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Guanotrophy: Waterbirds Pay for Using Resources at Their Wintering Habitats

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ABSTRACT

Nutrients present in the guano of the aquatic birds might alter the water quality and nutrient loading in the wetland ecosystem. We recorded the changes in waterbird abundance for two consecutive wintering seasons, October–March (2018–2019 and 2019–2020), in four wetlands of Bankura and Purulia district, West Bengal, India, on Central Asian and East Asian-Australasian Flyways. The monthly variation in the water parameters, along with total guano and nutrient loadings by waterbirds, were evaluated during the study. Waterbird species varied from 37 to 61 in these wetlands. Guano loading in the study tenure ranged from 50.2 to 2979.1 kg $month^{-1}$, depending on the wetland resources and the abundance of waterbird species. In most cases, total guano loading showed significant positive correlations with total N and P loading and, consequently, NO_3 and PO_4 concentrations in water. In all four wetlands, guano and nutrients added by herbivorous waterbirds were significantly higher than carnivorous and omnivorous waterbirds due to the much higher abundance of herbivorous waterbirds. Linear regression analyses showed that the abundance of the wintering waterbird community significantly impacted the nitrate and phosphate availability in most of the sites. Sustainable management of these wetlands depends on the delicate balance of guanotrophic nutrient enrichment and habitat fitness to attract migratory waterbirds.

1 | Introduction

Wetlands are globally recognised as one of the most important ecosystems due to their high productivity and biodiversity (Ghermandi et al. 2008). The abundance of dissolved and particulate nutrients in wetlands supports diverse planktonic and benthic communities, while dissolved nutrients also promote macrophyte growth. These wetland areas provide food, shelter, breeding grounds, and wintering sites for numerous waterbird species (Adhurya, Das, and Ray 2020). Changes in waterbird abundance and species richness often indicate wetland changes caused by environmental impacts. Therefore, understanding the population dynamics of migratory waterbirds is essential for developing sustainable wetland conservation mechanisms (Randin et al. 2006; Bassi et al. 2014).

Ma et al. (2010) reported that studies on the richness and abundance of waterbirds are imperative for both qualitative and quantitative evaluations of wetland habitats. During the winter months, various migratory and resident bird species inhabit wintering sites along the East Asian-Australasian Flyway (EAAF) and Central Asian Flyway (CAF) in West Bengal

Summary

This study looked at how bird droppings (guano) from waterbirds affect water quality and nutrient levels in four wetlands in Bankura and Purulia districts, West Bengal, during two wintering seasons (2018–2019 and 2019–2020). Researchers tracked changes in waterbird abundance and water quality, finding that guano loads, ranging from 50.2 to 2979.1 kg per month, contributed significantly to increased nitrogen (N) and phosphorus (P) levels in the water. These nutrients, especially nitrates (NO_3) and phosphates (PO_4), were linked to the abundance of herbivorous birds, which were more common than carnivorous or omnivorous species. The study highlighted the need for careful management to balance nutrient enrichment from guano and habitat conditions to ensure the wetlands remain attractive to migratory birds.

Practitioner Points

- Bird guano significantly increases nitrogen (N) and phosphorus (P) levels in wetlands, especially nitrates (NO_3) and phosphates (PO_4), affecting water quality.
- Wetland nutrient loading is strongly influenced by the abundance of waterbirds, mainly herbivorous species, which contribute more guano than carnivorous or omnivorous birds.
- Tracking monthly variations in waterbird abundance and water quality parameters is essential for understanding nutrient dynamics in wetland ecosystems.
- Sustainable wetland management should strike a balance between guano-driven nutrient enrichment and maintaining habitat conditions favourable for attracting migratory waterbirds.

(Mazumdar, Mookherjee, and Saha 2007; Nandi et al. 2007; Chatterjee et al. 2013; Chowdhury and Nandi 2014; CAF-National Action Plan-India 2018). The availability of foraging resources and the physical characteristics of these wetlands play a significant role in shaping waterbird community structure. Additionally, waterbird assemblages can influence the physicochemical properties of wetlands (Paracuellos 2006; Singha et al. 2011; Ramírez-Albores et al. 2014; Mukherjee et al. 2022a, 2022b).

Nutrients such as nitrate and phosphate from waterbird excreta can significantly alter water's physicochemical parameters, making these birds important contributors to nutrient cycling in wetlands (Manny, Johnson, and Wetzel 1994; Chatterjee, Adhikari, and Mukhopadhyay 2017, 2020; Adhurya, Das, and Ray 2020). Scherer et al. (1995) noted that when bird abundance is high relative to the size of a wetland, a considerable portion of the nutrient pool may cycle through waterbirds via guanotrophy. Several noteworthy studies have explored the relationship between waterbirds and the limnochemical parameters of wetlands, highlighting the reciprocal impact of birds on water quality and vice versa. Manny, Johnson and Wetzel (1994), Pettigrew, Hann and Goldsborough (1998), Hanson (2003), Longcore et al. (2006), Singha et al. (2011), Dessborn, Hessel and Elmberg (2016) and Duda et al. (2021) have all contributed to this field. Manny, Johnson and Wetzel (1994) and Duda et al. (2021) found that waterbird guano contributes to water quality deterioration. In contrast, Hanson (2008) and Singha et al. (2011) observed a negative correlation between major nutrient concentrations and high avian densities, noting that bird excreta enhances gross primary productivity, which in turn boosts secondary production in waterbodies. Moreover, Pettigrew, Hann and Goldsborough (1998) and Dessborn, Hessel and Elmberg (2016) reported that avian guanotrophication could lead to eutrophication but did not appear to impact the habitat food web significantly. However, certain studies have yet to establish a definitive correlation between avian congregation and nutrient enrichment (Gremillion and Malone 1986; Scherer et al. 1995).

The present study extrapolates the Quantitative Structure–Activity Relationship (QSAR), a computational modelling technique traditionally employed to study molecular associations, to analyse avian community structure and function. This approach is based on the premise that altering community structural components impacts their functional dynamics (Pal et al. 2017; Rumschlag et al. 2020). Quantitative models were employed to avoid direct intervention with wildlife while predicting species-specific activities within avian populations (Watkins et al. 1999; Marzio and Saenz 2004; Ruiz et al. 2012). Since directly estimating ornithogenic nutrient loading (NL) is challenging (Manny, Johnson, and Wetzel 1994), QSAR was used to infer NL indirectly from bird count data, leveraging allometric relationships in faecal matter production due to the similar digestive performance among waterbird species (Hahn, Bauer, and Klaassen 2008, 2007; Nagy, Girard, and Brown 1999). Key factors influencing nutrient enrichment include species composition, waterbody area, foraging behaviour, food preferences, and time spent in water (Manny, Johnson, and Wetzel 1994; Boros 2021; Laguna et al. 2021).

Anatids, in particular, are notable contributors to nutrient importation from terrestrial feeding grounds, promoting hydrophyte growth, water quality degradation and accelerated sediment deposition in wetlands (Manny, Johnson, and Wetzel 1994; Boros et al. 2008; Robledano Aymerich, Pagán Abellán, and Calvo Sendín 2008; Verstijnen et al. 2021). Several wetlands in India face severe anthropogenic pressures, and West Bengal is no exception (Bassi et al. 2014; Mukherjee et al. 2021). This study was conducted at four key wetlands in West Bengal, which are already recognised as significant wintering habitats for waterbirds (Mukherjee et al. 2021, 2022a, 2022b). These wetlands harbour diverse waterbird populations, including both resident and migratory species (Nandi et al. 2007; Mukherjee et al. 2021, 2022a, 2022b). Water quality assessments of wetlands in the Bankura district have been previously reported by Mukherjee and Palit (2013), while Siddiqi and Chandrasekhar (2010) and Mandal (2017) recorded the physicochemical conditions of Adra Sahebbandh, a lake in Purulia. Dutta et al. (2017) examined the water quality and trophic status of Purulia Sahebbandh, another body of water in the same district. These studies on Adra Sahebbandh and Purulia Sahebbandh concluded that Adra Sahebbandh had cleaner and safer water.

This study hypothesises that avian abundance and species richness influence guanotrophic nutrient enrichment during the wintering season, potentially sustaining the nutrient requirements of wetland ecosystems throughout the year. The objectives of this study are: (1) to study the changes in waterbird assemblages across four study sites during two consecutive wintering seasons (October–March 2018–2019 and 2019–2020) in West Bengal; (2) to record variations in the physicochemical parameters of surface water during the study period and (3) to determine species-wise and/or food choice-wise guano and nutrient loadings at the study sites. It is hypothesised that waterbirds significantly impact nutrient loading in these freshwater ecosystems.

2 | Materials and Methods

2.1 | Study Areas

Four sites were selected for this study. A location map is provided in Supporting Information S1: Supplement 1. Two sites are located in the Bankura district: Gangdoa Dam (GAD), at 23°40′ N, 87°08′ E, is a reservoir of the Shali River, primarily surrounded by agricultural lands. However, this site faces significant pressure from fishing activities and illegal hunting, which pose threats to the habitat. The second site in the Bankura district, Kadamdeuli Dam (KDM), at 23°10′ N, 86°85′ E, is a reservoir of the Shilabati River. This site experiences less anthropogenic pressure due to its remote location.

The other two sites are in the Purulia district. Purulia Sahebbandh (PSB), at 23°33′ N, 86°35′ E, is an artificial waterbody located in the heart of Purulia town and managed by the Purulia Municipality. This site faces considerable threats from wastewater discharge, plastic pollution, and various human activities in the surrounding area. The second site in the Purulia district, Adra Sahebbandh (ASB), at 23°28′ N, 86°42′ E, benefits from scientific management of its floating vegetation cover and effective protection by the Indian Railway Department, making it an ideal wintering ground. Detailed descriptions of these study sites are available in Mukherjee et al. (2023).

2.2 | Sampling Period and Frequency

Sampling was conducted fortnightly during the winter months (October to March) to estimate waterbird population sizes at four selected wetlands over two consecutive wintering seasons (2018–2019 and 2019–2020; $n = 24$). In South Asian countries, winter is considered the optimal period for studying migratory and resident waterbirds (Mazumdar, Mookherjee, and Saha 2007; Chatterjee et al. 2020). Observations were carried out at specific intervals – 06:00–07:00, 11:00–12:00, and 16:00–17:00. On each study day, the physicochemical properties of water samples were also analysed alongside avian population sampling. Monthly data were represented as mean values.

2.3 | Sampling of Avian Population

The avian population was estimated using the total count method as described by Mukherjee et al. (2022a). Observations were conducted using a Nikon Fieldscope (25–75 × 82 ED) and Olympus binoculars (8 × 40) to detect detailed features of the birds in view. Bird identification and nomenclature followed Grimmett, Inskipp and Inskipp (2011).

2.4 | Calculation of Diversity Indices

To analyse the avian community structure, the Shannon–Wiener diversity index ($H^{/}$), Simpson's dominance index (DSIPM), and Margalef's richness index (DMARG) were calculated. Data were processed using PAST version 4.12. The $H^{/}$and DSIPM indices were based on species richness at the study sites, with $H^{/}$placing greater emphasis on rare species and DSIPM favouring dominant species. DMARG accounted for both abundance and species richness.

2.5 | Estimation of Physicochemical Parameters

Water samples were collected from 5 to 10 sampling spots, depending on the wetland site, using clean glass bottles with stoppers (1 L). Bottles were submerged entirely to a depth of 6–8 cm below the surface to avoid floating debris. Subsurface water temperature (WT), pH, salinity, total dissolved solids (TDS), and electrical conductance (EC) were measured on-site by using an Eutech PCSTester 35 Multi-Parameter. Dissolved oxygen (DO), phosphate (PO_4^{3-}), and nitrate (NO_3^{-}) concentrations were analysed on-site using Aquamerck Field-testing kits (Merck, Germany).

2.6 | Species-Specific Nutrient and Guano Loading

2.6.1 | Guano Loading

Monthly guano loading (GL) or input (kg month^{-1}) by individual waterbird species was calculated by multiplying the daily faecal matter production rate (DFP) by the number of days in the month and the species' corresponding monthly average count. The total monthly guano input (kg month^{-1}) for a particular wetland was determined by summing up the guano input values for all individual species.

2.6.2 | Species-Specific and Total Nutrient (N and P) Loading

To estimate nutrient loading (NL), the number of diverse waterbird species was converted to an equivalent quantity of a particular reference species. Reference species were selected based on their availability in the study system and the existence of NL estimation parameters in the literature, scaled according to body mass (Adhurya, Das, and Ray 2022). Biomass data for different species were sourced from relevant literature (Dunning 2008; Lepage et al. 2014). The DFP rate was then multiplied by the equivalent waterbird number to calculate the total daily faecal matter produced by a given species.

Estimating DFP is challenging due to limited data availability. To address this, Boros (2021) classified waterbird species into groups and provided generalised daily faecal nutrient (C, N, and P) load values per individual. While this method is effective for groups with relatively consistent biomass, it is less suitable for groups with highly variable biomass (e.g., dabbling ducks, diving ducks, cormorants, herons, etc.). To overcome this limitation, two approaches were employed. In the first and most conventional approach, the DFP was calculated based on dropping mass (DrM) and dropping rate (DrR) (Equation 1) using the following equations:

$$\mathrm{DrM} = 10^{-3.065} \times \mathrm{M}^{0.8901} \text{ and } \mathrm{DrR} = 10^{2.1299} \times \mathrm{M}^{-0.3065}$$

where M is the species' biomass (Hahn, Bauer, and Klaassen 2008).

The DFP was then derived as:

$$DFP = DrR \times DrM \quad (1)$$

This approach has been widely used in previous studies (Gremillion and Malone 1986; Hahn, Bauer, and Klaassen 2008; Mallin et al. 2016; Manny, Wetzel, and Johnson 1975; Scherer et al. 1995).

In the second method, a bioenergetic approach (Hahn, Bauer, and Klaassen 2008, 2007; Post et al. 1998), DFP was estimated from food intake, calculated using daily energy requirements (DER), food energy content (E), and apparently metabolisable energy (AM). DER follows an allometric relationship and was calculated using the following formula:

$\mathrm{DER} = 10^{1.0195} \times \mathrm{M}^{0.6808}$ (Nagy, Girard, and Brown 1999).

The DFP was then derived using

$$DFP = \frac{\alpha \times DER}{E \times AM} \quad (2)$$

where α is the ratio between daily faecal production and daily food intake (Hahn, Bauer, and Klaassen 2007).

Both approaches produced comparable results and were chosen based on data availability.

The proportion of daily faecal production entering the lake depended on the time (fraction of day (f_d)) waterbird species spent on the lake. Residence time data were sourced from previous studies (Boros 2021; Adhurya, Das, and Ray 2022). For species residing on the lake for nearly the entire day (e.g., jacanas, coots, moorhens, diving ducks, etc.), f_d was set to 1 (24 h/24 h). For species that typically only the daytime on the lake (e.g., herons, cormorants, dabbling ducks, geese, etc.), f_d was calculated as *day length in hours*/24. For nocturnal lake users (e.g., bitterns, night-herons, etc.), f_d was calculated as *night length in hours*/24. For the Woolly-necked Stork, f_d was set to 0.167 based on personal observations and previous studies (Kittur and Gopi Sundar 2021). Data on day length was collected from web resources for the nearby city of Bankura ('Sunrise and sunset times in Bankura, 2022).

The effective number of individuals of each species was obtained by multiplying their counts by f_d. Daily NL was then estimated as

$$NL = \sum_{1}^{S} DFP \times f_d \times N_b \times \frac{a}{b} \times X_{drop} \quad (3)$$

where a and b are the biomass of the species in question (for which the NL will be estimated) and the reference species (for which the data regarding X_{drop} is available), respectively; X_{drop} is the elemental concentration (N, P, or C) of the faecal matter; and S is the number of species. Monthly NL was calculated by averaging fortnightly census data and multiplying daily NL by the number of days in the month.

X_{drop} value varied with the feeding habits of the species. Droppings from carnivorous waterbirds were more phosphatic than those from herbivorous waterbirds (Adhurya, Das, and Ray 2020). Therefore, it was necessary to group species based on their feeding habits before calculating nutrient loading. Waterbirds were broadly categorised into three groups: (i) herbivorous waterbirds, (ii) carnivorous waterbirds and (iii) omnivorous waterbirds. The feeding ecology of the birds was determined using del Hoyo et al. (2017). For herbivorous waterbirds, the Greylag Goose (*Anser anser*) was used as a reference species due to the availability of X_{drop} data (Kear 1963), and Equation 2 was used for DFP estimation. Carnivorous waterbirds were further divided into seven groups to account for their highly heterogeneous feeding habits. The Great Cormorant (*Phalacrocorax carbo*) was used as a reference species for NL estimation in cormorants and darters (piscivorous birds). The Grey Heron (*Ardea cinerea)* was used as a reference species for the NL estimation for species reliant on arthropods and small fish, including herons, egrets, bitterns, grebes, and waterhens. X_{drop} data for these species were obtained from Marion et al. (1994). Storks, ibises, and Tufted Ducks, which primarily consume molluscs, were grouped together. For this group, the White Ibis (*Eudocinus albus*) was selected as the reference species, with X_{drop} data sourced from Bildstein, Blood and Frederick (1992). Equation 3 was applied to estimate DFP for these three carnivorous waterbird groups. Other carnivorous waterbirds were classified and their NL was estimated following Boros (2021). For example, sandpipers of the genus *Actitis* and stints were classified as Small Sandpipers; sandpipers of the genus *Tringa*, along with snipes, were classified as Large Sandpipers; and Lapwings and Plovers formed two additional groups. The proportion of carnivorous and herbivorous diets varied in species like the Common Moorhen and Northern Shoveler, depending on food availability. For these species, a 50:50 split between carnivorous and herbivorous diets was assumed. NL for these species was estimated using the Greylag Goose and Grey Heron as reference species. Parameter values used in NL estimation are given in Supporting Information S1: Supplements 2 and 3. In addition, scientific names, species-specific food preferences, residence time in wetlands, and reference species are detailed in Supporting Information S1: Supplement 4.

2.6.3 | Exclusion of Certain Species From NL and GL Estimation

Certain species were excluded from NL estimation due to their minimal contribution to guanotrophication, as a result of their significantly lower residence time in the waterbody. These species include raptors, lapwings (except the Grey-headed Lapwing), kingfishers, wagtails, swallows, terns, gulls, and the Red-naped Ibis. Among the three lapwing species recorded during this study, Grey-headed Lapwings showed habitat preferences for marshy laces, wetland edges, and wet grazing grounds within the wetlands, making them relevant for inclusion. This habitat preference aligns with earlier observations by Ali and Ripley (1987). In contrast, the other two lapwing species preferred drier biotopes and were excluded from the analysis (Ali and Ripley 1987). The Red-naped Ibis, which primarily inhabits dry open lands and agricultural areas (Anjali and Rana 2021), was also excluded. Conversely, the Black-headed Ibis and Glossy Ibis were included in the analysis, as they predominantly use wetlands as roosting and feeding grounds (Taylor and Taylor 2015; Anjali and Rana 2021).

2.6.4 | Uncertainty in NL Estimation

All model estimations are subject to potential errors due to underlying model assumptions, measurement inaccuracies, and data limitations. Likewise, the NL estimation in this study involved several assumptions that contribute to prediction uncertainty. First, the parameter values for DER, DrR, DrM, E, and AM were taken from previously published literature based on temperate zones. Since temperature positively influences the DER of waterbirds, this reliance on temperate-zone data may have led to an underestimation of NL in this tropical region (Kendeigh, Dol'nik, and Gavrilov 1977; Post et al. 1998). Additionally, our estimations did not account for the flight costs of birds. Foraging grounds for externally feeding ducks and geese were not identified, and only a single visit to foraging grounds was assumed in our study. However, these species may perform multiple foraging trips depending on environmental temperature and wind speed, which would increase flight costs and, consequently, DER, leading to higher NL (Post et al. 1998). Further studies on the dropping mass and dropping rate of waterbirds in this region are necessary to validate the applicability of the model by Hahn, Bauer and Klaassen (2008) in tropical areas like India. Moreover, E values, which represent the energy content of food, are likely to be lower for agricultural food produced through conventional practices in this region compared to the E values reported in developed temperate nations. Similarly, AM, which depends on the diet of the concerned avian species, requires detailed investigation. The generalised use of this parameter may result in underestimations of DFP and NL. Furthermore, this study did not account for variations in X_{drop} caused by pre-migratory weight gain or post-migratory weight loss (Post et al. 1998).

2.7 | Statistical Analyses

Waterbird abundance: (a) t-tests (significance level: $p < 0.05$) were performed to assess significant differences in waterbird abundances between the two wintering seasons (2018–2019 and 2019–2020). (b) Sorensen's Similarity Index (SSD) was calculated to measure species composition similarity between site pairs (Magurran 2004).

Physicochemical variables and nutrient loading: (a) ANOVA (Analysis of Variance), followed by Tukey's Honestly Significant Difference (Tukey HSD) test ($p < 0.05$), was performed to identify significant differences in pH ranges across study sites and the mean monthly guano loaded by three guilds (carnivorous, herbivorous, and omnivorous). (b) Pearson correlation coefficients (*with significant correlations at $p < 0.05$) were calculated to evaluate relationships between total GL, total N loading, total P loading, NO_3-N concentrations, PO_4-P concentrations, and physicochemical variables at the study sites.

Abundance-diversity indices and nutrient concentration: Linear regression analyses were used to assess the relationships between diversity indices (DSIMP, H, and DMARG), abundance, and nutrient concentrations (nitrate and phosphate) at the four study sites.

All statistical analyses were conducted using Statistica for Windows (version 7, Statsoft Inc.) and PAST (version 4.12b). Graphical representations were created using Origin 2016.

3 | Results

3.1 | Waterbird Diversity

Family-wise waterbird species, their abundance, IUCN status, and migration status are detailed in Supporting Information S1: Supplement 5a–d. A detailed report on the diversity and turnover of waterbirds across these four sites, alongside nine additional important wintering wetland habitats during the peak wintering period (December 15, 2018 to January 31, 2019), has been previously published (Mukherjee et al. 2022a).

GAD harboured 52 waterbird species across 15 families (Supporting Information S1: Supplement 5a). Barn Swallow was the most abundant species (mean 54.1 ± 49.968), followed by Lesser Whistling-duck (mean 47.3 ± 32.464) and Red-crested Pochard (mean 39.3 ± 43.934). The highest diversity was recorded in December ($H' = 3.00$), while richness peaked in January (DMARG = 7.30) (Supporting Information S1: Supplement 6).

KDM harboured 61 species of waterbirds from 15 families (Supporting Information S1: Supplement 5b). Cotton Pygmy-goose was the most dominant species (mean 156.2 ± 81.427), followed by Pheasant-tailed Jacana (mean 56.1 ± 27.576) and Gadwall (mean 49.3 ± 54.845). The highest diversity was recorded in November ($H' = 2.85$), while both dominance and richness were highest in February (DSIMP = 0.21; DMARG = 7.22).

PSB recorded 37 waterbird species across 10 families (Supporting Information S1: Supplement 5c). Lesser Whistling Duck was the most dominant species (mean 369.2 ± 698.071), followed by Common Moorhen (mean 32.5 ± 34.321) and Red-crested Pochard (mean 25.9 ± 31.039). Dominance was highest in March (DSIMP = 0.69), while diversity peaked in December ($H' = 2.35$).

ASB supported 44 waterbird species from 14 families (Supporting Information S1: Supplement 5d). Lesser Whistling Duck was the predominant species (mean 271.4 ± 212.406), followed by Red-crested Pochard (mean 124.2 ± 147.060) and Cotton Pygmy Goose (mean 82.3 ± 36.687). Richness peaked in January

(DMARG = 5.19), while the highest dominance was recorded in March (DSIMP = 0.34).

Both Bankura district wetlands showed significant increases in total waterbird abundance from 2018 to 2019 to 2019–2020 (KDM: $t = 52.9$, $p < 0.05$; GAD: $t = 313.4$, $p < 0.05$). In contrast, ASB showed a minor decrease of nearly 3% ($t = 5.9$, $p < 0.05$), while PSB recorded a dramatic 95% decline in waterbird abundance over the same period ($t = 1305.9$, $p < 0.05$).

Sorensen's Similarity Index (SSD) was highest between ASB and PSB (81%), followed by KDM and GAD (75%). The lowest similarity was observed between ASB and GAD (67%).

3.2 | Physicochemical Conditions

Fluctuations in key physicochemical factors are depicted in Online Supplement 7a–d. The pH range at ASB significantly differed from those at PSB and GAD in the post hoc test ($p = 0.0012$ and $p = 0.0005$, respectively). Similarly, the pH range at PSB was significantly different from KDM ($p = 0.0030$), and the pH range at KDM was significantly different from GAD ($p = 0.0013$). At KDM and ASB, nitrate and phosphate concentrations showed a significant negative relationship with water temperature and phosphate concentration (Table 1). However, at PSB, only phosphate concentration exhibited a significant positive relationship with water temperature. Conversely, at GAD, neither nitrate nor phosphate concentrations showed any significant relationship with water temperature. Interestingly, pH, TDS, and salinity showed a significant positive correlation with both nitrate and phosphate concentration in KDM, PSB, and ASB. However, in GAD, pH showed a significant positive relationship with only phosphate concentration, and salinity was significantly positively correlated with nitrate concentration. DO showed a negative correlation with nitrate and phosphate concentrations in most instances (Table 1).

TABLE 1 | Pearson's correlations (* significant at $p < 0.05$) between physicochemical factors at four study sites ($n = 24$) (GAD: Gangdoa Dam, KDM: Kadamdeuli Dam, ASB: Adra Sahebbandh, PSB: Purulia Sahebbandh) (TDS: Total dissolved solids, DO: Dissolved oxygen).

	pH	TDS	Salinity	DO	Nitrate	Phosphate
GAD						
Water temperature	−0.318	−0.923*	−0.543*	−0.269	0.100	−0.386
pH		0.432	0.132	−0.517*	−0.233	0.945*
TDS			0.568*	0.318	−0.119	0.443
Salinity				−0.180	0.709*	0.335
DO					−0.429	−0.604*
Nitrate						−0.675*
KDM						
Water temperature	−0.617*	−0.740*	−0.791*	0.032	−0.746*	−0.740*
pH		0.934*	0.923*	−0.658*	0.938*	0.858*
TDS			0.876*	−0.459	0.988*	0.979*
Salinity				−0.571*	0.905*	0.819*
DO					−0.437	−0.336
Nitrate						0.977*
PSB						
Water temperature	0.314	0.092	−0.021	−0.457	0.481	0.567*
pH		0.954*	0.914*	0.115	0.976*	0.879*
TDS			0.944*	0.389	0.898*	0.734*
Salinity				0.258	0.847*	0.779*
DO					0.018	−0.243
Nitrate						0.931*
ASB						
Water temperature	−0.926*	−0.777*	−0.622*	−0.896*	−0.748*	−0.800*
pH		0.681*	0.695*	0.815*	0.637*	0.633*
TDS			0.821*	0.826*	0.992*	0.959*
Salinity				0.533*	0.804*	0.768*
DO					0.533*	0.804*
Nitrate						0.968*

3.3 | Total GL, Nutrient (N and P) Loading by Waterbirds, and NO_3-N and PO_4-P Concentrations at the Study Sites

Overall, GL during the study period was highest at ASB, followed by PSB, KDM, and GAD. At GAD, KDM and ASB, total GL was highest in January and lowest in October (Figure 1). In contrast, at PSB, the highest GL was recorded in March 2020, while the lowest occurred in November 2019. A sharp decline (approximately 94% from 2018 to 2019 to 2019–2020) in the total GL was observed at PSB. Similar trends were noted for N and P Loading across all study sites (Figure 1). The highest nitrate and phosphate concentrations were estimated from PSB in March 2019 (Figure 1). The lowest nitrate concentrations were estimated from KDM in October 2018, while the lowest phosphate concentrations were recorded at ASB in October 2018.

At all four study sites, herbivorous waterbirds contributed significantly more guano compared to carnivorous and omnivorous waterbirds. Guano from carnivorous waterbirds ranged from 3.1% to 14.3%, and from omnivorous waterbirds, it ranged from 0% to 4.5% (Figure 2). Carnivorous waterbird guano loading was highest at GAD, followed by KDM, PSB, and ASB. Meanwhile, omnivorous waterbird guano loading was highest at PSB, followed by ASB, KDM., and GAD. Significant differences in guano loading among the three waterbird guilds across the four study sites are presented in Table 2.

3.4 | Correlations Between Total GL, Total Nutrient (N and P) Loading, NO_3-N and PO_4-P Concentrations

Pearson correlation coefficients ($*p < 0.05$) are presented in Table 3, highlighting the relationships between total GL, N loading, P loading, NO_3-N and PO_4-P concentrations across the four study sites. Total GL showed significant positive correlations with both N and P loading at all study sites. Total GL also showed a significant positive correlation with nitrate and phosphate concentrations at ASB and KDM. At GAD, total GL positively correlated with phosphate concentration, while at PSB, it correlated positively with nitrate concentration. N loading exhibited significant positive correlations with nitrate concentration, P loading, and phosphate concentration at all the wetlands except GAD, where N loading was not significantly correlated with nitrate concentration.

3.5 | Linear Regression Analysis

Linear regression analyses were conducted to assess the relationships between diversity indices, abundance, and nutrient values (Figure 3). Significant correlation coefficients (r) ($p < 0.01$) between waterbird abundance and nitrate and phosphate concentrations were observed in most cases (KDM: Abundnace-NO_3: 0.972, Abundance-PO_4: 0.958; ASB: Abundnace-NO_3: 0.941, Abundance-PO_4: 0.869; PSB: Abundnace-NO_3: 0.975, Abundance-PO_4: 0.968). According to Mukaka (2012), correlations are considered strong when the r values lie between ± 0.50 and ± 1. The results indicate a strong positive linear correlation between waterbird abundance and nutrient concentrations at these three wetlands. However, at GAD, such strong correlations were not observed (Abundnace-NO_3: 0.25, Abundance-PO_4: 0.732). Notably, at PSB, strong positive correlations were recorded between two diversity indices (DSIMP and H) and nutrient concentrations in surface water (DSIMP-NO_3: 0.973, DSIMP-PO_4: 0.913; H-NO_3: 0.933, H-PO_4: 0.880).

4 | Discussion

The four wetlands studied are situated in the *Rarh* region of western West Bengal, a transitional zone between the Chottanagpur Plateau fringe and the lower Gangetic plain. These wetlands, located at the intersection of the CAF and EAAF, serve as key habitats for both migratory and resident waterbirds (Dhanjal-Adams et al. 2017; CAF-National Action Plan-India 2018; Mukherjee et al. 2021). Previous studies by Nandi, Bhuinya, and Das (2004, 2007) also recorded a high diversity of wintering waterbirds in this physiographic region. Wetlands within similar geographic areas often exhibit comparable species compositions of wintering waterbirds (Ma et al. 2010). Given that the distance between the wetlands is less than 100 km, the observed similarity in species composition is consistent with the findings of this study.

4.1 | Abundance of Wintering Waterbirds

Over 60% of the waterbird population in Asia is experiencing a declining trend, particularly among dabbling ducks such as Mallards, Northern Pintails, Common Teals and Spot-billed Ducks (Delany and Scott 2006; Li et al. 2009). In the present study, Northern Pintail was observed at all sites, while Common Teal was recorded only at ASB and KDM. The study sites supported sizeable populations of three vulnerable species and one near-threatened species. Additionally, a small population of the Critically Endangered (CR) Baer's Pochard was also recorded at ASB during the present study, underscoring the importance of these wetlands as indispensable wintering grounds. Hearn, Tao and Hilton (2013) identified habitat loss, degradation of breeding areas, hunting, and other anthropogenic factors as the primary drivers of waterbird population declines in Asia. These findings affirm the conservation value of the four studied wintering wetland habitats as key habitats for migratory waterbirds (Mahato, Mandal, and Das 2021; Mukherjee et al. 2021, 2022a, 2022b).

The Lesser Whistling Duck, a local migrant, was the most dominant waterbird species at both PSB and ASB and the second most dominant at GAD. High congregations of Lesser Whistling Ducks in March contributed to the highest dominance indices in these habitats during that month. Previous studies by Nandi et al. (2007) and Mukherjee et al. (2021) similarly reported the dominance of Lesser Whistling Ducks throughout West Bengal during the winter season. The significant decline in waterbird abundance at PSB in 2019–2020 could be attributed to increased anthropogenic pressures, including 'Sikra' boating and the complete removal of floating hydrophytic vegetation (Pal 2020). Begam et al. (2021) also noted that

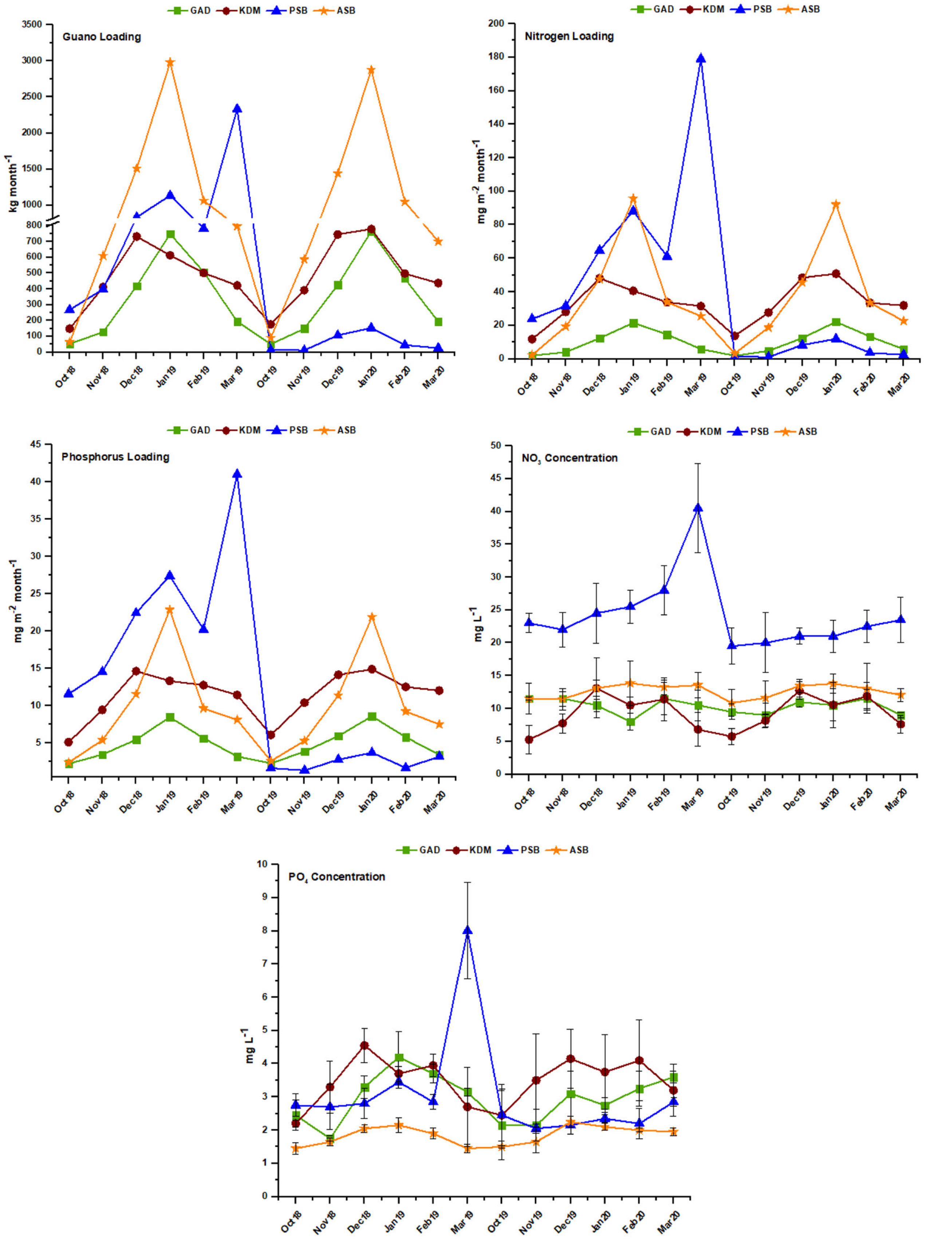

FIGURE 1 | Guano loading (kg month^{-1}), nitrogen (N) loading (mg m^{-2} month^{-1}), phosphorus (P) Loading (mg m^{-2} month^{-1}) rate and NO_3 concentration (mg L^{-1}) and PO_4 concentration (mg L^{-1}) in water of the four study sites (GAD: Gangdoa Dam, KDM: Kadamdeuli Dam, ASB: Adra Sahebbandh, PSB: Purulia Sahebbandh).

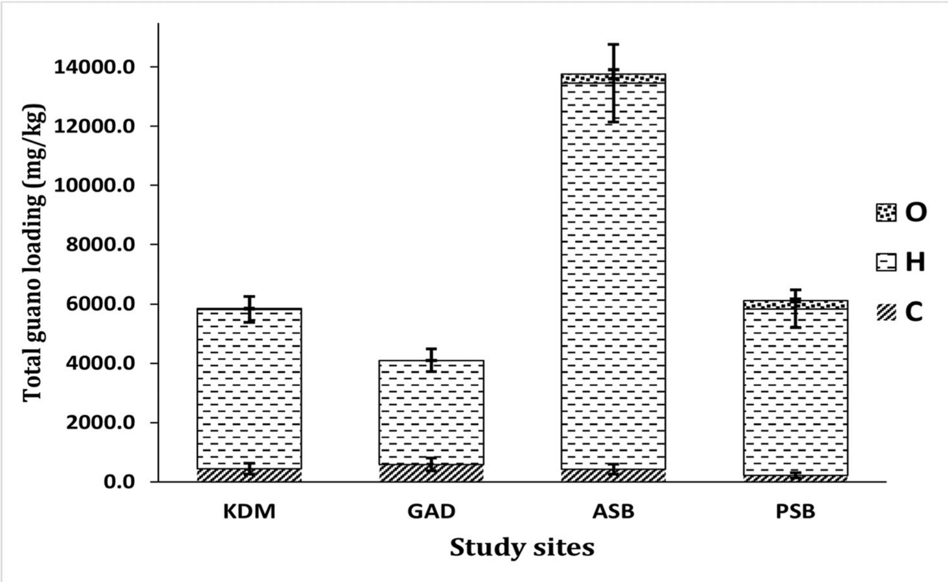

FIGURE 2 | Guild-wise (O: Omnivorous, H: Herbivorous, C: Carnivorous) guano loading (kg month^{-1}) (mean ± SD) by waterbirds in the study sites (GAD: Gangdoa Dam, KDM: Kadamdeuli Dam, ASB: Adra Sahebbandh, PSB: Purulia Sahebbandh).

unregulated management of *Eichhornia* sp. can negatively impact migratory waterbird density.

4.2 | Physicochemical Ambience

Surface water temperature is influenced by numerous factors like latitude, altitude, time of day, air circulation, cloud cover, and wetland depth (Chapman 1996). Subsurface water temperatures at the study sites ranged from 20°C in January to 33°C in March. Since all the sites were in the same physiographic zone, the water temperatures were comparable. The lowest subsurface water temperatures were consistently recorded in January, the coldest month in both Gangetic and sub-Himalayan West Bengal (NCCO 2008).

Published findings (Arfi 2003; Li, Xu, and Xu 2013) indicate that increasing water temperatures lead to decreased DO concentrations, a trend corroborated by this study. DO levels serve as indicators of wetland pollution by organic matter and the natural purification capacity of the waterbody (Slack 1971; Jane et al. 2021). Among our study sites, DO levels were highest at KDM, followed by ASB, reflecting differences in water quality. DO levels were lowest at PSB. Chatterjee, Mukherjee and Bhattacharjee (2014), Chatterjee and Bhattacharjee (2015), and Dutta et al. (2017) reported that in recent years, the PSB wetland has been increasingly polluted by untreated effluents from automobile servicing garages, nursing homes, private residences, housing complexes, bathing ghats and an amusement park. Dutta, Gupta and Gupta (2019) also noted significant pollution from city wastewater and domestic sewage discharged into PSB through five major wastewater inlets at a mean flow rate of 277 m^3h^{-1}. Kumar and Reddy (2008) reported that such municipal waste discharge reduced DO levels in an urban canal. This was also observed at PSB, where waste containing high organic matter led to a decrease in DO level. This elevated organic matter content increased microbial respiration (Manitcharoen, Pimpunchat, and Sattayatham 2020) and algal blooms (Mitsch and Gosselink 2015), resulting in elevated DO consumption. These factors explained the negative correlations between DO and nitrate or phosphate concentrations recorded in this study.

No distinct seasonal fluctuations in pH were observed at the study sites, with pH values remaining in the weakly alkaline range throughout the wintering period. Weakly alkaline pH levels likely augment higher macroinvertebrate diversity, providing more foraging opportunities for waterbirds (Longcore et al. 2006).

EC and TDS, both electro-physical collinear factors, are often used for monitoring temporal changes in water quality (Pal et al. 2015). An upsurge in conductance in a wetland may indicate pollution, often driven by increased levels of chloride, phosphate and nitrate ions (Pal, Chattopadhyay, and Mukhopadhyay 2013, 2015). Among the study sites, the highest EC, TDS, and salinity values were recorded at PSB, indicating poor water quality, while the lowest values were recorded in ASB, signifying better water quality. Consistent with this, Siddiqi and Chandrasekhar (2010) reported on the overall physicochemical and biological milieu of the ASB wetland, categorising it as oligotrophic with clean, safe water.

Significant positive correlations between pH, TDS, and salinity with both nitrate and phosphate concentrations were noted at KDM, PSB, and ASB. Previous research (Akpor and Momba 2008) reported that nitrate release is optimum at pH 6, which aligns with the higher nitrate concentrations observed at elevated pH levels at our study sites. High pH levels likely facilitated phosphate desorption from suspended surface sediments, increasing phosphate concentrations in the waterbody (Jensen and Andersen 1992).

High TDS levels were directly linked to increased nitrate concentrations at the study sites, consistent with studies by Fadlelmawla et al. (2008) and Kent and Landon (2013).

TABLE 2 | ANOVA with Tukey HSD test to highlight the pair-wise significant differences between mean monthly ($n = 12$) guano loading (kg/month) by three guilds of waterbirds (C: carnivorous, H: herbivorous, O: omnivorous) in four study sites. (GAD: Gangdoa Dam, KDM: Kadamdeuli Dam, ASB: Adra Sahebbandh, PSB: Purulia Sahebbandh).

	H_KDM	O_KDM	C_GAD	H_GAD	O_GAD	C_ASB	H_ASB	O_ASB	C_PSB	H_PSB	O_PSB
C_KDM	0.0045*	0.0031*	0.4377	0.0479*	0.0001*	0.5118	0.0009*	0.4657	0.1528	0.1230	0.2145
H_KDM		6.5E-09*	0.0386*	0.3861	3.4E-11*	0.0005*	0.6489	0.0004*	1.9E-05*	0.1928	4.3E-05*
O_KDM			0.0002*	7.9E-07*	0.4107	0.0214*	3.9E-10*	0.0259*	0.1266	6.8E-08*	0.0861
C_GAD				0.2293	5.2E-06*	0.1521	0.0116*	0.1322	0.024*	0.4433	0.0437*
H_GAD					8.5E-09*	0.0084*	0.1862	0.0068*	0.0007*	0.6630	0.0013*
O_GAD						0.0018*	1.4E-12*	0.0023*	0.0188*	1.0E-07*	0.0111*
C_ASB							7.6E-05*	0.9415	0.4392	0.0279*	0.5585
H_ASB								5.5E-05*	2.2E-06*	0.0788	5.5E-06*
O_ASB									0.4838	0.0231*	0.6089
C_PSB										0.0030*	0.8505
H_PSB											0.0054*

Note: Significant differences at $p < 0.05$ are marked with *.

Their findings showed a direct correlation between nitrate and TDS concentrations. However, TDS trends were not correlated with factors like land use, indicating that TDS sources are more complex, arising from both natural and anthropogenic influences. Higher salinity levels were also associated with increased nitrate and phosphate concentrations, as supported by Baek et al. (2009), who found significant positive correlations between salinity and these nutrients.

4.3 | Guanotrophic Nutrient Dynamics

Waterbirds influence nutrient dynamics in waterbodies through nutrient cycling and external loading (Hahn, Bauer, and Klaassen Bauer, and Klaassen 2007, 2008). Overwintering flocks can substantially enrich freshwater lakes with nutrients, mainly through guano, which adds nitrates and phosphates, altering water quality and potentially leading to eutrophication (Manny, Johnson, and Wetzel 1994; Post et al. 1998). Even low levels of inorganic nitrogen ($0.5\,mg\,L^{-1}$) and organic phosphorus ($0.01\,mg\,L^{-1}$) can trigger undesirable algal growth (Bassi et al. 2014), reducing open water areas and negatively impacting waterbird foraging and roosting. Waterbird droppings contribute significantly to wetland nutrient levels, with estimates showing that bird guano accounts for 27% of nitrate and 70% of phosphorus inputs in these areas (Manny, Johnson, and Wetzel 1994; Wetzel, Manny, Wetzel, and Johnson 1975). While some studies (Marion et al. 1994; Scherer et al. 1995; Wambach and Mallin 2002) found no significant impact of bird guano, others (Andrikovics et al. 2003; Singha et al. 2011; Zwolicki et al. 2013) support its role in nutrient enrichment in wetlands.

In this study, three of the four study sites (GAD, KDM and ASB) reached peak waterbird abundance in January, corresponding with the high guano and nutrient loading in this month. A previous study by Mukherjee et al. (2022a) also attested to a similar high waterbird abundance from these study sites in earlier years. However, at PSB, the highest waterbird abundance was recorded in March, primarily due to a huge, almost mono-specific congregation of Lesser Whistling Ducks, resulting in a distinct pattern of guano and nutrient loading. PSB also exhibited higher nitrate and phosphate concentrations than the other three wetlands, even at the outset of migration season (early October). Although a decline in waterbird abundance from 2018 to 2019 to 2019–2020 influenced both guano and nutrient loadings across sites, phosphate levels at PSB were unaffected. This could be attributed to inputs from five major wastewater inlets carrying industrial and municipal effluents into the wetland habitat (Dutta, Gupta, and Gupta 2019).

Orthophosphate (PO_4^{3-}) is particularly significant, as it bioaccumulates in the food chain and is a limiting nutrient for both primary productivity and algal growth in freshwater wetlands (Wetzel 1999, 2001). Anthropogenic activities contributing to elevated phosphate levels can accelerate eutrophication (Olson et al. 2005; Fadiran, Dlamini, and Mavuso 2008). Without proper management, PSB, with its high phosphate concentrations, risks becoming hypertrophic in the near future.

Previous studies (Manny, Johnson, and Wetzel 1994; Post et al. 1998) demonstrated that waterfowl significantly

TABLE 3 | Pearson's correlations (* Significant at $p < 0.05$) between total guano loading, total N loading, total P loading, NO_3-N, and PO_4-P concentrations at four study sites (GAD: Gangdoa Dam, KDM: Kadamdeuli Dam, ASB: Adra Sahebbandh, PSB: Purulia Sahebbandh).

	Guano loading	N loading	Nitrate concentrations	P loading
GAD				
N loading	0.999*			
Nitrate concentrations	−0.116	−0.123		
P loading	0.986*	0.988*	−0.159	
Phosphate concentrations	0.639*	0.634*	−0.277	0.556
KDM				
N loading	0.997*			
Nitrate concentrations	0.868*	0.849*		
P loading	0.952*	0.965*	0.857*	
Phosphate concentrations	0.851*	0.836*	0.971*	0.861*
PSB				
N loading	0.999*			
Nitrate concentrations	0.940*	0.939*		
P loading	0.969*	0.972*	0.869*	
Phosphate concentrations	−0.041	0.916*	0.953*	0.820*
ASB				
N loading	0.999*			
Nitrate concentrations	0.801*	0.799*		
P loading	0.997*	0.997*	0.815*	
Phosphate concentrations	0.761*	0.758*	0.675*	0.747*

contribute to nutrient loading, especially phosphorus, through guano. Findings from this study align with earlier research by Kear (1963), Gould and Fletcher (1978), Gwiazda (1996), and Purcell (1999), who also recorded the presence of N and P in the guano of waterbirds from different families, corroborating the fact that as total guano input increases, total N and P loading will also increase proportionately. Adhurya, Das and Ray (2020) showed that a large population of waterbirds could contribute a substantial amount of nutrients (0.4%–28.7% N and 2.4%–92% P of total N and P input to the lake, respectively) to a wetland. Similar findings were also recorded from the present study. Total GL was significantly positively correlated with both N and P loading across all study sites. Likewise, total GL correlated positively with nitrate and phosphate concentrations at ASB and KDM, with site-specific variations at PSB (nitrate) and GAD (phosphate). Linear regression analyses further highlighted the strong relationship between waterbird abundance and nitrate and phosphate concentrations, with PSB also showing strong correlations between DSIMP and nutrient concentrations, emphasising the importance of dominant species in nutrient loading at that wetland. Gwiazda et al. (2014) and Laguna et al. (2021) similarly reported that waterfowl are nutrient importers in wetlands, especially when bird population density is high, e.g., in wintering or breeding periods.

Grouping waterbirds based on their feeding habits introduces some uncertainty in nutrient-loading model predictions. Most herbivorous species consume some proportion of carnivorous diets and vice versa (Zhang et al. 2018; Verstijnen et al. 2021), influenced by food availability, season, and developmental stage (Bakker and Nolet 2014; Laguna et al. 2021). Estimating NL for omnivorous species, such as the Common Moorhen and the Northern Shoveler, was particularly challenging. While Tufted Ducks were grouped with openbills for NL estimation in our study due to their similar molluscan diets, differences in digestive performance warrant further investigation. Marion et al. (1994) showed that carnivorous waterbirds contribute more P than N due to P-rich guano. Hahn, Bauer and Klaassen (2008) and Zhang et al. (2018) reported that on a local scale, carnivorous and omnivorous waterbirds could also play significant roles in terms of P or N enrichment. Zhang et al. (2018) also reported that omnivores always preferred animal food over plant material.

In the present study, as noted in Supporting Information S1: Supplement 4, the occurrence of omnivores in the wintering waterbird community was negligible (0.5%) compared to herbivores (30%) and carnivores (64.5%). Consequently, herbivores and carnivores had a more substantial role in guanotrophication. This guanotrophic nutrient enrichment by herbivores and carnivores and its importance has been well documented by Gwiazdaet al. (2014), Laguna et al. (2021) and Verstijnen et al. (2021). Among the study sites, herbivorous waterbirds contributed significantly higher levels of guano and nutrients than carnivorous or omnivorous waterbirds due to their larger populations. Hahn, Bauer and Klaassen (2007) at a landscape scale and Adhurya, Das and Ray (2022) at a local scale similarly reported that nutrient loading by carnivorous waterbirds was significantly lower than that of herbivorous waterbirds in freshwater habitats.

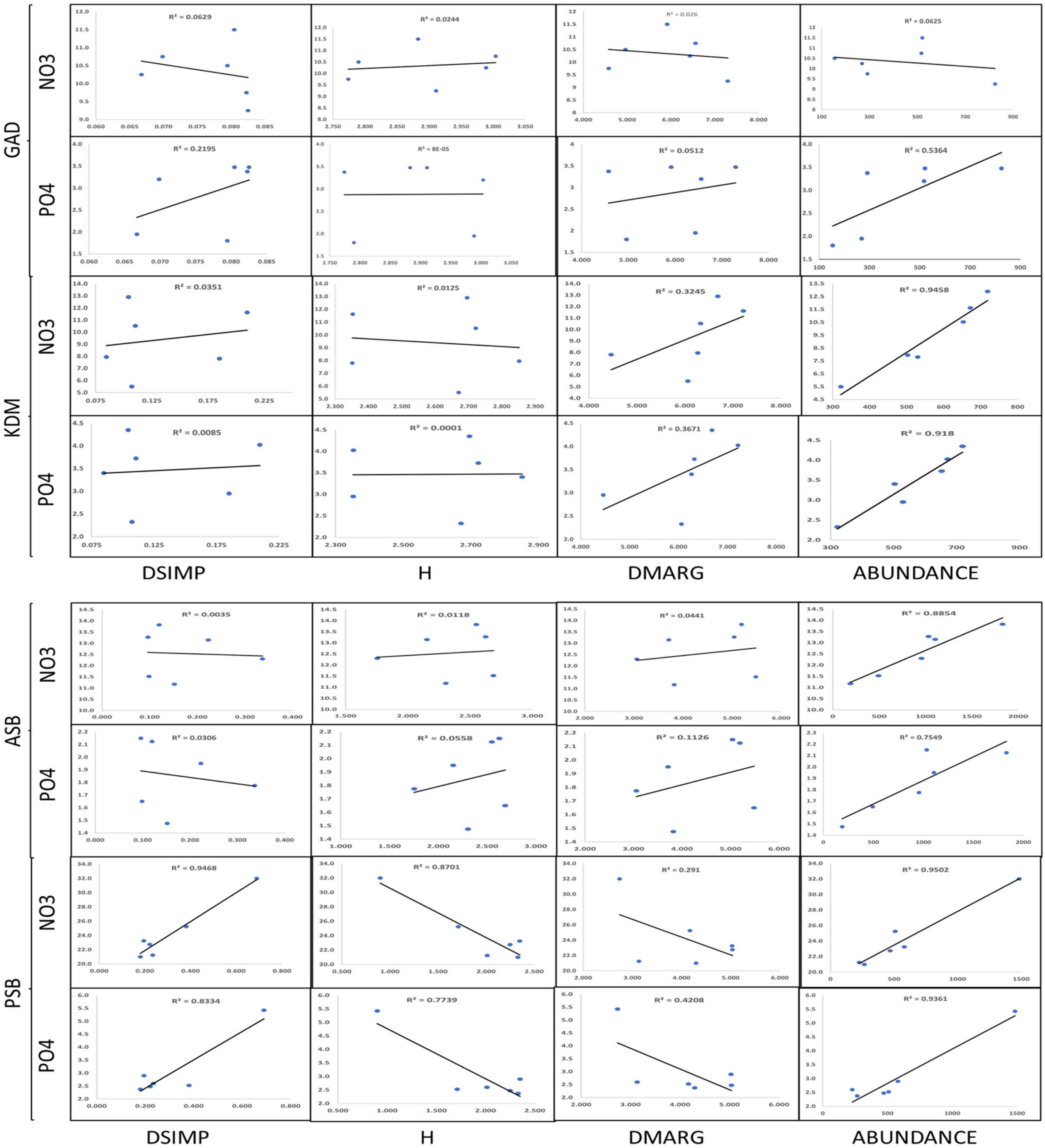

FIGURE 3 | Linear regression analyses between different diversity indices (Shannon–Wiener diversity index (H/), Simpson's dominance index (DSIPM), and Margalef's richness index (DMARG)) and abundance with the nutrient values (nitrate and phosphate concentration) of the study sites (GAD: Gangdoa Dam, KDM: Kadamdeuli Dam, ASB: Adra Sahebbandh, PSB: Purulia Sahebbandh) (R^2: Coefficient of determination).

5 | Conclusion

The wetlands of the Gangetic plains face varying levels of anthropogenic interference (Chatterjee et al. 2020). Despite this, these sites, located along the East Asia-Australasia and Central Asian Flyways, continue to attract a sizeable number of winter migratory birds. These waterbirds play a significant role in nutrient cycling through guanotrophy. Elevated nutrient levels in wetlands influence the growth of aquatic biota, forming a key food base for waterbirds (Rader and Richardson 1994). Moreover, bird droppings promote the proliferation of phytoplankton, hydrophytes, micro- and macroinvertebrates, benthic organisms, and fish (Scherer et al. 1995; Longcore et al. 2006; Hanson 2008). Avian guanotrophy during the waterbird wintering season likely sustains the nutrient requirements of the study sites throughout the year. As hypothesised, our study found that in most of the wetlands, waterbird abundance plays a significant role in nutrient enrichment. Herbivorous waterbirds were the main contributors to nitrate and phosphate loading, followed by carnivorous species. Managing wetland ecosystems that support winter migratory birds requires a delicate balance between the nutrient enrichment effects of waterbirds and maintaining habitat sustainability to continue attracting these seasonal visitors. Regular monitoring of water quality and control of external anthropogenic inputs to these wetlands are essential for preserving these historical wintering grounds for the future.

Author Contributions

Arkajyoti Mukherjee: conceptualisation, data curation, investigation, writing–original draft. **Sudin Pal:** methodology, software, writing–review & editing. **Sagar Adhurya:** data curation, investigation, methodology. **Subhra Kumar Mukhopadhyay:** conceptualisation, investigation, methodology, supervision, validation, visualisation.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.