



Spatio-temporal variation in avian taxonomic, functional, and phylogenetic diversity and its relevance for conservation in a wetland ecosystem in Myanmar

Thazin Htay^{1,2} · Eivin Røskraft¹ · Thor Harald Ringsby^{1,3} · Peter Sjolte Ranke^{1,3}

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Abstract

Wetland ecosystems host an extensive number of avian species and play therefore a key role in biodiversity conservation. However, avifauna in wetlands is severely impacted by the anthropogenic transformation of natural habitats into other land uses. Understanding how habitat changes influence avian community dynamics is crucial for effective management and conservation of bird habitats. Here, we assessed spatio-temporal variation in taxonomic, functional, and phylogenetic diversity, and assembly structures of the bird community in the Indawgyi Wetland Ecosystem in Myanmar. Bird surveys were seasonally conducted at 120 sample plots, which were equally distributed among four habitat types subject to different level of human influences (natural lake habitat, seasonally flooded grasslands, riparian forest, and agricultural land). Across habitat types, functional and phylogenetic diversity were the highest in the lake habitat, especially during the migration season, and the lowest in the cultivated habitat. Our results indicated over-dispersed functional and phylogenetic structures in the lake habitat, with clustered structures in the remaining habitats. Diversity of species important for conservation was also higher in the lake habitat and in areas far away from human disturbances. Spatial variation of bird community diversity suggests that conservation efforts in this ecosystem should concentrate more on the lake habitat and associated grassland habitats. Moreover, our results suggest the need for habitat restoration in riparian forests and increased sustainable agricultural practices in order to improve the contribution of these habitats to the diversity in the avifauna community. Our study highlighted the importance of integrating functional and phylogenetic dimensions into biodiversity analyses providing broader ecological insights for conservation.

Keywords Bird diversity · Biodiversity conservation · Ecological traits · Evolutionary history · Anthropogenic disturbance · Indawgyi · Spatio-temporal patterns

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Thor Harald Ringsby and Peter Sjolte Ranke are joint senior authors.

Extended author information available on the last page of the article

Introduction

In the face of the sixth mass extinction, avian diversity is severely threatened by habitat loss and fragmentation (Jetz et al. 2007; IPBES 2019). Land use and land cover changes driven by anthropogenic activities have reduced the global abundance of birds by 20–25% since industrial development (Birdlife International 2022; Lees 2022). Currently, 48% of all bird species are undergoing population declines and 13% (i.e., one in eight species) are threatened with extinction (Birdlife International 2022). Agriculture and logging have caused degradation of valuable bird habitats such as wetlands and therefore they have been recognized as main drivers for avian population declines (Convention on Wetlands 2021; Birdlife International 2022; Lees et al. 2022). Ramsar convention reported that 35% of natural wetlands have been lost between 1970 and 2015 (Convention on Wetlands 2021). As wetlands are among the most productive ecosystems supporting a wide range of biota, deterioration of these habitats has affected many groups of avian taxa (Xu et al. 2019; Lees et al. 2022). In Asia alone, 5000 km² of wetlands are annually converted into agriculture and its related land uses (McAllister et al. 2001). An extensive wetland loss caused by various kinds of land use changes has posed an enormous pressure on wetland-dependent birds (Fluet-Chouinard et al. 2023). As the biodiversity crisis is projected to increase with the current rate of increase in land use changes, effective mitigation measures and targeted conservation actions are urgently needed to preserve vulnerable wetland habitats (Jetz et al. 2007).

With increasing global concerns about anthropogenic impacts on natural ecosystems, assessment of biodiversity has received much attention for habitat management (Devictor et al. 2010). Traditionally, measurements of biodiversity have relied on taxonomic diversity (TD), an approach that considers that all species in the ecosystem are equally important (Webb et al. 2002). However, conservation decisions based only on TD are not sufficient as it ignores the ecological function and evolutionary relatedness of co-occurring species and therefore provides little information about the species contribution to ecosystem structure and dynamics (Webb et al. 2002; Swenson 2014). Accordingly, functional diversity (FD) which quantifies variability of species-specific morphological, behavioral, and ecological traits that influence ecosystem function or species responses to environmental changes, and phylogenetic diversity (PD) that characterizes species evolutionary history, are increasingly integrated in biodiversity analyses to acquire a more comprehensive ecological information (Devictor et al. 2010; Meynard et al. 2011; Cisneros et al. 2015; He et al. 2018; Che et al. 2019; Lee 2022). Measures of FD and PD provide mechanistic links to ecosystem resilience and evolutionary potential to persist future environmental perturbations (Petchey and Gaston 2007; de Bello et al. 2021). Functional-, and phylogenetic structures could also reveal underlying mechanisms defining community assemblages (Weiher et al. 2011; de Bello et al. 2021). For instance, if the functional traits are phylogenetically conserved, functional and phylogenetic clustering suggests that closely related species or only species with similar functional traits, will coexist in a given environment (i.e., the ecology assemblage is driven by environmental filtering) (Webb et al. 2002; Weiher et al. 2011; de Bello et al. 2021). On the other hand, functional and phylogenetic overdispersion suggests interspecific competition where ecologically similar species are excluded due to resource competition, and coexisting species are evolutionally or functionally different from each other (Webb et al. 2002; de Bello et al. 2021).

Birds are sensitive to ecosystem changes and thus function as biological indicators to understand biodiversity and habitat relationships (Lees et al. 2022). Previous studies have

demonstrated that bird-habitat relationships are primarily determined by habitat composition and configuration, as proposed by two prevailing hypotheses (Cisneros et al. 2015; Godet et al. 2016; Klingbeil and Willig 2016; He et al. 2018). “The habitat heterogeneity hypothesis” predicts that bird species diversity increases with structural complexity (for instance, number of land cover types in a landscape) because of niche differences and variability in available food resources (MacArthur and MacArthur 1961; Ke et al. 2018). Alternatively, “the habitat amount hypothesis” suggests that species diversity is a function of the area or extent of suitable habitats in a landscape (Fahrig 2003, 2013; Bennett et al. 2006). Although habitat factors positively influence TD, its effects may not necessarily be the same for other biodiversity facets (Cisneros et al. 2015; Klingbeil and Willig 2016; Häkikilä et al. 2017; He et al. 2018; Li et al. 2019). Especially in human dominated landscapes, bird response to habitat factors is mediated by anthropogenic actions and often results in inconsistent patterns of biodiversity facets (Meynard et al. 2011; Häkikilä et al. 2017; Lee and Martin 2017). For instance, in forest patches surrounded by agricultural landscapes in Poland, Belcik et al. (2020) found that TD increased with forest area while PD decreased, and FD remained unaffected. A study by Li et al. (2019) on wetlands in North China Plain also reported that FD of waterbirds responded positively to habitat diversity, while the PD showed no response. In addition to these proven influences of habitat factors, ecological mechanisms driving community assembly can change with disturbance intensity (Lopez et al. 2016); for example, selective pressure and habitat filtering can be more prominent in the disturbed portion of a disturbance gradient where bird communities are dominated by species that can survive in stressful habitats (Lopez et al. 2016). Several other studies have found that the effect of habitat fragmentation and isolation are stronger on PD because phylogenetically distinct species prefer less degraded habitats (Cisneros et al. 2015; Klingbeil and Willig 2016; Ke et al. 2018; Belcik et al. 2020). These studies, showing different responses in TD, FD, and PD, highlights that conservation decisions based solely on one facet, would give misleading recommendations to conservation (Devictor et al. 2010; Meynard et al. 2011). Therefore, predictions using multi-facet approaches are required to better characterize the biodiversity, especially in the face of the ongoing global change (Andrén 1994; Devictor et al. 2010; Ke et al. 2018; Zeng et al. 2019).

Myanmar is located in the Indo-Burma biodiversity hotspot and its diverse ecosystems are different in terms of avian species richness and abundance of threatened birds (Davies et al. 2004; Forest Department 2015). Among all ecosystems, wetlands cover almost 85,000 km² of the country’s area and are thus important for bird conservation (Nature and Wildlife Conservation Division 2020). Nonetheless, wetlands are the most disturbance-prone ecosystems due to proliferation of human land uses. As an agricultural-based country, its wetlands are under pressure from agricultural expansion and intensification (Nature and Wildlife Conservation Division 2020). Transformation of natural wetlands into other land uses (agriculture, village development) causes homogenization of available resources which could further impose serious ecological and evolutionary consequences to avifauna (Şekercioğlu 2012; Liang et al. 2019). However, a less intensive agricultural matrix could lead to an alternative habitat for birds if managed sustainably (Lee 2022). Tscharnkte et al. (2012) suggested that agri-environmental schemes are potential conservation strategies in areas where large natural and semi-natural landscapes remain, and that many bird species are able to utilize these habitats. These kinds of sustainable agricultural practices are especially important for Myanmar because more than half of the wetland areas are human created and managed, as for instance rice paddies (Nature and Wildlife Conservation Division 2020). Understanding the impacts of wetland transformation and the conservation potential of existing agricultural systems is very important for future wetland management (Xu

et al. 2019). High priority should be given to conserve all facets of diversity (Devictor et al. 2010). However, wetland ecosystems in Myanmar are underrepresented within ecological research and no study has simultaneously assessed TD, FD, and PD of bird communities in wetlands in this region. Additionally, these wetlands are wintering sites for migratory birds flying through the East Asian Australasian Flyway and the Central Asian Flyway (Nature and Wildlife Conservation Division 2020). Therefore, it is important to consider both temporal and spatial variation in the analyses of diversity and structure of the avian community (Bennett et al. 2006; Che et al. 2019).

The Indawgyi wetland ecosystem in Myanmar is a multi-designated conservation area as it is an Important Bird Area (IBA), a Ramsar Site, as well as a flyway network site and a UNESCO Biosphere Reserve (Forest Department 2018). The area includes a multitude of land cover types experiencing different levels of human disturbances which can be categorized into four main landcover habitats: open lake habitat, seasonally flooded grassland, riparian forests, and agricultural land (Convention on Wetlands 2022). The Indawgyi wetland system is therefore well-suited to investigate how bird communities differ regarding land uses and their annual variation in a human-dominated landscape. Specifically, we aim to assess seasonal patterns of bird diversity in four different habitat types, quantify impacts of disturbances and reveal drivers of bird community assemblages. Given a heterogeneous landscape consisting of both water and aquatic vegetation, providing more ecological niches, and a low level of human influences, we hypothesized that bird diversity to be higher in the open lake habitats than other habitats (seasonally flooded grassland, riparian forest, and agricultural land). Accordingly, we expected over dispersed functional and phylogenetic structures in this habitat, indicating that community assembly deviated from random structure due to biotic interactions acting upon diverse resources, large extent of the lake area and stability of the habitat (Bennett et al. 2006; Tscharntke et al. 2012; Che et al. 2019; Sinha et al. 2022). In contrast, we hypothesized that bird community diversity in agricultural land is predicted to be the lowest (particularly in the functional, and phylogenetic diversity) due to environmental filtering driven by homogenous habitat structures and intensified agricultural uses (Devictor et al. 2008; Şekercioğlu 2012; Liang et al. 2019; Jayathilake et al. 2021). Because of seasonal variation in available resources following flooding, crop production-harvest cycles (Bennett et al. 2006; Şekercioğlu 2012) and the arrival of migratory birds (Yabuhara et al. 2019), we hypothesized that bird diversity patterns would differ among seasons, especially in seasonally inundated grasslands and riparian forests that are bordering cultivated lands (Che et al. 2019; Li et al. 2019). Our main aim is to elucidate spatiotemporal variation of bird diversity and thereby provide helpful ecological information to enhance conservation and management efforts in an internationally important wetland.

Methods

Study area

The study was conducted in the Indawgyi wetland, an important bird conservation area in northern Myanmar (Fig. 1). The ecosystem encompasses 47,884 ha comprising a large lake in the center, surrounded by seasonally flooded grasslands, riparian forests, and an extensive agricultural land in its outermost areas (Convention on Wetlands 2022). The Indawgyi lake is the largest freshwater lake in Myanmar and the third largest in Southeast Asia. The

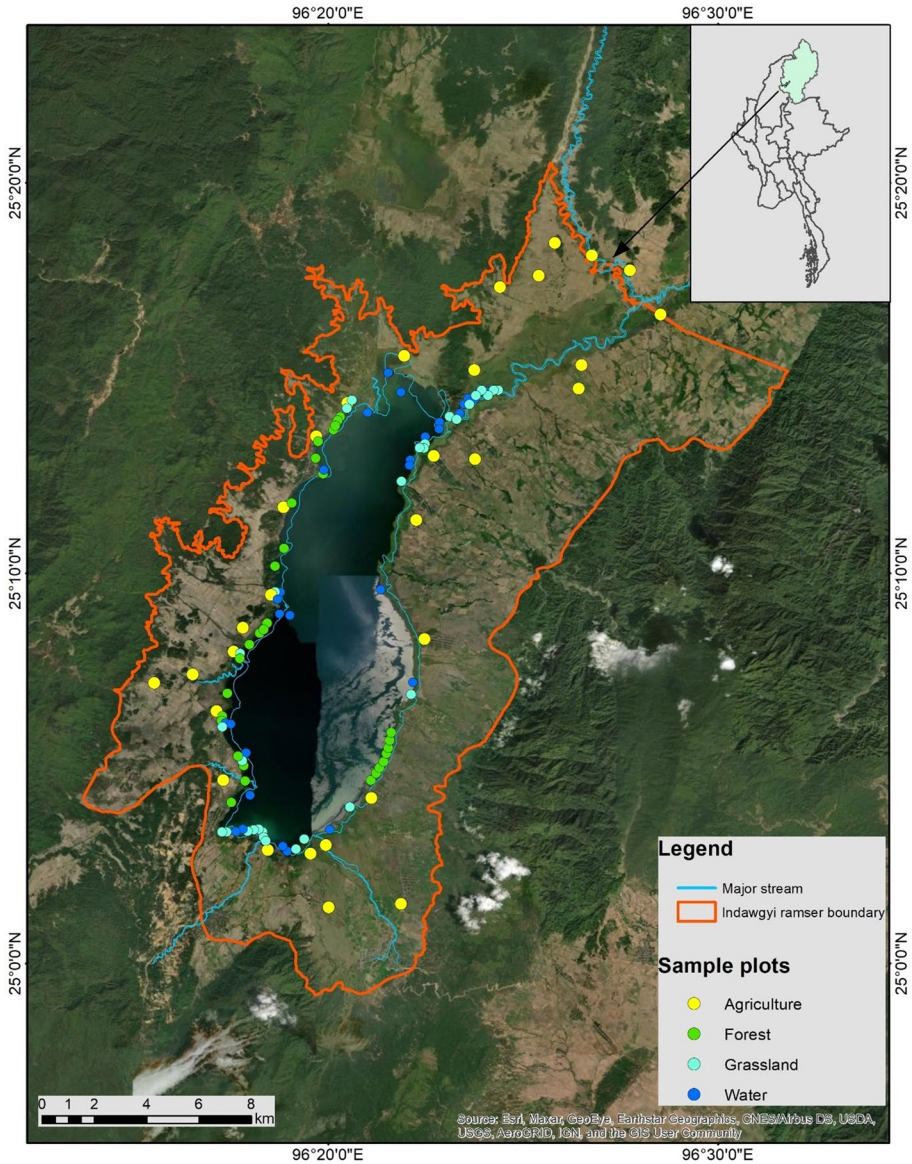


Fig. 1 Location of the Indawgyi Wetland within Myanmar in the upper right corner and distribution of bird sample plots ($n=120$) in four habitat types (yellow dots are sampling points in agricultural land, green in riparian forest, cyan in grassland, and blue in water)

area has a subtropical climate with the lowest temperature of 5.5 °C while the highest is 33.6 °C. The annual rainfall ranges from 1048 to 2060 mm. The lake and its associated wetland regularly support at least 1% of the abundance of the flyway community of water-birds in Myanmar (Forest Department 2018). The study area is also an important migratory

stop over site as it is situated along the East-Asian-Australasian Flyway (Convention on Wetlands 2022).

A large area of waterbody with reeds and floating vegetation consisting of 22 species, dominantly *Salvinia cucullate* and *Eichhornia crassipes* is the primary habitat for waterbirds including ducks, grebes, rails, and crakes (Forest Department 2018). Subsistence fishing, regulated through an appropriate zonation system is the only human activity in the lake (Forest Department 2018). Grasslands and herbaceous marshes are seasonally inundated and are dominated by wild grasses, *Polygonum* and *Cyperaceae* genera, providing suitable habitat for wetland-dependent birds such as stints, plovers, and sandpipers. The riparian forests characterized by *Barringtonia* species are also inundated during the monsoon and this habitat is used by darters, kingfishers, and cormorants. In these habitats, cattle grazing in the dry season, collection of animal fodder and non-timber forest products are main anthropogenic activities (Forest Department 2018).

In the study area, 36 villages surrounding the wetland alluvial plain practice agriculture as their main livelihood. Rainfed rice is the major crop grown in the whole region (start growing in June and harvest the latest in November) and some areas in the northern part cultivate soybeans after the rice harvest (Forest Department 2018). Since these farmlands surround the lake and its associated wetlands, all agrochemicals applied to the farms impact the quality of the lake. Furthermore, sedimentation due to gold mining in the upstream areas impedes the inflow of water into the lake and its wetland. Due to population pressure and large-scale land acquisition, much of the grassland and riverine vegetation have also been transformed into agricultural land, causing the habitat contraction and fragmentation for wetland-dependent birds (Forest Department 2018).

Bird surveys

The land cover types based on the latest landcover map of the Indawgyi ecosystem, which was developed in 2015, were used to establish a stratified random sampling design for bird surveys (Forest Department 2018). The main land cover types are a large waterbody, seasonally flooded grasslands, riparian forests, and agricultural land. Using this landcover map, we first generated 50 random sample points for each land cover types using “create random point tools” in ArcGIS Ver 10.8.1. Each sampling point was separated 200 m from each other (Ralph et al. 1995). However, after ground truthing and pilot surveys, we included 30 sample plots per land cover due to accessibility and local security constraints (Ralph et al. 1995). Thus, a total of 120 sample plots were established for bird surveys across the four different habitat types (Fig. 1).

Data were collected seasonally from June 2021 to March 2022, using point counts (Ralph et al. 1995). In Myanmar, the monsoon season coincides with the crop growing season and lasts for four months, from mid-May to September. The winter lasts from October to mid-February, which also includes the crop harvest season, and the summer is from late February to mid-May, which is the fallow period or after harvest season. Migratory birds normally arrive at the study area in winter (October) and leave in the middle of summer (March) (Forest Department 2015). Sampling across seasons, therefore, allowed us to study the dynamics of the bird community during the breeding and the migratory seasons, in interaction with seasonal agricultural practices. Furthermore, this study is part of a project investigating “Socio-ecological perspectives of avian conservation in the Indawgyi Wetland Ecosystem in Myanmar”, where we examined spatio-temporal variation in bird

community diversity (ecological perspective) as well as human-wildlife conflicts with a focus on avian species and prevalence of illegal killing of birds (socio-biological perspective). To be consistent among all three perspectives, we followed a seasonal division by agricultural calendar (Htay et al. 2022).

Bird community data (i.e., bird species and their abundances) was recorded in the sample plots during the three seasons, and each sample plot was visited two times within each season; the growing season (sampled in June and July), the harvest season (sampled in October and November) and after the harvest season (sampled in February and March). Accordingly, each sample plots were visited six times throughout the study and the total number of counts was 720 (i.e., 6 surveys x 120 sample plots). In each visit, all birds recorded by sound and/or observed within 50 m radius of the plot were counted for 15 min (Ralph et al. 1995). We recorded both the presence of species as well as their abundances. The bird survey was conducted within 5 h after sunrise and 3 h before sunset. A local ornithologist (Zwe Zaw Zaw Hein) with more than 10 years of experience as a bird guide in Indawgyi Local Tourism Group and previously involved in multiple bird surveys identified bird species in all conducted surveys. The classification of the birds followed the guidelines of Birds of Southeast Asia (Robson 2005). All bird counts were conducted only when weather conditions allowed reliable counts.

Assessment of environmental characteristics

Vegetation and environmental variables were sampled in three 10 × 10 m plots, which were established within each of the 50 m radius bird sample plots (Lee 2022). Each quadratic plot was established 15 m from the center of the bird sampling point and at 120 degrees from each other. This method is commonly used for vegetation surveys (Rajpar and Zakaria 2011; Menon et al. 2019). In each quadratic plot, we recorded the number of plant species, and visually estimated percent cover of tree, shrubs, herbs, short grasses (height < 1 m), long grasses (height > 1 m), shallow water (depth < 1 m), and deep water (depth > 1 m). As agricultural crop cover changed with different seasons (i.e., germinating, and growing rice paddy in the monsoon, flowering and ripening paddy in the harvest season, and rice stubble, fallow riceland, or soybean after harvest), we therefore recorded agricultural crop cover as presence or absence for two major crops: rice and soybean (Han et al. 2021). We also recorded the presence or absence of temporary trails, grazing, fishing, and hunting in each sample plot. However, these variables were later pooled into one variable as level of human disturbance, which ranked from 0 to 4 (Mereta et al. 2021). If there was no disturbance in the sampling plot, the level of human disturbance would be 0, if there was one type of disturbance, it would be 1, and so forth. To measure each sample plot's distance to human settlement, we first plotted the coordinates of our sampling points in Google Earth and then we measured the straight-line distance from each plot to the nearest human settlement by using "Ruler Tools". All environmental variables recorded in the three quadratic plots were averaged as a single value for each bird sampling point (Rajpar and Zakaria 2011; Menon et al. 2019; Han et al. 2021; Lee 2022; Schmidt et al. 2022).

Functional traits and phylogenetic data

For all recorded bird species, we collected 10 functional traits including six traits related to fitness and resource acquisition of each bird species (i.e., body size, body mass, generation length, clutch size, diet, and foraging strata ; Ding et al. 2013; Zhang et al. 2020), and

four traits related to importance for conservation of each species (i.e., habitat specialization, population status, migration status and conservation status; Devictor et al. 2008; Lee and Martin 2017; Zeng et al. 2019; Santangeli et al. 2022) (Table S1). We selected these functional traits because they represent important life history characteristics which reflects adaptation to the environment, the trophic level, and the food web, and they are commonly used in functional diversity studies (Petchey and Gaston 2007; Ding et al. 2013; Lee and Martin 2017; Jayathilake et al. 2021). Data for body size, body mass, clutch size and habitat specialization were compiled from Handbook of the Bird of the World (del Hoyo et al. 1992). Data on diet and foraging strata were extracted from the Elton Traits database 1.0 (Wilman et al. 2014). This dataset estimated proportion of nine different food categories in diet: invertebrates, endotherms, ectotherms, fish, scavengers, fruit, nectar, seed, and plant. Likewise, the preferred foraging strata was recorded in percent use of seven different foraging strata: below water surface, around water surface, on ground, understory, mid to high vegetation, canopy, and aerial (Wilman et al. 2014). Population status, migration status and conservation status of each species were retrieved from IUCN (<https://www.iucnredlist.org/>). Traits for resource acquisition were recorded as continuous traits while those for conservation were recorded as binary traits (Table S1). Phylogenetic signals of continuous traits were tested using the Pagel's λ , where the value range from 0 to 1 according to the strength of phylogenetic signal (Münkemüller et al. 2012; Li et al. 2019). Accordingly, a λ close to 0 indicates functional traits are phylogenetically independent and a λ value close to 1 suggests a strong phylogenetic signal (Pagel 1999). We used D statistics to test phylogenetic signal in categorical traits, where D approaches to 0 as the phylogenetic signal increases and negative values suggests the trait is phylogenetically more conserved (Fritz and Purvis 2010). Phylogenetic signals were calculated using *Phytools* (Revell 2012) and *Caper* Packages (Orme 2018).

For phylogenetic data, we pruned phylogenetic trees covering all bird species found in our study area from the BirdTree database (<https://birdtree.org/>) (Jetz et al. 2012). We sampled 1000 trees using the option specified for “Erison All Species: a set of 10,000 trees with 9993 OUT each”. These trees were subsequently used to build a maximum clade credibility tree (Rubolini et al. 2015). The maximum clade credibility tree was constructed using the mean node height in *Tree Annotator Version 1.10* of the *BEAST* package (Drummond and Rambaut 2007). This tree was then used for all phylogenetic analyses. However, functional traits and phylogenetic data were not available for two species (Oriental reed warbler *Acrocephalus orientalis* and Two-barred warbler *Phylloscopus plumbeitarsus*), and we excluded these species in the construction of functional and phylogenetic tree.

Diversity metrics

Before computing diversity metrics, we checked the adequacy of our sampling effort using sampling completeness curve (Chao and Jost 2012; Chao et al. 2020) and ensured that the sample size was enough to detect 95% of species in all habitats (Fig. S1). To characterize three facets of bird diversity, we calculated two indices for each facet, where the first index considered presence/absence data (i.e., species richness for taxonomic diversity, functional diversity, and phylogenetic diversity) and the second one used abundance data (abundance for taxonomic diversity, mean pairwise functional distance and mean pairwise phylogenetic distance). Species richness and abundance for each sample plot were calculated using the *Vegan* package (Oksanen et al. 2022).

For functional diversity, we calculated functional trait dissimilarity for all pairs of species using Gower distance, which is flexible for datasets that consist of both continuous and categorical traits (Gower and Legendre 1986). Gower distance was calculated using *gowdis* function from the *FD* package (Lalibert et al. 2014). However, body size, body mass and generation lengths are highly correlated to each other ($r > 0.8$), and we excluded body mass and generation length in calculating Gower distance. After that, we constructed a functional dendrogram through the “Unweighted Pair Group” method with arithmetic mean using *hclust* function in the *Phangorn* package (Schliep 2011). Then, we calculated functional diversity (FD) of each bird sample plot using the summed branch lengths of functional dendrogram for all species contained in the assemblage (Petchey and Gaston 2007). As FD used only presence/absence data, we additionally calculated abundance-weighted mean pairwise functional distance (MFD) (Webb et al. 2002; Swenson 2014).

In addition to overall functional diversity, we calculated functional diversity and mean pairwise functional distance separately for (1) life-history strategy traits (i.e., body size, clutch size, diet, and foraging strata; hereafter resource utilization based functional diversity- RFD- and mean pairwise functional distance - MRFD), to assess the species interaction for resource acquisition; and (2) traits that are important for conservation (i.e., habitat specialization, declining population, migratory species and threatened species; hereafter conservation important functional diversity- CFD- and mean pairwise functional distance - MCFD) (Lopez et al. 2016; Che et al. 2021). Separation of traits into two functional processes not only filter the ecological function that are of main interests, but also reduce unwanted confusion of the effects of functional traits in calculating overall functional diversity (Cisneros et al. 2016; Lopez et al. 2016).

For phylogenetic diversity (PD), we used the maximum clade credibility tree and calculated Faith’s phylogenetic diversity (Faith 1992) and mean pairwise phylogenetic distance (MPD) (Webb et al. 2002; Swenson 2014). As functional and phylogenetic diversity metrics are positively related to species richness, we calculated standardized effect sizes to determine whether the observed diversity values were higher or lower than expected by chance (Swenson 2014). Standardized effect sizes were calculated by comparing the observed functional and phylogenetic diversity against those obtained from null models that corrected for species richness (i.e., Standardized effect size = observed value – mean expected values from randomized communities/ standard deviation of the expected values from randomized communities). We calculated standardized effect sizes for functional diversity (SES.FD and SES.MFD), life-history strategies (SES.RFD and SES.MRFD), conservation function (SES.CFD and SES.MCFD) and phylogenetic diversity (SES.PD and SES.MPD) from 1000 randomly generated communities using the “taxa.labels” option, which shuffled species on the functional and phylogenetic trees (Kembel et al. 2010). These standardized values are used to infer underlying community assembly process (Webb et al. 2002; Swenson 2014). Positive SES values indicate that diversity is higher than expected (bird species are functionally or phylogenetically overdispersed) whereas negative values indicate lower diversity (bird species are functionally or phylogenetically clustered). SES values that are not different from zero suggest stochastic or random community structures (Webb et al. 2002; Swenson 2014). All functional and phylogenetic diversity indexes were calculated using packages *ape* (Paradis and Schliep 2019) and *picante* (Kembel et al. 2010) from R (R Core Team 2022).

Data analysis

To analyze how the environmental characteristics could explain patterns in bird community diversity among four habitat types and seasons, we constructed generalized linear mixed models (GLMM) in which diversity indices (species richness, abundance, SES.FD, SES.MFD, SES.RFD, SES.MRFD, SES.CFD, SES.MCFD, SES.PD and SES.MPD) were included as response variables. However, environmental variables, which were mostly recorded as percent cover of vegetation, were not possible to be included in the same model because they were strongly correlated with habitat types (for instance, in the forest habitat, there was a high percent of forest, shrub, and herb cover while the grassland habitat was dominated by grass, see Fig. S2). Therefore, we constructed two GLMMs where the first model tested the effects of habitat, season, their interactions, and distance to nearest human settlement. The identity of the sampling plot and sampling occasion were included as random factors to account for non-independence among sampling points and sampling visits. The model was constructed using the full dataset as well as datasets separated for each season and for each habitat. As the results did not differ noticeably between the full dataset and separate datasets (Fig.S3–9), we presented results from the models fitted using the full dataset, considering the absence of opposing seasonal effects. Then, we constructed the second model which included only environmental predictors to understand seasonal environmental changes on community diversity indices. As the inclusion of interaction between environmental variables and seasons would lead to over parametrization of models in the full dataset, we used seasonal datasets for this model. The model was fitted using environmental variables and sampling occasion as predictors and the identity of the sample plot as random factor. Models were fitted using a Poisson distribution for species richness, a Negative binomial distribution for abundance (due to overdispersion) and a Gaussian distribution for functional and phylogenetic diversities. Before constructing models, all continuous variables were standardized with mean zero and one standard deviation. A variable was considered to have significant effect if the confidence interval of its estimate did not include zero (Nakagawa and Cuthill 2007). We checked multicollinearity among predictors using *Performance* package (Lüdtke et al. 2021) and dropped level of human disturbance due to its high correlation with distance to human settlement (Pearson's $r=0.818$). All models were constructed using *glmmTMB* package (Brooks et al. 2017) and the residual diagnostics of the models were checked using *DHARMA* package (Hartig 2020). Spatial autocorrelation of the residuals was evaluated using Moran I statistics under *spdep* package and no significant effects were detected in our fitted residuals (Bivand et al. 2022). All analyses were conducted in R version 4.1.1 (R Core Team 2022).

Results

We recorded a total of 35,941 individuals belonging to 200 species of birds across 720-point counts. In the growing season, we recorded 116 species and 12,529 individuals and the most abundant species were baya weaver (*Ploceus philippinus*), lesser whistling duck (*Dendrocygna javanica*) and blue-tailed bee-eater (*Merops philippinus*). In the harvest season, 134 species and 9414 individuals were recorded and Brown-headed gull (*Larus brunicephalus*), lesser whistling duck (*D. javanica*) and little cormorant (*Microcarbo niger*) were the most common species. After harvest season, 158 species and 13,998 individuals

were recorded. The most abundant species were purple swamphen (*Porphyrio porphyrio*), lesser whistling duck (*D. javanica*) and barn swallow (*Hirundo rustica*).

Among all recorded species, 15 were threatened, 49 were habitat specialists, 66 experienced globally population decline and 93 were migratory species (see supplementary materials for the species list). The median body size of all species was 25 cm (range: 8–176 cm) and the median clutch size was 4 (range: 1–11 eggs). Invertebrates constituted the diet of 89% of all bird species followed by seeds and plants (49.5%), and fruits and nectar (40%). Other categories included ectothermic vertebrates, for instance amphibians in 31% of species, fish in 22.5% of species and endothermic vertebrates in 17.5% of species. The percentage of species within each of the categories of foraging location was: on the ground, 65.5%; understory or vegetation below 2 m, 45%; in water, 39%; mid to high vegetation, 37%; canopy, 21%; and aerial, 7.5%. Most life-history traits showed strong phylogenetic signals while traits related to conservation showed weak phylogenetic effects (Table S1).

Analysis of bird diversity patterns

Taxonomic diversity

Bird species richness differed among seasons (Table S3a and Fig. 2a). In agricultural land, the highest number of bird species was in the growing season ($\beta = 2.242$ [2.046, 2.438], $SE = 0.100$). In grassland, the highest number of bird species was in the harvest season ($\beta = 0.259$ [0.093, 0.425], $SE = 0.085$). In forest and lake, however, the highest species richness was found in the season after harvest (forest: $\beta = 0.331$ [0.161, 0.501], $SE = 0.087$; lake: $\beta = 0.268$ [0.105, 0.431], $SE = 0.083$; Table S3a and Fig. 3). Species richness was positively related to number of plant species in all seasons (Growing: $\beta = 0.088$ [0.030, 0.147], $SE = 0.030$; Harvest: $\beta = 0.194$ [0.115, 0.272], $SE = 0.040$; Afterharvest: $\beta = 0.107$ [0.025, 0.188], $SE = 0.042$; Table S3b). Species richness during the growing season increased with the presence of rice crop, percent cover of long grass, and floating vegetation. In the harvest season, species richness increased with areas of short grass, water coverage and paddy fields. After harvest, area of waterbody was the only significant environmental variable influencing species richness. More species were recorded during the second visits in all seasons.

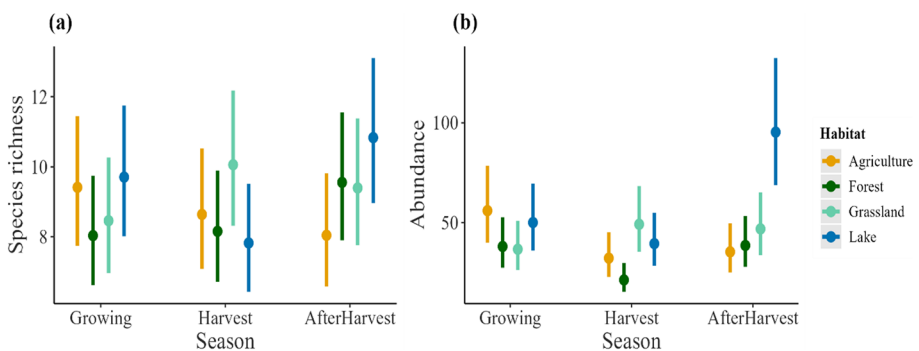


Fig. 2 Seasonal patterns of **a** bird species richness based on estimates and 95% confidence interval from the model in Table S3a, and **b** total abundances based on estimates and 95% confidence interval from the model in Table S4a in four different habitats of Indragyi wetland ecosystem

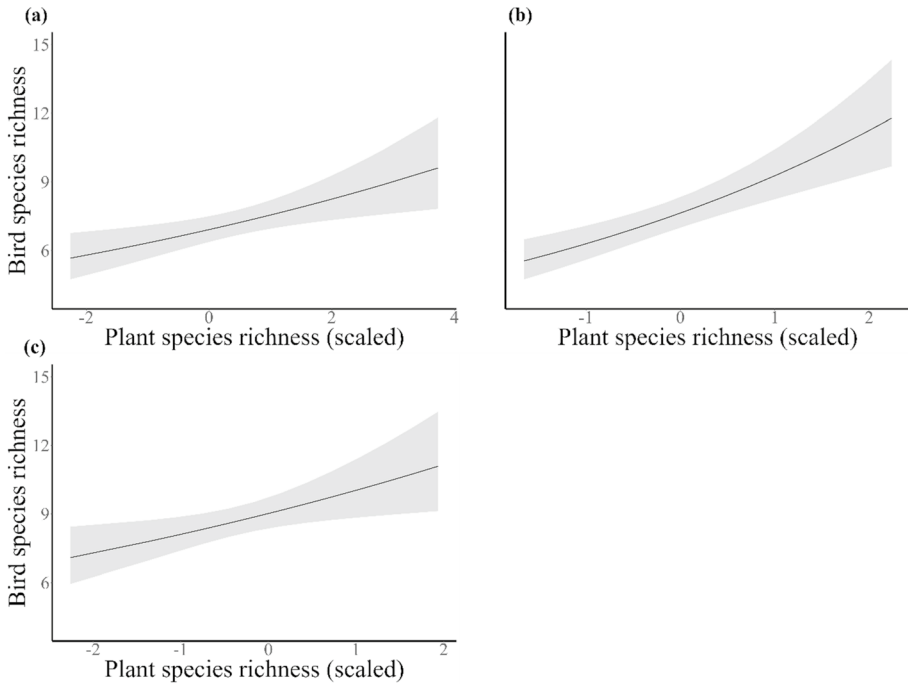


Fig. 3 Bird species richness in relation to plant species richness in **a** growing season, **b** harvest season and **c** after-harvest season based on estimates and 95% confidence interval from the models in Table S3b

A similar seasonal variation pattern was found for bird abundance (Table S4a and Fig. 2b). In agricultural land, birds were most abundant in the growing season ($\beta=4.026$ [3.689, 4.363], $SE=0.172$). However, abundance in grassland was the highest in the harvest season ($\beta=0.844$ [0.463, 1.225], $SE=0.195$). In forest and lake, highest abundances were recorded in the season after harvest (forest: $\beta=0.472$ [0.093, 0.851], $SE=0.193$; lake: $\beta=1.102$ [0.725, 1.479], $SE=0.192$; Table S4a and Fig. 2b). In the growing season, birds were more abundant in areas with climbing plants or herbs (Table S4b). During the harvest season, species abundance increased with coverage of waterbody, sand, grass, and rice crop. After the harvest period, only water coverage affected bird abundance positively. Bird abundances were higher during the second visits in all seasons.

Functional diversity

Among four habitats, bird species were functionally more diverse in the lake than those were in forest, grassland, and agricultural land ($\beta=1.076$ [0.711, 1.441], $SE=0.186$; Table S5a and Fig. 4a). We found a seasonal variation in bird functional diversity (SES.FD) in lake and forest. SES.FD in forest was the lowest in season after harvest ($\beta=-0.461$ [-0.917, -0.006], $SE=0.232$; Table S5a). SES.FD in the lake was the highest in the harvest season ($\beta=0.592$ [0.136, 1.047], $SE=0.232$; Table S5a). During the growing season, SES.FD decreased with the number of plant species (Table S5b). During the harvest season, SES.FD was higher in areas with water, but lower in long grass cover and rice fields.

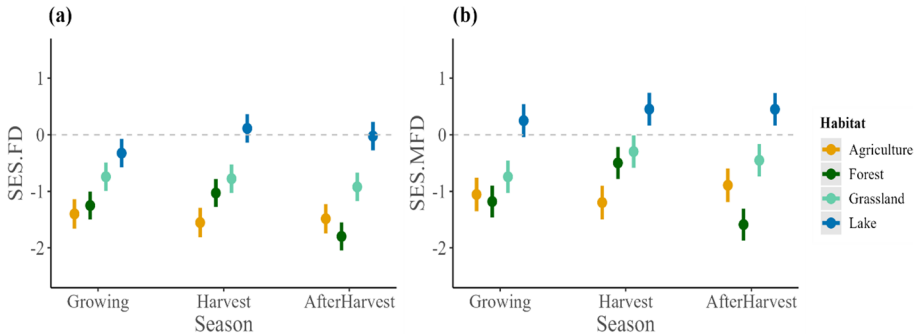


Fig. 4 Seasonal patterns of **a** bird functional diversity (SES.FD) based on estimates and 95% confidence interval from the model in Table S5a and, **b** mean pairwise functional distance (SES.MFD) based on estimates and 95% confidence interval from the model in Table S6a in four different habitats of Indawgyi wetland ecosystem

After harvest, SES.FD increased with waterbody and long grass cover, but it decreased with increasing plant species, herb cover, and soybean. Bird species were functionally less diverse in the second visit of the growing season. SES.FD indicated random structures in lake during harvest and after harvest seasons, whereas a clustered structure during growing season. However, SES.FD in agriculture, forest and grassland showed clustered structures in all seasons (Fig. 4a).

The mean pairwise functional distance showed a similar pattern. SES.MFD was higher in lake than those were in grassland, forest, and agricultural land ($\beta = 1.308$ [0.878, 1.737], $SE = 0.219$; SES.MFD; Table S6a and Fig. 4b). There was a seasonal variation in SES.MFD in grassland and forest. In both habitats, SES.MFDs were the highest during the harvest season (grassland: $\beta = 0.589$ [0.045, 1.134], $SE = 0.278$; forest: $\beta = 0.826$ [0.282, 1.371], $SE = 0.278$; Table S6a and Fig. 4b). In all seasons, SES.MFD increased with coverage of waterbody and floating vegetation (Table S6b). However, it decreased with expanding areas of shrub, herb, and agricultural crop after harvest. SES.MFD in the growing season was lower during the second visit while there were no differences during the harvest and after-harvest seasons. SES.MFD showed random to over-dispersed structures in lake, especially during the harvest and after harvest seasons. In agriculture land, forest and grassland, bird communities were clustered in all seasons (Fig. 4b).

Phylogenetic diversity

Phylogenetic diversity of bird communities (SES.PD) was higher in the lake than those in grassland, forest, and agricultural land ($\beta = 1.913$ [1.462, 2.365], $SE = 0.230$; Table S7a and Fig. 5a). There was no seasonal variation in SES.PD except in the forest habitat where the highest phylogenetic diversity was observed in the growing season ($\beta = 0.902$ [0.473, 1.330], $SE = 0.219$; Table S7a). In all seasons, SES.PD increased with the coverage of water and decreased with presence of agricultural crop. After the harvest season, number of plant species influenced the SES.PD negatively (Table S7b). SES.PD in forest, agriculture and grassland indicated clustered structures in all seasons. In the lake, however, the avifauna were phylogenetically random in all seasons (Fig. 5a).

The mean pairwise phylogenetic distance (SES.MPD) was also higher in lake than those were in the remaining habitats ($\beta = 1.996$ [1.444, 2.548], $SE = 0.281$; Table S8a and

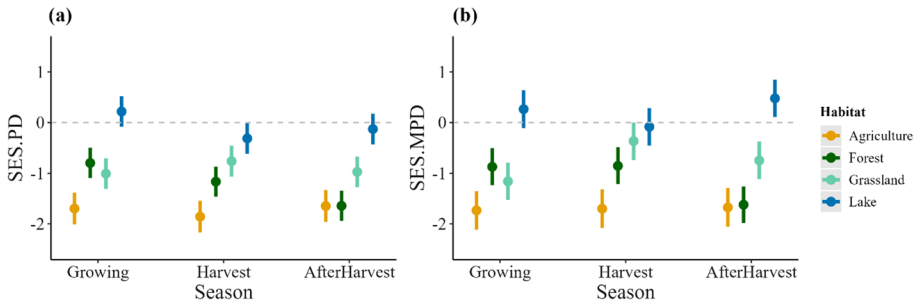


Fig. 5 Seasonal patterns of **a** bird phylogenetic diversity (SES.PD) based on estimates and 95% confidence interval from the model in Table S5a and, **b** mean pairwise phylogenetic distance (SES.MPD) based on estimates and 95% confidence interval from the model in Table S6a in four different habitats of Indawgyi wetland ecosystem

Fig. 5b). Seasonal variation in SES.MPD was found in grassland and forest. In grassland, SES.MPD was the highest in the harvest season ($\beta = 0.757$ [0.007, 1.436], $SE = 0.347$; Table S8a). In forest, SES.MPD was the lowest in the season after harvest ($\beta = -0.809$ [-1.488, -0.013], $SE = 0.347$; Table S8a). SES.MPD increased with the coverage of water and decreased with presence of agricultural crop in all seasons (Table S8b). SES.MPD was lower during the second visit in the growing season. However, in the harvest season, it was higher during the second visit. SES.MPD in the lake habitat indicated an over dispersed phylogenetic structure after harvest season and random structures in other seasons. SES.MPDs of agricultural land, forest and grassland were phylogenetically clustered (Fig. 5b).

Functional diversity of the traits important for conservation

Among all habitats, functional diversity of bird species that were crucial for conservation (SES.CFD) was the highest in the lake ($\beta = 0.960$ [0.638, 1.281], $SE = 0.164$; Table S9a

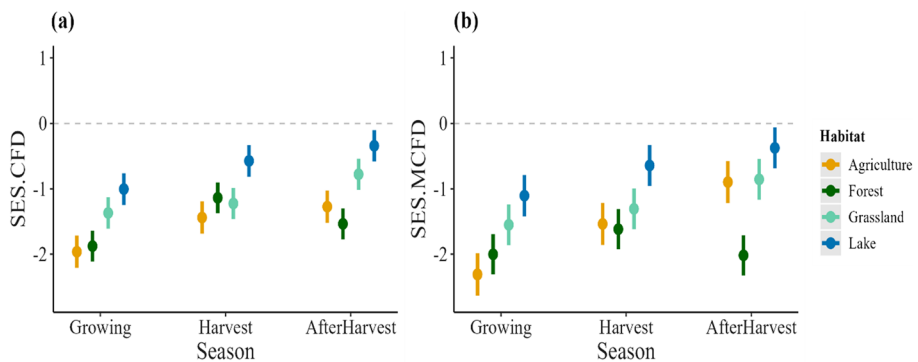


Fig. 6 Seasonal patterns of **a** conservation important function (SES.CFD) based on estimates and 95% confidence interval from the model Table S9a and, **b** mean pairwise functional distance in conservation (SES.MCFD) based on estimates and 95% confidence interval from the model in Table S10a in four different habitats of Indawgyi wetland ecosystem

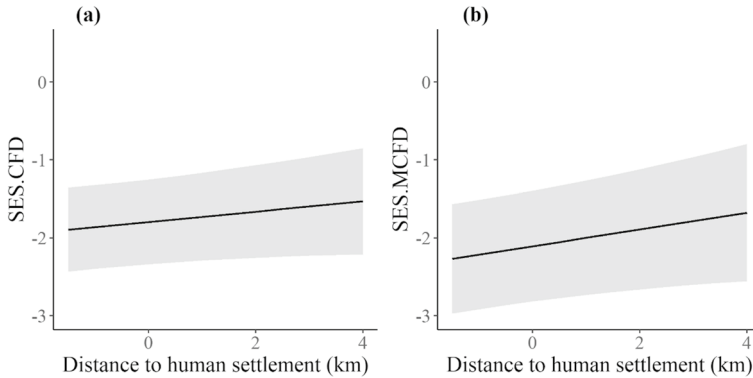


Fig. 7 **a** Functional diversity (SES.CFD) and **b** mean pairwise functional distance (SES.MCFD) of conservation important functional traits in relation to distance to the nearest human settlement (km), based on estimates and 95% confidence interval from the models in Table S9a and Table S10a

and Fig. 6a). In most habitats, species of conservation concern were consistently the most numerous during the season after harvest (Fig. 6a). However, in forest, SES.CFD tended to be the highest in harvest season (Fig. 6a). Furthermore, conservation important function tended to be higher in areas faraway from human settlement (Table S9a, Fig. 7a). In the growing season, SES.CFD increased with waterbody area. In the harvest season, SES.CFD decreased with the number of plant species. After harvest, SES.CFD was higher in areas of waterbody, floating vegetation, long grass and lower in areas with herbs. SES.CFD was higher during the second visit of the harvest season (Table S9b).

Mean pairwise functional distance of conservation important traits (SES.MCFD) was also higher in lake than other habitats ($\beta = 1.203$ [0.788, 1.618], $SE = 0.212$; Table S10a and Fig. 6b). While SES.MCFD in forest was the lowest in after-harvest season ($\beta = -1.427$ [-1.938, -1.281], $SE = -0.916$; Table S10a), those of remaining habitats were the highest in the after-harvest season (agricultural land: $\beta = 1.411$ [0.997, 1.826], $SE = 0.212$; grassland: $\beta = -0.715$ [-1.226, -0.204], $SE = 0.261$; lake: $\beta = -0.679$ [-1.193, -0.166], $SE = 0.262$; Table S10a). SES.MCFD was also higher in areas far away from human disturbances (Table S10a and Fig. 7b). In the harvest season, SES.MCFD increased with water cover and decreased with number of plant species. After harvest, it increased with floating vegetation cover and decreased with tree, shrub, and herb cover (Table S10b). Functional diversities (SES.CFD and SES.MCFD) of bird species that were crucial for conservation were clustered in all habitats.

Functional diversity of the life-history strategies

There was a seasonal variation in functional diversity of life-history strategies (SES.RFD) in studied habitats (Table S11a and Fig. 8a). Although SES.RFD in the lake was slightly higher in the harvest season ($\beta = 1.174$ [0.734, 1.613], $SE = 0.224$; Table S11a), the overall pattern was not different among seasons (Table S11a and Fig. 7a). In grassland, it was quite similar in the growing ($\beta = -0.411$ [-0.773, -0.049], $SE = 0.185$) and harvest season ($\beta = 0.995$ [0.555, 1.434], $SE = 0.224$) but the lowest in the season after harvest (Fig. 8a). In forest and agricultural land, the highest SES.RFD was found in growing season (grassland:

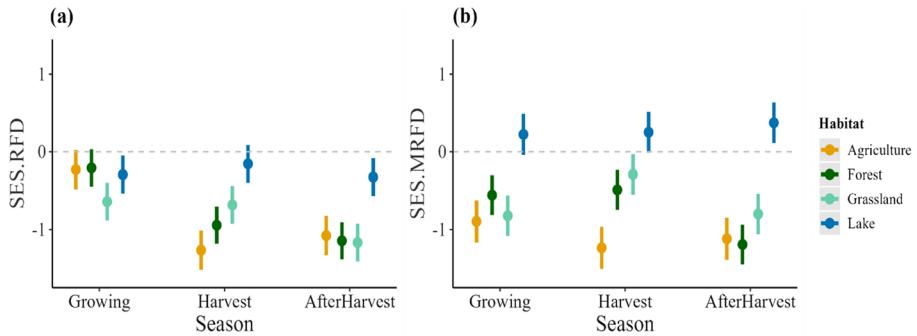


Fig. 8 Seasonal patterns of **a** life-history strategies (SES.RFD) based on estimates and 95% confidence interval from the model in Table S11a and, **b** mean pairwise functional distance in life-history strategies (SES.MRFD) based on estimates and 95% confidence interval from the model in Table S12a in four different habitats of Indawgyi wetland ecosystem

$\beta = -0.715$ [$-1.226, -0.204$], $SE=0.261$; lake: $\beta = -0.679$ [$-1.193, -0.166$], $SE=0.262$; Table S11a). Life history strategies were less diverse in areas far away from the human settlement (Table S11a). SES.RFD was lower in areas with short grass cover in the growing season and with long grass cover in the harvest season. It also decreased with floating vegetation cover and sand cover during after-harvest season (Table S11b). SES.RFDs of agricultural land, forest and grassland showed clustered structures in all seasons. In lake habitat, SES.RFD indicated random structure in the harvest season whereas clustered structures in other seasons (Fig. 8a).

Mean pairwise functional distance in life-history strategies (SES.MRFD) was higher in the lake than other habitat types and no seasonal variation was found there ($\beta=1.119$ [$0.726, 1.512$], $SE=0.201$; Table S12a and Fig. 8b). In grassland, it was the highest in the harvest season ($\beta=0.871$ [$0.406, 1.336$], $SE=0.237$; Table S12a). SES.MRFD in forest also tended to be higher in harvest season (Table S12a and Fig. 7b). However, SES.MRFD of agricultural land was the highest in the growing season ($\beta = -0.896$, [$-1.167, -0.624$], $SE=0.139$; Table S12a, Fig. 7b). In the growing season, SES.MRFD decreased with shrub cover (Table S12b). In the harvest season, it increased with coverage of waterbody. After harvest, SES.MRFD increased with areas of water but decreased with areas of shrub and agricultural crop. SES.RFDs of agricultural land, forest and grassland showed clustered structures in all seasons. In lake habitat, SES.RFD indicated over dispersed structure after harvest season whereas random structures in other seasons (Fig. 8b).

Discussion

The present study has demonstrated substantial spatial and temporal variation in taxonomic, functional, and phylogenetic diversity across habitat types in a heterogeneous wetland ecosystem within an agricultural landscape in Myanmar. The highest functional and phylogenetic diversities were recorded in the migratory season, especially in the remote and heterogeneous lake habitats, indicating that the species assemblages in avian communities were influenced by common ancestral evolutionary history as well as environmental processes. Also, our results highlight habitats and seasons where the bird community included

the most threatened species, based on their conservation values. The study emphasizes the importance of evaluating several indices of community diversity (taxonomic, functional, phylogenetic diversity) as well as diversity of species of conservation concern to assess the ecological-, evolutionary-, and conservation importance. Given the scarcity of research investing in comprehensive assessments of bird community diversity patterns and structures in the Southeast Asia's flyway network sites, this study provides useful ecological information that are linked with other previous studies to upscale conservation efforts both at the local level and regional scale.

Seasonal patterns of bird diversity in wetland habitats

Among studied habitat types, the overall diversity was highest in lake habitat and lowest in agricultural land as we hypothesized. However, we found habitat-specific seasonal differences in our biodiversity facets, highlighting an asynchrony in the temporal importance of each habitat type for the conservation of the avian community at the ecosystem level.

Lake habitat

In the lake habitat, bird species were taxonomically most diverse in the season after harvest (Fig. 2). The observed pattern could be explained by influx of migratory birds to the study site because the study area is located along the East Asian Australasian Flyway and important staging site (Li et al. 2019; de Deus et al. 2020). However, in the harvest season, which is also the beginning of the migration season, the number of species present and their abundances were comparatively lower than after-harvest season (Fig. 2). This difference indicated that migratory species accumulated more in the lake during the late migration season. Our finding is congruent with the seasonal pattern depicted by a year-round study of bird species composition in the Okhla wetland sanctuary in India (Mazumdar 2019) and in the lowland Tokachi plain in central Hokkaido, northern Japan (Yabuhara et al. 2019). Additionally, this variation could be related to crop ripening because both wild rice grass (*Zizania spp.*) in seasonally flooded grassland and cultivated rice (*Oryza sativa*) were ripened in the harvest season. Results also indicated that species richness increased in rice fields and higher grass cover during the harvest season (Table S3b). Furthermore, birds are more attracted to grasslands (Fig. 2) and even to the agricultural land than lake in the harvest season (Fig. 2a). Tschardt et al. (2012) and Ngcobo et al. (2022) reported that this type of cross-habitat spillover effects is very common in bird communities using heterogeneous landscapes, especially at the time of high resource flux. Results also reveal that functional diversity (FD) is higher in harvest and after-harvest times than those in the growing season, indicating that the migratory birds contributed to be functionally more diverse in the lake (Fig. 4). This pattern is also reflected in functional diversity of conservation important traits (SES.CFD), where the species of conservation concern were also higher in latter two seasons (Fig. 6). Results also showed that FD and SES.CFD increased in areas with waterbody and floating vegetation during the harvest season and after the harvest period (Table S5b and S9b). However, species life-history strategy types did not differ across seasons (especially among abundant species), suggesting that differences in overall functional diversity in the lake was driven by the species of conservation concern (Table S12a). This is also in line with the pattern depicted by mean pairwise functional

distance (MFD), which is consistent across seasons revealing that the most common species in the lake are functionally redundant species (Che et al. 2019; Li et al. 2019). Likewise, phylogenetic diversity was not significantly different among seasons (Table S7a and S8a). Taken all these findings together, our study suggests that the lake area is especially important during migration seasons to conserve overall bird diversity as well as bird species that are of conservation value.

Grassland habitat

Our study showed that species richness and abundances in seasonally flooded grassland were higher in migration period, especially during the harvest season (Fig. 2). This may be related to abundant resources from rice ripening in grassland and its associated agricultural lands (Andrén 1994). We found that the most common species in this season included granivorous birds like weavers, munia and starlings. Although grass and rice crop cover had positive effects on the taxonomic diversity (Table S3b), they revealed negative effects on functional diversity during the harvest season (Table S5b). Despite this, changes in hydrological cycles were shown to influence functional diversity (de Deus et al. 2020). In the harvest season, most parts of the grasslands are flooded, and this habitat is also used by other functional groups such as ducks, gulls, egrets, cormorants, ibises, swampheens, and herons. Results also indicated that functional, and phylogenetic diversity responded positively in relation to the area of waterbody (Table S6b and S8b). Therefore, both the functional and phylogenetic diversity of common species seems to be higher in inundated grassland during the harvest season (i.e., high mean pairwise functional distance-MFD and mean pairwise phylogenetic distance- MPD, Figs. 4b and 5b). These findings are again supported by the life-history strategies where functional diversity in the grassland bird communities related to resource acquisition of each bird species was also higher in this period (Fig. 8b). Although species important for conservation were also present during the harvest season, diversity within this group of species was found higher after harvest time (Fig. 6). This finding indicates that species that are important for conservation functions, including species that are red listed, such as lesser adjutant *Leptoptilos javanicus*, woolly-necked stork *Ciconia episcopus*, white-rumped vulture *Gyps bengalensis* and Himalayan griffon *Gyps himalayensis* were more likely to use grassland after harvest times. We also found that grass cover along with floating vegetation and water were found to promote functional diversity of conservation important species after the harvest period (Table S9b). Therefore, in this grassland habitat, conservation of overall diversity is important in early migration season (harvest season) and conservation concern species in late migration season (after-harvest season).

Riparian forest

Although taxonomic diversity (species richness and abundances) of riparian forest was highest after harvest times (Fig. 2), bird functional diversity was interestingly the lowest in this period (Fig. 4). Instead, functional diversity was found to be higher in the growing season and harvest season. Phylogenetic diversity showed a similar pattern as functional diversity (Fig. 5). These findings suggest that bird species using riparian forests in these seasons are functionally and phylogenetically distinct species, despite their lower taxonomic richness. The onset of breeding season with monsoon and reproduction-associated uses (e.g.,

nesting) in forests could be possible reasons for such high functional and phylogenetic diversity (Bennett et al. 2006; He et al. 2018; de Deus et al. 2020). The observed pattern could further be explained by the ecology of *Barringtonia* forests, which usually flower in the growing season (June and July) and fruit from August to October (Nath et al. 2016). Our results also indicated that bird abundances increased with percent cover of climbing plants or herbs in this season (Table S4b). Results also showed that the number of plant species was shown to have a positive effect on bird species richness (Fig. 3a, Table S3b), but it had a negative effect on the functional diversity (Table S5b). These findings suggest that riparian forests during this period might be important foraging sources for specific functional groups like frugivorous and nectivorous species (de Deus et al. 2020). Nonetheless, lakeside forests are inundated from monsoon until the end of the harvest season, and during this period, waterbirds, and fish-eating birds might use these habitats (de Deus et al. 2020). Riparian forests also serve as intermediary to resource-rich grasslands and rice land in the harvesting time. A study by Yabuhara et al. (2019) in Toakachi plain in northern Japan found that the seasonal changes in resource availability influenced the distribution of riparian forest birds especially insectivores, frugivores and granivores. Their findings are also mirrored in our analysis about the functional diversity of life-history strategies in lakeside forests (Fig. 8). In the season after harvest, when the water recedes and understory vegetation regrow, bird communities are again dominated by functionally similar and closely related species that specialized in forest habitats (Yabuhara et al. 2019). In this season, we also found that environmental characteristics mostly associated with the forests (plant species richness, percent cover of trees, shrubs, and herbs) resulted in a decline of overall functional diversity (Table S5b and S6b), as well as functional diversity of species with high conservation value (Table S9b and S10b). Therefore, riparian forests are important in the breeding season to maintain diversity in bird community.

Agricultural land

Although agricultural land is functionally and phylogenetically less diverse than other habitat types, its species richness and abundances are notably high during the rice growing season (Fig. 2, Table S3b). In the growing season, flooded rice fields rich in invertebrates are primary sources for breeding birds to increase chick growth and ensure breeding success (Best et al. 1995). Similarly, a gut analysis study of waterbirds in a Mediterranean wetland found that aquatic macro-invertebrates from the rice fields are main prey for waterbirds during the breeding season (Antón-Tello et al. 2021). An increase in bird species richness and abundances during the harvesting season were shown to be related to presence of rice crops (Tables S3b and S4b). Despite the fluctuation in taxonomic diversity, functional and phylogenetic diversity of agricultural land were consistent across seasons (Tables S5a, S6a, S7a and S8a). This homogenous pattern indicated that agricultural lands select to some generalist clades such as omnivores and granivores that possess higher degree of plasticity which enables them to thrive under the novel environment (Best et al. 1995; Ngcobo et al. 2022). Life-history strategies also showed that the most abundant species in the agricultural land were functionally similar species (Fig. 8b), although there were few functionally different species during the growing season (Fig. 8a). We also found that agricultural land uses reduced functional and phylogenetic diversity during the harvest and after harvests (Tables S5b, S6b, S7b, S8b). Findings from our study echoed previous studies that agricultural land uses lead to biotic homogenization through continuous removal of less tolerant species (Devictor et al. 2008; Tscharnkte et al. 2012; Jayathilake et al. 2021).

Şekercioğlu (2012) found that intensified agricultural land uses gradually excluded dietary specialists and lead to a shift in functional structure of the bird communities. Such functional and phylogenetic homogenization comes at the cost of important ecosystem services, posing the risk of ecosystem stability and resilience to environmental changes (Devictor et al. 2008). However, the highest functional diversity of conservation important species in agricultural land after harvest season (Fig. 6) highlights a considerable contribution of fallow crop fields to bird conservation, especially to crane species that use rice stubble fields.

Underlying mechanisms shaping bird community structure

In a human-dominated landscape, understanding the structuring mechanisms for bird communities is crucial for effective management of their habitats. Functional and phylogenetic diversity metrics are complementary measures that could reveal the underlying mechanisms of biodiversity and habitat relationships. Several studies have demonstrated that coexistence of species is determined by environmental deterministic process, dispersal mechanisms, and stochastic processes (Lopez et al. 2016; Che et al. 2019; Li et al. 2019; Sinha et al. 2022). Generally, communities with high functional and phylogenetic diversity are governed by niche differentiation in heterogenous environments (over-dispersed structures) and low diversity are due to environmental filtering effects in homogenous habitats (clustered structures) (Webb et al. 2002). However, random functional and phylogenetic structures are caused by two processes (Lopez et al. 2016). On the one hand, this could be interpreted as neither competition nor environmental filtering are important in community assembly processes. Instead, randomly fluctuating demographic and stochastic process governs the composition of the community (Almeida et al. 2017; Che et al. 2019). On the other hand, both competition and environmental filtering are simultaneously occurring (Lopez et al. 2016; Almeida et al. 2017). According to niche-based theory, the general assumption is that environmental filtering dominates homogenous habitats and competition dominates in heterogenous environment, despite other ecological mechanisms might interact in these processes (Webb et al. 2002). If this assumption is true for our study system, we should have observed functional and phylogenetic overdispersion in structurally heterogenous habitats (i.e., forests, grassland, and the lake) whereas clustering should be dominant in human-modified agricultural habitats. Instead, our study found clustered structures in agriculture, forest, and grassland, and random to over dispersed structure in the lake (Figs. 4 and 5). This suggests that ecological process other than niche partitioning are involved in underlying community structures and a further study is recommended to identify these processes (Lopez et al. 2016; Almeida et al. 2017). Previous studies also demonstrated that habitat heterogeneity did not always have monotonic relationships with diversity as its effect on bird species compositional and functional structures depend on the spatial scale (Best et al. 1995; Turner 2005; Bennett et al. 2006; Häkkinä et al. 2017). Furthermore, the structural connectivity influences the ecological mechanisms and habitats should be large enough to support high diversity of species (Best et al. 1995; Fahrig 2003; Bennett et al. 2006; Cisneros et al. 2015; Lee and Martin 2017; Ke et al. 2018). Otherwise, if the amount of habitat is too small, heterogeneity itself often lead to habitat fragmentation and isolation (Fahrig 2003; Bennett et al. 2006; Häkkinä et al. 2017; Lee and Martin 2017). Therefore, large waterbody enriched with floating wetland vegetation seems to have higher diversity and over dispersed community structure (Fahrig 2013; Almeida et al. 2017). Furthermore, co-occurrence of species in the lake due to variable

water depths providing diverse prey-base (Che et al. 2019) and habitat stability might increase functional and phylogenetic diversity than in other habitats (Tscharnke et al. 2012; Liang et al. 2019; Sinha et al. 2022).

Proximity to human settlements and associated edge effects were found as important factors influencing bird community structures (Andr n 1994; Fahrig 2003; Arias-Sosa et al. 2021; Jayathilake et al. 2021; Sinha et al. 2022). Habitat types of the Indawgyi ecosystem follow an anthropogenic gradient, from human-dominated agricultural land, forests, and seasonally flooded grasslands to a large area of a little-disturbed lake (Forest Department 2018). This might also explain the observed clustered functional and phylogenetic structures in forest, grassland, and agricultural land because riparian forests and grasslands of the Indawgyi ecosystem are narrowly located along the edges of the lake, circled by huge areas of human-modified cultivated land. Furthermore, forest areas are not continuous and fragmented in most parts of the wetland, especially in the eastern part of the lake (see Fig. 1). Ngcobo et al. (2022) also found that bird species richness and its phylogenetic diversity decreased in fragmented habitats despite its structural complexity. Bird community analysis in an Ethiopian wetland also found that, although local habitat variables explained the largest amount of compositional variation, these habitat effects were moderated by human disturbances (Mereta et al. 2021). Cisneros et al. (2016) found that spatially structured environmental effects explained more variation of functional and phylogenetic structures of bat communities than unique effects of space and environment in a human-modified landscape of Costa Rica. Although our study focuses on the local level habitat factors, our results revealed that area of waterbody and floating wetland vegetation had positive effects while agricultural crop cover had negative effects on functional and phylogenetic structures (Table S2). In the present study, functional diversity in conservation importance increased with distance to human settlements, suggesting that persistent anthropogenic actions would undermine conservation function of the Indawgyi ecosystem (Table S10a, Fig. 7). Furthermore, findings from our study are also consistent with the disturbance dominance hypothesis, which postulates that community assembly processes change with environmental conditions, where habitat filtering is more prevalent in stressful parts of the gradient and biotic competition is common in favorable parts (Lopez et al. 2016). This is supported by several previous studies of bird community ecology along land cover gradients (Liang et al. 2019), elevational gradients (He et al. 2021), urbanization gradients (Morelli et al. 2016), habitat fragmentation gradients (Ngcobo et al. 2022), where bird species are functionally and phylogenetically less diverse in stressful part of the gradient. However, our study merits future research that could reveal the effects of landscape level habitat factors as well as the relative importance of abiotic filtering and biotic interaction for a more comprehensive understanding of bird community assemblages (Cisneros et al. 2016; Mereta et al. 2021).

Conclusion and conservation implications

This study provides a first comprehensive assessment of the bird diversity patterns in an internationally important wetland in Myanmar. Our study found substantial variation in the structure of the bird communities in the habitats of the Indawgyi ecosystem. The study reveals that the habitats host bird communities with high occurrence of threatened species that are important for conservation, including both breeding and wintering species.

Seasonal variation of site-specific diversity values indicated complementary roles of each of four different wetland habitats in bird conservation. To maintain and improve overall diversity, the lake habitat and its associated grassland should be prioritized for conservation. These habitats are additionally important for migratory species, revealed by the seasonal variation in diversity. Our results also suggest that water coverage and floating vegetation are important habitat variables to ensure long-term conservation function. Currently, the flow of water into the lake is largely impacted by huge load of sedimentation because of goldmining in upstream areas. To sustain the conservation value of these habitats, the quality and quantity of water flowing into the lake should be monitored and maintained at optimal conditions. As intensified agriculture would lead to functional and phylogenetic homogenization of bird diversity, particular efforts should be made to control agricultural encroachment into seasonally flooded grasslands. Habitat restoration initiatives are very important to sustain ecological functions in lakeside forests and floodplain grasslands. Also, sustainable land use strategies are important to secure the livelihoods of the local communities as well as to safeguard the spatio-temporal dynamics in the diversity of the bird community in wetland systems. Agricultural practices should also be transformed towards more biodiversity-friendly, for instance organic farming, which will enhance conditions for species with high conservation value. Furthermore, human disturbances should be reduced because most biodiversity metrics tended to be higher in area faraway from disturbances. Finally, our study underlines that an integrative approach using different facets of biodiversity provide broader insight into the ecological and evolutionary drivers of community diversity than traditional taxonomic-based analysis for effective management intervention in vulnerable wetland ecosystems.

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Author contributions All authors contributed to the conceptualization and study design. Material preparation, data collection and analysis were performed by TH, under supervision of ER, THR and PSR. The first draft of the manuscript was written by TH. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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Authors and Affiliations

Thazin Htay^{1,2}  · Eivin Røskaft¹  · Thor Harald Ringsby^{1,3}  · Peter Sjolte Ranke^{1,3} 

✉ Thazin Htay
thazinh@stud.ntnu.no

¹ Department of Biology, Norwegian University of Science and Technology (NTNU), Realfagbygget, NO- 7491 Trondheim, Norway

² Nature and Wildlife Conservation Division, Forest Department, Ministry of Natural Resources and Environmental Conservation, Nay Pyi Taw, Myanmar

³ Centre for Biodiversity Dynamics (CBD), Department of Biology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway