



## Article

# Assessing the Influence of Anthropogenic Land-Use Changes on Bird Diversity and Feeding Guilds—A Case Study of Kalametiya Lagoon (Southern Sri Lanka)

Tom Bernard <sup>1,\*</sup>, K. A. S. Kodikara <sup>2</sup>, Jani Sleutel <sup>3</sup>, G. G. N. K. Wijeratne <sup>2</sup>, Jean Hugé <sup>1,3,4,5</sup>, M. P. Kumara <sup>6</sup>, M. A. Y. N. Weerasinghe <sup>7</sup>, D. P. D. Ranakawa <sup>2</sup>, W. A. K. G. Thakshila <sup>8</sup> and Farid Dahdouh-Guebas <sup>1,3,9</sup>

<sup>1</sup> Systems Ecology and Resource Management Research Unit (SERM), Department of Organism Biology, Université Libre de Bruxelles, 1050 Brussels, Belgium

<sup>2</sup> Department of Botany, Faculty of Science, University of Ruhuna, Matara 81000, Sri Lanka

<sup>3</sup> Ecology & Biodiversity Research Unit, Biology Department, Vrije Universiteit Brussel, 1050 Brussels, Belgium

<sup>4</sup> Department of Environmental Sciences, Open University of The Netherlands, 6401 Heerlen, The Netherlands

<sup>5</sup> Centre for Environmental Sciences, Research Group Zoology: Biodiversity and Toxicology, Hasselt University, 3500 Diepenbeek, Belgium

<sup>6</sup> Faculty of Fisheries and Ocean Sciences, Ocean University of Sri Lanka, Tangalle 82200, Sri Lanka

<sup>7</sup> Department of Zoology and Environment Sciences, Faculty of Sciences, University of Colombo, Colombo 00300, Sri Lanka

<sup>8</sup> Department of Zoology, Faculty of Science, University of Ruhuna, Matara 81000, Sri Lanka

<sup>9</sup> Mangrove Specialist Group (MSG), Species Survival Commission (SSC), International Union for the Conservation of Nature (IUCN), London NW1 4RY, UK

\* Correspondence: tombrnd.pro@gmail.com



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**Abstract:** Kalametiya Lagoon, a highly threatened Sri Lankan wetland, has undergone drastic hydrological changes in recent decades, due to an upstream irrigation project. These changes led to the invasion of the lagoon water by monospecific *Sonneratia caseolaris* mangrove stands and *Typha angustifolia* reedbeds. As Kalametiya has been a nationally recognized bird sanctuary since 1984, this invasion is expected to have brought significant changes upon local avifauna. Therefore, this study aimed at determining the lagoon's current bird diversity and distribution in relation with habitat types and environmental variables. Thirty-seven point-count stations were studied, between January and April 2022. Seventy-nine bird species, including four endemic and ten nationally threatened species, were encountered during the study period. Invertebrate feeders and polyphages were the richest and most diverse guilds. Bird communities were also found richer and more diverse in *T. angustifolia* reedbeds than in *S. caseolaris* mangroves. As feeding guild composition was significantly influenced by several environmental variables (i.e., water nitrate content, water TDS, water pH, soil pH), guilds could have great potential as bioindicators of the ecosystem if further studies are done to explore these relationships. Considering the important bird diversity found in the new habitats, this research brings additional proof that a management aiming at restoring the lagoon to its past state would bring significant changes to its avifaunal community. These changes could, in the future, be more precisely defined by a thorough comparison with past inventories of the lagoon's bird community.

**Keywords:** avian diversity; feeding guild; land-use changes; mangroves; reedbeds; lagoon

## 1. Introduction

In Sri Lanka, 82 lagoons have been recorded, with the majority located in the southern, south-eastern, and eastern coasts of Sri Lanka, where the littoral drift causes accreted sand to form barriers [1,2]. They are ecosystems that contribute to numerous ecosystem services such as food and water provisioning, coastal protection, water quality regulation, nutrient cycling, carbon storage, and several cultural services [3,4]. Mangrove forests associated

with coastal lagoons provide additional support to fisheries and additional natural hazard control and regulating and cultural services, and also contribute to wood, fuel, and ethnomedicinal provisioning [5–8]. Despite these ecological services and economic benefits, overexploitation of the resources, urbanization, eutrophication, pollution, and modification in their watersheds have been threatening coastal lagoons around the world [3]. Coastal ecosystems in Sri Lanka have not escaped from this pressure, as many lagoons have been subject to anthropogenic-driven changes in recent times [1,9–12]. Among the human activities that have been affecting coastal lagoons, inland irrigation projects are prominent in Sri Lanka [11,13]. Kalametiya Lagoon, on the southern coast of Sri Lanka, is an example of an altered ecosystem caused by such human pressure.

Kalametiya Lagoon, now home to a large mangrove forest, is part of the Kalametiya–Lunama Wetland Sanctuary (Lunama being a smaller lagoon connected to Kalametiya), created by the Fauna and Flora Protection Ordinance of 1984 [14,15]. For the past six decades, Kalametiya’s mangrove forest has been in constant expansion, increasing its cover from 77.5 ha in 1956 to 385.3 ha in 2016, while reducing the lagoon water surface of 86% in the same period [11]. Those changes have been linked to the Udawalawe Irrigation and Resettlement Project (UWIRP), which took place about 40 km upstream of the lagoon [11,13,15]. A direct consequence of the UWIRP has been the constant change of Kalametiya lagoon conditions in recent decades, as illustrated by the high turbidity and nutrient levels as well as the low salinity levels recorded in 2016 [11]. The modified physiochemical parameters, combined with a strong increase in siltation filling at least 40% of the lagoon between 1990 and 2005, caused the co-invasion of the lagoon by *Sonneratia caseolaris* (L.) Engl. mangrove stands, a low-saline mangrove species, and *Typha angustifolia* L., a brackish water marsh plant [11,16]. The associated land-use changes are very likely to have brought about changes for the fauna and flora of Kalametiya.

In an ecosystem subject to environmental modifications, species that can show early, clear and easily detected ecological changes are called indicator species [17,18]. They can be used to assess the environmental conditions since they provide an early warning signal of changes in the environment [19,20]. Particularly for mangroves, studying functional diversity of faunal assemblages has been put forward as one of the research priorities for the future [21]. Birds were investigated as indicator species in this study since: (i) they are sensitive to environmental change; (ii) their ecology is generally well-known; (iii) they are ecologically versatile; (iv) they are conspicuous and easily surveyed in many environments; and (v) Kalametiya Lagoon is an important bird sanctuary [14,15,22–26].

Several studies have been conducted on avifaunal changes in response to environmental alterations in Sri Lankan coastal ecosystems. A direct relationship was established between anthropogenic disturbance intensity and the loss of avifaunal diversity in a Sri Lankan estuary [27]. Waterbird abundance and species composition were also linked to salinity levels, water depth, and aquatic macrophyte abundance in three Sri Lankan lagoons, which had been impacted by a similar irrigation scheme as Kalametiya’s [28]. By comparing two of those lagoons, hydrology alterations were shown to impact the same parameters, as well as the bird foraging ecology [29]. Relationships between ecological alterations and bird diversity, assemblage, and foraging guilds have also been recorded in several wetlands around the world. In a lagoon in south-eastern Spain, a strong relationship was observed between the nitrogen load and the abundance of two grebes species [30]. Lake morphometry and water chemistry were found to be significantly connected to the richness and composition of different foraging guilds in eutrophic boreal lakes in Canada [31]. Additionally, in Ethiopian lakes, overall species richness as well as insectivore and granivore species richness were correlated to anthropogenic disturbances [32].

The avifauna of Kalametiya has been well documented by ornithologists and official reports. In 1995, a site report was published on Kalametiya and Lunama lagoons, recording around 151 bird species, with 54 migrant species [33]. Another biodiversity record of the Kalametiya–Lunama Sanctuary was published in 2005, with 168 bird species recorded in a 6-month survey, including 121 residents, 46 winter migrants, and one offshore marine

bird [14]. Among those residents, five species were endemic and five were nationally threatened. These reports demonstrated the rich avifaunal diversity and thus conservation importance of the Kalametiya area.

However, variation in species richness or abundance has not been regularly studied, particularly not in response to the ongoing land-use and associated ecological changes. Thus, the aim of this research was to evaluate the current avifaunal diversity and establish a current baseline relationship between ecological variables and bird populations, against which future changes may be compared in Kalametiya. Four specific objectives were formulated: (i) preparation of an extensive list of bird species currently present in the study area; (ii) investigation of habitat-wise differences and overall pattern of diversity indices; (iii) analysis of the relationship between avifaunal species composition and the lagoon's environmental parameters; and (iv) analysis of the relationship between avifaunal feeding guilds and the lagoon's environmental parameters.

## 2. Materials and Methods

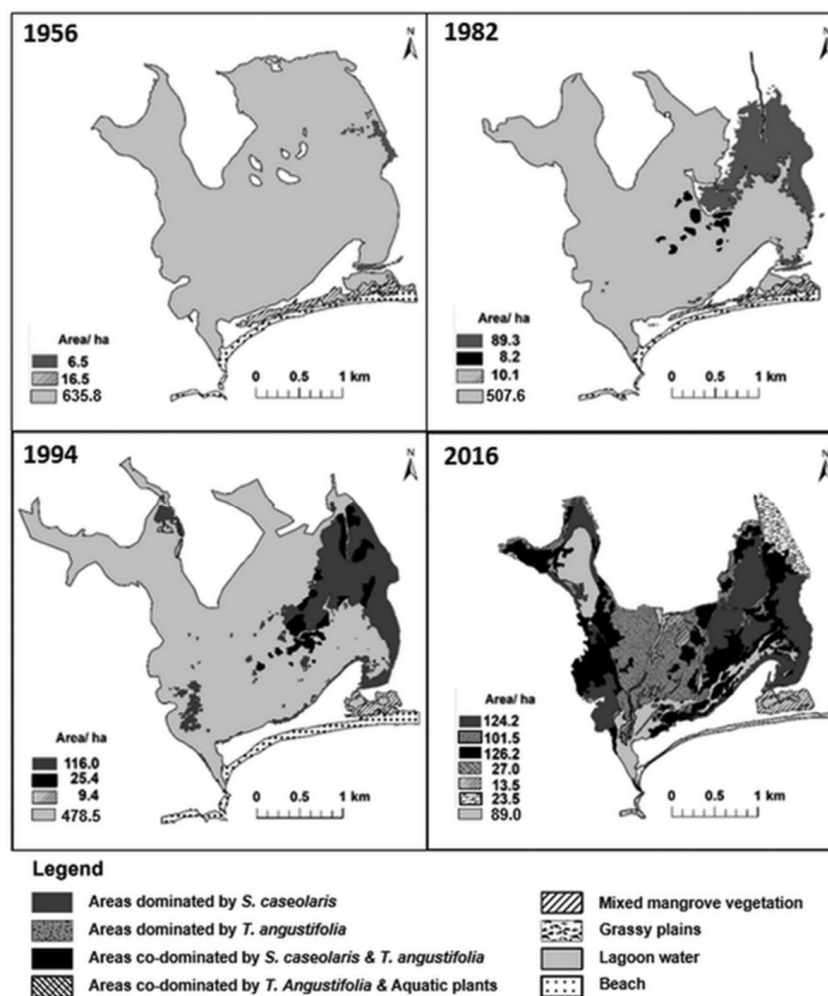
### 2.1. Study Area

The study area is Kalametiya Lagoon and its direct surroundings. It is located on the southern coast of Sri Lanka in the district of Hambantota, situated in the Low Country Dry Zone of Sri Lanka [34]. Three main habitats were considered since they represent the major land covers of the Kalametiya area: (1) Mature *S. caseolaris*-dominated habitat (*Sc*); (2) Young *S. caseolaris* and *T. angustifolia* co-dominated habitat (*Sc-Ta*); and (3) *T. angustifolia*-dominated habitat (*Ta*). Maps depicting the years 1956, 1982, 1994, and 2016, combined with the different habitat covers for each period are presented in Figure 1.

### 2.2. Sampling Design

The study area boundaries and vegetation distribution were obtained from S.K. Madarasinghe (University of Ruhuna, Sri Lanka) (Figure 2). The location of three transects mainly following the waterways of Kalametiya Lagoon were defined using ArcMap 10.3 Software (Transect I = 06°4'47.486" N, 080°56'5.586" E–06°6'20.506" N, 080°55'44.422" E; Transect II = 06°5'5.957" N, 080°56'7.5912" E–06°5'34.919" N, 080°56'13.787" E; Transect III = 06°5'7.775" N, 080°56'10.691" E–06°5'36.420" N, 080°57'4.824" E; Figure 2). The three transects included the three aforementioned vegetation regions (i.e., *Sc*, *Sc-Ta*, and *Ta*), and their physiochemical parameters had already been measured. An additional fourth transect going through the *Sc* dense vegetation was surveyed (Transect IV = 06°6'0.508" N, 080°57'15.127" E–06°6'31.7664" N, 080°57'4.468" E; Figure 2). It allowed for including birds not present at the edge of the mangrove habitat and thus not visible from the waterways. As the mangroves were dense habitats, the point-count method was selected over the line transect method for bird surveys, to allow for a higher detection rate.

Based on field accessibility, we established 37 point-count stations, further referred to as "sites", following the previously mentioned transects. Coordinates of each site were determined using the Google Earth Pro mobile application (Table S1). The sites were placed on a 2021 LULC map of the study area (Figure 2). Sites were located at a minimum distance of 100 m for the first three transects. The recommended distance of 200 m between sites [35–38] was not respected for three main reasons: (i) to account for the high density of birds in the Kalametiya sanctuary, (ii) to reduce time spent between sites, as the paddle boat was slow, and (iii) the high visibility from the waterway already reduces the probability of double counting birds. A shorter minimum distance of 50 m between sites was used for the fourth transect, because of its reduced accessibility. A pilot study was also made in August to check the relevance of the sampling method and obtain a preview of the bird community.

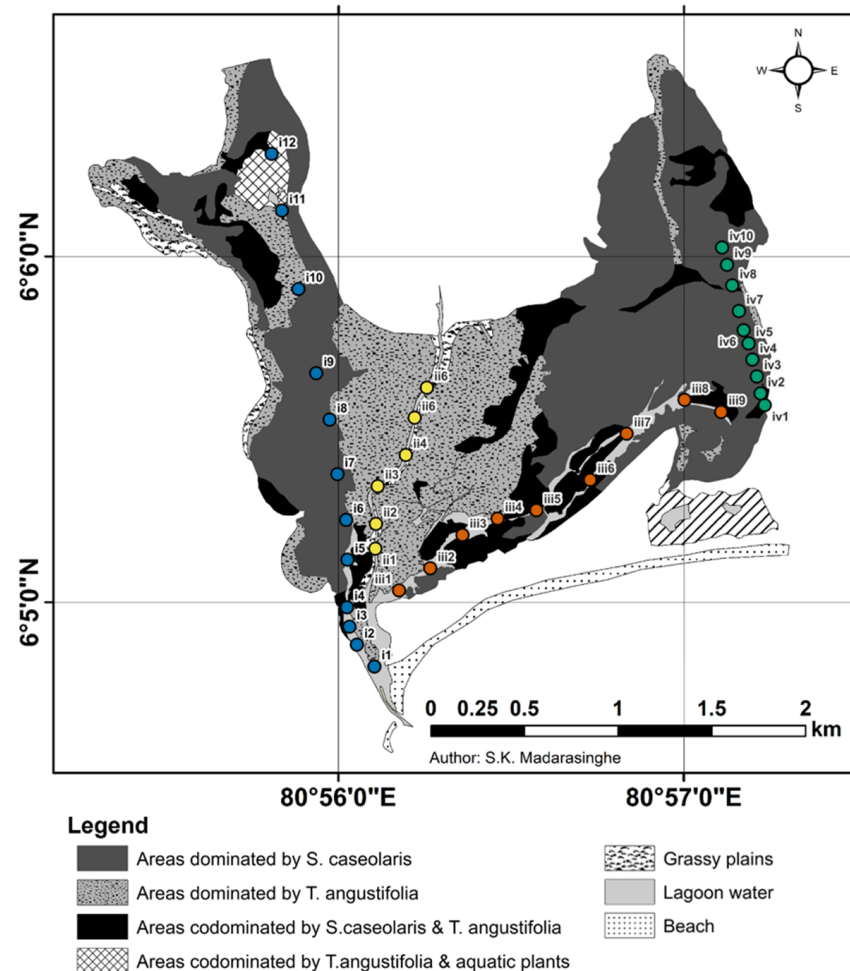


**Figure 1.** Maps of Kalametiya Lagoon showing spatio-temporal changes of vegetation over the last six decades (1956–2016). Eight considered habitat types are described in the legend, along with their respective patterns: (i) areas dominated by *S. caseolaris* (dark grey), (ii) areas dominated by *T. angustifolia* (grey with black spots), (iii) areas co-dominated by *S. caseolaris* and *T. angustifolia* (black), (iv) areas co-dominated by *T. angustifolia* and aquatic plants (white with two layers of black stripes), (v) mixed mangrove vegetation (white with one layer of black stripes), (vi) grassy plains (white with grass symbols), (vii) lagoon water (light grey), (viii) beach (white with black spots). When habitats are present in the map, corresponding area is added in ha on the side of the map. A scale in kilometres is presented under each map. Figure adopted from Madarasinghe et al. (2020) [11].

### 2.3. Bird Surveys

Sampling was performed in small observer groups at sunrise and ended before noon as birds are mostly active during that time [35,36]. Evening surveys were also conducted, starting at 4 pm and closing shortly before sunset, as some birds are also active during that time and different species may be observed [35]. No waiting time was needed before the start of the survey located in the waterway, as the paddle boat was discrete enough to not disturb the birds. When walking was necessary to access a certain site, the observations began after an approximate wait of one minute to allow the birds to settle again [38]. The chosen count period was 5 min, in correspondence to the time range advised by several studies [35–38]. Thus, birds were surveyed in an approximate 50 m radius for 5 min at each site, using both visual and auditive recognition. Birds in flight were not recorded during the surveys, except if their origin or landing point was observed. PENTAX SP 8 × 40 WP binoculars were used for the survey. The *Birds of Sri Lanka* guidebook was used to identify the birds if needed [39]. The survey period lasted for four months, from January to April

2022. During this period, all sites were surveyed twice in the morning and twice in the evening. The dates of the surveys are as follows: (i) 08 April (morning and evening) and 28 April (morning and evening) for Transect I, (ii) 14 January (morning and evening) and 06 April (morning and evening) for Transect II, (iii) 10 January (evening), 11 January (morning), and 18 April (morning and evening) for Transect III, and (iv) 20 March (morning and evening) and 07 April (morning and evening) for Transect IV.



**Figure 2.** Land-Use Map of Kalametiya Lagoon (© S. K. Madarasinghe) with the 37 point-count station sites. Seven considered habitat types are described in the legend, along with their respective patterns: (i) areas dominated by *S. caseolaris* (dark grey), (ii) areas dominated by *T. angustifolia* (grey with black spots), (iii) areas co-dominated by *S. caseolaris* and *T. angustifolia* (black), (iv) areas co-dominated by *T. angustifolia* and aquatic plants (white with two layers of black stripes), (v) grassy plains (white with grass symbols), (vi) lagoon water (light grey), (vii) beach (white with black spots). Sites are displayed in four different colours: blue for Transect I, yellow for Transect II, red for Transect III, green for Transect IV. Sites labels show their respective transect (i = Transect I, ii = Transect II, iii = Transect III, iv = Transect IV) and numbers. The area coordinates are present on the left and bottom sides of the map. A scale in kilometres is presented under the map.

The vernacular name in English, order, family, genus, and species were collected for all species observed on the study site. Species taxonomy followed the IOC Master List V12.1 [40]. The Global Conservation Status (GCS) of each species was extracted from the recently updated IUCN Red List [41]. The species' phenological status was also extracted for each species, using the 2021 National Red List of Sri Lanka [42]. The Birds of the World database was used to describe the feeding guilds [43], mainly based on the categories defined by [44]: Carnivorous (Car), (ii) Piscivorous (Psc), (iii) Invertebrate feeders (Inv),



(iv) Herbivorous (Hrb), or (v) Polyphage (combination of two or more of the previous categories; Pol). Herbivorous then was divided in four feeding guilds: frugivorous (Hrb-F), granivorous (Hrb-G), frugivorous–granivorous (Hrb-FG), and a guild containing species primarily consuming plants' vegetative parts (Hrb-P). Hrb-P was considered in the analysis to include the specific diet of *Porphyrio poliocephalus* (Latham, 1801) (i.e., plants' vegetative parts), which represented a significant portion of the observations. Thus, eight feeding guilds in total were considered. Habitat was mentioned when species were observed on affiliated sites.

#### 2.4. Vegetation Sampling

Vegetation sampling was performed at the 37 sites, in the last week of May. Two parameters, tree height, and tree girth at 130 cm above the soil and along the stem ( $G_{130}$ ), were measured in the field. These parameters were collected for the 10 closest trees to each site centre within a radius limit of 50 m. If no or less than 10 trees were present within the 50 m radius, then no or less than 10 trees were measured. Only trees with a  $G_{130}$  superior to 16 cm were considered, to avoid underestimates for sites displaying a high density of both mature and juvenile trees. Based on all the trees measured in the 50 m radius, the height and  $G_{130}$  means were calculated for each site. The mean basal area ( $\overline{\text{Basal Area}}$ ) was then computed with the following formula:

$$\overline{\text{Basal Area}} = \pi \times (\overline{D}_{130}/2)^2 \quad (1)$$

where  $\overline{D}_{130}$  is the mean diameter at 130 cm above the soil and along the stem, which was calculated as follows:

$$\overline{D}_{130} = \overline{G}_{130}/\pi \quad (2)$$

where  $\overline{G}_{130}$  is the mean girth at 130 cm above the soil and along the stem. To assess variations in forest structures, the variances of the basal area and height were also determined for each site.

#### 2.5. Environmental Sampling

Six water variables were used to assess the environmental conditions of Transect I/II/III sites: water pH, water Total Dissolved Solids (TDS), water salinity, water Biochemical Oxygen Demand (BOD), water phosphate content, water nitrate content. As no water body was remotely close to Transect IV, five sediment variables were used instead for its sites: soil pH, soil salinity, soil phosphate content, and soil nitrate content. The water and sediment variable dataset was shared by G.G.N.K. Wijeratne, from her previous study on Kalametiya's soils [45].

#### 2.6. Habitat Affiliation

Spatial analysis was needed to affiliate a specific habitat to each site, as several were surrounded by more than one habitat type. This analysis was performed on QGIS 3.24.3, using the 2021 LULC-map of the Kalametiya area (Figure 2) and the mobile-based Google Earth Pro site coordinates (Table S1). First, a 100 m radius buffer was created around every sampling site. The distance of 100 m was chosen to compensate for the inaccuracy of mobile-based coordinates. The area covered by every habitat type was then measured within each buffer, and those values were converted to percentages of the 100 m radius area. Areas belonging to the Grassy Plain habitat were not considered in the percentage calculations since they accounted for a low proportion of the buffer area while hiding the overall Ta-habitat affiliation. A minimum coverage of 75% of the buffer area by one habitat was chosen as the threshold for the habitat-site affiliation.

#### 2.7. Avifauna Analysis

Two types of index values were used in the analysis: (i) the total index value using the pooled data of all sites included in a category, and (ii) the mean index value corresponding

to the mean of individual index values of each site included in a category. Mean index values were calculated to account for the difference in site sample size between habitats.

Along with the number of observations (N), three estimates of species richness were computed for the overall study and each habitat: observed species richness (S), and two incidence-based nonparametric estimators Chao2 and Jackknife2 [46,47]. The aim of the nonparametric methods was to control for sampling effort effect and estimate the lower boundary of the actual species richness. Both total and mean index values were calculated for S and N ( $\bar{S}$  and  $\bar{N}$  for the respective means).

Six diversity indices were additionally computed in PRIMER 7 v.7.0.21 for the overall study, the feeding guilds, and the habitats: (i) the commonly used Shannon–Wiener Index H, (ii) a modified form of Simpson’s dominance index  $1-\lambda$ , (iii) an equitability index, Pielou’s evenness J, (iv) the average taxonomic distinctness  $\Delta^*$ , (v) the average taxonomic breadth  $\Delta^+$ , and (vi) the taxonomic distinctness variation  $\Lambda^+$ . The average taxonomic distinctness estimates taxonomic diversity based on abundance data, whereas the average taxonomic breadth uses incidence data. The taxonomic distinctness variation estimates the variation of the average taxonomic breadth within a sample. Formulas of the indices are as defined by [48]:

(i) Shannon–Wiener’s Index:

$$H = - \sum_i p_i \log(p_i) \quad (3)$$

where  $p_i$  is the proportion of the total abundance of species  $i$ .

(ii) Simpson’s Index:

$$1 - \lambda = 1 - (\sum_i p_i^2) \quad (4)$$

where  $p_i$  is the proportion of the total abundance of species  $i$ .

(iii) Pielou’s Evenness:

$$J = H/H_{\max} \quad (5)$$

where  $H_{\max}$  is the maximum value of Shannon–Wiener diversity, reached if all species are equally abundant.

(iv) Taxonomic Distinctness:

$$\Delta^* = \left[ \sum \sum_{i < j} \omega_{ij} x_i x_j \right] / \left[ \sum \sum_{i < j} x_i x_j \right] \quad (6)$$

where  $x_i$  is the number of individuals of species  $i$ ,  $x_j$  is the number of individuals of species  $j$ , and  $w_{ij}$  is the taxonomic distance between species  $i$  and species  $j$ .

(v) Taxonomic Breadth:

$$\Delta^+ = \left[ \sum \sum_{i < j} \omega_{ij} \right] / [S(S-1)/2] \quad (7)$$

where  $i$  and  $j$  are a pair of distinct species,  $w_{ij}$  is the taxonomic distance between species  $i$  and species  $j$ , and  $S$  is the observed species richness.

(vi) Taxonomic Distinctness Variation:

$$\Lambda^+ = \left[ \sum \sum_{i < j} (\omega_{ij} - \Delta^+)^2 \right] / [S(S-1)/2] \quad (8)$$

where  $i$  and  $j$  are a pair of distinct species,  $w_{ij}$  is the taxonomic distance between species  $i$  and species  $j$ ,  $S$  is the observed species richness, and  $\Delta^+$  is the Taxonomic Breadth. For the overall study and feeding guilds, total diversity indices were calculated using data from all the sites. For habitats, mean diversity indices and their standard deviations were calculated using affiliated sites data. To compare habitats, statistical tests were performed

in R-Studio 2022.02.3 [49]. Normality and homoscedasticity were verified with the Shapiro–Wilk test (package *stats* [49], function *shapiro.test*) and the Levene test (package *car* [50], function *leveneTest*), respectively. When those two assumptions were met, a two-sided Welch *t*-test (package *stats*, function *t.test*) was performed to account for differences in sample size. When they were not met, a two-sided nonparametric Wilcoxon test (package *stats*, function *wilcox.test*) was used. Means and standard deviations were also calculated for S and Relative Abundances (RA) for each guild within each habitat. Their statistical comparisons were performed as explained above and plotted on a bar chart (package *ggplot2* [51], function *ggplot*).

R-Studio 2022.02.3 was also used for multivariate analysis. To visualize species composition differences between sites and habitats, the Principal Component Analysis (PCA) (package *vegan* [52], function *rda*) unconstrained ordination method was used. To model relationships between environmental variables and species composition, the Redundancy Analysis (RDA) (package *vegan*, function *rda*) constrained ordination method was used. Both methods follow [53]. Abundance data was transformed in Hellinger distances (package *vegan*, function *decostand* and *rda*) with the formula [53,54]:

$$D_{\text{Hellinger}}(x_1, x_2) = \sqrt{\sum_{j=1}^p \left[ \sqrt{\frac{y_{1j}}{y_{1+}}} - \sqrt{\frac{y_{2j}}{y_{2+}}} \right]^2} \quad (9)$$

where  $x_1$  and  $x_2$  are two distinct sites,  $j = \{1 \dots p\}$  is the species,  $y_{ij}$  is the number of individuals of species  $j$  at site  $i$ , and  $y_{i+}$  is the sum of species numbers of individuals of site  $i$ . Two sets of ordination analysis were performed: (i) on species transformed abundances and (ii) on feeding guild transformed abundances. Feeding guild abundances of a site are further referred to as feeding guild composition. Each set of ordination included one PCA and two RDA ordinations: one RDA on Transects I/II/III sites for which water variables were available, and one on Transect IV sites for which sediment variables were available. For Transect I/II/III RDA ordinations, twelve explanatory variables were used: latitude, longitude, water pH, water TDS, water salinity, water BOD, water phosphate content, water nitrate content, mean tree basal area, mean tree height, tree basal area variance, and tree height variance. For Transect IV RDA ordinations, ten explanatory variables were used: latitude, longitude, soil pH, soil salinity, soil phosphate content, soil nitrate content, mean tree basal area, mean tree height, tree basal area variance, and tree height variance. Explanatory variables were first standardized (package *base* [49], function *scale*). A matrix of correlation was then created for each set of variables (package *stats*, function *cor*) using nonparametric Spearman's rank correlation coefficient. The variable with the highest mean absolute correlation was then removed for each pair of variables with a correlation coefficient superior to 0.7 (package *caret* [55], function *findCorrelation*). Final RDA models were created with a forward selection of explanatory variables using the double  $R^2$  stopping criterion (package *vegan*, function *ordiR2step*), in order to reduce the overestimation of explained variance and the high Type 1 error [56]. Variables were added randomly to the model in order to maximize its adjusted  $R^2$  ( $R^2_{\text{adj}}$ ). It stopped when the adjusted  $R^2$  decreased or exceeded the model including all explanatory variables, or when the permutation  $p$ -value limit of 0.05 was exceeded. RDA ordinations were plotted using their first two ordination axis, explaining the most amount of variance (package *ggplot2*, function *ggplot*).

### 3. Results

#### 3.1. Habitat Affiliation

Out of the 37 sites sampled, 16 were affiliated to a specific habitat (i.e., *Sc*, *Ta*, *Sc-Ta*). Five sites, all from Transect II (i.e., ii2, ii3, ii4, ii5, ii6), were affiliated with the *Ta* habitat. Ten sites, from both Transect I and Transect IV (i.e., i7, i9, iv3, iv4, iv5, iv6, iv7, iv8, iv9, iv10), were affiliated with the *Sc* habitat. Only one site, from Transect III (i.e., iii6), was



affiliated with the Sc-Ta habitat. As one site is not a statistically sufficient sample size, the Sc-Ta habitat was not included in most of the following analyses.

### 3.2. Diversity Analysis

The extensive list of birds encountered during the study period in Kalametiya is provided in the Supplementary Materials (Table S2). Over the totality of the study period (including observations made outside of survey periods), 79 species, belonging to 40 families and 14 orders, were observed. A total of four endemic species were encountered: *Cecropis hyperythra* (Blyth, 1849), *Dicaeum vincens* (Sclater, 1872), *Dinopium psarodes* (Lichtenstein, 1793), and *Gallus lafayettii* (Lesson, 1831). Ten nationally threatened species were observed: three critically endangered (*Sterna hirundo* (L., 1758), *Columba livia* (Gmelin, 1789), and *Merops philippinus* (L., 1767)), three endangered (*Acrocephalus stentoreus* (Hemprich and Ehrenberg, 1833), *Dicaeum vincens*, and *Ixobrychus sinensis* (Gmelin, 1789)), one vulnerable (*Sternula albifrons* (Pallas, 1764)), and three near threatened (*Streptopelia decaocto* (Frisvaldszki, 1838), *Merops leschenaulti* (Vieillot, 1817), and *Lonchura malacca* (L., 1766)). Additionally, seven of the 79 encountered species were considered globally threatened, and all were classified as near threatened. A large majority of the birds were residents, with only 10 observed migrant species.

During the surveys, the three most abundant birds were *Himantopus himantopus* (L., 1758), *Tringa totanus* (L., 1758), and *Corvus splendens* (Vieillot, 1817), accounting for 10.29%, 9.35%, and 5.67% of the total number of observations, respectively. Five of the ten most abundant species belonged to the invertebrate feeder guild. Relative abundances, number of observations, feeding guild, and affiliated habitats are presented below for all species observed during the surveys (Table 1).

**Table 1.** List of bird species, in order of relative abundances, observed during point-count surveys performed in Kalametiya Lagoon, Sri Lanka. This table only includes observations made during the surveys. Feeding Guild labels: (i) Inv = Invertebrate feeder, (ii) Pol = Polyphage, (iii) Hrb-FG = Frugivorous–granivorous, (iv) Hrb-F = Frugivorous, (v) Hrb-G = Granivorous, (vi) Hrb-P = Species consuming plants’ vegetative parts, (vii) Psc = Piscivorous. Habitat labels: (i) Sc = *Sonneratia caseolaris*-dominated habitat, (ii) Sc-Ta = *S. caseolaris* – *Typha angustifolia* co-dominated habitat, (iii) Ta = *T. angustifolia*-dominated habitat. Taxonomic authorities are provided for all species in the Supplementary Materials (Table S2).

Latin Name	Vernacular Name	Relative Abundance	Number of Observations	Feeding Guild	Habitat
<i>Himantopus himantopus</i>	Black-winged Stilt	10.29%	252	Inv	Sc/Ta
<i>Tringa totanus</i>	Common Redshank	9.35%	229	Inv	Sc
<i>Corvus splendens</i>	House Crow	5.67%	139	Pol	Sc/Sc-Ta/Ta
<i>Leptocoma zeylonica</i>	Purple-rumped Sunbird	5.22%	128	Inv	Sc/Sc-Ta/Ta
<i>Spilopelia chinensis</i>	Spotted Dove	4.57%	112	Hrb-FG	Sc/Ta
<i>Acridotheres tristis</i>	Common Myna	4.41%	108	Pol	Sc/Ta
<i>Vanellus indicus</i>	Red-wattled Lapwing	3.59%	88	Inv	Sc/Ta
<i>Merops philippinus</i>	Blue-tailed Bee-Eater	3.31%	81	Inv	Sc/Sc-Ta/Ta
<i>Plegadis falcinellus</i>	Glossy Ibis	3.18%	78	Pol	—
<i>Microcarbo niger</i>	Little Cormorant	2.90%	71	Psc	Sc-Ta/Ta
<i>Ardea purpurea</i>	Purple Heron	2.90%	71	Pol	Sc/Sc-Ta/Ta
<i>Hirundo rustica</i>	Barn Swallow	2.16%	53	Inv	Sc/Ta
<i>Ducula aenea</i>	Green Imperial Pigeon	2.12%	52	Hrb-F	Sc/Sc-Ta/Ta
<i>Ardea intermedia</i>	Intermediate Egret	2.12%	52	Psc	Sc/Sc-Ta/Ta
<i>Egretta garzetta</i>	Little Egret	2.12%	52	Pol	Sc/Ta
<i>Psittacula krameri</i>	Rose-ringed Parakeet	2.12%	52	Hrb-FG	Sc/Ta
<i>Porphyrio poliocephalus</i>	Grey-headed Swamphen	2.08%	51	Hrb-P	Sc/Ta

Table 1. Cont.

Latin Name	Vernacular Name	Relative Abundance	Number of Observations	Feeding Guild	Habitat
<i>Dendrocygna javanica</i>	Lesser Whistling-Duck	1.88%	46	Pol	Sc/Sc-Ta/Ta
<i>Eudynamis scolopaceus</i>	Asian Koel	1.84%	45	Hrb-F	Sc/Ta
<i>Ardeola Grayii</i>	Indian Pond Heron	1.76%	43	Pol	Sc/Ta
<i>Sternula albifrons</i>	Little Tern	1.76%	43	Pol	Sc/Ta
<i>Psilopogon zeylanicus</i>	Brown-headed Barbet	1.51%	37	Hrb-F	Sc/Sc-Ta/Ta
<i>Ardea cinerea</i>	Grey Heron	1.47%	36	Psc	Ta
<i>Lonchura punctulata</i>	Scaly-breasted Munia	1.39%	34	Hrb-G	Sc
<i>Threskiornis melanocephalus</i>	Black-headed Ibis	1.31%	32	Pol	Sc/Sc-Ta/Ta
<i>Columba livia</i>	Rock Dove	1.31%	32	Hrb-FG	Sc/Ta
<i>Pelecanus philippensis</i>	Spot-billed Pelican	1.31%	32	Psc	Sc/Ta
<i>Lonchura malacca</i>	Tricolored munia	1.10%	27	Hrb-G	Sc/Ta
<i>Orthotomus sutorius</i>	Common Tailorbird	1.06%	26	Inv	Sc/Ta
<i>Anthus rufulus</i>	Paddyfield Pipit	1.02%	25	Inv	Sc/Sc-Ta
<i>Hydrophasianus chirurgus</i>	Pheasant-tailed Jacana	0.82%	20	Inv	Ta
<i>Pycnonotus cafer</i>	Red-vented Bulbul	0.82%	20	Hrb-F	Sc
<i>Dinopium psarodes</i>	Red-backed Flameback	0.78%	19	Inv	Sc/Ta
<i>Anastomus oscitans</i>	Asian Openbill	0.69%	17	Inv	Sc/Ta
<i>Anhinga melanogaster</i>	Oriental Darter	0.69%	17	Psc	Sc/Sc-Ta/Ta
<i>Halcyon smyrnensis</i>	White-throated Kingfisher	0.69%	17	Pol	Sc/Sc-Ta/Ta
<i>Argya affinis</i>	Yellow-billed Babbler	0.65%	16	Pol	Sc/Ta
<i>Centropus sinensis</i>	Greater Coucal	0.61%	15	Pol	Sc/Sc-Ta/Ta
<i>Tringa glareola</i>	Wood Sandpiper	0.57%	14	Pol	Sc
<i>Prinia socialis</i>	Ashy Prinia	0.53%	13	Inv	Ta
<i>Sterna hirundo</i>	Common Tern	0.49%	12	Pol	Ta
<i>Mycteria leucocephala</i>	Painted Stork	0.49%	12	Psc	Sc/Ta
<i>Chalcophaps indica</i>	Common Emerald Dove	0.45%	11	Hrb-FG	Ta
<i>Pycnonotus luteolus</i>	White-browed Bulbul	0.45%	11	Hrb-F	Sc
<i>Lalage melanoptera</i>	Black-headed Cuckooshrike	0.41%	10	Inv	Sc/Ta
<i>Oriolus xanthornus</i>	Black-hooded Oriole	0.37%	9	Hrb-F	Sc/Ta
<i>Alcedo atthis</i>	Common Kingfisher	0.37%	9	Psc	Sc/Ta
<i>Prinia inornata</i>	Plain Prinia	0.37%	9	Inv	Sc
<i>Ixobrychus sinensis</i>	Yellow Bittern	0.37%	9	Inv	Ta
<i>Vanellus malabricus</i>	Yellow-wattled Lapwing	0.37%	9	Inv	Sc
<i>Pavo cristatus</i>	Indian Peafowl	0.33%	8	Pol	Sc/Ta
<i>Ceryle rudis</i>	Pied Kingfisher	0.29%	7	Psc	Ta
<i>Motacilla cinerea</i>	Grey Wagtail	0.24%	6	Inv	Sc
<i>Gallus lafayettii</i>	Sri Lanka Junglefowl	0.24%	6	Pol	—
<i>Rhipidura aureola</i>	White-browed Fantail	0.20%	5	Inv	Ta
<i>Merops orientalis</i>	Asian Green Bee-Eater	0.16%	4	Inv	Sc
<i>Copsychus saularis</i>	Oriental Magpie-Robin	0.16%	4	Inv	Sc
<i>Gallinula chloropus</i>	Common Moorhen	0.12%	3	Pol	—
<i>Lanius cristatus</i>	Brown Shrike	0.08%	2	Inv	Sc
<i>Treron bicinctus</i>	Orange-breasted Green Pigeon	0.08%	2	Hrb-F	Sc
<i>Pelargopsis capensis</i>	Stork-billed Kingfisher	0.08%	2	Pol	Sc
<i>Amaurornis phoenicurus</i>	White-breasted Waterhen	0.08%	2	Pol	Sc
<i>Dicaeum vincens</i>	Legge's Flowerpecker	0.08%	2	Hrb-F	Sc
<i>Ardea alba</i>	Great Egret	0.04%	1	Psc	—

Among the seven considered feeding guilds, the invertebrate feeder and polyphage guilds displayed a notably higher total observed species richness (i.e., 21 and 19 species, respectively) and relative abundance (i.e., 41.18% and 28.86%). The piscivorous guild only included nine species with a total relative abundance of 9.67%. The herbivorous guild, when all sub-categories were combined, was represented by 15 species and a relative abundance of 20.29%. Within the herbivorous guild, eight species were frugivorous,

four frugivorous–granivorous, two granivorous, and one primarily consumed plants’ vegetative parts (Grey-headed Swamphen). Both the Shannon–Wiener (H) and Simpson’s indices (1–λ) showed higher values for guilds with a higher observed species richness, although it was lower for the richest guild (invertebrate feeders) ( $H_{Inv} = 2.263$ ) than for the polyphage guild ( $H_{Pol} = 2.483$ ). The polyphage guild displayed the second highest evenness ( $J_{Pol} = 0.8432$ ) whereas the invertebrate feeders exhibited the lowest ( $J_{Inv} = 0.7434$ ). The highest taxonomic diversity was found in the frugivorous guild when the index factored in abundances ( $\Delta_{Hrb-F}^* = 97.54$ ). When only incidence of species was considered, the polyphage guild showed the highest taxonomic diversity ( $\Delta_{Pol}^+ = 96.05$ ). The variation of taxonomic distances between the species of a same guild was the highest in the frugivorous–granivorous guild ( $\Lambda_{Hrb-FG}^+ = 625$ ) and the lowest in the polyphage guild ( $\Lambda_{Pol}^+ = 141.6$ ). All diversity indices for each feeding guild are displayed below (Table 2).

**Table 2.** Comparison of number of observations (N), relative abundance (RA), observed species richness (S), and six diversity indices in the overall study and in the seven different bird feeding guilds of Kalametiya Lagoon, Sri Lanka. For feeding guild labels, cf. Table 1. The presented diversity indices are Shannon–Wiener’s Index (H), Simpson Index (1–λ), Pielou’s Evenness (J), Average Taxonomic Distinctness (Δ\*), Average Taxonomic Breadth (Δ+), and Variation in Taxonomic Distinctness (Λ+).

Feeding Guild	N	RA	S	H	1–λ	J	Δ*	Δ+	Λ+
Overall	2450	—	64	3.584	0.9594	0.8618	95.66	95.51	140.40
Inv	1009	41.18%	21	2.263	0.8503	0.7434	91.38	91.07	214.9
Pol	707	28.86%	19	2.483	0.8942	0.8432	93.05	96.05	141.6
Psc	237	9.67%	9	1.842	0.8108	0.8383	88.95	89.58	499.1
Hrb-F	178	7.27%	8	1.70	0.79	0.82	97.54	91.07	322.1
Hrb-FG	207	8.45%	4	1.12	0.62	0.81	80.47	75	625
Hrb-G	61	2.49%	2	0.69	0.49	0.99	25	25	—
Hrb-P	51	2.08%	1	—	—	—	—	—	—

Total S, Total N, Chao2, and Jackknife2 were higher in the Sc habitat than in the Ta habitat (Table 3).  $\bar{S}$  was found statistically higher in Ta ( $\bar{S}_{Ta} = 22.6 \pm 2.61$ ) than in Sc ( $\bar{S}_{Sc} = 14.4 \pm 2.17$ ) ( $t = 5.06$ ,  $df = 6.88$ ,  $p$ -value = 0.00054). Species richness estimators and number of observations for the overall study are also presented in Table 3.

**Table 3.** Comparison of species richness estimators (S, Chao2, Jackknife2) and number of observations (N) of birds between the overall study site and the Sc and the Ta habitats. For habitat labels, cf. Table 1. SD stands for Standard Deviation. An asterisk represents a statistically significant ( $p$ -value < 0.05) difference between the two habitats.

Categories	N		S		Chao2 (±SD)	Jackknife2
	Total	$\bar{N} (\pm SD)$	Total	$\bar{S} (\pm SD)$		
Overall	2450	66.22 (56.04)	64	15.59 (4.01)	65 (1.46)	64.32
Sc	619	61.9 (9.86)	51	14.4 * (2.17)	69.18 (10.69)	77.18
Ta	372	74.4 (13.59)	44	22.6 * (2.61)	48.55 (3.83)	53.05

Among the six diversity indices of Sc and Ta habitats (Table 4), only the Shannon–Wiener Index was found to be significantly different. Its mean was significantly higher in the Ta habitat ( $\bar{H}_{Ta} = 2.83 \pm 0.31$ ) than in the Sc habitat ( $\bar{H}_{Sc} = 2.39 \pm 0.16$ ) ( $t = 3$ ,  $df = 5.10$ ,  $p$ -value = 0.029).

**Table 4.** Comparison of the mean diversity indices of the avifaunal community between the Sc and Ta habitats. For habitat labels, cf. Table 1. For diversity indices symbols, cf. Table 2. SD stands for Standard Deviation. An asterisk represents a statistically significant difference ( $p$ -value < 0.05) between the two habitats.

Categories	$\bar{H}$ ( $\pm$ SD)	$\bar{1-\lambda}$ ( $\pm$ SD)	$\bar{J}$ ( $\pm$ SD)	$\bar{\Delta}^*$ ( $\pm$ SD)	$\bar{\Delta}^+$ ( $\pm$ SD)	$\bar{\Lambda}^+$ ( $\pm$ SD)
Sc	2.39 * (0.16)	0.88 (0.03)	0.9 (0.04)	93.12 (3.41)	94.03 (2.61)	167.13 (65.62)
Ta	2.83 * (0.31)	0.92 (0.05)	0.91 (0.08)	94.72 (1.62)	95.9 (0.71)	152.86 (28.31)

Among their five most abundant species (Table 5), Sc and Ta habitats only shared one: *Leptocoma zeylonica* (L., 1766). *Leptocoma zeylonica*, *Spilopelia chinensis* (Scopoli, 1786), and *Vanellus indicus* (Boddaert, 1783) were the three most abundant species in the Sc habitat with 13.57%, 12.12%, and 7.43% of total bird count, respectively. For the Ta habitat, the three most abundant species were *Himantopus himantopus*, *Ardea purpurea* (Sykes, 1832), and *Leptocoma zeylonica* with 9.14%, 5.91%, and 5.65% of total bird count, respectively. *Corvus splendens* represented a significant part of the observations in both habitats (sixth most abundant species in Sc, fifth most abundant species in Ta).

**Table 5.** List of the five most abundant bird species, in order of relative abundances, in the Sc and Ta habitats. For habitat labels, cf. Table 1. RA stands for Relative Abundance.

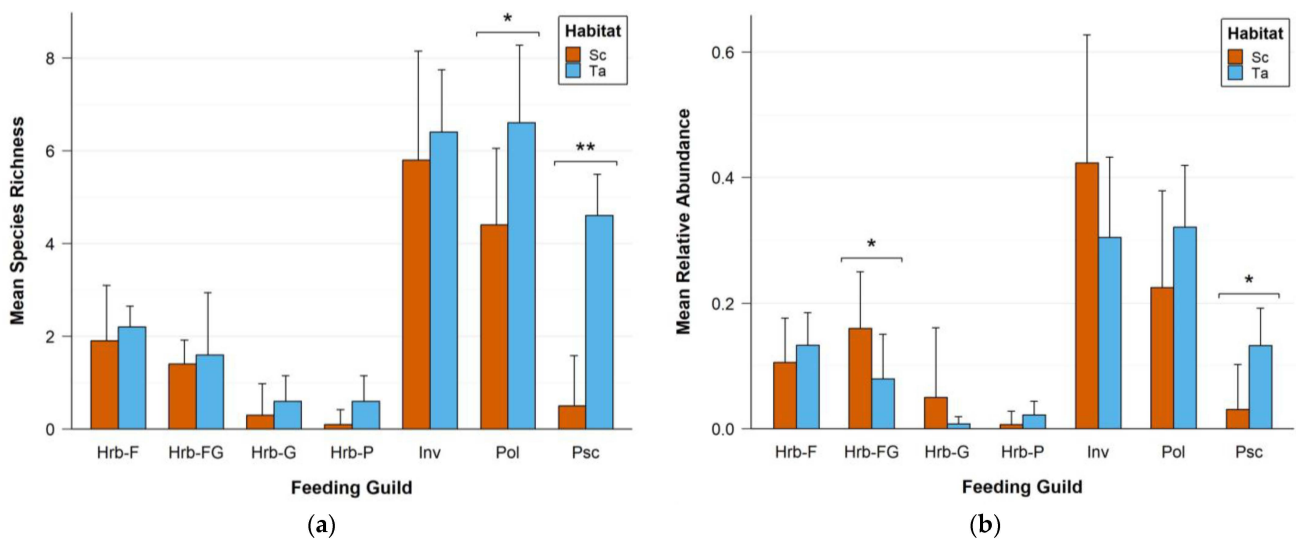
Sc		Ta	
Common Name	RA	Common Name	RA
<i>Leptocoma zeylonica</i>	13.57%	<i>Himantopus himantopus</i>	9.14%
<i>Spilopelia chinensis</i>	12.12%	<i>Ardea purpurea</i>	5.91%
<i>Vanellus indicus</i>	7.43%	<i>Leptocoma zeylonica</i>	5.65%
<i>Acridotheres tristis</i>	5.98%	<i>Ducula aenea</i>	5.38%
<i>Merops philippinus</i>	4.52%	<i>Corvus splendens</i>	4.57%

Comparison of the foraging guilds mean observed species richness and relative abundance between the Sc and Ta habitats is displayed on Figure 3. The polyphage guild ( $\bar{S}_{Pol-Ta} = 6.6 \pm 1.67$ ,  $\bar{S}_{Pol-Sc} = 4.4 \pm 1.65$ ;  $t = -2.41$ ,  $df = 7.98$ ,  $p$ -value = 0.042) and the piscivorous guild ( $\bar{S}_{Psc-Ta} = 4.6 \pm 0.89$ ,  $\bar{S}_{Psc-Sc} = 0.5 \pm 1.08$ ;  $W = 0.5$ ,  $p$ -value = 0.0013) showed a higher species richness in Ta than in Sc. The frugivorous–granivorous guild ( $\bar{RA}_{FG-Sc} = 0.16 \pm 0.09$ ,  $\bar{RA}_{FG-Ta} = 0.08 \pm 0.071$ ;  $t = 2.83$ ,  $df = 12.27$ ,  $p$ -value = 0.015) was significantly more abundant in Sc than in Ta, in contrast to the piscivorous guild ( $\bar{RA}_{Psc-Ta} = 0.13 \pm 0.06$ ,  $\bar{RA}_{Psc-Sc} = 0.03 \pm 0.07$ ;  $W = 6$ ,  $p$ -value = 0.014).

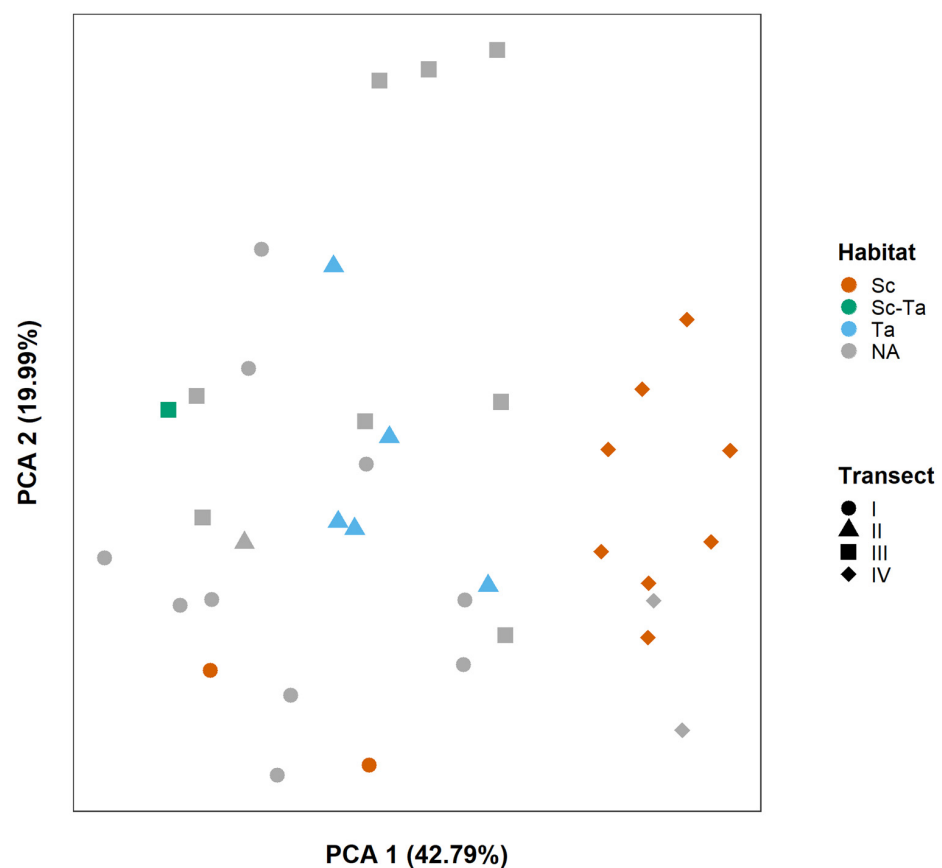
### 3.3. Multivariate Analysis

As multivariate analysis of species composition poorly explained the variation in both PCA (proportion of explained variation of 29.74% when the two first ordination axes were added) and RDA ( $R^2_{adj}$  of 8.96% and 14.52% for the first and second model, respectively) compared to feeding guild composition, and guild abundances were used for both ordination methods.

The PCA ordination diagram was built with the two first ordination axes PC1 (Eigenvalue = 0.089, Explained Proportion = 42.79%) and PC2 (Eigenvalue = 0.041, Proportion Explained = 19.99%), accounting for a total of 62.78% of the guild composition variation among sites (Figure 4). The only observed pattern was a cluster of Transect IV sites, as habitat affiliation did not show significant impact on the grouping of affiliated sites.



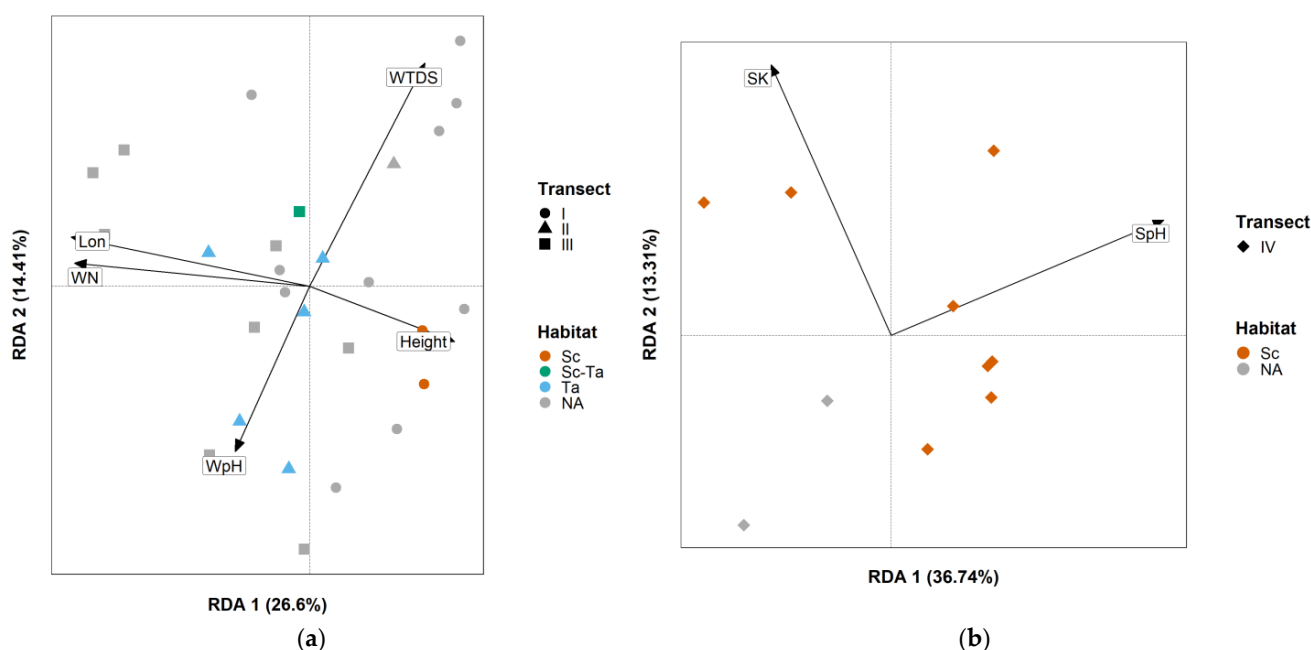
**Figure 3.** Comparison of (a) mean observed species richness and (b) mean relative abundance of the seven feeding guilds between the Sc and Ta habitats. For habitat and feeding guild labels, cf. Table 1. An asterisk represents a statistically significant difference between the two habitats (\* for  $p$ -values < 0.05, \*\* for  $p$ -values < 0.01). Error bars represent the standard deviations.



**Figure 4.** PCA ordination diagram on Kalametiya Lagoon feeding guilds abundance variation among study sites. It uses the two first ordination axes, PC1 and PC2, displayed on the left and bottom sides of the figure with their explained proportion in percentages. For habitat labels, cf. Table 1, except for NA, which is used for sites with no habitat affiliation. The shape of the dots displays transect affiliation: circle for Transect I, triangle for Transect II, square for Transect III, and diamond for Transect IV.



In the Transect I/II/III environmental dataset, mean tree basal area and water salinity were removed because of their respective correlation with mean tree height ( $r_s = 0.769$ ) and latitude ( $r_s = 0.758$ ). Following the forward selection, five variables were found to have significantly influenced feeding guild composition: water nitrate content ( $p$ -value = 0.001), water TDS ( $p$ -value = 0.006), longitude ( $p$ -value = 0.006), water pH ( $p$ -value = 0.014), and mean tree height ( $p$ -value = 0.023). The final RDA model was strongly significant ( $p$ -value = 0.001, variance = 0.077,  $F = 3.90$ ) and explained more than a third of the guild abundances' variations ( $R^2_{adj} = 0.36$ ). Habitat affiliation did not show any significant pattern in the RDA ordination diagram (Figure 5A). After the removal of correlated variables in the Transect IV environmental dataset, five variables remained: soil pH, soil salinity, soil phosphate content, tree basal area variance, and tree height variance. After the forward selection, only soil pH ( $p$ -value = 0.006) was found to significantly influence feeding guild composition. Soil phosphate content was also added to the model as it almost reached the significance threshold ( $p$ -value = 0.066), and in order to explore possible patterns. The final model was strongly significant ( $p$ -value = 0.008, variance = 0.057,  $F = 3.51$ ) and explained again more than a third of the guild composition variation ( $R^2_{adj} = 0.36$ ). A no habitat affiliation visual pattern was also observed (Figure 5B).



**Figure 5.** RDA ordination diagram for (a) Transect I/II/III and (b) Transect IV, linking Kalametiya Lagoon environmental variables and feeding guild composition among study sites. They use the two first ordination axes, RDA 1 and RDA 2, displayed on the left and bottom sides of each figure with their explained proportion in percentages. For habitat labels, cf. Table 1, except for NA, which is used for sites with no habitat affiliation. The shape of the dots displays transect affiliation: circle for Transect I, triangle for Transect II, square for Transect III, and diamond for Transect IV. Labels for environmental variables are: Lon = longitude, WN = water nitrate content, WTDS = water total dissolved solids, WpH = water pH, Height = mean tree height, SK = soil phosphate content, SpH = soil pH.

#### 4. Discussion

During this research, 15% of the 522 bird species present in Sri Lanka were encountered, encompassing nearly half of the country's taxonomic families [57]. Locally, the observed avifaunal richness of Kalametiya Lagoon was slightly lower than neighbouring Rekawa Lagoon, where 104 bird species have been recorded [58]. Kalametiya Lagoon thus includes more than 40% of the 184 bird species present in the Rekawa, Ussangoda, Kalametiya inland coastal area [59]. Four of the 34 nationally endemic bird species were

encountered in Kalametiya Lagoon: *Dicaeum vincens*, *Dinopium psarodes*, *Gallus lafayettii*, and *Cecropis hyperythra*.

In the last inventory of the area, 168 species were recorded including five endemic birds [14]: *Gallus lafayettii*, *Treron pompadora* (Gmelin, 1789), *Cecropis hyperythra*, *Tephrodornis affinis* (Blyth, 1847), and *Pellorneum fuscocapillum* (Blyth, 1849). The lower number of species observed in the current study could likely be due to the lower sampling effort, as the previous inventory was conducted for 6 months at fortnightly intervals both day and night. This supposition is however not supported by the fact that non-parametric species richness estimators were almost equal to the observed species richness for the overall study site. The previous study also used line transects in addition to point-counts, whereas this study only relied on point-counts. As the last inventory surveyed the entire Lunama–Kalametiya Wetland Sanctuary, the covered area was at that time much larger and included several additional habitats (e.g., anthropogenic habitats, sand dunes, salt marches) [14]. Furthermore, no sampling site was placed in the Kalametiya Lagoon mixed-mangrove patch (Figure 2), which could be the reason for some of the missed diversity. The difference in species richness and assemblage (e.g., new endemic species) could finally be the result of the rapid evolution of Kalametiya Lagoon, due to a continuous co-invasion of lagoon water by *T. angustifolia* reedbeds and *S. caseolaris* mono-specific mangrove forests [11]. Several nationally important species were however observed in both studies, such as *Merops philippinus*, *Colomba livia*, and *Sterna hirundo*, which are globally common but critically endangered in Sri Lanka [42]. Four of the five most abundant species observed in this study were also labelled as very abundant in the last inventory [14], suggesting that the bird community did not experience a complete turn-over in the last two decades.

The abundant presence of *Corvus splendens*, species known to be an anthropogenic disturbance indicator [27], indicates that the lagoon itself is subject to important human influence. This is in agreement with the “High Threat” status given by the National Wetland Directory to Kalametiya–Lunama lagoons [58]. *Corvus splendens* did not, however, dominate the lagoon bird assemblages (i.e., relative abundance of 5.67%), suggesting that the lagoon avifauna could still be driven by natural variables. However, abundance-based results must be considered carefully in this research as bird counts are strongly influenced by the detectability variation between species, caused by differences in species’ physical and behavioural attributes such as body size and vocalization characteristics [60,61].

Among the feeding guilds, the invertebrate feeders were the most abundant and displayed the highest species richness. This pattern could be explained by the abundance of mangrove patches in Kalametiya, which tend to support important insectivorous communities [62]. It is however not consistent with the history of the lagoon, as insectivores has been shown to respond negatively to disturbances [63]. The polyphages were the second richest and most abundant guild, as well as the most diverse. It could be due to the multiplicity of habitats in Kalametiya Lagoon (Figure 2), creating an important diversity of available resources.

The total species richness was found to be higher in the *S. caseolaris*-dominated habitat (mangrove habitat, *Sc*) than in the *T. angustifolia*-dominated habitat (reedbed habitat, *Ta*). This pattern could be explained by the larger number of sites affiliated to *Sc* than to *Ta* (respectively 10 and 5 sites), which lead to a relatively higher sampling effort and a higher absolute number of observations (619 in *Sc*, 372 in *Ta*). As more birds were observed, more species could be affiliated with the mangrove habitat. To overcome this sample size effect, the mean species richness and diversity indices were compared between habitats. *Ta* harboured a higher mean species richness than *Sc*, as well as a higher mean diversity (i.e., Shannon–Wiener Index). First, it can be hypothesized that a species detectability varied in the different habitats. Species traits and distinct habitat structures have already been shown to bring heterogeneity in bird detectability [64,65]. It could thus be one explanation for the decrease in species richness in the mangrove forest, which is notably more complex and hosts forest specialists. The presence of one of the lagoon’s main waterways running across reedbeds might be another reason for their higher mean bird richness, by promoting

the presence of birds relying on flowing water resources. Indeed, the *Ta* habitat included a higher piscivores mean and total species richness than the *Sc* habitat. The presence of fruiting trees (i.e., mangrove apples of *S. caseolaris*) would be expected to lead to an opposite increase in the richness of frugivorous and granivorous species, and thus the general bird richness in mangroves. However, this hypothesis was not entirely supported by our findings, since no significant difference was found between mangroves and reedbeds in the frugivores/granivores/frugivores–granivores mean species richness. A factor that could play an important role in both richness and diversity differences is the relative location of the affiliated sampling sites in the lagoon. *Ta*-affiliated sites were almost exclusively located at the centre of the lagoon, whereas most of the *Sc*-affiliated sites were located near the right border of Kalametiya area. The proximity with areas under anthropogenic influence (e.g., habitations, roads) could be the reason for the lower diversity in *Sc*-affiliated sites [28,66].

Apart from those differences, these two main habitats resulting from lagoon modification in recent decades, as well as the entire study area, displayed strong species and taxonomic diversities. This suggests that the lagoon currently supports a diverse community of birds that not only relies on *S. caseolaris* mangrove stands but also on *T. angustifolia* reedbeds. Indeed, even though the reedbeds resulted from a recent invasion of the lagoon, they now sustain an important part of Kalametiya's avifaunal diversity. This confirms that, as mentioned by [12], a management plan with the objective of returning the entire lagoon to its past state could disturb this community and lead to significant changes in bird species composition. The removal of vegetated areas to retrieve past water surfaces could be expected to negatively impact bird species relying on the new habitats while benefiting species relying on water resources, leading to a shift in the community composition. Despite methodological differences with previous inventories, a more thorough comparison of bird diversity and community composition of this study dataset and datasets collected in 1995 and 2004 would help to understand the changes a restoration of the lagoon would imply.

Feeding guild composition was used as a surrogate of changes in bird assemblages in a multivariate analysis, as species composition variation was not properly summarized by the PCA. Feeding guild composition seemed more influenced by the site transect, and thus position in the lagoon, than by its affiliation to the *Sc* or *Ta* habitat. Indeed, guild composition was found to be similar for all sites from Transect IV, which is the closest to the lagoon borders and human infrastructures. This finding, if confirmed, would support the previously mentioned hypothesis that proximity with anthropogenic pressure influences Kalametiya bird assemblages. Transect IV is also the furthest from the large patches of *T. angustifolia* reedbeds, Kalametiya's second main habitat, which could induce weaker interactions with its avifauna community. It has indeed been shown that mangroves should be considered as part of a landscape mosaic, in which bird communities are heavily influenced by surrounding habitats [67,68]. The mosaic effect could also explain the differences in feeding guild composition for the last three sites of Transect III (isolated cluster of three sites in the upper part of Figure 4: iii7, iii8, iii9; Figure 2), which are relatively far from the *T. angustifolia* patches without being inside the *S. caseolaris* mangrove forest.

Species composition was not found to be significantly driven by the studied physiochemical and vegetation variables, as final RDA models explained a low proportion of the variation (Transect I/II/III:  $R^2 = 9\%$ ; Transect IV:  $R^2 = 15\%$ ). Feeding guilds were a more reliable indicator of bird community responses to environmental variables, as respective RDA models explained a higher proportion of variation ( $R^2 = 36\%$  for both models). Several physiochemical variables (i.e., water nitrate content, water TDS, water pH, soil pH) were found to significantly influence guild assemblages, though no prominent site clustering was observed in response to those. This supports the fact that bird communities experienced great changes with the hydrological modifications resulting from the Udawalawe inland irrigation project [11]. The observed influence of these variables on birds is consistent with several other studies on wetlands [28,29,31].

## 5. Conclusions

Overall, this study showed that Kalametiya Lagoon supported an important and diverse avifauna despite the recent invasion of *S. caseolaris* and *T. angustifolia*. It suggested that *T. angustifolia* reedbeds harboured a higher richness and stronger bird diversity than *S. caseolaris* mangroves. However, multivariate analysis showed that habitat types did not have a great influence on bird assemblages composition. These assumptions need further verification for two main reasons: (i) mean and not total diversity indices were used, (ii) most of the *S. caseolaris*-affiliated sites were significantly closer to the lagoon border than the *T. angustifolia*-affiliated sites. An additional study with random stratified design and equal sampling effort for both habitats could confirm the diversity differences between *S. caseolaris* mangroves and *T. angustifolia* reedbeds, as well as include *S. caseolaris*—*T. angustifolia* co-dominated patches in the analysis. As bird feeding guilds were significantly influenced by several environmental variables, they could have great potential as proxies in Kalametiya Lagoon state. It is recommended that additional research is performed to confirm their bioindicator statuses.

**Supplementary Materials:** The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d15030383/s1>. Table S1: Sampling sites coordinates, habitat affiliation, and species richness; Table S2: Complete list of the avifauna encountered during the study period in Kalametiya.

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