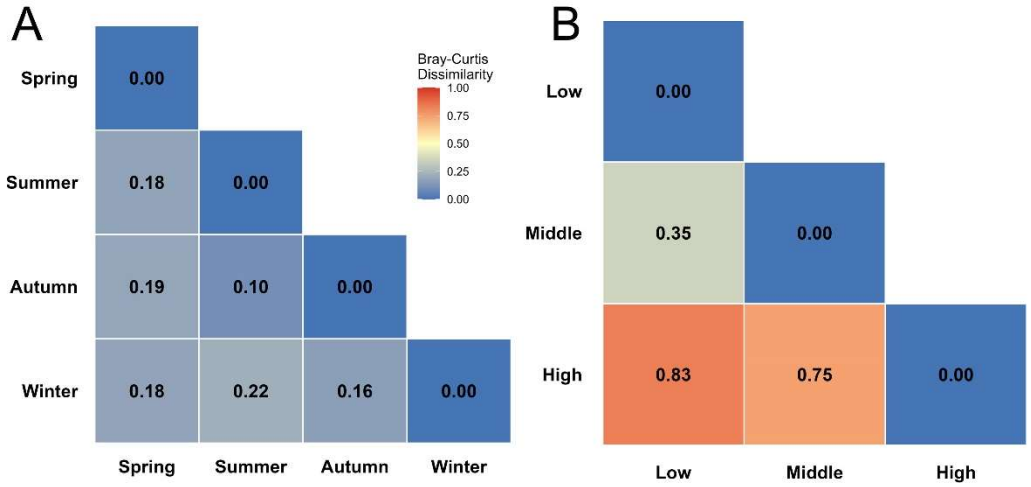

Fig. 4. Bray-Curtis dissimilarity matrices showing differences in the compositional similarity of avian communities among **A.** seasons and **B.** elevational categories based on relative abundance indices. Elevational categories were defined as low elevation (< 1,500 m), middle elevation (1,500–2,500 m), and high elevation (> 2,500 m).

considered (Fig. 5A; Table 1). For species richness (q = 0), extrapolated estimates exceeded observed values across the overall dataset as well as across seasonal and elevational assemblages, and none of the richness curves reached an asymptote, indicating incomplete detection and likely presence of undetected rare species. However, diversity curves for common (q = 1) and dominant species (q = 2) plateaued not only in the overall dataset but also across seasonal and elevational assemblages, suggesting that our sampling effort was sufficient to characterize the core bird community structure captured by camera traps.

The results in seasonal assemblages showed similar richness patterns, with overlapping confidence intervals for q = 0 across seasons (Fig. 5B). Differences among seasons became more apparent when considering abundance-weighted diversity, where q = 1 and q = 2 estimates were higher in summer and winter compared to spring and autumn (Fig. 5B; Table 1). Along the elevational gradient, estimated species richness (q = 0) declined with increasing elevation, with low-, middle-, and high-elevation assemblages expected to contain 91, 78, and 38 species, respectively. Patterns for q = 1 and q = 2 differed, with high-elevation assemblages showing comparable or higher Shannon diversity and Simpson diversity than the low- and middle-elevation assemblages despite lower overall richness (Fig. 5C). Although sampling effort was uneven across elevations, with substantially more independent detection events at low

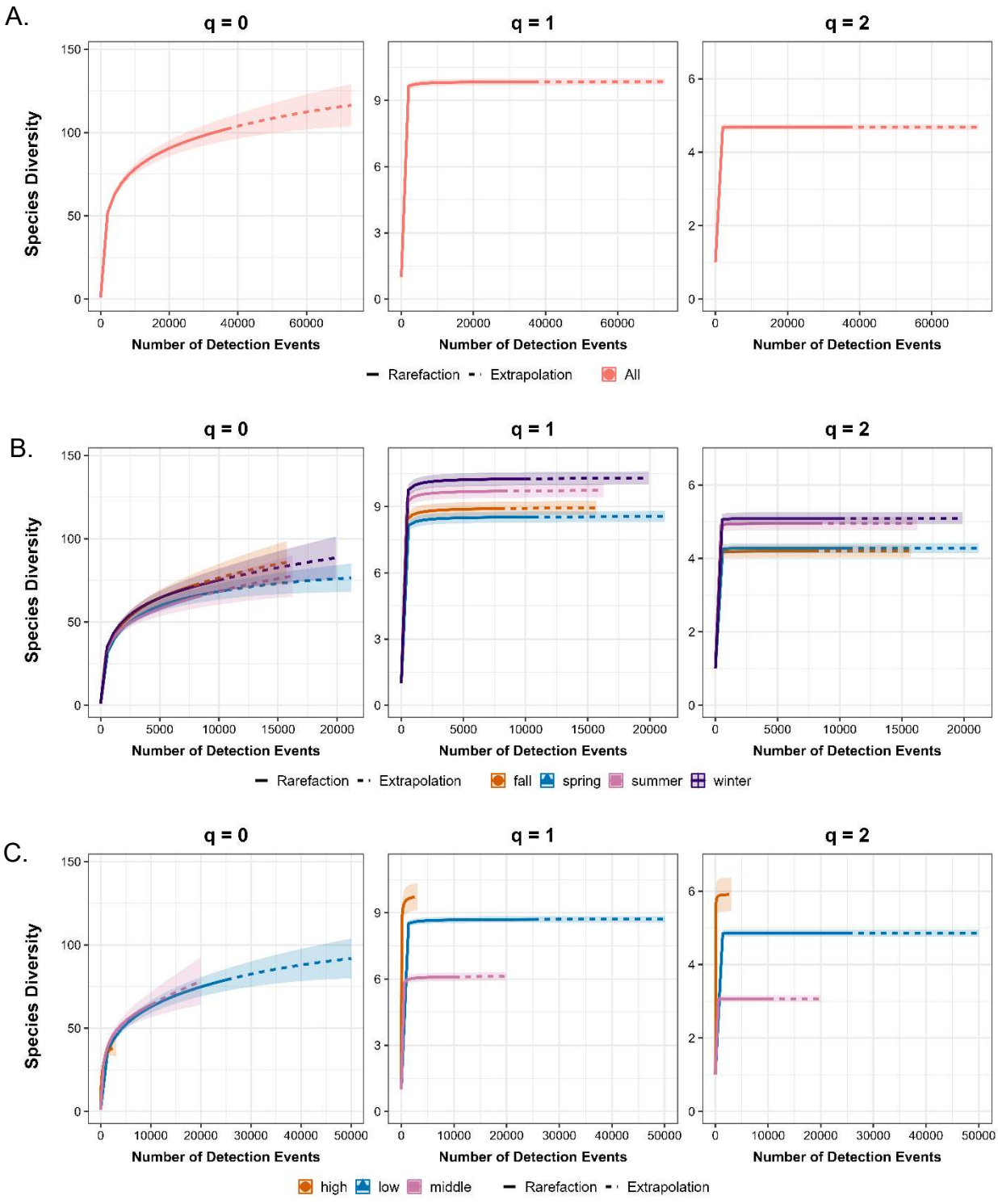

Fig. 5. Hill-number-based rarefaction and extrapolation curves for avian bycatch data from March 2015 to February 2023 across **A.** the overall assemblage, **B.** seasonal assemblages, and **C.** elevational assemblages. Curves are shown for species richness (q = 0), Shannon diversity (q = 1), and Simpson diversity (q = 2), with shaded areas representing 95% confidence intervals. Solid lines indicate rarefaction based on observed data, and dashed lines represent extrapolation. Elevational categories were defined as low elevation (< 1,500 m), middle elevation (1,500–2,500 m), and high elevation (> 2,500 m).

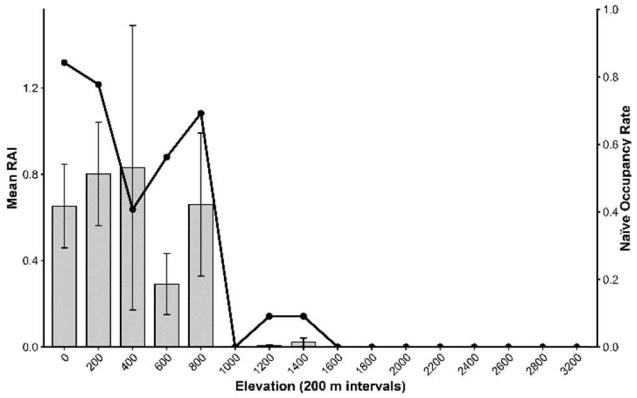

Fig. 6. Elevational distribution of Malayan Night-Heron (***Gorsachius melanolophus***) based on camera-trap records across the study period. Bars represent mean relative abundance index (RAI ± SE), and the solid line indicates naïve occupancy, expressed as the proportion of camera stations with at least one independent detection within each 200 m elevational band.

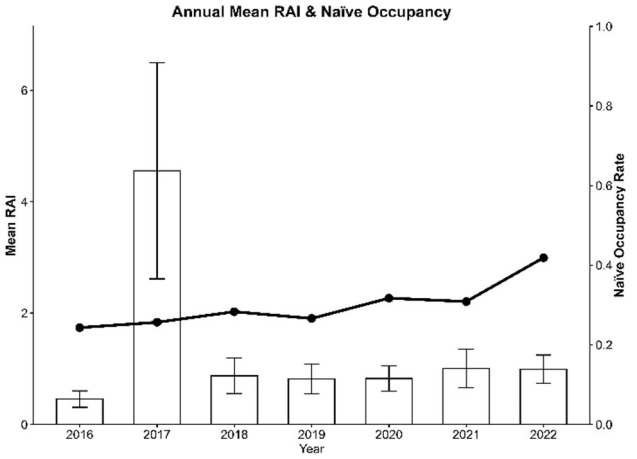

Fig. 7. Interannual variation in detections of Malayan Night-Heron (***Gorsachius melanolophus***) below 1,000 m elevation from 2016 to 2022. Bars indicate mean annual relative abundance index (RAI ± SE) after excluding outlier values exceeding three standard deviations, and the line shows naïve occupancy, expressed as the proportion of working camera stations that detected the species in each year. Data from 2015 and 2023 were excluded because only partial-year records were available.

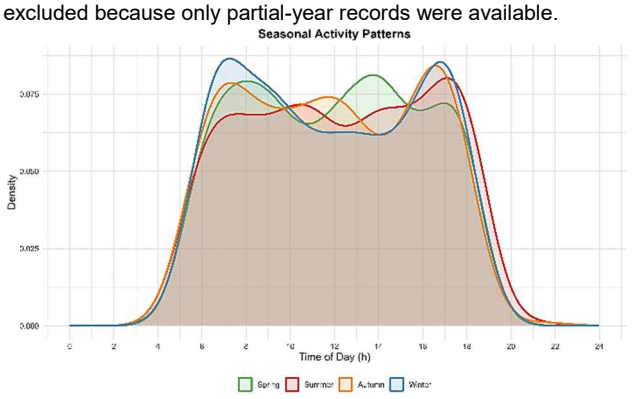

Fig. 8. Seasonal diel activity patterns of Malayan Night-Heron (***Gorsachius melanolophus***) based on kernel density estimation of independent camera-trap detection events. Curves represent kernel density estimates of activity across the 24-hour cycle for each season.

elevation (>25,000) than at high elevations (around 1,500; Fig. 2), diversity estimates for common and dominant species converged across elevational assemblages, indicating stable representation of commonly recorded species despite differences in total camera-trap effort.

Species-level illustration: Malayan Night-Heron

Malayan Night-Heron was consistently recorded by camera stations at low elevations and represented one of the most frequently detected ground-dwelling species in the dataset. Based on the RAI (ranked fifth at low elevation) and naïve occupancy, detections were concentrated below 1,000 m, with both metrics declining sharply at higher elevations (Fig. 6). Across the study period, mean annual RAI and the proportion of camera stations detecting Malayan Night-Heron generally increased from 2016 to 2022 (Fig. 7), suggesting broader detection within monitored lowland forest sites. The daily activity patterns of Malayan Night-Heron showed a pronounced diurnal rhythm (Fig. 8). The kernel density analysis revealed that activity typically started near sunrise and declined toward sunset, with some variation among seasons. Despite these shifts in timing among seasons, the overall shape of the daily activity curve remained consistent throughout the year.

DISCUSSION

This study provides a nationwide, exploratory assessment of avian bycatch data from a long-term, spatially extensive camera-trap monitoring program in Taiwan, demonstrating that a substantial number of bird species can be recorded incidentally through monitoring programs primarily designed for mammals. Across nearly a decade of sampling, camera traps captured a diverse avian assemblage, with community composition showing limited seasonal variation but pronounced differentiation along the elevational gradient. Analyses of sampling completeness further revealed that while rare species were incompletely detected, the diversity of common and dominant species was consistently characterized across seasons and elevations. Together, these results highlight the potential value of using existing camera-trap data without additional survey costs and resonate with a growing global trend in conservation biology that emphasizes the maximization of bycatch data to broaden biodiversity insight (Burton *et al.*, 2015; Murphy *et al.*, 2018).

Although camera-trap bycatch revealed similar dominant species across seasons, this pattern is likely influenced by the sampling bias of ground-based cameras toward resident and frequently detected species and does not necessarily reflect seasonal patterns of the entire avian community. In particular, species-specific detection probabilities may vary substantially depending on body size, movement behavior, habitat use, and camera

placement configuration, potentially increasing the detectability of larger-bodied or ground-active species. Seasonal variation was still apparent for certain taxa, particularly among ground-foraging species that occur primarily during winter. For example, thrushes such as the Pale Thrush and Brown-headed Thrush showed markedly higher detection frequencies during winter, consistent with the seasonal presence of migratory species. Additionally, altitudinal migration of resident species descending from high to lower elevation during colder months has been documented in Taiwan (Tsai *et al.*, 2021) and may also contribute to the increased seasonal detectability at low and middle elevations. In contrast to these taxon-specific seasonal signals, community composition differed more strongly along elevational gradients, a pattern widely reported in avian studies, where differences in temperature, vegetation structure, and habitat heterogeneity act as strong environmental filters (Shiu and Lee, 2003; Lee *et al.*, 2004; Alvarez-Alvarez *et al.*, 2018). Together, these findings suggest that while seasonal changes in detectability occur for specific ecological groups, elevational gradients remain the dominant structuring force shaping avian assemblages captured by camera-trap bycatch.

Patterns of sampling completeness based on Hill numbers indicate that the camera-trap dataset did not fully capture rare species ($q = 0$), whereas common ($q = 1$) and dominant ($q = 2$) species were consistently well represented across seasons and elevational zones. This contrast between richness estimates and abundance-weighted diversity is a well-recognized feature of biodiversity assessment, and rarefaction and extrapolation methods provide a formal framework for evaluating how completely sampling effort captures underlying diversity (Chao *et al.*, 2014; Hsieh *et al.*, 2016). Despite uneven sampling effort across elevations and seasons, the curves of abundance-weighted diversity estimates plateaued rapidly, indicating reliable representation of frequently detected components of avian assemblages. However, the failure of species richness curves ($q = 0$) to reach asymptote highlights an inherent limitation of ground-based camera trapping, as many rare, canopy-dwelling, or arboreal bird species were systematically under-detected due to the ground-oriented placement and mammal-focused configuration of camera traps. Therefore, camera trapping should be viewed as a complementary approach to traditional transect or point count surveys, rather than a replacement, especially for characterizing ground-associated and frequently encountered components of avian communities. This also demonstrates the importance of integrating sampling completeness diagnostics when interpreting biodiversity patterns from incidental observations.

The Malayan Night-Heron provides a clear illustration of how avian bycatch from camera-trap networks can provide meaningful ecological information for species that are difficult to monitor using conventional survey methods. This species was consistently and frequently detected by ground-level cameras in lowland forests, reflecting its ground-foraging behavior. In contrast, large-scale visual and auditory surveys such as the Taiwan Breeding Bird Survey have explicitly noted that population indices for nocturnal species, including the Malayan Night-Heron, should be interpreted with caution due to the methodological limitations of survey design (Fan *et al.*, 2025). Historically, Malayan Night-Heron has been regarded as a cryptic, forest-associated species that is difficult to observe directly (Severinghaus *et al.*, 2012). In recent decades, however, increased observations in urban and suburban habitats have substantially improved public awareness and understanding of this species, while its status within forest habitat, the presumed core of its original distribution, has remained understudied. Camera-trap data therefore provide a valuable and cost-effective source of information that helps address this imbalance by documenting occurrence, distribution, and activity patterns within forest environments that are difficult for direct observation.

The elevational distribution observed, characterized by a strong concentration of detections at low elevations under 1,000 m, and only occasional detections at four camera stations above 1,000 m, is consistent with current ecological understanding of the species (Martínez-Vilalta *et al.*, 2020). Moreover, both RAI and the proportion of camera stations detecting Malayan Night-Heron generally increased during the study period, indicating broader detection of the species within lowland forest sites covered by the camera-trap monitoring program. Such data provide a valuable empirical basis for further studies examining habitat use and long-term distributional dynamics. In addition to the spatial and temporal pattern of occurrence, the camera-trap dataset also captured fine-scale diel activity information. The predominantly diurnal activity pattern observed in our camera-trap data is broadly consistent with previous observations suggesting that the Malayan Night-Heron are not strictly nocturnal. Although the species has traditionally been described as crepuscular or nocturnal (Martínez-Vilalta *et al.*, 2020), daytime observations are frequently reported in Taiwan (Jang, 2021). Similarly, Sawada (2023) documented parental feeding activity from morning to early evening at a breeding nest in Japan, indicating substantial daytime activity during the breeding season. However, quantitative information on year-round activity patterns remains limited, making direct validation of seasonal differences difficult. Because our analyses were derived from ground-level camera traps, seasonal variation in habitat use, such as changes in the relative use of ground versus arboreal strata, could also influence detection probability. Consequently, seasonal differences in activity patterns

should be interpreted cautiously. Nevertheless, our results demonstrate how long-term camera-trap bycatch can provide novel behavioral information for species whose activity patterns are otherwise difficult to quantify consistently across broad spatial and temporal scales.

This study demonstrates that avian bycatch from large-scale camera-trap monitoring programs represents a valuable and underutilized resource for understanding terrestrial bird communities, particularly in regions where long-term mammal monitoring networks are already established. While ground-based cameras are inherently selective and incomplete for documenting total avian species richness, they consistently record dominant and frequently detected species, particularly ground-dwelling and ground-foraging taxa that are often underrepresented in conventional monitoring programs such as Breeding Bird Surveys or New Year Bird Counts. When interpreted alongside these established surveys, camera-trap bycatch data therefore provide complementary information that helps fill taxonomic and ecological gaps rather than replacing existing methods. Our findings also suggest that camera-trap deployment protocols optimized for mammals could potentially be further refined for ground-dwelling birds, for example through lower camera placement, reduced focal distance, or camera orientations that increase coverage near the ground surface while still maintaining mammal-monitoring functions. However, the effectiveness of such modifications remains to be explicitly tested in future studies. Moreover, the spatial replication and temporal continuity of the camera-trap monitoring program create opportunities for future analytical approaches, including occupancy-based or hierarchical models that explicitly account for uneven sampling effort and imperfect detection. Importantly, the government-led nature of this long-term camera-trap network ensures ongoing data collection, creating a sustained and expanding archive of avian bycatch observations. This continuity enhances the value of these data for future ecological research and conservation planning beyond the network's original mammal-focused objectives, particularly across seasonal and elevational gradients in heterogeneous landscapes such as Taiwan.

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LITERATURE CITED

Alvarez-Alvarez, E.A., Corcuera, P., Almazán-Núñez, R.C. 2018 Spatiotemporal variation in the structure and diet types of bird assemblages in tropical dry forest in southwestern Mexico. Wilson J. Ornithol. **130(2)** : 457–469.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., Boutin, S. 2015 Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. J. Appl. Ecol. **52(3)** : 675–685.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M. 2014 Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. Ecol. Monogr. **84(1)** : 45–67.

Fan, M.-W., Hsu, W.-T., Tsai, M.-K., Wei, H.-Y., Ko, C.-J., Lin, R.-H., Chang, R.-L., Lu, Y.-W., Lee, P.-F., 2025 Taiwan breeding bird survey: 2024 annual report. Biodiversity Research Institute, Ministry of Agriculture, Taiwan. (in Chinese).

Fontúrbel, F.E., Rodríguez-Gómez, G.B., Fernández, N., García, B., Orellana, J.I., Castaño-Villa, G.J. 2020 Sampling understory birds in different habitat types using point counts and camera traps. Ecol. Indicators **119**: 106863.

Fontúrbel, F.E., Orellana, J.I., Rodríguez-Gómez, G.B., Tabilo, C.A., Castaño-Villa, G.J. 2021 Habitat disturbance can alter forest understory bird activity patterns: A regional-scale assessment with camera-traps. For. Ecol. Manage. **479**: 118618.

Fraixedas, S., Lindén, A., Piha, M., Cabeza, M., Gregory, R., Lehikoinen, A. 2020 A state-of-the-art review on birds as indicators of biodiversity: Advances, challenges, and future directions. Ecol. Indicators **118**: 106728.

Herzog, S.K., Soria A., R., Matthysen, E. 2003 Seasonal variation in avian community composition in a high-Andean Polylepis (Rosaceae) forest fragment. Wilson Bull. **115(4)**: 438–447.

Ho, H.-C., Ding, T.-S., Yuan, H.-W., Tsai, J.-S., Weng, G.-J., Lin, Y.-H., Chen, H. L., Huang, Y.-B., Yen, S.-C. 2025 Impacts of free-roaming dogs on spatiotemporal niches of native carnivores in Taiwan. Global Ecol. Conserv. **57**: e03411.

Hsieh, T.C., Ma, K.H., Chao, A. 2016 iNEXT: An R package for rarefaction and extrapolation of species diversity (hill numbers). Methods Ecol. Evol. **7(12)**: 1451–1456.

Hu, Y., Xu, Y., Hu, H., Scheffers, B.R. 2025 Seasonal variation in community structure and elevational distributions of mammals and birds in the central Himalayas. Ecography **2025(9)**: e07973.

Jang, J.-J. 2021 Understanding habitat preference of G*orsachius melanolophu*s in urban areas using systematic surveys and citizen science. Master thesis, National Taiwan University, Taipei, Taiwan.

Lee, P.F., Ding, T.S., Hsu, F.H., Geng, S. 2004 Breeding bird species richness in Taiwan: Distribution on gradients of elevation, primary productivity and urbanization. J. Biogeogr. **31(2)**: 307–314.

Liang, D., Pan, X., Luo, X., Wenda, C., Zhao, Y., Hu, Y., Robinson, S. K., Liu, Y. 2021 Seasonal variation in community composition and distributional ranges of birds along a subtropical elevation gradient in China. Divers. Distrib. **27(12)**: 2527–2541.

Lin, D.-L., Ko, C.-J., Amano, T., Hsu, C.-T., Fuller, R.A., Maron, M., Fan, M.-W., Pursner, S., Wu, T.-Y., Wu, S.-H., Chen, W.-J., Bayraktarov, E., Mundkur, T., Lin, R.-S., Ding, T.-S., Lee, Y.-J., Lee, P.-F. 2023a Taiwan's breeding bird survey reveals very few declining species. Ecol. Indicators **146**: 109839.

Lin, D.-L., Tsai, C.-Y., Pursner, S., Chao, J., Lyu, A., Amano, T., Maron, M., Lin, R.-S., Lin, K.-H., Chiang, K.-K., Lin, Y.-L., Lu, L.-C., Chang, A.-Y., Chen, W.-J., Fuller, R. A. 2023b Remote and local threats are associated with population change in Taiwanese migratory waterbirds. Global Ecol. Conserv. **42**: e02402.

Martínez-Vilalta, A., Motis, A., Kirwan, G.M. 2020 Malayan Night-Heron (*Gorsachius melanolophus*), version 1.0. In: Hoyo, J.D., Elliott, A., Sargatal, J., Christie, D.A., Juana, E.D. (eds.) Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.

Mere Roncal, C., Middendorf, E., Forsyth, A., Cáceres, A., Blake, J.G., Almeyda Zambrano, A.M., Broadbent, E.N. 2019 Assemblage structure and dynamics of terrestrial birds in the southwest Amazon: A camera-trap case study. J. Field Ornithol. **90(3)** : 203–214.

Meredith, M., Ridout, M.S., Campbell, L.A.D. 2024 Overlap: Estimates of coefficient of overlapping for animal activity patterns (version 0.3.9). https://cran.r-project.org/web/packages/overlap/index.html.

Murphy, A.J., Farris, Z.J., Karpanty, S., Kelly, M.J., Miles, K.A., Ratelolahy, F., Rahariniaina, R.P., Golden, C.D. 2018 Using camera traps to examine distribution and occupancy trends of ground-dwelling rainforest birds in north-eastern Madagascar. Bird Conserv. Int. **28(4)**: 567–580.

Nguyen, A.T., Nguyen, A., Le, M., Wilting, A., Tilker, A. 2025 Camera-trapping reveals both defaunation and conservation priority species in an unprotected forest in Vietnam. Global Ecol. Conserv. **61**: e03644.

O'Brien, T.G., Kinnaird, M.F., Wibisono, H.T. 2003 Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim. Conserv. **6(2)** : 131–139.

O'Brien, T.G., Kinnaird, M.F. 2008 A picture is worth a thousand words: The application of camera trapping to the study of birds. Bird Conserv. Int. **18(S1)** : S144–S162.

O'Brien, T.G., Baillie, J.E. M., Krueger, L., Cuke, M. 2010 The wildlife picture index: Monitoring top trophic levels. Anim. Conserv. **13(4)**: 335–343.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szöcs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Borman, T., Carvalho, G., Chirico, M., Cáceres, M.D., Weedon, J., 2025 Vegan: Community ecology package (version 2.7-2). doi: https://cran.r-project.org/web/packages/vegan/index.html.

Ridout, M.S., Linkie, M. 2009 Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. **14(3)**: 322–337.

Samejima, H., Ong, R., Lagan, P., Kitayama, K. 2012 Camera-trapping rates of mammals and birds in a Bornean tropical rainforest under sustainable forest management. For. Ecol. Manage. **270**: 248–256.

Sollmann, R. 2018 A gentle introduction to camera-trap data analysis. Afr. J. Ecol. **56(4)**: 740–749.

Sawada, A. 2023 A breeding record of Malayan Night-Heron *Gorsachius melanolophus* on Hateruma island. Ornithol. Sci. **22(2)**: 169–174.

Severinghaus, L. L., Ding, Z.-S., Fang, W.-H., Lin, W.-H., Tsai, M.-C., Yen, C.-W. 2012 The avifauna of Taiwan. 2nd ed. Forestry and Natural Conservation Agency, Taipei, Taiwan.

Shiu, H.-J., Lee, P.-F. 2003 Seasonal variation in bird species richness along elevational gradients in Taiwan. Acta Zool. Taiwan. **14(1)**: 1–21.

Sollmann, R., Mohamed, A., Samejima, H., Wilting, A. 2013 Risky business or simple solution – relative abundance indices from camera-trapping. Biol. Conserv. **159:** 405–412.

Tsai, P.-Y., Ko, C.-J., Chia, S. Y., Lu, Y.-J., Tuanmu, M.-N. 2021 New insights into the patterns and drivers of avian altitudinal migration from a growing crowdsourcing data source. Ecography **44(1)**: 75–86.

Weng, G.-J. 2025 Optimization of the long-term wildlife monitoring system and data integration (1/4). Forestry and Nature Conservation Agency, Taiwan. Available at https://www.forest.gov.tw/report/0003951.

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