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# ARTICLE



# Landscape-wide pulse events predict trait-based responses among wetland birds in perennial channels of a dryland wetland

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#### Abstract

Wetlands in arid or semiarid zones are vital for maintaining biodiversity but face growing threats. Flooding regime variability is a key driver of ecological dynamism in these systems, dictating primary productivity on a large spatial scale. The functional composition or diversity of wetland-dependent bird species has been found to be sensitive to fluctuations in hydrological regimes and can thus be indicative of cascading ecosystem responses associated with climate change. In this paper, we investigate whether large-scale changes in inundation and fire-a significant additional biodiversity determinant in (semi-)arid landscapes-are reliable predictors of functional group responses of wetland-dependent birds along a perennial channel of the Okavango Delta, Botswana. We fit generalized additive models (GAMs) to 6 years of bird survey data collected along ~190-km-long annual transects and use remotely sensed landscape-level inundation estimates, as well as spatiotemporal distance to fire, to predict the responsiveness of seven trait-based functional group abundances. During the surveys, a total of 89 different wetland-dependent bird species were recorded, including 76 residents, across all years, with below-surface feeding waders consistently the most abundant functional group. Including estimated spatiotemporal variability in flooding and fire, as well as their interactions, improved model fit for all seven functional groups, explaining between 46.8% and 68.3% of variability in functional group abundances. Covariates representing longer-term variability in inundation generally performed better than shorter-term ones. For example, variability in inundation over the 5 months preceding a survey best predicted the responses of all functional groups, which also all exhibited responsiveness to the interaction between flooding and fire. We were able to interpret the responses of individual functional groups, based on the resource exploitation assumption. Overall, our results suggest that perennial waters in dryland wetlands offer functional refugia to wetland-dependent birds and highlight the indicative power of large-scale traitbased bird monitoring. Our findings demonstrate the potential utility of such a

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made. © 2023 The Authors. *Ecological Applications* published by Wiley Periodicals LLC on behalf of The Ecological Society of America. monitoring regime for dryland wetland ecosystems vulnerable to industrial-scale anthropogenic pressure and associated climate change.

K E Y W O R D S

fire, flooding, functional groups, pulse events, waterbirds, wetlands

# INTRODUCTION

Dryland wetlands support high levels of biodiversity and harbor valuable natural resources in regions otherwise characterized by resource scarcities—especially, and paradoxically, water scarcity (Tooth & McCarthy, 2007). They are fed by a reliable provision of water, albeit with an often distinct seasonal variability (or flood pulse; Junk et al., 1989) that facilitates an interconnected mosaic of lentic and lotic conditions (Arias et al., 2013; Kobayashi et al., 2009; Lindholm et al., 2007; Ramberg et al., 2010). Within such systems, seasonally inundated floodplains become instrumental in supplementing primary productivity on a landscape level (Lindholm et al., 2007; Molinari et al., 2022). Wetland productivity further depends on interactions between the additive effects of flooding and other environmental forces, such as fire (Heim et al., 2021).

Fluctuations in hydrological regimes in flood-pulsed dryland wetlands can be predicted to some degree in both the short and long term. However, climate change and industrial-scale water consumption have aggravated the uncertainty of long-term predictions, particularly the duration and magnitude of such pulse events, and the capacity of adapted ecosystems to respond (Jentsch & White, 2019). In flood-pulsed wetlands, resource accumulation and distribution, which are both functions of water availability, dictate food web composition over space and time (Kobayashi et al., 2015) and are heavily reliant on sequential flow and the hydro-ecological connections within the river-floodplain complex (Leigh et al., 2010). Effectively tracking and exploiting these resources is overwhelmingly dependent on a combination of functional and life history traits (Ishiyama et al., 2014).

High mobility makes wetland-dependent birds particularly adept at accessing aquatic and semiaquatic habitats on a local and regional scale. Ecosystem functions performed by wetland-dependent birds include bioturbation, dispersal of native and non-native species, predation, and pest control (Green & Elmberg, 2014). This makes them key agents in maintaining the functioning of wetland ecosystems and, thus, useful indicators of changing environmental conditions (Everard & Noble, 2010; Farinós-Celdrán et al., 2017; Mistry et al., 2008).

Taxonomic composition and diversity among wetland-dependent birds have been linked to wetland

habitat condition and structure (Cintra, 2019; Gayen et al., 2020; Paillex et al., 2009). However, studies employing functional composition and/or diversity offer additional insights, as the response to the same variables might differ (Almeida et al., 2018) due largely to the different roles birds assume within food webs (Violle et al., 2007). Within pulse dynamics, Jentsch and White (2019) postulate that trait complementarity, diversity, and redundancy are all determinants of ecosystem responses to pulse events. In flood-pulsed wetlands, wetlanddependent bird responses in trait space are primarily dictated by hydrologically driven fluctuations in resource availability (Cumming et al., 2012). Over the last decade or so, more research investigating such responses to hydrological regime changes in flood-pulsed river or wetland systems has emerged, especially from the Southern Hemisphere (Almeida et al., 2017; Cumming et al., 2012; Garrett-Walker et al., 2020; Lorenzón et al., 2017, 2020). It does, however, remain underexplored, especially in arid regions, where bird mobility takes on even greater importance in maintaining the ecological functioning of wetlands. Conversely, the ecological integrity of wetlands becomes especially pertinent to wetland-dependent bird diversity and conservation in areas with low rainfall.

Several studies have demonstrated that trait-based responses of wetland-dependent birds present a promising analytical tool for understanding changing resource availability of ecosystems in flood-pulsed wetlands (Almeida et al., 2017; Cumming et al., 2012; Lorenzón et al., 2020). However, these studies were based on localized flooding conditions. In this study, we modeled responses of wetland-dependent birds to seasonal inundation variability along a landscape-level geohydrological gradient in the Okavango Delta in Ngamiland, northwestern Botswana.

Using multiyear data from a continuous large-scale bird survey along the longitudinal flow axis of the Okavango's terminal dryland wetland and remotely sensed inundation and fire hotspot estimates, we investigated the responsiveness of wetland-dependent bird functional groups to variations in and interactions between pulse events (flooding and fire). Our aim was to test whether functional-trait-based responses among wetland-dependent birds along the dryland wetland's core hydrological axis could be predicted by fluctuations in lateral inundation across the wetland's extent, based on additive modeling. We also incorporate spatiotemporal variables reflecting fire incidence in our modeling efforts since it is a major pulse event in dryland wetlands. Based on the performance of our models, we investigated the suitability of functional variability among wetland-dependent birds as a proxy for landscape-scale environmental conditions and, thus, a monitoring tool of ecosystem function in dryland wetlands.

Given the highly variable and complex hydrological cycle in flood-pulsed wetlands in general, examining functional groups within higher trophic levels could advance our understanding of large-scale ecosystem responses to this variability in space and time. This, in turn, could aid efforts to mitigate threats, such as climate change and industrial water extraction, to systems that are not only invaluable to regional and global biodiversity but also becoming increasingly vulnerable to climate-related impacts (Mitchell, 2013; Moses & Hambira, 2018).

# METHODS

#### **Study site**

The flood-pulsed endorheic Okavango Delta stretches across three southern African countries. In Botswana, it covers almost one-tenth of the country's surface area (55,599 km<sup>2</sup>) and comprises 95% of its surface water. Recognized by the Ramsar Convention on Wetlands of International Importance (in 1997) and the United Nations Educational, Scientific and Cultural Organization (UNESCO) as a Ramsar Site and UNESCO World Heritage Site, respectively, the Delta adds incomparable environmental, cultural and socioeconomic value, both locally and regionally. Water supply and flooding patterns within the delta are predominantly dictated by perennial flow, with localized summer rainfall (November to March) adding considerable volumes of water on an inconsistent basis (McCarthy et al., 2003). Average rainfall varies from almost 1500 mm per annum (p.a.) at the river's highaltitude headwaters in central Angola to about 400 mm p.a. at its alluvial fan in Botswana's semiarid northwest. A steady pulse means that inundation generally peaks during the dry winter months (Milzow et al., 2010). Current climatological conditions permit a maximum inundation expanse of up to 13,000 km<sup>2</sup>, while approximately 6000 km<sup>2</sup> are inundated perennially (Gumbricht et al., 2004; McCarthy, 2006). Distributaries are characterized by varying flooding behaviors, with water level fluctuations of 1.5-2 m in westerly and central distributary systems and less than 0.6 m in the eastern portions (Porter & Muzila, 1989).

The delta's high biological productivity is reflected in its species diversity and abundance (Junk et al., 2006; Ramberg et al., 2006), biomass (Bonyongo, 2004), and nutrient cycling (Frings et al., 2014; Mladenov et al., 2007). A total of 444 species of birds (belonging to 74 different families) have been confirmed within its expanses (Ramberg et al., 2006). Of these, 169 were classified as wetland-dependent by Ramberg et al. (2006).

## Annual surveys

Between 2013 and 2018, the National Geographic Okavango Wilderness Project conducted an annual wetland bird survey along a major channel (the Okavango-Jao-Boro system) in the Okavango Delta (Figure 1). These surveys were undertaken in dugout canoes by the same observer (R. Boyes) along a standardized transect route following traditional trails known by local guides. Transect routes varied little among years based on water levels and blockages caused by elephants. Birds encountered were identified and their abundance noted, with the observer audibly sharing each observation, so that observations could be augmented by other experienced observers on the team. Observations were made both visually (with binoculars when necessary) and aurally and were recorded by various team members using the Mobile Forms App (©Device Magic), which attaches a date/time and location stamp to each observation. Due to the habitat configuration and observational reliability, observations were generally limited to approximately 200 m. Flushed individuals that remained ahead of the research team were noted and disregarded from future counts, as were individuals flying overhead. Taxonomic classifications used here are in accordance with the latest Illustrated Checklist of the Birds of the World (HBW & BirdLife International, 2020).

Surveys were limited to months with sufficient water levels (August/September/October), and survey duration varied between 15 and 19 days. Daily survey efforts and their intensities were largely dependent on environmental and landscape factors (e.g., suitable habitat for camping, water levels, wildlife-related risks) but were restricted to diurnal hours. As launch locations were inconsistent over the years, we truncated our data set based on interannual transect alignment; this truncated transect was approximately 190 km long. To account for (interannual) spatial variability, we used ArcGIS (version 10.7.1) to place each observation within a  $300 \times 300$ -m grid, with each grid cell constituting a data point. A grid-based approach allows for some flexibility, which is needed to accommodate the positioning inaccuracies that come with a continuously moving observer. The fieldwork was conducted under the conditions of Research Permit EWT 8/36/4 XXXVII (2) issued by Botswana's Ministry of Environment, Natural Resources Conservation and Tourism.



**FIGURE1** (Top left) Image of Okavango Delta. The white solid line indicates the polygon to which inundation calculations were restricted. (Top right) The red square marks the location of the Okavango Delta, with Angola (AO), Botswana (BW), and Namibia (NA) also indicated. (Bottom) The blue line marks the surveyed grid cells from 2013 to 2018, with varying transparency indicating the number of years each grid cell was surveyed, illustrated at a finer spatial scale for demonstrative purposes (bottom).

## **Response variables**

## Functional groups

We based criteria for species' wetland dependence on the major importance of any of the listed inland wetland characteristics for respective species as outlined by the International Union for Conservation of Nature (IUCN) Red List (IUCN, 2021). We divided bird species into seven functional groups (Table 1) based on dietary and foraging traits, as quantified by Wilman et al. (2014), as well as expert knowledge. These traits relate primarily to a species' diet and foraging habitat. Counts for each group were aggregated by grid cell and year. Each functional group count constitutes a response variable. To aid oversight and readability, we will include the functional group description in parentheses upon first mention in each section of this manuscript. These short descriptions represent most of the functional group, but might not completely describe every species. Aspects of diet or foraging strata used might overlap to a lesser or greater degree between species but still align enough to warrant our chosen groupings.

# **Explanatory variables**

# Flooding

We calculated flood expanse by adapting the method used by Inman and Lyons (2020). We used a short-wave infrared thresholding method on the MCD43A4.006 Moderate Resolution Imaging Spectroradiometer (MODIS) Nadir Bidirectional Reflectance Distribution Function Adjusted Reflectance (NBAR) product to extract daily inundation area (in square kilometers) at a 500-m resolution for the polygon outlined in the top of Figure 1 from 1 January 2013 to 31 December 2018 (i.e., the time span of our data set). We removed any images with more than 5% cloud cover, which predominantly occurred during the rainy season (typically December to March).

Based on the consistency of these filtered values, we set our time frame of effect to 5 months prior to each survey up to the date of the survey for all explanatory variables (Figure 2). This period captures the most substantial changes in inundation area, as well as potential responses from wetland bird communities to these changes (Francis et al., 2021). For inundation area (in square kilometers), we used grid-cell-based mean values for the survey period and five 1-month intervals predating this period. In addition, we calculated the SD of inundation area (in square kilometers). These variables are designed to capture flooding regime patterns and accommodate environmental factors, such as local evapotranspiration rates, which are decoupled from the hydrology primarily driving the annual flood.

As additional explanatory variables (or predictors) we included median days passed since the maximum inundation area was observed for respective years.

# Fire

We extracted data on fire using the National Aeronautics and Space Administration's (NASA) Fire Information for Resource Management System (FIRMS; https://firms. modaps.eosdis.nasa.gov/). These data are represented as hotspots, based on satellite imagery from the MODIS and

TABLE 1 Overview and description of the seven functional groups used in this study.

Functional group	Description	No. species	Example species
FG1 (Invertivorous shore feeders)	Species primarily feeding on invertebrates along shoreline	10	African snipe, blacksmith lapwing, glossy ibis
FG2 (Omnivorous shore feeders)	Primarily species with wide-ranging diet, foraging along shoreline	11	Cattle egret, little stint, spur-winged goose
FG3 (Surface feeders)	Species primarily foraging on or around water surface	14	African jacana, little bittern, rufous-bellied heron
FG4 (Below-surface feeding nonwaders)	Nonwading species foraging in upper stratum of water column	9	African pygmy-goose, little grebe, white-faced whistling duck
FG5 (Below-surface feeding waders)	Wading species foraging in upper stratum of water column	16	African spoonbill, hamerkop, wattled crane
FG6 (Diving piscivores)	Species feeding on fish in open water through partial or complete immersion	13	African darter, giant kingfisher, Pel's fishing-owl
FG7 (Nonaquatic feeders)	Wetland-dependent species primarily foraging in nonaquatic habitats	16	Chirping cisticola, hadada ibis, southern carmine bee-eater



**FIGURE 2** Annual fluctuations in inundated area, with only values generated from images with less than 5% cloud cover displayed. Color gradient indicates survey periods temporally displaced in 1-month intervals. These displaced values were used to construct the floodx and changex variable set.

Visible Infrared Imaging Radiometer Suite (VIIRS) instruments. We only included fire hotspots that (a) exceeded the 50% confidence threshold and (b) occurred within 5 months of the survey start (Appendix S1: Figure S1). Spatial (or planar, in kilometers) and temporal (number of days separating the start of a survey and the acquisition of the satellite image in which the fire hotspots appear) distances for each fire hotspot from a given grid cell were computed.

# Statistical analysis

To model possible lagged responses to inundation, we tested a range of inundation estimates prior to the survey for each year. These were calculated in monthly intervals, with the number at the end of a variable name representing the number of months preceding the survey for a given year. For example, flood2 is the inundation value 2 months prior to the survey, while change3 is the SD from the mean inundation during the 3 months before the survey (Table 2).

We established a set of explanatory variables considered for final analysis by evaluating the variance inflation factor (VIF) of all eligible variables and eliminating them one by one until the VIF for all independent variables was below 3 (Zuur et al., 2009). This helped avoid concurvity (a generalization of collinearity).

For each functional group, we fitted generalized additive models (GAMs; Hastie & Tibshirani, 1991) to evaluate the strength of respective explanatory variables. This modeling approach was deemed suitable

because GAMs are capable of fitting nonlinear relationships between response and predictor (Wood, 2017), and our knowledge of the system and relevant literature (Ramberg et al., 2010) suggested that relationships between bird responses and flooding and fire would be nonlinear. We conducted all analyses in the R programming environment (R Core Team, 2020), using the "gam" function in the mgcv package (Wood, 2020). Given the nature of our dependent variables (counts) and overdispersion within our data set and based on our inspection of model residuals, we found that a negative binomial error distribution with a log-link function was the most suitable (O'Hara & Kotze, 2010; Wood, 2017). Every model was fitted with nested interaction terms to accommodate potential spatial and temporal autocorrelation. The spatial term comprised the coordinates of a given grid cell centroid, while the temporal term comprised the day of the year and the time of day. We let both these terms vary by year. We also included an offset term for sampling effort (hours per day) to correct for sampling variability. To determine the presence of autocorrelation, we compared models using a likelihood ratio test (LRT), with and without spatiotemporal terms (Zuur et al., 2009).

Based on the final set of variables, we constructed a set of models per functional group, of which each one included a different interaction between each flood- and fire-related variable term using a tensor product (Wood, 2020), in addition to the smoothed main effects of the variable set. One model per set was left without an interaction term to evaluate its performance. We estimated smoothing parameters for explanatory variables using

TABLE 2 Explanatory variables considered for model construction.

Variable	Minimum	Maximum	Description	Reference
Changex	-33.47	17.75	Standard deviation for inundated area (in square kilometers) during range of periods (1–5 months) prior to the survey (x represents a placeholder for respective intervals)	Wolski et al. (2017); Inman and Lyons (2020)
Daysmax	25	244	Median no. days between maximum observed inundation value and respective survey day	Cumming et al. (2012)
Fire_days	39	158	No. days between date of satellite image acquisition and survey start	Heinl et al. (2006); Ramberg et al. (2010)
Fire_distance	5.22	98.84	Distance (in kilometer) between fire hotspot and a given grid cell	Heinl et al. (2006); Ramberg et al. (2010)
Floodx	4678.47	10,897.81	Mean inundation area (in square kilometers) during survey and at 1-month intervals (1–5) prior to survey ( <i>x</i> represents a placeholder for respective intervals)	Wolski et al. (2017); Inman and Lyons (2020)

restricted maximum likelihood (REML; Marra & Wood, 2011). Variable selection was undertaken using the double penalty approach described by Marra and Wood (2011), which allows for smoothing parameter estimation to eliminate variables by penalizing a function component in the null space. Models took on one of these two basic forms:

- 1.  $E(n_{gij}) = f_1(\text{latitude}_j, \text{longitude}_j, \text{year}_i) + f_2(\text{day of year}_j, \text{time of day}_j, \text{year}_i) + f_3(\text{flooding}_{ij}, \text{fire}_{ij}) + f_4(\text{flooding}_{ij}) + f_5(\text{fire}_{ij}) + \text{offset}(\text{sampling effort}),$
- 2.  $E(n_{gij}) = f_1(\text{latitude}_j, \text{longitude}_j, \text{year}_i) + f_2(\text{day of year}_j, \text{time of day}_j, \text{year}_i) + f_4(\text{flooding}_{ij}) + f_5(\text{fire}_{ij}) + \text{offset(sampling effort)},$

in which  $n_{gij}$  represents the bird count per functional group g for the *i*th year in the *j*th grid cell, while  $f_1$  and  $f_2$  are autocorrelation structures, and  $f_3$ - $f_5$  represent the main effects and interactions considered in our analysis. Where necessary, we made adjustments to variable selection and/or selected variables based on model diagnostics generated by the "gam.check" function. Model performances were assessed using the Akaike information criterion (AIC) and compared using the difference in AIC values ( $\Delta$ AIC), with  $\Delta$ AIC < 2 indicating substantial support for a given model (Anderson & Burnham, 2004). For all environmental predictors, we retained the default thin plate spline regression as a penalization basis. For day of the year and time of day, we let the smoothing penalty be defined by cyclical regression splines, while the grid cell centroid coordinates were defined by Duchon splines. We restricted all predictors passing through a smoothing function to four degrees of freedom to prevent overfitting and enhance interpretability.

## RESULTS

We recorded 89 wetland-dependent bird species (Appendix S1: Table S1), with between nine and 16 species per functional group (Table 1). On average, FG5 (below-surface feeding waders) was consistently the most abundant functional group each year (2296.5  $\pm$  908.8, n = 6; Becker et al., 2023) and FG7 (nonaquatic feeders) yielded the lowest mean annual counts (573.3  $\pm$  110.7, n = 6). Out of the 89 species recorded, 13 were entirely nonresident to the Okavango Delta and either intra-Africa or Palearctic migrants (Appendix S1: Table S2).

Overall, inundation expanse across survey years varied up to 3.46 times with maxima observed in 2017 (11,238.81 km<sup>2</sup>; Table 3; Appendix S1: Figure S2) and minima observed in 2018 (3250.10 km<sup>2</sup>). In 2017, inundation also experienced the largest difference in extreme values (maximum–minimum). The highest annual mean inundation expanse was recorded in 2014 (7948.91  $\pm$  57.56 km<sup>2</sup>; n = 313).

# **Correlation between predictors**

Following the stepwise elimination of variables, based on their contribution to the VIF, we were left with a final variable selection of five: daysmax (days since maximum inundation), flood3 (inundation extent during 3 months prior to survey), change3 (inundation variability during 3 months prior to survey), change5 (inundation variability during 5 months prior to survey), fire\_days (days between survey start and fire hotspot image acquisition). The temporal distance of fire hotspots (fire\_days) was significantly and negatively correlated with the spatial distance of fire hotspots (fire\_distance; r = -0.83; p < 0.01).

e	e				
Year	Minimum	Maximum	Range	Mean (±SE)	N
2013	4819.02	10,074.04	5255.02	$6990.99 \pm 54.71$	314
2014	4918.12	9210.52	4292.40	$7948.91 \pm 57.56$	313
2015	3690.38	7963.19	4272.81	$6398.27 \pm 72.34$	352
2016	3479.01	7266.08	3787.07	5759.98 ± 65.67	296
2017	3935.71	11,238.81	7303.10	$7610.19 \pm 93.25$	313
2018	3250.10	7041.08	3790.98	$5401.09 \pm 59.99$	322

**TABLE 3** Range of moderate-resolution imaging spectroradiometer (MODIS)-based inundation expanse across surveyed years, with *N* indicating number of images with less than 5% cloud cover.

Note: Minimum, maximum, range, and mean (±SE) are expressed in square kilometers.

Temporal distance can also be interpreted as the inverse of spatial distance, meaning that the most recent fire hotspots were also the furthest away.

## Model performances

For all functional groups, models including spatiotemporal interaction terms significantly improved model fit (p < 0.01), which suggests autocorrelation and justifies the inclusion of these terms as a corrective measure (Zuur et al., 2009). This ensures that any modeled environmental effects are independent of autocorrelated structures within the model residuals. The most parsimonious model for each functional group outperformed competing models by a  $\triangle AIC$  value >2 in most functional groups (Table 4). However, FG3 (surface feeders) and FG6 (diving piscivores) were characterized by more model uncertainty, with relative support for model parsimony offered by more than one model. Overall, the model explaining the most deviance was fitted to FG5, with the most parsimonious model accounting for 68.3% of the deviance. The deviance explained by the bestperforming GAM for FG4 (below-surface feeding nonwaders) was the lowest overall at 46.7%. For most functional groups, variability over the 5 months preceding the survey (change5) emerged as the strongest determinant in the most parsimonious model iteration. High model parsimony was also linked to the inclusion of flooding-fire interaction terms, which are present in all the top-performing models.

Overall, only three different main effects were included across all functional groups, namely, change3, change5, and fire\_days. The only models that retained fire\_days as a main effect were those for FG1 (invertivorous shore feeders; Appendix S1: Table S3; edf = 1.00,  $\chi^2 = 3.34$ , p = 0.07), FG2 (omnivorous shore feeders; effective degrees of freedom [edf] = 1.36,  $\chi^2 = 5.25$ , p = 0.11), and FG7 (edf = 1.00,  $\chi^2 = 4.72$ , p < 0.05). Only two functional groups exhibited

responsiveness to the shorter-term inundation variability (change3): FG1 (edf = 1.00,  $\chi^2$  = 3.75, *p* = 0.05) and FG5 (edf = 2.66,  $\chi^2$  = 14.58, *p* < 0.01).

Flooding-fire interaction terms varied relatively between functional groups. FG3 (edf = 2.48,  $\chi^2 = 0.45$ , p = 0.85) and FG6 (edf = 1.20,  $\chi^2 = 1.38$ , p < 0.01) were most responsive to the interaction between days passed since maximum inundation (daysmax) and days passed since a fire hotspot detection (fire\_days). FG2  $(edf = 5.61, \chi^2 = 12.66, p = 0.05), FG4 (edf = 4.06,$  $\chi^2 = 20.24$ , p < 0.01), FG6 (edf = 8.51,  $\chi^2 = 70.28$ , p < 0.01), and FG7 (edf = 2.45,  $\chi^2 = 9.80$ , p < 0.05) displayed heightened responses to change3 and fire days interacting. The interaction between change5 and fire\_days was retained in the best-performing models of FG1 (edf = 1.69,  $\chi^2 = 1.61$ , p = 0.45) and FG3 (edf = 1.88,  $\chi^2 = 1.62$ , p = 0.36), while the interaction term consisting of absolute inundation expanse 3 months prior to the survey (flood3) and fire days only appeared in the top-performing model for FG5  $(edf = 3.00, \chi^2 = 5.06, p = 0.29)$  and FG6 (edf = 2.47, $\chi^2 = 5.32, p = 0.14$ ).

# **GAM response curves**

For most functional groups, responses to long-term variability in inundated area (change5) assumed a similar shape (Figure 3). Abundances increased up to a point (~600–800 km<sup>2</sup>) before declining again toward the end of our measured range. Only the abundance of species in FG2 responded positively along a linear trajectory, while FG5 exhibited a near-linear negative response. For the two functional groups whose most parsimonious models included change3, responses were contrasting. FG1 abundances decreased linearly with growing inundation variability in the 3 months leading up to the survey, whereas FG5 abundances increased along the same gradient.

Responses to the temporal distance of fire hotspots followed a similar trend across respective functional

r					
		Model	$D^2$	AIC	$\Delta AIC$
FG1	~	fire_days×change5 + fire_days + change3 + <b>change5</b>	65.7	7386.00	
FG2	~	<pre>fire_days×change3 + fire_days + change5</pre>	56.2	7700.74	0.00
		fire_days + change5	55.6	7709.16	8.42
		fire_days×flood3 + <b>fire_days</b> + change5	55.6	7711.94	11.20
FG3	~	fire_days×change5 + <b>change5</b>	54.9	10,502.18	0.00
		fire_days×daysmax + <b>change5</b>	54.9	10,504.10	1.92
		change5	54.8	10,504.28	2.10
FG4	~	<pre>fire_days×change3 + change5</pre>	46.7	8675.42	0.00
		change5	46.3	8680.00	4.58
FG5	~	fire_days×flood3 + change3 + change5	68.3	12,962.80	0.00
		change3 + change5	67.9	12,977.30	14.50
		fire_days×daysmax + change5	67.8	12,979.05	16.25
		<pre>fire_days×change3 + fire_days + change5</pre>	67.8	13,009.42	46.62
FG6	~	fire_days×change3 + change5	66.4	12,286.50	0.00
		fire_days×flood3 + <b>change5</b>	66.4	12,287.61	1.11
		fire_days×daysmax + <b>change5</b>	66.4	12,287.65	1.15
		change5	66.2	12,290.63	4.13
FG7	~	fire_days×change3 + fire_days + change5	63.7	6227.04	0.00
		fire_days×daysmax + change3 + change5	63.4	6236.50	9.46
		fire_days + change5	63.5	6237.64	10.60

**TABLE 4** Generalized additive model (GAM) comparisons, with counts of respective functional groups among wetland-dependent birds as response variables.

*Note*: Model fit and associated performance are represented by deviance explained ( $D^2$ ) and the Akaike information criterion (AIC). Model comparisons are illustrated by difference in AIC values ( $\Delta$ AIC), with the most parsimonious model registering a  $\Delta$ AIC value of 0.00. Significant terms (p < 0.05) are indicated in bold. Where  $\Delta$ AIC is absent, only one competing model was generated.

groups. FG1, FG2, and FG7 abundances responded positively to days since a fire was detected. We observed the most pronounced responses to flooding-fire interaction for FG2, FG4, FG6, and FG7 (Appendix S1: Figure S3). Abundances for all these functional groups exhibited strong positive responses to the interaction between high medium-term inundation variability (change3) and a low number of days passed since a fire hotspot was observed. This effect inverted with more recent fire hotspots. FG4 abundances were also relatively strongly affected by an interactive relationship between long-term inundation variability (change5) and recent fire hotspots. However, here the strongest positive effect corresponded with high inundation variability and high temporal distance to fire hotspots. Interaction terms for the other functional groups were characterized by relatively small effect sizes.

# DISCUSSION

Disentangling the ecosystem implications of hydrological variability in flood-pulsed wetlands on a landscape level

is difficult. We expressed these implications by modeling the abundance of wetland-dependent bird functional groups using remotely sensed environmental variables. Our models capture a considerable amount of the variability in our data and robustly illustrate functional group responses to variation in inundated area and recent fire hotspots, as well as their interactions, in a dryland wetland. Given the system's dynamism, it is perhaps unsurprising that our findings suggest that inundation variability, and not inundation extent per se, is the primary determinant of wetland-dependent bird abundances. Finer scale spatial variability along perennial channels still requires further scrutiny but falls outside the scope of this study and presents opportunities for future research.

Environmental predictors in our models revealed responses meeting the assumptions of the exploitation hypothesis described by Cumming et al. (2012). When applied to our study, its premise stipulates that population responses of wetland-dependent bird species in different functional groups along the core channel system can be predicted by changes in wetland-wide inundation



FIGURE 3 Legend on next page.

and fire proximity across the entire landscape. Our findings at least partially support this hypothesis across all functional groups on a large spatial scale, which also shows the potential to employ this approach as an indicative monitoring tool for wider ecosystem processes in these systems.

# PREDICTING TRAIT-BASED RESPONSES TO VARIATIONS IN PULSE EVENTS

# Main effects

Inundation as a determinant of resource flux in floodpulsed wetlands is relatively well understood (Ramberg et al., 2010). Wetland-dependent bird species can respond to short-term changes in resource availability, which our models also suggest in relation to fluctuations in inundated area. In fact, variability in inundated areas proved to be a stronger predictor across all functional groups than any other flood-related variable. Moderate inundation variability over a longer period elicited a positive response from almost all functional groups and could suggest that, beyond a certain threshold in flooding stability, wetland-dependent birds are pushed away by unfavorable conditions or pulled away by favorable conditions elsewhere. This result is also somewhat consistent with the findings of Cumming et al. (2021), who noted that bird encounter rates and species diversity at Lake Ngami (which is part of our study's landscape) were highest during the midpoint of the drying-down period.

Only FG5 (below-surface feeding waders) responded entirely negatively to increasingly unstable flooding conditions over a period of 5 months prior to our surveys. Given that these birds' foraging behaviors are heavily reliant on water depth on a localized scale, highly variable flooding conditions are likely to dictate their movements to a greater extent than other functional groups, who might rely more on shoreline availability or

perennially inundated channels, whose depths are not determined as much by landscape inundation. The adverse response of FG1 (invertivorous shore feeders) to increasing inundation variability in the shorter term suggests that these birds favor more stable flooding conditions immediately preceding their occupation of an area. Due to their predominantly invertivorous diet, this could be linked to prey life cycles, which, depending on the taxon, are also reliant on relatively stable or predictable flooding conditions (Dube et al., 2017). For FG5 we observed an inverse trend, with the group's abundance responding positively to an increase in shorter- or medium-term variability in an inundated area. Given the strong fish-based component of their diet, this observation too offers a prey-related explanation. Ramberg et al. (2010) and Linhoss et al. (2012) determined that highflood conditions favored fish production in the Okavango Delta. For the purpose of this study, that could mean that high-flood conditions in the preceding 3 months ensured high fish production and, with relatively rapidly shrinking inundation, highly concentrated fishing grounds for these birds along our surveyed transect. However, based on this reasoning alone, we would also expect to make a similar observation for FG6 (diving piscivores). Perhaps, then, higher fish concentrations, coupled with habitat preference (i.e., shallower waters on floodplains), are a likelier determining factor than fish availability alone.

As we noted earlier, the precise composition of certain functional groups is to some degree subjective. During the analysis, we fitted models with variations in some of these categorizations, and our results for the most parsimonious models were unchanged by these changes.

Habitat- and landscape-dependent fire-induced alterations to vegetation structure have been found to influence avian trait-based assemblages (Hidasi-Neto et al., 2012). Fire-related variables in wetland systems apply environmental filters that select for traits associated with both the accessibility and availability of food/prey. Their cascading effects, in tandem with hydrological events, on ecosystem functioning and vegetation structure in

**FIGURE 3** Generalized additive model response curves (white lines) for each smoothed predictor in most parsimonious model per functional group (FGx). Color-coded shade represents the confidence intervals (95%) for each smoothing function. Black lines on *x*-axes indicate distribution of raw data points. More transparent confidence intervals indicate greater model uncertainty within a functional group (models with  $\Delta$ AIC <2), with the given variable and associated response maintained throughout the model set. The annotation s(...) represents the partial effect size of a given variable. The numbers inside the parentheses indicate the effective degrees of freedom (edf). Note that scales on the *y*-axis may vary among individual plots. Bird silhouettes were sourced from PhyloPic (https://www.phylopic.org/) and are attributed to the following illustrators: Rebecca Groom (FG1, FG2), Alexandre Vong (FG3), Andy Wilson (FG4), Jon Hill (FG5), Ferran Sayol (FG6), Mathieu Pélissié (FG7); they were used under the following Creative Commons licenses: Attribution 3.0 Unported (FG1, FG2, FG3; license link: https://creativecommons.org/licenses/by/3.0/), CC0 1.0 Universal Public Domain Dedication (FG4, FG6; license link: https://creativecommons.org/licenses/by/3.0/), Attribution-NonCommercial-ShareAlike 3.0 Unported (FG7; license link: https://creativecommons.org/licenses/by-sa/3.0/).

dryland wetlands have also been well documented especially for our study system (Heim et al., 2019, 2021; Heinl et al., 2006, 2007). Temporal distance to fire hotspots across the landscape exerted a positive effect on the abundance of FG2 (omnivorous shore feeders). The dominant species in this group (Egyptian goose and spurwinged goose) are heavily reliant on grazing, which would be promoted by fires (Heinl et al., 2004). A temporal lag in fire-related effects could thus explain potentially better foraging habitat for these birds.

For FG1 and FG7 (nonaquatic feeders), the only other functional groups that included temporal distance to fire hotspots as a main effect in the most parsimonious model, fire events played a slightly different role. For these groups, abundances also responded positively to temporal distance. One of the most common species in FG1, the blacksmith lapwing, largely relies on foraging behaviors that flush invertebrate prey items (Cantlay et al., 2019), so more frequent fires could provide these birds with better access to preferred prey. This notion (or a version of it) could also help explain the relatively large contribution of fire frequency to the FG7-based model, where probe-feeding species, such as the African sacred ibis and the hadada ibis, the group's most abundant species, might benefit from more open ground. Affinity to frequently burned habitats has been documented among ibis species, both regionally and globally (Kopij, 2001; Venne & Frederick, 2013). Fires on the Okavango Delta's floodplains remove almost 80% of dead plant material (Rutz, 2004), which we hypothesize favors solely or predominantly ground-foraging species with a primarily invertivorous diet, such as those in FG1 and FG7.

# Interactions between fire and flood

The fact that model terms representing the interaction between a given inundation-related variable and the firerelated variable appear in every best-performing model (to varying degrees) signals the relative importance of this dynamic to wetland-dependent bird distribution in the Okavango Delta. The importance of flooding-fire interactions has already been established for other taxa or in other climates (Heim et al., 2019; Heinl et al., 2006). The strongest responses to the flooding-fire interaction emerged among FG2, FG4 (below-surface feeding nonwaders), FG6, and FG7. All four of these groups' responses peaked with interacting high (medium-term) inundation variability and recently documented fire hotspots and then again with the interaction between low inundation variability and temporally distant fires. Depending on the functional group, this might be

attributable to several factors. Organic matter mineralized through fires causes a resource pulse, which Heinl et al. (2004) suggested could contribute to the dominance of highly palatable perennial grasses after a fire on seasonal floodplains in the Okavango Delta. This process is, however, reliant on seasonal flooding to facilitate the grasses' growth in the longer term (Heinl et al., 2007). Such grasses' early successional appearance on these floodplains could therefore explain the effect on FG2, or at least its dominant species.

Pulse events are likely to interact differently as a driver of FG7 abundances, despite exerting a similar effect. Fire's ability to create a foraging habitat for more ground-based feeders, coupled with the high-flooding conditions' promotion of heterotrophy (in other words, prey availability), offers a theory as to why nonaquatic feeders responded positively to the interaction between recent fires and high (medium-term) inundation variability (Ramberg et al., 2010). This means that abundant prey items would be more easily accessible immediately after a fire event. This theory also supports the interactions' inverted effect as time since a given fire event increases, while high inundation variability is maintained. However, on this reasoning we would also expect these effects to have emerged in the top-performing model for FG1, so these interpretations should be treated with caution.

FG6 also exhibited a particularly positive response to the interplay between recent fires and highly variable inundation. For a predominantly piscivorous collection of birds, this potentially points to the suppressive effects of fire on fish production (especially on floodplains; Ramberg et al., 2010). This interpretation is reaffirmed by the interactive role of high inundation variability, which would have to facilitate the nutrient cycling needed to inhibit fish production (Mosepele et al., 2022).

# **Study limitations**

Our findings were limited by the fact that environmental variables were restricted to remotely sensed data. Fine-scale spatial variability description might benefit from other data sources to help identify its drivers. However, given the greater accessibility, availability, and spatial coverage of these data, remote sensing holds increasing promise for spatiotemporally extensive studies.

Habitat structure also certainly influenced functional group distributions, both for breeding and foraging compatibility, especially given the close link between vegetation structure and flooding regime (Murray-Hudson et al., 2014, 2015). Incorporating more detailed habitat information could thus improve insights into more localized trait-based exploitation of flood-prone environments by wetland-dependent birds.

Another limitation of our study is that the models did not account for nomadic or migratory behavior. The timing of our survey closely coincided with the return of migratory species, most of which were only observed in selected years and in low numbers, which should minimize any potential confounding effects.

Lorenzón et al. (2020) have also made a case for including non-wetland-dependent species in investigations of hydrological implications for bird assemblages in flood-pulsed river systems. Where possible, a more extensive time series would provide even more perspective. Subsequent studies would benefit from complementing this survey technique with other methods, such as point counts, which would also reduce observers' reliance on contiguous and seasonally aligning waterways, which are prone to channel migration (Yan et al., 2021), making it difficult to collect consistent long-term data; it would also enhance bird count certainty. Moreover, corresponding variables relating to other biota and abiotic environmental components (e.g., water chemistry, water depth) would help contextualize associated ecosystem processes.

# Significance of trait-based responses to changes in inundation and potential to use bird functional groups as indicators

Our findings not only agree with those of other studies, in that they demonstrated trait-based wetland-adapted avifaunal responses to varying water levels in flood-prone ecosystems (Almeida et al., 2017, 2018; Cumming et al., 2012; Francis et al., 2021; Lorenzón et al., 2017), but we also presented evidence of these responses based on landscape-wide dynamics. The longevity of dryland wetlands is reliant on continuous and periodic inundation in areas with low rainfall (Tooth & McCarthy, 2007). While periodically inundated floodplains fulfill a vital role in biogeochemical cycling, perennial inundation serves as a source to which seasonally flooded (productive) systems connect. Wetland-dependent birds are among the higherorder consumers driving cyclical processes between channels and floodplains.

Our models' predictive powers highlighted wetlanddependent birds' functional reliance on perennially flooded habitats in a flood-pulsed dryland wetland. By doing so, they also demonstrated the potential of contiguous bird monitoring regimes along a perennial channel system to gain insights into landscape-wide ecological processes in a dryland wetland. Our study further demonstrated the utility of remote sensing data in wetland ecology research (Arias et al., 2018; Molinari et al., 2022; Murray-Hudson et al., 2019). As large-scale data are further accumulated, our approach also presents an opportunity to eventually make relatively confident (albeit general) wide-ranging ecological inferences from remotely sensed data.

With the burgeoning impacts of climate change and freshwater resource extraction, perennial inundation in dryland wetlands is under threat, with changes in the frequency and size of pulse events, such as flooding and fire. The potential impacts of substantially altered or reduced flooding regimes on dryland river systems have already been documented (Capon, 2007; Leigh et al., 2010; Mitchell, 2013; Molinari et al., 2022). These persistent threats not only signal habitat loss to resident, nomadic, and migratory wetland-dependent birds but also the associated decline in ecosystem function that they provide. Our findings highlight the value and potential of longterm, large-scale monitoring of wetland-dependent birds in dryland wetlands as a predictive mechanism of ecosystem changes on a landscape scale. Using trait-based functional responses of a highly mobile, wetland-dependent taxon across perennial waters as a surrogate for wider ecosystem processes can certainly further our understanding of dryland wetland dynamics. However, coupled with remotely sensed data, this approach has also shown promise of providing an effective ecological monitoring tool that could help inform wetland management efforts, which are becoming increasingly relevant through the intensifying effects of corporate/industrial freshwater extraction/ pollution and climate change. These not only risk reliable water provision but also amplify other pulsed events like fire, with potentially detrimental consequences for the ecosystem. Being able to make landscape-wide ecological inferences is particularly useful for dryland wetlands that traverse political boundaries, which are often subjected to asymmetric management strategies.

#### **AUTHOR CONTRIBUTIONS**

Rutledge S. Boyes designed and led the field survey, while Frowin K. Becker, Heiko U. Wittmer, and Stephen Marsland helped conceptualize the research. Victoria Inman computed the remotely sensed inundation data. Frowin K. Becker conducted the data analysis and drafted the manuscript. All authors reviewed and offered critical contributions to various versions of this manuscript and were asked for approval before submission.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

All data (Becker et al., 2023) are available in Figshare at https://doi.org/10.6084/m9.figshare.20317185. Raw fire hotspot data were downloaded from the National Aeronautics and Space Administration's Fire Information for Resource Management System (FIRMS; https://firms.modaps.eosdis.nasa.gov/) by searching for "Okavango Delta" and adjusting the timeline (1 January 2013–31 December 2018). These data were cleaned and truncated and are available in that form within the Figshare repository.

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#### SUPPORTING INFORMATION

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