

Article

# Landscape-Level Associations of Wintering Waterbird Diversity and Abundance from Remotely Sensed Wetland Characteristics of Poyang Lake

Iryna Dronova <sup>1,\*</sup>, Steven R. Beissinger <sup>2</sup>, James W. Burnham <sup>3,4</sup> and Peng Gong <sup>2,5,6</sup>

<sup>1</sup> Department of Landscape Architecture & Environmental Planning, College of Environmental Design, University of California Berkeley, Berkeley, CA 94720-2000, USA

<sup>2</sup> Department of Environmental Science, Policy and Management, Division of Ecosystem Science, College of Natural Resources, University of California, Berkeley, CA 94720-3114, USA; beis@berkeley.edu (S.R.B.); penggong@tsinghua.edu.cn (P.G.)

<sup>3</sup> Department of Forest and Wildlife Ecology, College of Agriculture and Life Sciences, University of Wisconsin-Madison, Madison, WI 53706-1598, USA; burnham@wisc.edu

<sup>4</sup> The International Crane Foundation, Baraboo, WI 53913, USA

<sup>5</sup> Ministry of Education Key Laboratory for Earth System Modeling, Center for Earth System Science, Tsinghua University, Beijing 100084, China

<sup>6</sup> Poyang Lake Ecological Research Station for Environment and Health, Duchang 332600, China

\* Correspondence: idronova@berkeley.edu; Tel.: +1-510-642-2930

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**Abstract:** Poyang Lake, the largest freshwater wetland in China, provides critical habitat for wintering waterbirds from the East Asian Flyway; however, landscape drivers of non-uniform bird diversity and abundance are not yet well understood. Using a winter 2006 waterbird survey, we examined the relationships among metrics of bird community diversity and abundance and landscape characteristics of 51 wetland sub-lakes derived by an object-based classification of Landsat satellite data. Relative importance of predictors and their sets was assessed using information-theoretic model selection and the Akaike Information Criterion. Ordinary least squares regression models were diagnosed and corrected for spatial autocorrelation using spatial autoregressive lag and error models. The strongest and most consistent landscape predictors included Normalized Difference Vegetation Index for mudflat (negative effect) and emergent grassland (positive effect), total sub-lake area (positive effect), and proportion of submerged vegetation (negative effect). Significant spatial autocorrelation in linear regression was associated with local clustering of response and predictor variables, and should be further explored for selection of wetland sampling units and management of protected areas. Overall, results corroborate the utility of remote sensing to elucidate potential indicators of waterbird diversity that complement logistically challenging ground observations and offer new hypotheses on factors underlying community distributions.

**Keywords:** wetlands; lakes; remote sensing; waterbird; biodiversity; conservation; spatial autocorrelation; object-based image analysis; ecology; habitat

## 1. Introduction

More than 400 waterbird species, including long-distance migrants, critically depend on wintering habitat in wetlands of warm low-latitude regions, large extents of which have been lost to agriculture, residential sprawl and modifications to store or manage water resources in recent decades [1–8]. The United Nations has designated a number of conservation targets and wetlands of international

importance under the Ramsar Convention [9]. However, the understanding of specific factors behind non-uniform distributions and “hotspots” of bird diversity in wetlands is often limited by constrained site access, logistics and financial costs [10,11]. These challenges may hinder allocation of management, conservation and research targets within large wetlands and selection of meaningful habitat features in predictive models of bird population dynamics and diversity.

Recognition of these constraints has stimulated efforts to characterize wetland habitat properties relevant to landscape-scale bird distributions from cost-efficient geospatial and remote sensing data [12–18]. For instance, significant statistical associations of wetland bird species richness and spatial variables, such as wetland area, proportion of emergent wetland vegetation, or water depth, have been reported by studies in the Rainwater Basin and Prairie Pothole Region of the USA [17,19]. Similarly, a number of terrestrial studies found strong relationships between bird diversity and remote sensing indices of vegetation greenness, compositional heterogeneity, and structure based on both passive and active remote sensing [20–26]. However, few studies have used remote sensing in the analyses of broad-scale bird community patterns in large wetland regions with limited field access yet high concentrations of resident and migratory avifauna [7,8].

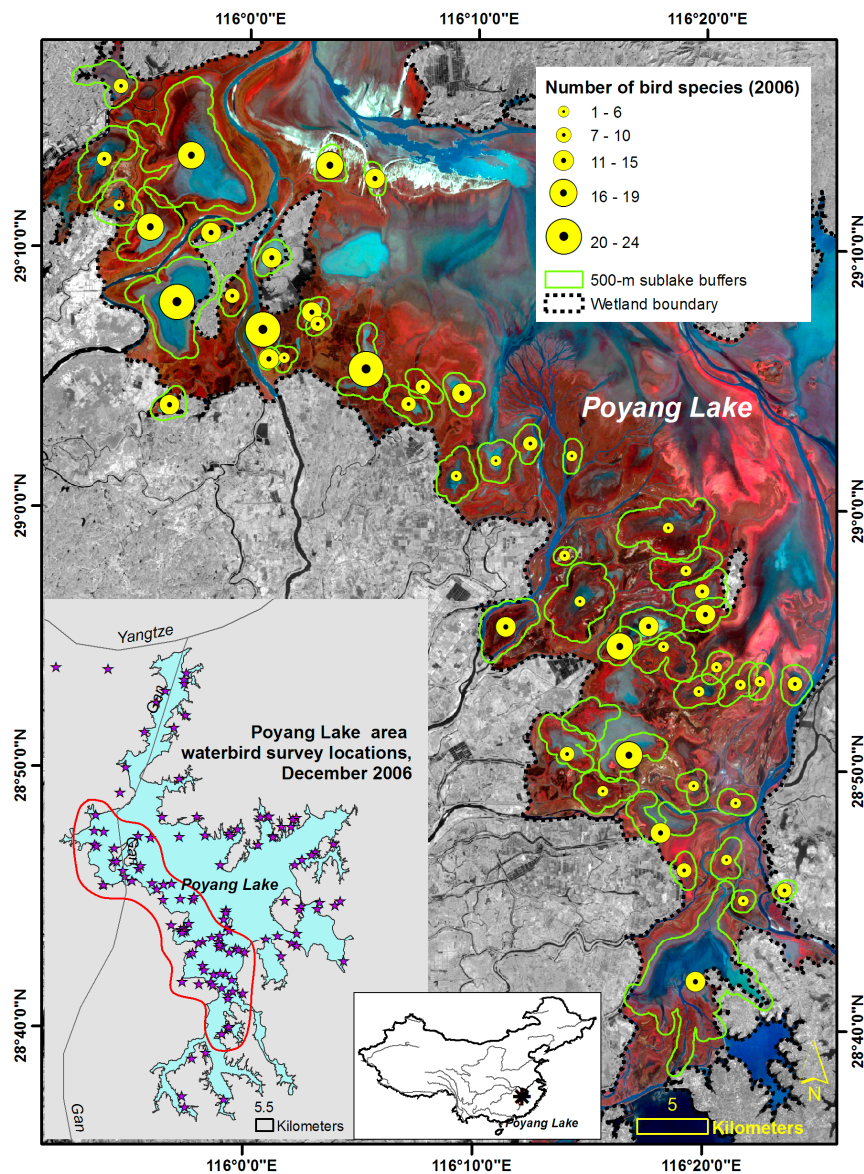
This limitation can be also attributed to known constraints of remote sensing and spatial analyses in wetlands, such as infamous “salt-and-pepper” noise arising from high spectral variation within individual patches of wetland cover types [10,16,27,28]. Novel object-based image analysis (OBIA) methods and machine learning image classification algorithms offer promise to enhance the quality of wetland cover mapping and interpretation, although these techniques are still relatively under-utilized [29–32]. Another caveat to spatial analyses of ecosystem and habitat properties is presented by potential spatial dependence (autocorrelation), which may violate the assumptions of independent and identically distributed errors in landscape models but in some cases indicate ecological processes such as dispersal or species interactions [33–39].

The goal of this study was to explore the variation in diversity and abundance of resident and migratory wintering waterbirds at Poyang Lake, the largest freshwater lake in China (Figure 1) and an internationally important wetland conservation site under the Ramsar convention since 1992 [9,40] using landscape characteristics derived from satellite remote sensing data. In the winter, this area hosts large numbers of resident and migratory waterbirds from the East Asian Flyway, including 11 endangered and six globally threatened species [41,42]. Most of them utilize the habitats within sub-lakes, or water bodies within the major wetland that become isolated during the low-water winter stage [43,44]. Of particular conservation concern are tuber-feeding waterbirds, including the critically endangered Siberian White Crane (*Leucogeranus leucogeranus*), which depend on multiple species of *Vallisneria*, a submerged aquatic macrophyte (SAM) [43,45].

Land use and climate change, novel aquaculture practices and hydrological control projects threaten the future ecological integrity of Poyang Lake wetlands and their long-term capacity to sustain wintering birds [1,7,8,45–50]. However, the understanding of factors behind spatial patterns of bird diversity and abundance is still limited [7,45,51,52], while primary habitat requirements have been studied mainly for specific species and foraging guilds [43,45,53]. Previous multi-year analyses of waterbird diversity and abundance have investigated their associations with basin-wide hydrological and climatic factors [8] and remotely sensed extents and heterogeneity of major habitat cover types [7]. These studies, however, were based on bird censuses from 10–12 spatial observation units [7,8], while whole-region monitoring has been limited by the high logistical cost of repeated basin-wide surveys in this large wetland [42,44,54]. These constraints call for further exploration of remote sensing’s potential to characterize habitat features related to diversity and abundance at spatial scales relevant to conservation and management of Poyang Lake protected areas.

To address this call, we examined the associations between several metrics of waterbird diversity and abundance based on a basin-wide ground survey in December 2006 and remotely sensed landscape characteristics of the sub-lake neighborhoods extracted by the object-based image analysis of the Landsat TM satellite data. Here we explored which landscape characteristics of the sub-lakes were

most consistently and strongly associated with the observed bird diversity and abundance patterns across the seasonally flooded wetland area and to what extent the detection and interpretation of these relationships was affected by spatial autocorrelation in waterbird and landscape variables and their statistical models.



**Figure 1.** Study area and waterbird survey in December 2006. The background images represent Landsat 5 TM scene as a color composite of bands 4 (near-infrared), 3 (red) and 2 (green) for the wetland area (RGB), and a grayscale image of band 4 for the surrounding mixed-cover landscape.

## 2. Materials and Methods

### 2.1. Study Area

Poyang Lake is located in the middle Yangtze River basin, Jiangxi Province, China ( $28^{\circ}25'N$ – $29^{\circ}45'N$ ,  $115^{\circ}48'E$ – $116^{\circ}44'E$ ; Figure 1). Its surface exhibits considerable year-round hydrological variation where water coverage at the highest summer flood stage in July–August can exceed  $4000\text{ km}^2$ , while in winter it reduces to less than  $1000\text{ km}^2$  [55,56] exposing rivers, channels and smaller sub-lakes. At these sub-lakes, waterbirds are often observed within 500 m or less of the water

boundary along the inundation gradient from water 0.5–5 m deep to mudflats and higher-elevation emergent grasslands [44,45]. Some of these sub-lakes have been important diversity hotspots in local nature reserves [43,44,54,57].

The immediate spatial neighborhoods of winter sub-lakes often have gentle slopes with slow change in elevation and belt-shaped zonation of emergent wetland cover types ranging from shallow water to mudflats to emergent grassland dominated by sedges (*Carex* spp.) and forbs [45,57,58]. Some of the submerged aquatic macrophyte species (e.g., *Vallisneria* spp. and *Stuckenia pectinata*) overwinter in the form of tubers buried in lake sediment. Although “invisible” to remote sensors, these tubers provide critical food resources to bird foragers from the tuber-feeding guild [40,43,45,59]. Some areas of Poyang Lake also retain photosynthetically active submerged and floating macrophytes from other taxa during the cool growing season [44,51]; however, the specific role of this vegetation in wintering waterbird habitat relationships remains unclear to date.

## 2.2. Waterbird Survey of 2006 and Dependent Variables

Our study used the data from the basin-wide point-count waterbird survey in 15–25 December 2006, obtained with permission from the State Key Lab of Remote Sensing Science (the Chinese Academy of Sciences, Beijing, China) who jointly organized it with the State Key Lab of Poyang Lake Ecology and Environment at Jiangxi Normal University, Nanchang, China, and local nature reserves [44,60]. The survey included 138 target locations representing permanent sub-lakes, water reservoirs near cities and selected vantage points at the shorelines of rivers and channels within the Poyang Lake area (Figure 1). Bird species identification and counts were performed by field technicians using binoculars and telescopes [42,60] and then reported as summaries for each observation location along with one, rarely two, geolocated GPS point(s) marking the primary spatial position of observers. For the purposes of this study, we focused on the data from 51 sub-lakes representing permanent water bodies in western, southwestern and southern part of the lake basin (Figure 1) that were part of the seasonally inundated wetland area. Because of the uncertainty in spatial position of observers relative to birds [60], the whole sub-lakes were used as the units of spatial analysis. It should be also acknowledged that the single-event 2006 bird survey represented only a phase in the wintering season and did not allow us to estimate the observation error or extrapolate results beyond this time frame. We further discuss the implications of this constraint in Section 4.3 below.

Our analysis specifically targeted resident and migratory Poyang Lake waterbirds from the orders of Podicipediformes, Pelecaniformes, Suliformes, Ciconiformes, Anseriformes, Gruiformes and Charadriiformes. Six major foraging guilds were defined among them based on the long-term Poyang Lake ecological research by the International Crane Foundation [40,45] and other studies in this region [7,8,43,44,53,59,61,62] and other wetlands [63]: (1) tuber feeding; (2) sedge/grass eating; (3) seed eating/dabbling; (4) benthic insect/larvae eating; (5) fish eating; and (6) zooplankton eating. Four size groups were also designated: (1) larger floating birds; (2) smaller floating birds; (3) large waders; and (4) small shorebirds. From the bird counts at 51 selected sub-lakes, we quantified dependent variables (Table 1) for the models of their relationships with remotely sensed wetland characteristics. These included four alpha-diversity indices (species richness, or the total number of species per sub-lake; Shannon index; number of foraging guilds and number of size groups), total number of waterbirds and the number of tuber-feeders. This latter guild was given special attention because it includes conservation targets of international importance with four out of five species that are threatened or endangered with recently reported declines in the study region [41,59].

Both abundance variables had non-normal distributions due to large number of small values, similar to other studies [7,8,18]. For the number of birds, natural logarithm transformation significantly improved the normality. However, the number of tuber-feeders had zero values at 12 sub-lakes. Thus, for the number of tuber-feeders, we applied and compared two different strategies: (1) statistical transformation of their counts using natural logarithm+1 for linear regression models to alleviate the skewness and compare results with models with other response variables; and (2) the alternative



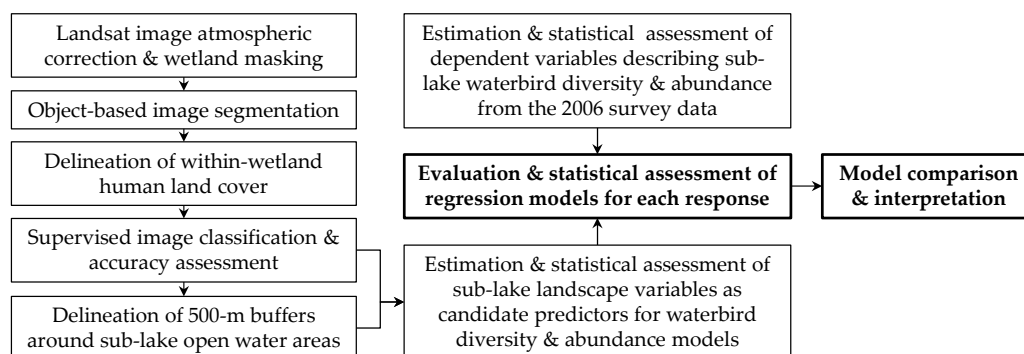
negative binomial regression modeling of the non-transformed variable to address the potential zero inflation (discussed in Section 2.4 below).

**Table 1.** Dependent (response) variables used in regression models and their basic descriptive statistics for 51 sub-lakes from December 2006 Poyang Lake survey.

Variable	Description	Min–Max	Mean (st. dev.)
Species richness	Number of waterbird species per sub-lake	2–23	9.1 (5.44)
Shannon index	Diversity index which accounts for both the number of species and evenness of their abundance calculated as $H' = -\sum_{i=1}^R p_i \ln p_i$ , where $p_i$ is the proportion of individuals from species $i$ in the whole dataset and $R$ is the total number of species in the dataset	0.2–2.03	1.1 (0.44)
Number of food guilds	The number of foraging guilds represented per sub-lake, out of 6 groups after [45]: tuber-feeding, sedge/grass-eating, seed eating/dabbling, benthic insect/larvae eating, fish eating and zooplankton eating birds	1–6	3.9 (1.38)
Number of size groups	The number of bird groups defined by foraging habit (wading versus floating/diving birds) and size (average body mass greater or less than 2 kg for floating birds, average body length greater or less than 0.8 m for waders)	1–4	3.2 (0.98)
Total waterbird abundance	Total number of waterbirds per sub-lake	17–94,658	7201 (16,262)
Abundance of tuber feeding birds	The number of birds from the tuber-feeding foraging guild including <i>Leucogeranus leucogeranus</i> , <i>Grus monacha</i> , <i>Grus vipio</i> , <i>Anser cygnoides</i> and <i>Cygnus columbianus</i>	0–46,395	2750 (8185)

### 2.3. Independent Variables Based on Remote Sensing Data

We characterized major wetland cover types and their landscape metrics for subsequent bird diversity and abundance analyses (Figure 2) using a terrain-geocorrected (Level 1T) Landsat 5 TM satellite image of 6 January 2007. Digital numbers from six 30-m spatial resolution bands representing visible (bands 1–3), near-infrared (band 4) and shortwave-infrared (bands 5 and 7) portions of the electromagnetic spectrum were corrected to radiance at the sensor using sensor-specific radiometric calibration coefficients [64] and then to ground surface reflectance using 6S algorithm [65,66]. We then isolated wetland area by digitizing its hydrological boundaries shaped by levees using a high-resolution basemap imagery layer in ArcGIS 10 (Esri Inc., Redlands, CA, USA). Basemap images in ArcGIS are compiled from high-resolution remote sensing data provided by Esri partners and streamlined directly into the ArcMap window [67].



**Figure 2.** Major steps in the study analysis of remote sensing and waterbird survey data.

We then segmented wetland area into small spectrally homogeneous groups of pixels, *i.e.*, objects, followed by their statistical classification into wetland cover types (Figure 2) using a multiresolution segmentation tool in eCognition 8.0 software (Trimble Inc., Sunnyvale, CA, USA) which allows for flexibility in the output object sizes. Due to the lack of prior information on wetland patch structure, segmentation parameters prioritized spectral band values in object generation, while shape and

compactness were kept at low values of 0.1 each. Following Reference [57], we used a value of 8 for the scale parameter which controls maximum level of heterogeneity and object size [68]. As a result, most primitive objects exceeded Landsat pixels, and their median size was ~19 pixels.

Prior to classification, we visually interpreted and labeled objects corresponding to residential and other human land cover within sub-lake neighborhoods using again the high-resolution basemap imagery in ArcGIS 10. Then, we classified wetland area into common cover types that were hypothesized to represent suitable and non-suitable habitat (Table 2): Open water, mudflat, sand, flooded vegetation, green emergent C3 grasses, senescent grasses and burned vegetation. For these classes, we assigned 222 objects for classification training and 300 separate objects for accuracy assessment using several sources of reference data from March 2006 to April 2008 (because no field assessments of wetland cover were performed at the time of the 2006 bird survey). Reference objects were selected to represent homogeneous regions of target cover types (Table 2) based on (1) their spatial overlap with transects and locations of several field surveys at Poyang Lake in March 2006, March 2007, December 2007, April 2008 where vegetation and other types were recorded along with field photographs of surveyed areas (performed by the State Key Lab of Remote Sensing Science (the Chinese Academy of Sciences, Beijing, China); and (2) visual interpretation of cover types from the reference high-resolution imagery from DigitalGlobe Worldview-1 and QuickBird satellites for November and December 2007, provided for a portion of the study area by the National Aeronautics and Space Administration (NASA) and The National Geospatial-Intelligence Agency (NGA) NextView program [69]. Classification was performed in open-source Weka 3.6.5 software (University of Waikato, Hamilton, New Zealand; [70]) using a supervised k-nearest neighbor algorithm. Object mean values of Landsat bands 3–5 and 7 and spectral indices representing normalized differences between bands 3 and 4, 2 and 4 and 2 and 5 were used as discriminating features. Classification accuracy was quantified as the agreement between reference classes of test objects and their respective mapped categories using confusion matrices.

**Table 2.** Poyang Lake wetland cover types used in satellite image classification.

Cover Type Name	Description
Water	Inundated areas with water coverage above the ground or vegetation surface: sub-lakes, channels, pools, rivers <i>etc.</i>
Mudflat	Exposed lake bottomland directly adjacent to the water body with sparse (<30%) or no plant cover
Emergent grassland	Green photosynthetically active emergent wetland vegetation dominated by C3 grasses and forbs
Flooded vegetation	Green photosynthetically active vegetation with “wet” spectral signal (significantly lower near- and short-wave-infrared range than emergent grasses); includes inundated emergent, floating and submerged aquatic macrophytes and their mixtures
Senescent grasses	Perennial vegetation that maintains senescent biomass during the winter, typically dominated by mixed warm-season C4-grasses and reeds that grow in higher-elevation sub-lake and channel periphery
Burned vegetation	Recently burned grassland with distinct dark soil/ash and little or no vegetation regrowth
Human land use	Areas of active human land use adjacent to Poyang Lake wetlands (residential, agriculture, extraction, <i>etc.</i> )

From the classification results, we selected open water and flooded vegetation together as proxies of the extent of inundated areas at the time of image acquisition. We then constructed 500-m buffer neighborhoods around these sub-lake areas in ArcGIS 10 (Figures 1 and 2) and within those estimated thirteen metrics subsequently used as candidate predictor variables in diversity and

abundance models (Table 3). These variables were informed by previous research at Poyang Lake and other wetlands [17,19,43,45,60] and selected so as to minimize both conceptual redundancy and statistical multi-collinearity. Several independent variables had highly skewed distributions that were corrected to improve normality using natural log transformation (total sub-lake area) and square root transformation (proportions of mudflat, emergent grassland and flooded vegetation).

**Table 3.** Independent variables used in regression models of Poyang Lake waterbird abundance and diversity, summarized for 500-m neighborhoods around sub-lakes within the natural wetland area.

Category	Name (Model Code)	Definition
Area	Total sub-lake unit area (area)	Total area of the sub-lake water body and its 500-m buffer neighborhood, m <sup>2</sup>
Prevalence of habitat cover types within sub-lake neighborhood	Percent mudflat (%mudflat)	Proportion of the area classified as mudflat within the sub-lake neighborhood
	Percent emergent vegetation (%emgrass)	Proportion of the area classified as emergent grassland within the sub-lake neighborhood
	Percent flooded vegetation (%floodveg)	Proportion of the area classified as flooded vegetation within the sub-lake neighborhood
Spectral greenness	Normalized Difference Vegetation Index (NDVI) of emergent grassland (ndvi emgrass)	Spectral index of vegetation greenness, here calculated as mean object-level NDVI from Landsat TM bands 3 (red) and 4 (near-infrared) within green emergent grass class for each sub-lake: $NDVI = (Band\ 4 - Band\ 3) / (Band\ 4 + Band\ 3)$
	Normalized Difference Vegetation Index (NDVI) of mudflat (ndvi mudflat)	Calculated using the same formula as above as mean of the objects within the mudflat class
Spectral heterogeneity of habitat cover types	Spectral heterogeneity of mudflat (stdev Red mud)	Standard deviation of the object-level mean values for Landsat TM band 3 (red) among the mudflat image objects
	Spectral heterogeneity of flooded vegetation (stdev Red floodveg)	Standard deviation of the object-level mean values for Landsat TM band 3 (red) among the flooded vegetation image objects
	Spectral heterogeneity of emergent vegetation (stdev Red emgrass)	Standard deviation of the object-level mean values for Landsat TM band 3 (red) among the emergent C3 grass image objects
Heterogeneity of primitive patch shapes within habitat cover types	Heterogeneity of shape index for mudflat (stdev SI mud)	Standard deviation of the shape index (perimeter of the image object divided by four times the square root of its area [66]) for primitive image objects classified as mudflat within the sub-lake neighborhood
	Heterogeneity of shape index for emergent vegetation (stdev SI emgrass)	Standard deviation of the shape index (perimeter of the image object divided by four times the square root of its area [66]) for primitive image objects classified as emergent grassland within the sub-lake neighborhood
Potential human disturbance within sub-lake neighborhood	Percent of burned vegetation area (%burnveg)	Proportion of the area classified as burnt vegetation within the sub-lake neighborhood
	Percent of human land use (%human LU)	Proportion of the area representing active human land use (residential or agriculture) within the sub-lake neighborhood

#### 2.4. Model Selection and Diagnostics for Spatial Autocorrelation

For each response variable (Table 1), we first constructed multivariate ordinary least squares (OLS) linear regression models with different sets of predictors in MATLAB R2012a software (MathWorks Inc., Natick, MA, USA). We then ranked these models using the Akaike Information Criterion corrected for the small sample size ( $AIC_c$ ) following [71]:

$$AIC_c = -2\ln L + 2k + \frac{2k(k+1)}{(n-k-1)}, \quad (1)$$

where  $\ln L$  is the model log-likelihood,  $k$  is the number of parameters to be estimated and  $n$  is the number of observations in the model. This approach was chosen to allow the relative comparison of models with different predictor sets, as well as OLS and spatial regression results for a given predictor combination. However, with 13 predictor variables, the number of their theoretically possible combinations becomes extremely large, and the risk of multi-collinearity increases as more predictors

are included in regression. For these reasons, we estimated regression parameters and  $AIC_c$  only for the models with 5 or fewer predictors, and for the final set of candidate models we considered only the models within 2  $AIC_c$  units from the minimum  $AIC_c$  [71]. To further account for the zero values in the number of tuber-feeders, we separately estimated a zero-inflated negative binomial regression in R (Version 3.2.4; R Development Core Team 2016, Vienna, Austria) with the package `pscl` (Version 1.4.9 [72,73]). This approach estimates a two-component negative binomial model for bird counts with the assumption that the data may include both “true” zero counts for the tuber-feeders, and “excess” zeros, e.g., sub-lakes that are never visited by this guild [73]. The output models were ranked using  $AIC_c$ , and selected predictor sets with the strongest support were compared to those in OLS results.

Next, we examined spatial dependence in response and predictor variables using Anselin’s local indicators for spatial association (LISA; [74]) in GeoDa spatial analysis software [75] and then tested for significant spatial autocorrelation in OLS regression. A matrix of spatial weights  $W$  was calculated based on Euclidean distances between sub-lakes and then used to perform Lagrange Multiplier (LM) tests for spatial dependence in OLS. When significant spatial autocorrelation was detected, we further estimated two maximum-likelihood linear spatial autoregressive models in GeoDa [75]. The first one was the spatial lag model, which accounts for a second-order spatial interaction between localities based on their proximity:

$$y = X\beta + \rho Wy + \varepsilon, \quad (2)$$

where  $\beta$  indicates coefficients for the predictor variables  $X$ ,  $\rho$  is the spatial autoregressive coefficient on the matrix of weights  $W$  applied to response values from spatial neighbors of each data point and  $\varepsilon$  is the random error term. The second form of spatial regression was the spatial error model which accounts for spatial autocorrelation in the model error structure:

$$y = X\beta + \lambda W\varepsilon + \varepsilon, \quad (3)$$

where  $\lambda$  is the spatial autoregressive coefficient for the error term. We then compared statistics for individual predictors and model  $AIC_c$  among OLS and spatial regression results.

### 3. Results

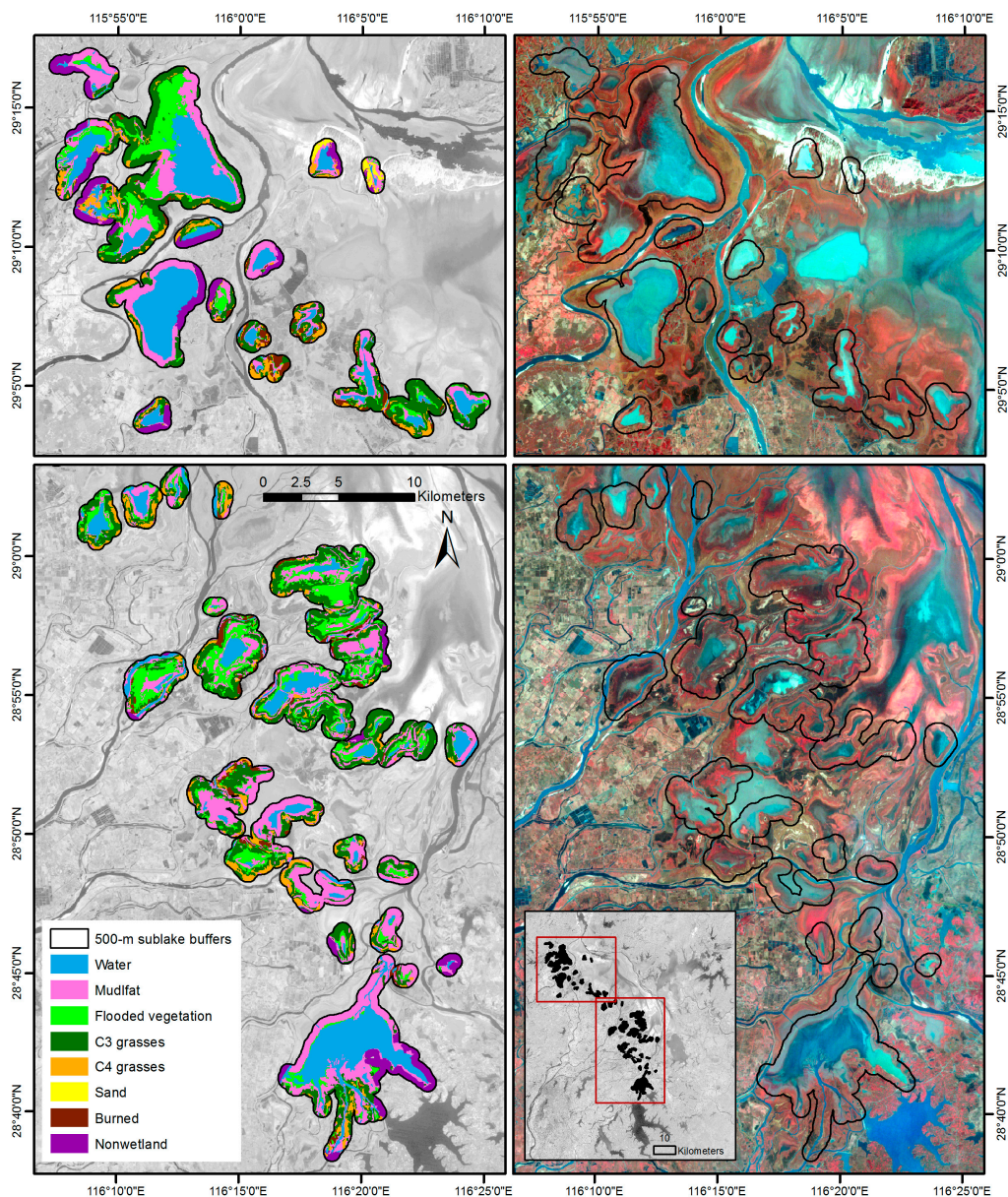
#### 3.1. Image Classification Results

The supervised classification of the Landsat image had the overall accuracy of 94.3% and kappa statistics value of 0.93 (Table 4). The confusions occurred between turbid shallow water and mudflat, flooded vegetation and mudflat or burned vegetation, and between emergent and senescent vegetation in mixed-cover areas, similar to other studies of this region [10,57,58]. Sand was detected in 15 sub-lakes, and only in three cases exceeded 2% of sub-lake area. Given limited presence of this class and its primary concentration near dunes in the upper northern part of the study region (Figure 3), sand metrics were not included in subsequent regression analysis.

**Table 4.** Confusion matrix for the object-based k-nearest neighbor classification of the study area.

Assigned Class:	Reference Class							User's Accuracy %
	Emergent Grassland	Mudflat	Senescent Grassland	Flooded Vegetation	Water	Burned Vegetation	Sand	
Overall Accuracy 94.3%, Kappa 0.934								
Emergent grassland	48		3			2		90.6
Mudflat		47	1	2				94.0
Senescent grassland	2		36					94.7
Flooded vegetation		1		37		3		90.2
Water		2		1	40			93.0
Burned vegetation						35		100
Sand							40	100
<b>Producer's accuracy,%</b>	96.0	94.0	90.0	92.5	100	87.5	100	



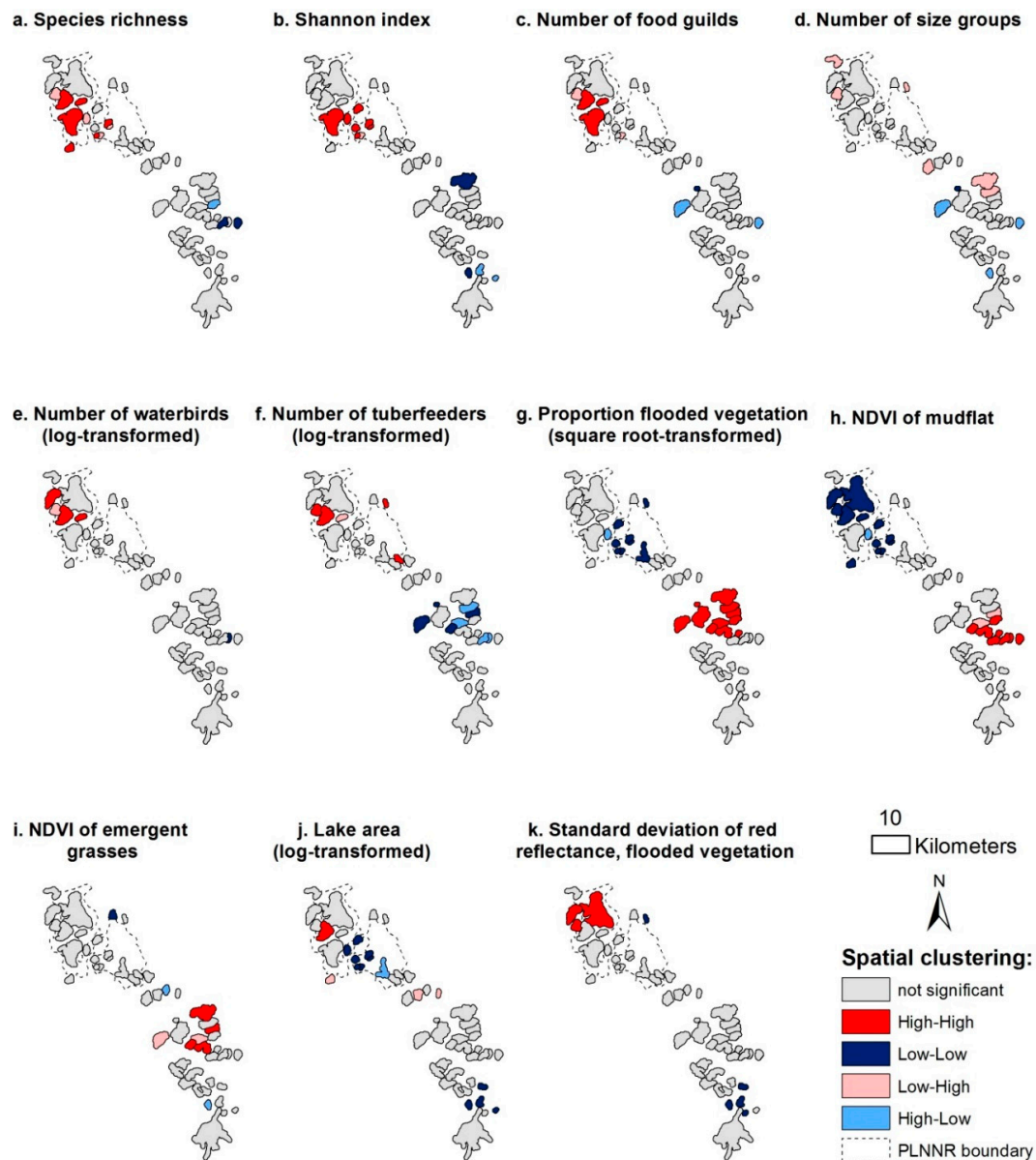


**Figure 3.** Major wetland cover types within sub-lakes included in December 2006 Poyang Lake waterbird surveys (left; overlaid on Landsat 5 TM grayscale image of band 4 (near-infrared) and characterized with supervised object-based k-nearest neighbor classification of the Landsat satellite image from 6 January 2007) and sub-lake 500-m neighborhood buffers (right; overlaid on Landsat 5 TM RGB composite of bands 4, 3 (red) and 2 (green)).

### 3.2. Spatial Patterns of Response and Predictor Variables

Total number of species varied from two to 23 among 51 sub-lakes (Table 1), and the proportional species turnover [76] was equal to 0.86, suggesting that an average sub-lake contained only ~14% of the overall species richness. Local spatial autocorrelation of response variables was not uniform across the landscape and concentrated in a few statistically significant “hotspots” (Figure 4). Species richness, Shannon index, number of food guilds, number of birds and number of tuber-feeders showed significant clustering of spatially close high values at several lakes within Poyang Lake National Nature Reserve (PLNNR; Figure 4a–c,e,f). For species richness, Shannon index and the number of tuber-feeders there were also clusters of low values and high-low associations in the southeastern part

of the study area (Figure 4a,b,f) within the Nanjishan National Nature Reserve. The number of size groups showed several low-high and high-low instances of negative spatial dependence, including those in PLNNR reserve (Figure 4d).



**Figure 4.** Sub-lake clusters of significant spatial dependence ( $p < 0.05$ ) determined using Local Indicators of Spatial Association (LISA) for (a) species richness; (b) Shannon index; (c) number of food guilds; (d) number of size groups; (e) number of waterbirds; (f) number of tuberfeeders; (g) proportion of flooded vegetation; (h) NDVI of mudflat; (i) NDVI of emergent grasses; (j) lake area; and (k) standard deviation of red reflectance for flooded vegetation. For positive spatial dependence, “High-High” indicates significant clustering of high values in each variable and “Low-Low”—significant clustering of low values. Negative spatial dependence is represented by “High-Low” and “Low-High” significant associations.

Among predictor variables, the proportion of flooded vegetation and mudflat NDVI had significant aggregations of high values in the southeastern portion of study area and clusters of low values in PLNNR (Figure 4g,h). The NDVI of emergent grasses also showed clusters of high values in the southeastern region and several clusters of high and low values (Figure 4i). Sub-lake area

had clusters of low values associated with small lake groupings in northeastern and southern portions of the study area (Figure 4j). Standard deviation of red reflectance of the flooded vegetation showed a cluster of high values in PLNNR and clusters of low values in other parts of the region (Figure 4k). Significant local clustering in both response and predictor variables based on these results indicated potential risk of violating assumptions of the ordinary linear regression due to spatial dependence.

### 3.3. Variable Selection in Regression Models

Relative importance of independent variables in the univariate OLS models varied among diversity and abundance metrics (Table 5). Spectral greenness (NDVI) of mudflat with a negative effect was consistently among the strongest predictors, while other important variables included proportion of flooded vegetation with negative effect, for the numbers of food guilds and size groups—total sub-lake area with positive effect, and for species richness and Shannon index—spectral heterogeneity of mudflat or flooded vegetation, respectively (Table 5). Combinations of 2–3 of these variables were also frequently included in the lowest AIC<sub>c</sub> multivariate models for each response variable (Table 6). However, none of the univariate models in Table 5 was within 2 AIC<sub>c</sub> units from the minimum-AIC<sub>c</sub> multivariate models in Table 6.

**Table 5.** Relative importance of independent variables with  $p$ -value > 0.05 in univariate ordinary least squares (OLS) regression models of diversity and abundance response variables, sorted by Akaike Information Criterion (AIC<sub>c</sub>) in ascending order. The AIC<sub>c</sub> values of the intercept-only models are provided as reference.

Dependent Variable:		Species Richness		Shannon Index		Number of Food Guilds		
Independent Variable	R <sup>2</sup>	AIC <sub>c</sub>	Independent Variable	R <sup>2</sup>	AIC <sub>c</sub>	Independent Variable	R <sup>2</sup>	AIC <sub>c</sub>
ndvi mudflat	0.35	303.2	ndvi mudflat	0.15	64.1	ndvi mudflat	0.21	178.5
Sqrt (%floodveg)	0.21	313.4	Sqrt (%floodveg)	0.12	65.5	Sqrt (%floodveg)	0.12	184.1
Stdev Red mud	0.11	319.3	Stdev Red floodveg	0.08	67.9	Ln(area)	0.08	186.1
Intercept-only	0.00	322.7	Intercept-only	0.00	69.81	Intercept-only	0.00	188.3
Dependent Variable:		Number of Size Groups		Ln (Number of Birds)		Ln (Number of Tuber Feeding Birds + 1)		
Independent Variable	R <sup>2</sup>	AIC <sub>c</sub>	Independent Variable	R <sup>2</sup>	AIC <sub>c</sub>	Independent Variable	R <sup>2</sup>	AIC <sub>c</sub>
ndvi mudflat	0.15	149.2	Ln(area)	0.2	216.0	ndvi mudflat	0.09	267.3
ndvi emgrass	0.09	152.4	ndvi mudflat	0.13	220.4	Sqrt (%floodveg)	0.08	267.4
Ln (area)	0.08	153.2	Intercept-only	0.00	225.2	Intercept-only	0.00	269.6
Intercept-only	0.00	155.2						

Multivariate models within 2 units from the lowest-AIC<sub>c</sub> outcome included three to eight candidate sets for a given response variable (Tables 6 and 7). These frequently included sub-lake area with positive effect and mudflat NDVI and proportion of flooded vegetation with negative effects (Table 6). The NDVI of emergent grasses with positive effect was also included in OLS models for all dependent variables except the number of tuber-feeders (Table 6). Other predictors in the highest-support multivariate models differed among response variables and included spectral heterogeneity of flooded vegetation with positive effect, proportions of human land use with positive effect and burned vegetation with negative effect, and for abundance response variables—also, object shape heterogeneity of emergent grassland with negative effect (Table 6). Predictors selected by the highest-rank zero-inflated negative binomial models for the number of tuber-feeders (Table 7) were consistent with the OLS results (Table 6), including sub-lake area and NDVI of emergent grassland with positive effects and object shape heterogeneity of emergent grassland, proportion of burned vegetation, NDVI of mudflat, and proportion of flooded vegetation with negative effects in the count model component. The latter two predictors were also selected in the zero-inflated model component with positive effects (Table 7).



**Table 6.** Multivariate ordinary least squares (OLS) and spatial regression models for waterbird diversity and abundance response variables within 2 units of AIC<sub>c</sub> from the lowest AIC<sub>c</sub> OLS model.

Models	R <sup>2</sup> OLS	AIC <sub>c</sub> OLS	AIC <sub>c</sub> Lag	AIC <sub>c</sub> Error	Akaike Weight
<b>Dependent Variable: Species Richness</b>					
Ln(area) – Sqrt(%floodveg) + ndvi emgrass – ndvi mudflat – stdev SI emgrass	0.54	294.38	297.17	291.54	0.60
–Sqrt(%floodveg) + ndvi emgrass – ndvi mudflat – stdev SI emgrass	0.50	295.94	298.60	293.92	
–Sqrt(%floodveg) + ndvi emgrass – ndvi mudflat – stdev SI emgrass + stdev Red emgrass	0.52	296.15	298.83	292.34	0.40
<b>Dependent Variable: Shannon Index</b>					
–Sqrt(%floodveg) + ndvi emgrass + stdev Red floodveg + stdev Red emgrass	0.40	52.69 *			0.27
–Sqrt(%floodveg) + ndvi emgrass + stdev Red floodveg	0.37	52.76 *			0.26
Ln(area) – Sqrt(%floodveg) + ndvi emgrass + stdev Red floodveg	0.39	53.01 *			0.23
Ln(area) – Sqrt(%floodveg) + ndvi emgrass + stdev Red floodveg + stdev Red emgrass	0.42	53.90 *			0.15
–Sqrt(%floodveg) + ndvi emgrass + stdev Red floodveg + stdev Red emgrass – ndvi mudflat	0.41	54.58 *			0.10
<b>Dependent Variable: Number Of Food Guilds</b>					
Ln(area) – Sqrt(%floodveg) + ndvi emgrass	0.38	169.73	170.45	172.24	0.35
Ln(area) – Sqrt(%floodveg) + ndvi emgrass – ndvi mudflat	0.41	170.23 *			0.4
Ln(area) – Sqrt(%floodveg) + ndvi emgrass – %emgrass	0.41	170.29	171.18	172.96	0.25
Ln(area) – Sqrt(%floodveg) + ndvi emgrass + %human LU	0.39	171.55	172.72	174.24	
Ln(area) – Sqrt(%floodveg) + ndvi emgrass – stdev SI emgrass	0.39	171.73	172.55	174.42	
<b>Dependent Variable: Number of Size Groups</b>					
Ln(area) – Sqrt(%floodveg) + ndvi emgrass	0.33	140.55 *			0.25
Ln(area) – Sqrt(%floodveg) + ndvi emgrass + %human LU	0.35	141.59 *			0.15
Ln(area) – Sqrt(%floodveg) + ndvi emgrass – ndvi mudflat	0.35	141.71 *			0.14
Ln(area) – Sqrt(%floodveg) + ndvi emgrass – %emgrass	0.35	141.72 *			0.14
Ln(area) – Sqrt(%floodveg) + ndvi emgrass – %burnveg	0.35	141.89 *			0.13
Ln(area) – Sqrt(%floodveg) + ndvi emgrass – %mudflat	0.34	142.41 *			0.10
Ln(area) – Sqrt(%floodveg) + ndvi emgrass + stdev Red floodveg	0.34	142.45 *			0.10
<b>Dependent Variable: Natural Log of the Total Number of Birds</b>					
Ln(area) + ndvi emgrass – ndvi mudflat – stdev SI emgrass	0.4	207.90	209.62	210.56	0.23
Ln(area) – ndvi mudflat – stdev SI emgrass	0.35	209.19 *			0.44
Ln(area) + ndvi emgrass – ndvi mudflat – stdev SI emgrass – %burnveg	0.41	209.24	211.47	211.59	
Ln(area) – ndvi mudflat – stdev SI emgrass – %burnveg	0.38	209.83 *			0.33
Ln(area) + ndvi emgrass – ndvi mudflat – stdev SI emgrass – Sqrt(%floodveg)	0.41	209.84	211.55	212.63	
<b>Dependent Variable: (Natural Log + 1) of the Number of Tuber Feeding Birds</b>					
Ln(area) – Sqrt(%floodveg)	0.16	264.41	263.87	265.17	0.36
Ln(area) – Sqrt(%floodveg) – stdev SI emgrass	0.19	264.79	264.56	266.11	0.22
– ndvi mudflat – stdev SI emgrass	0.14	265.19	264.54	265.61	0.28
Ln(area) – Sqrt(%floodveg) – %burnveg	0.17	266.15	266.03	267.45	
Ln(area) – ndvi mudflat – stdev SI emgrass	0.17	266.19	265.51	266.97	0.14
– ndvi mudflat	0.09	266.25 *			
%emgrass – ndvi mudflat – stdev SI emgrass	0.17	266.31 *			
– Sqrt(%floodveg)	0.08	266.39 *			

\* Spatial autocorrelation diagnostics not significant with *p*-value > 0.05.



Notably, the strongest multivariate models for different response variables often included similar predictors. For instance, sub-lake area, proportion of flooded vegetation and NDVI of emergent grassland were often selected together and formed the key component of all lowest AIC<sub>c</sub> models for number of food guilds and number of size groups (Table 6). In the models for species richness and two abundance metrics, NDVI of mudflat was often included together with heterogeneity of object shape index for emergent grasses (Tables 6 and 7). The interactions among predictors were also tested; however, most of them appeared to be not significant and did not contribute explanatory power comparable to the best-fit multivariate sets in Table 6.

**Table 7.** Predictors selected by the highest-rank zero-inflated negative binomial regression models for the number of tuber-feeding birds within 2 units of AIC<sub>c</sub> from the lowest AIC<sub>c</sub> model.

Count Model	Zero-Inflation Model	AIC <sub>c</sub>	Akaike Weight
Ln(area) – stdev SI emgrass	ndvi mudflat + Sqrt(%floodveg)	661.4	0.28
Ln(area) – stdev SI emgrass	Sqrt(%floodveg)	661.5	0.27
Ln(area) – stdev SI emgrass – Sqrt(%floodveg)	Sqrt(%floodveg)	663.0	0.13
Ln(area) – stdev SI emgrass – Sqrt(%floodveg)	ndvi mudflat + Sqrt(%floodveg)	663.3	0.11
Ln(area) – stdev SI emgrass – ndvi mudflat	Sqrt(%floodveg)	663.3	0.11
ndvi emgrass – ndvi mudflat – %burnveg	Sqrt(%floodveg)	663.3	0.11

### 3.4. Spatial Autocorrelation in Linear Regression Models

Significant spatial autocorrelation was detected in the OLS models for species richness, number of food guilds and two abundance variables (Table 6). Spatial regression successfully corrected this effect in most cases as indicated by GeoDa diagnostics of these models; however, goodness-of-fit was only marginally affected. Most of the changes in AIC<sub>c</sub> with spatial regression were within 2 units from a corresponding OLS model (Table 6), in part because both spatial models estimate one additional parameter relative to OLS, which penalized their AIC<sub>c</sub> values.

For species richness, spatial error model had stronger support than spatial lag model when significant spatial autocorrelation was detected (Table 6), and the lambda coefficient in spatial error model was significant with  $p$ -value < 0.05. For the number of food guilds and the number of birds, spatial lag model had higher support than spatial error regression (Table 6) in case of significant spatial dependence in OLS. Applying the lag model also slightly changed model ranks and reduced the number of candidate models within 2 units of AIC<sub>c</sub> from the minimum (Table 6). For the number of tuber-feeders, spatial lag models had slightly lower AIC<sub>c</sub> than corresponding spatial error models (Table 6). However, the latter models for this response variable no longer had significant spatial dependence for weight matrix ( $p$ -values > 0.05). For the number of size groups and Shannon index, LM tests in GeoDa did not detect significant spatial dependence in favor of spatial regression.

## 4. Discussion

### 4.1. Remotely Sensed Indicators of Poyang Lake Bird Diversity and Abundance

The degree to which spatial and temporal biodiversity patterns can be interpreted with indirect but cost-effective geospatial habitat proxies is an important pre-requisite for comprehensive landscape-scale monitoring of vulnerable ecosystems globally. Our analysis highlighted several landscape variables associated with waterbird diversity and abundance at Poyang Lake, China based on the remotely sensed characteristics of their wintering habitat from Landsat satellite data. In particular, statistical importance of sub-lake open water area was consistent with evidence from other wetland regions [12,13,17,77,78] and the significance of shallow water extent in waterbird abundance models in a previous Poyang Lake study [7]. This outcome likely represented the effect of lake size on the amount and potential diversity of food resources and foraging space.

Strong negative effect of mudflat NDVI on all response variables indicated the importance of mudflats with lower green vegetation cover and/or wetter surface. Mudflats with such properties may represent lake beds with more recent post-flood exposure [10,51] that contain aquatic invertebrates,

vegetation seeds, propagules and tubers of the summer-season aquatic macrophytes [40,43] and, thus, support birds of different size and foraging preferences. The size of mudflat was previously reported to positively contribute to bird abundance, and negatively—to species richness based on the study of 10 Poyang Lake sub-lakes [7]; however, in our models the proportion of mudflat area was not as important. The latter result may indicate potential availability of unoccupied wintering habitat, with sub-lake environments providing more suitable territories and resources than current bird populations could utilize.

Positive association of emergent grassland NDVI with bird diversity and abundance was consistent with previous terrestrial studies [14,20,24,37] and a recent analysis of selected waterbird species' habitat across Yangtze River wetlands [12]. These relationships may be attributed to potential correlations between NDVI and plant density, biomass and foliar nutrient content [79,80], which play important role in habitat quality [53,62]. At Poyang Lake, green sedges provide a critical food resource to *Anatidae* of the grass-eating guild, which forage in large numbers [12,45,49,53,60] and contribute to both bird diversity and abundance at sub-lakes with this vegetation type. However, relative size of emergent grassland was not among the main predictors, suggesting, again, that the available grassland habitat could exceed the demand of surveyed bird populations.

The importance of metrics related to variation in spectral and shape properties within grasslands and flooded vegetation was consistent with the expectation that more heterogeneous habitats may favor diverse avian communities and foraging opportunities [7,13,21,26,81]. A previous study of Poyang Lake bird diversity and abundance from 10 sub-lakes [7] reported the importance of the number of wet meadows and a form of shape index for waterbodies that were also related to habitat complexity. While specific ecological roles of heterogeneity should be investigated in the future, this collective evidence suggests that landscape complexity of wetland habitats should be considered in the analyses of diversity and abundance in addition to presence and extent of the relevant cover types. Estimation of heterogeneity metrics may especially benefit from remote sensing due to comprehensive spatial coverage of limited-access wetlands.

Significant negative correlation of most diversity and abundance variables with the proportion of flooded vegetation raises a question on what features make the sub-lakes *less* conducive to high diversity and abundance [60]. Potential ecological benefits of aquatic macrophytes growing in winter to waterbirds are less well understood at Poyang Lake than the importance of emergent grasses [49,53] or tubers of the warm-season aquatic plants [43,45]. Flooded vegetation types that are not preferential to birds or compete with their primary food species may indicate sub-lake differences in habitat quality, which may be important in light of reported declines in tuber-producing species along central Yangtze River [1,59,82,83]. Higher proportion of flooded vegetation could also indirectly signal other habitat characteristics; for instance, shallower water column allowing for greater abundance of macrophytes may restrict activities of diving and swimming species.

Although proportions of cover types directly associated with potential human disturbance within lake neighborhoods were not frequently associated with response variables, similar to evidence from other wetlands [18], we cannot rule out the potential effects of human disturbance on bird distributions and statistical importance of other variables. For instance, larger sub-lakes may provide better opportunities to avoid human presence, while higher greenness of some emergent grasslands may be driven by lower grazing pressure by domestic livestock due to limited wetland access. A variety of human-driven stressors at Poyang Lake, such as poaching, fishing, and livestock herding [5,43,49], may not be captured with remote sensing data alone. Hence, future work should incorporate the information on roads, elevation, and soil characteristics to more explicitly address the effect of human activities on bird spatial distribution and behavior.

Our results also show that sets of predictors describing complementary habitat features may be more useful in models of diversity and abundance than single variables. Consistent inclusion of several predictors in the lowest AIC<sub>c</sub> models (Table 6) suggests that not only their individual importance, but also their synergy could elucidate conditions favoring certain diversity levels. Collectively, results

indicate that bird community diversity and abundance were on average higher in larger sub-lakes with relatively small but heterogeneous component of flooded vegetation, non-vegetated mudflat and green emergent grassland with more uniform patches. This description matches several spatially close lakes that have been previously reported as diversity hotspots [42,43,45,54]. In contrast, smaller sub-lakes with more flooded vegetation in winter and the lack of bare mudflat were associated with lower diversity and abundance and exhibited spatial clustering with respect to these two characteristics. However, the latter conditions should not be immediately interpreted as “non-desirable” for wetland management, since theoretically they might be critical for selected bird species or their diet components, which should be investigated in the future.

#### 4.2. Spatial Autocorrelation in Diversity and Abundance Models

Significant spatial autocorrelation detected in multiple models with high support presents an important caveat for landscape analyses of bird diversity and abundance due to the risk of violating key assumptions of linear regression. Our results suggest that significant spatial autocorrelation in selected models could arise both from model specification and from the underlying spatial patterns in landscape variables (Figure 4). Specifically, higher effectiveness of spatial error models at correcting for spatial autocorrelation for species richness likely reflected the absence of important but spatially structured variables [84], such as the availability of tubers from warm-season summer aquatic plants [43] that were not sampled in the 2006 bird survey. The importance of spatial error models may also question the utility of sub-lake units to represent spatial patterns in diversity, particularly among adjacent water bodies which may be utilized by the same bird flocks more frequently and thus function as a single landscape unit in representing bird communities (Figure 4).

At the same time, stronger support for spatial lag models for the number of food guilds, the number of birds and the number of tuberfeeders suggests potential importance of yet unknown second-order spatial interactions [34,39] among sub-lakes that should be studied further. For instance, moderate intra-specific or intra-guild competition for resources and foraging space may be hypothesized to force large groups of birds to disperse over spatially close sub-lakes, producing similar community composition and autocorrelated bird counts. Alternatively, spatial autocorrelation in food resources caused by distance-sensitive dispersal of aquatic vegetation, fish and invertebrates could make close sub-lakes attractive to similar bird species and foraging guilds [18]. Location of significant response and predictor clusters within natural reserve territories also suggest that reserve management and restriction of human activities could play a role in these interactions and the overall habitat suitability for avifauna.

#### 4.3. Uncertainties in Models and Study Limitations

Several limitations of this study should be considered in the interpretation and generalization of the findings. A particularly important constraint was the timing of 2006 bird survey which represented only a short-term portion of waterbird distributions during the wintering season. From these data alone, we could not estimate observation error or assess the dynamics of sub-lake habitat use by different species and of the wetland landscape itself. Although major clusters of bird diversity in these data were generally consistent with reports from other years [44,54], one-time surveys make it problematic to verify whether bird distribution displayed their “typical” spatial pattern of the winter season or had been affected by a temporary “aggregate shock” e.g., due to prior burning of reeds across the wetland in 2006. Unfortunately, most of the basin-wide Poyang Lake surveys to date has been conducted as a one-time effort per winter, with different method of observation and timing within the season, which limits the possibility of their comparisons and remains an important challenge for monitoring programs [42,44,54].

The unexplained variation in regressions also suggests that useful predictors could be missing from the model structure. Water level may be such a key missing factor which often determines spatial location of waterbirds within the study area and access to food resources [8,43,45]; however, spatially

explicit water level data have not been monitored at the sub-lake scale in the Poyang Lake region. Finally, study results could be affected by more general constraints of remote sensing analyses in wetlands, such as heterogeneity of wetland surface as a challenge to classification accuracy that may be partially addressed by OBIA [29,57,85] and relatively coarse resolution of 30-m Landsat data obscuring local patterns of vegetation composition and micro-topography [57].

#### 4.4. Implications for Wetland Management and Conservation

Our results corroborate the utility of remote sensing to provide cost-effective, landscape-scale habitat variables to complement ground observations and ultimately inform monitoring, management and conservation in vulnerable wetland regions such as Poyang Lake [1,3,12,49,59,61]. In particular, non-vegetated seasonal mudflat and shallow water interfaces with low spectral greenness appear to be important potential targets for these efforts. At Poyang Lake and other periodically inundated wetlands globally [13,77,86], these habitat components may change their spatial position throughout the low water winter season due to fluctuations in adjacent water bodies and spread of emergent grasses [10,51]. Although with the one-time 2006 survey it was not possible to examine whether birds had been “tracking” mudflats, a survey later in winter season of 2009 reported higher waterbird aggregations close to Poyang Lake center [42] where mudflats are expected to become flood-free later than in peripheral sub-lakes [51]. Being directly adjacent to water bodies, mudflat habitats and hence their supported avian groups may be particularly vulnerable to hydrological changes caused by shifts in climate and new water control structures [45,47]. Thus, future management and projections of waterbird habitat should consider pre-allocating for potential redistributions of these cover types throughout the winter season.

Importantly, the “snapshot” patterns of bird distributions and habitat properties from individual surveys and remote sensing images are shaped by seasonal and inter-annual ecological processes and interactions underlying the distribution of foraging space, resources and risk factors [7,8,18,40,43]. Thus, to better understand the effects of selected habitat predictors on bird diversity and abundance, their associations need to be further investigated in the broader spatio-temporal context of wetland dynamics, which can also be greatly facilitated by remote sensing. For instance, seasonal transitions of Poyang Lake habitats may be captured by multi-date remote sensing analyses as “dynamic cover type” analyses of wetland zones with similar patterns of change within annual flood cycles [51,52,58] and then coupled with seasonally repeated waterbird surveys [7,8]. Such analyses are urgently needed at the whole-wetland scale given recent declines in several important waterbird species along the Yangtze River [49] and threats to wetland hydro-ecological regimes from the water control projects [8,45,47,48].

Efforts to improve the frequency of waterbird surveys and incorporate habitat dynamics into the analyses of diversity and abundance may also benefit from complementary remote sensing technology. Near-surface wireless acoustic sensors, phenocam photography and uninhabited aerial vehicle surveys may be used to provide local observations of both bird communities and landscape properties at high spatial resolution and temporal frequency. These datasets may be further combined with the analyses of optical and active remote sensing (e.g., radar) images [51] to fill the gaps in their time series, provide local reference information on limited-access sites and ultimately inform selection and validation of wetland biodiversity and habitat models.

## 5. Conclusions

Remote sensing offers important strategies to characterize landscape ecosystems and habitats in large wetland regions with constrained field access and limited ecological data. This capacity is critical for understanding the habitat utilization and non-uniform patterns of bird community diversity and abundance that are of high interest to conservation, management and adaptation to future environmental changes. This study investigated spatial relationships among several metrics of waterbird diversity and abundance and remotely sensed characteristics of their wetland habitat at 51 sub-lakes within the Poyang Lake basin, one of the largest Ramsar protected biodiversity hotspots



in Southeast Asia. Several landscape variables from Landsat satellite data were strongly associated with bird community metrics, including sub-lake area and spectral greenness (NDVI) of emergent grassland with positive effect and the proportion of flooded vegetation and NDVI of mudflats with negative effect. These associations elucidate the importance of lake size and specific wetland habitat features along the local inundation gradients in explaining bird diversity and abundance patterns beyond species- or guild-specific analyses alone.

Our results also revealed significant spatial dependence in some of the habitat variables and bird diversity and abundance metrics, as well as in their regression models. This spatial autocorrelation leads to violation of linear regression assumptions and points to shortcomings of the model specification, such as the lack of potentially important predictors related to water depth and food resources that have not been yet characterized at the whole-basin scale. At the same time, significant local clustering of both waterbird and landscape variables and stronger support for spatial lag models in some instances suggest that more complex ecological connectivity and second-order spatial interactions may exist among individual sub-lakes and ultimately contribute to the observed bird distributions. This evidence calls for more in-depth future investigations of the second-order spatial interactions among the waterbird community metrics and sub-lake characteristics, as well as for alternative testing of sub-lake aggregations as spatial units of bird diversity, abundance and habitat analyses. Association of detected clusters with local nature reserve territories further supports the relevance of waterbird community analyses using remote sensing-based habitat descriptors to conservation and management at Poyang Lake. To expand the cost-effective potential of remote sensing and improve temporal contiguity of bird and habitat surveying, future efforts should take advantage of complementary sensors including near-surface platforms such as wireless sensor and *in situ* phenological observations.

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## Abbreviations

The following abbreviations are used in this manuscript:

MDPI	Multidisciplinary Digital Publishing Institute
DOAJ	Directory of open access journals
NDVI	Normalized Difference Vegetation Index
OBIA	Object-based image analysis
AIC	Akaike Information Criterion
PLNNR	Poyang Lake National Nature Reserve
ICF	International Crane Foundation
OLS	Ordinary least squares regression
LISA	Local indicators of spatial autocorrelation

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