

Hierarchy of the factors influencing the broad-scale waterbirds functional diversity gradients in temperate China

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Abstract

Geographical gradients in species diversity have long fascinated biogeographers and ecologists. However, the extent and generality of the positive/negative effects of the important factors governing functional diversity (FD) patterns are still debated, especially for the freshwater domain. We examined lake productivity and functional richness (FRic) of waterbirds sampled from 35 lakes and reservoirs in northern China with a geographic coverage of over 5 million km². We used structural equation modelling (SEM) to explore the causal relationships between geographic position, climate, lake productivity and waterbirds FRic. We found unambiguous altitudinal and longitudinal gradients in lake productivity and waterbirds FD, which were strongly mediated by local environmental factors. Specifically, we found 1) lake productivity increased northeast but decreased with altitude, and the observed gradients were driven by climate and nutrient availability, with 93% of variation explained in the individual SEM; 2) waterbirds FD showed similar geographic and elevational gradients; the environmental factors which had direct and/or indirect effects on these geographic and elevational gradients included climate, lake productivity and morphology, which collectively explained more than 56% of the variation in waterbirds FD; and 3) a significant ($P = 0.029$) causality between lake productivity and waterbirds FD was confirmed. Nevertheless, the causality link was relatively weak in comparison with climate and lake area (standardized path coefficient was 0.65, 0.21, and 0.17 for climate, area, and productivity, respectively). Through articulating the dominant causality paths, our results could contribute to the mechanistic explanations underlying the observed broad-scale biodiversity gradients.

Introduction

One of the oldest and most important macroecology patterns is the spatial variability in biodiversity over broad geographical extents (Field et al., 2009; Hawkins, 2001; Stein, Gerstner, & Kreft, 2014), an appropriate knowledge of which is an essential key to guarantee the provision of multiple ecosystem services (Benedetti et al., 2020). The planet Earth shows striking gradients in the diversity of plants and animals, from high biodiversity in the tropics to low biodiversity in polar and high-mountain regions (Gaston, 2000; Rosenzweig, 1995; Whittaker, Nogues-Bravo, & Araujo, 2007; Willig, Kaufman, & Stevens, 2003). Due to the alarming rate of biodiversity loss in the last decades caused by anthropogenic interruption (Prescott et al., 2016; Waide et al., 1999), a modern resurgence of interests in taxonomic diversity patterns is likely to contribute important insights for developing a more general theory of species diversity (Castro-Insua, Gómez-Rodríguez, & Baselga, 2016). Studies in the past decades has documented the broad-scale spatial patterns of species diversity, and explored the mechanisms for such patterns, leading to conceptual insight on the biogeographical variation of species diversity (Devictor et al., 2010; Field et al., 2009; Gaston, 2000). For example, diversity is often highest at intermediate levels of ecosystem productivity (Grime, 1973; Mittelbach et al., 2001; Waide et al.,

1999), and species diversity generally increases with habitat area (MacArthur & Wilson, 1967; Rosenzweig, 1995). In addition, environmental heterogeneity is considered as a universal driver of species diversity across taxa, biomes and spatial scales (Stein et al., 2014). Importantly, both theoretical considerations and empirical analyses suggest that patterns are likely scale dependent (Field et al., 2009; Mittelbach et al., 2001; Mouchet et al., 2015).

Most macroecology researches have been focused on terrestrial ecosystems (Currie & Paquin, 1987; Qian, Ricklefs, & White, 2005), and relative fewer studies have explored geographic biodiversity gradients and the underlying mechanisms for aquatic ecosystems (Astorga, Heino, Luoto, & Muotka, 2011; Barbour & Brown, 1974; Heino, 2002, 2011; Irz, Argillier, & Thierry, 2004; Jacobsen, 2004), especially the aquatic ecosystems in the arid and semi-arid region, which provide important habitat for diverse species and water resource for human living (Williams, 1999). Moreover, the geographical distribution of study sites is strongly biased towards Europe and North America, with particularly poor coverage in Asia (Field et al., 2009; Fu, Wu, Wang, Lei, & Chen, 2004). Study of species diversity in aquatic ecosystems is as essential as in their terrestrial counterparts (Stendera et al., 2012). Declines in biodiversity are far greater in freshwaters than in most terrestrial ecosystems (Sala et al., 2000), and freshwater ecosystems may well be the most endangered ecosystems in the world (Dudgeon et al., 2006; Millennium Ecosystem Assessment, 2005). In addition, the actual rates of freshwater species extinction due to human interruptions are much higher than natural extinction rates (Naiman & Dudgeon, 2011). Therefore, a better understanding of the global freshwater diversity gradients and the major environmental drivers remains a major topic (Heino, 2011); and such studies serve to address some fundamental questions for conserving freshwater taxa (Tisseuil et al., 2013).

In addition, biodiversity assessments are an important component of conservation planning and increasingly used to identify land-use management practices that maximise both evolutionary value and ecosystem function (Chapman, Tobias, Edwards, Davies, & Vamosi, 2018). Key requirements are to maintain community resilience to environmental disturbance and to preserve ecosystem functions and services across time and space (Socolar, Gilroy, Kunin, & Edwards, 2016). Consequently, it is often proposed that we need to look beyond merely conserving species richness towards maintaining the maximum diversity of evolutionary lineages and associated ecological functions (Bregman et al., 2016). The idea that functional diversity or functional complementarity performs better than species richness as predictors of ecosystem functions is supported by a range of empirical studies (Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011; Frund, Dormann, Holzschuh, & Tschardtke, 2013; Petchey & Gaston, 2007). Functional diversity (FD) is a biodiversity component that represents the extent of the functional differences among species based on the distinction of their morphological, physiological and ecological traits (Petchey & Gaston, 2006). Species loss may lead to a reduction in FD depending on the intrinsic redundancy of assemblages (Flynn et al., 2009; Petchey, Evans, Fishburn, & Gaston, 2007). A decrease on the FD of local and regional assemblages could have dramatic consequences for ecosystem functioning because the traits of species, not just the number of taxonomic units, ultimately drive biodiversity-ecosystem functioning relationships (Diaz & Cabido, 2001; Hooper et al., 2005). Worldwide, strong geographic differences exist in the ecological attributes of birds (Kissling, Sekercioglu, & Jetz, 2012). Thus, we ask how these factors combined to affect the diversity of species assemblages under different environmental conditions.

Waterbirds are ubiquitous components of freshwater systems, and their diversity and abundance have long been recognized as suitable bioindicators of environmental change in aquatic systems (Caro & O'Doherty, 1999; Wen, Saintilan, Reid, & Colloff, 2016) and serves multiple significant functional roles in ecosystems (Barbet-Massin & Jetz, 2015) (Figure 1). However, as with other freshwater biota, macroecological studies of environmental drivers of waterbirds diversity are rare (Shah, Domisch, Pauls, Haase, & Jähnig, 2014; Stendera et al., 2012; Zeng et al., 2019). It is unclear whether similar latitudinal and other broad geographical (e.g. altitudinal) gradients apply to waterbirds as well. In a recent review, Heino (2011) found no clear latitudinal gradients at regional scale while species richness typically attains highest levels in mountainous regions. Using river basins as the spatial unit, however, Tisseuil et al. (2013) found that the 'climate/productivity' hypothesis (Field et al., 2009) explained large portion of geographic variance in waterbirds richness, which is consistent to land avian species (Storch et al., 2006). Several factors are known to affect waterbirds diversity

at a local scale, such as lake productivity, lake size, and habitat heterogeneity (Barbour & Brown, 1974; Cintra, 2015; Xia et al., 2016). Linking these local scale variables with broad-scale geographical variations in an integrative analysis framework could potentially articulate the leading processes underlying the regional and global waterbirds richness patterns.

Lakes are ideal systems for studying the relationship between species richness and productivity (Dodson, Arnott, & Cottingham, 2000). It provides a unique system to examine macro-ecological pattern involving geographic and elevational gradients in inland aquatic systems. In this study, we apply multiple regression analysis and structural equation models (SEM) to lake productivity and waterbirds FD data collected from 35 lakes and reservoirs across the temperate zone of arid and semi-arid China to examine macro-ecological pattern involving geographic and elevational gradients in inland aquatic systems. Our primary goal is to test the causal path of geographic location climate lake productivity waterbirds FD. In particular, we first develop separate models for lake productivity and waterbirds FD to compare the dominant factors controlling the gradients of the two indicators. We then build an integrative SEM with explicit causality from productivity to waterbirds diversity to quantify the effect of lake productivity on waterbirds FD. Lake productivity is often a strong predictor of freshwater biodiversity (Dodson et al., 2000), including aquatic animals (and zooplankton as well) (Chase & Leibold, 2002) and phytoplankton (Stomp, Huisman, Mittelbach, Litchman, & Klausmeier, 2011). But its effect on waterbirds has rarely been tested. The productivity-richness hypothesis suggests a positive effect of primary productivity on species richness by allowing larger populations to persist, thereby reducing extinction risk and supporting a higher diversity of niche specialists (Tittensor et al., 2010; Willig et al., 2003). In this context, a significantly positive path coefficient from lake productivity to waterbirds could provide strong support to the productivity-richness hypothesis. However, a weak or no causal link between the two might suggest that waterbirds, not like other aquatic biota like fish (Dodson, 2008) that is constrained by water, have access to other energy sources; and their distribution is governed by other broad scale factors. In this study, we applied FD metrics to waterbird communities sampled in 35 lakes across the whole temperate arid and semi-arid northern China to test the productivity-richness hypothesis, and more importantly, to fill in the gaps in our understanding of ecological patterns in aquatic ecosystems across a large geographical scale.

Materials and methods

Study sites

We sampled a total of 35 lakes and reservoirs across the temperate zone of China (latitude 34.60° to 46.06°, longitude 85.69° to 124.29°, Figure 2). The study area covers more than 5 million km², including a range of landforms such as mountains, hills, plateaus, and plains with altitude ranging from 22.61 m to 4818.10 m, which have large precipitation and temperature gradients. The total area of all the lakes is 508,288.1 ha, ranges from about 70 to 98,800 ha. Mean depth of the lakes ranges from 0.05 to 30.00 m. Most of the lakes are located in the arid and semi-arid region of China, which are relatively independent wetland ecosystems (Wang & Dou, 1998). They provide critical habitats for diverse species (e.g. important breeding and staging sites for waterbirds, some are also used as wintering ground, like Hengshui Lake). The environment in the semi-arid area is sensitive to climate variation (Gong, Shi, & Wang, 2004). Human uses of the lakes mainly include fishery, tourism, water source for irrigation, and reed harvest.

Data collection

Data were collected from 35 lakes and reservoirs during the summers of 2011-2016. The lakes were sampled one to three times, with most of them sampled once in summer. In each lake, water samples were taken on the same day as waterbirds survey during daylight hours.

Waterbirds surveys

Waterbirds were surveyed using transect line method to cover the lakes. Fixed transects with variable lengths were established in each lake and reservoir. Based on the size of each lake and reservoir, the transect length varied from 1 to 5 km and the perpendicular searching distance varied from 0.1 to 0.6 km. We surveyed the transects on foot with constant speed by using binoculars (8×42) and telescopes (Swarovski ATS 80 HD 20-60 × 80). To increase detectability, the surveys were carried out on clear days during daytime and there were at least two fully trained observers for each transect. Visual and/or verbal communication enabled us to avoid duplicate recordings of the same flock of waterbirds by the observers. Waterbirds were all identified to species level. Lists of waterbirds species recorded by the nature reserves and published papers were also collected and incorporated.

Functional trait data

To estimate functional diversity, we collected biometric trait data that describe key ecological attributes of species from published literature for all 148 species. We collected 16 traits for each bird species, including generation length (the average age of breeding individuals), clutch size (number of eggs), incubation times, body size, body mass, wingspan, migratory types (full migration, altitudinal migration, and not migration), breeding habitat range, diet (percentage of scavenger, and invertebrate, fish, seed, fruit and other plant materials), habitat mode (percentage usage of water, riparian, and ground), and pelagic species (0/1) (Table 1). These selected traits measure many aspects of resource used by birds, such as the quantity and the quality of resource consumed (Petchey & Gaston, 2007), as well as the fitness of the species such as reproduction strategies and generation length (Luck, Andrew, Lisa, & Davies, 2013). For example, body mass is highly related to birds' energy requirements (Blendinger & Villegas, 2011). Diet is related to ecosystem functions such as seed dispersal and food-web structure (Sekercioglu, 2006). The main sources of the trait measurements are Planet of Birds, BirdLife International, and a database compiled by Wilman et al. (2014) (Table 1). Any missing data were filled based on information in the ornithological literature, such as the Handbook of the Birds of the World (<http://www.hbw.com/>). A brief summary is available in the Appendix S1.

We used functional richness (FRic) as the measure of functional diversity. FRic represents the amount of functional space filled by the community (Villéger, Mason, & Mouillot, 2008). A community with high FRic would be one with many traits (and potentially high utilization of resources), whereas one with lower FRic might have some traits missing, suggesting that some niches are completely empty (Prescott et al., 2016).

Lake chemical characteristics and morphology

Indicators for lake chemical characteristics include total nitrogen (TN), total phosphorus (TP) and chlorophylla (Chl-a). Water samples for TN and TP in each lake were collected and preserved using 100-ml jars on the same day with waterbirds surveys. All the water samples were sent to and processed in lab by using Ultrospec 6300 pro spectrophotometer (GE Healthcare, America). Water samples for chlorophylla (Chl-a) concentration were collected synchronously on site. We used 2-litre bottles to collect water samples in each lake and reservoir and then filtered the water by using GF/C filter membrane, each filter membrane was filtered with 500 mL water and three filter membranes (3*500 mL) were requested for every sampling point. All water samples and filter membranes were preserved in <5 refrigerator and sent to lab for further test by using Ultrospec 6300 pro spectrophotometer (GE Healthcare, America). Sample size ranges from 3 to 18 based on the area of lake. We set three, six, nine, 12 and 18 sampling points for lakes with area < 10,000 ha, 10,000-20,000 ha, 20,001-30,000 ha, 30,001-50,000 ha and >50,000 ha, respectively. Surface area of each lake and reservoir was calculated from remote sensing interpretation by using Google Earth images from year 2013 to 2016.

Climatic and geographical variables

To define the climate of the lakes, we used the 30 seconds WorldClim bioclimatic variables, which were downloaded from WorldClim website, publicly available at <https://www.worldclim.org/data/worldclim21.html>. The

following bioclimatic variables were included in the study based on collinearity test (see below): mean diurnal range (T1, mean of monthly (max temp-min temp)), mean temperature of the wettest quarter (T2), mean temperature of the warmest quarter (T3), annual total precipitation (P1), precipitation of the driest month (P2), precipitation of the warmest quarter (P3), and precipitation of the coldest quarter (P4). The variables of climate are spatial means of each lake.

Altitudes of the sampled lakes were retrieved from GPS Visualizer on site. Mean geographical coordinates of each site were calculated from remote sensing interpretation by using Google Earth images of each lake and reservoir between years 2013 to 2016. The data of the 35 lakes and reservoirs used in this paper are provided in the Appendix S2.

Data analyses

Our working hypothesis is that large-scale pattern of high trophic level species (waterbirds in this study) diversity can be interpreted as a multilevel biogeographical pattern. That is, we envision that the species diversity of a lake is to a large extent determined by local environmental factors (e.g. nutrients, lake surface area), and that these local environmental factors in turn vary along biogeographical gradients. This nested structure is reflected in our data analysis.

We combined our own survey data and historical records to compile a waterbirds community dataset for each lake. FD was then calculated based on the compiled community data set. It is necessary to have several years of observation because the species observed in a lake could vary from year to year. In addition, we used the total chlorophylla proxy of primary productivity (Eppeley, Stewart, Abbott, & Heyman, 1985; Falkowski & Raven, 2013).

Multiple linear regression –relationships between geography, lake productivity and waterbirds functional diversity

We used stepwise multiple regression with forward selection of variables to identify the most important local environmental variables explaining waterbirds FD in the 35 lakes and reservoirs. Environmental variables were \log_{10} -transformed if this resulted in a more uniform spread of data points. In addition, collinearity between variables was also checked based on variance inflation factor by using the VIF function with package “car” (Fox et al., 2012) in R software (R Development Core Team, 2019). Environmental variables tested in the multiple regression analysis were surface area of the lake (ha), total nitrogen (mg.L^{-1}), total phosphorus (mg.L^{-1}) and lake productivity (mg.m^{-3}), mean diurnal range (), mean temperature of the wettest quarter (), mean temperature of the warmest quarter (), annual total precipitation (mm), precipitation of driest month (mm), and precipitation of the warmest quarter (mm). We used the same stepwise multiple regression approach to investigate how each of these local environmental variables varied with the geographical coordinates of latitude, longitude and altitude (m). The analysis was performed using R version 3.6.1 (R Development Core Team, 2019).

Structural equation modeling – exploring the drivers of lake productivity and waterbirds richness

To gain further understanding of the linkages between waterbirds FD, productivity and environmental variables, we modeled lake productivity and waterbirds functional richness (FRic) in an integrated manner within the structural equation modeling (SEM) framework. SEM is a collection of procedures whereby complex hypotheses, particularly those involving networks of path relations, are evaluated against multivariate data (Grace, 2006). The resulting estimates for path coefficients in structural equation models represent the implied sensitivities of response variables to variations in individual predictors (Grace et al., 2012). We started with an initial SEM that included all plausible pathways between waterbirds functional diversity, the selected set of local environmental variables, and the geographical coordinates of the lakes. Our first attempt with the initial model revealed that it was under-identified, meaning that there was some redundancy such

that it was not possible to estimate all of the model's parameters. We therefore investigated the statistical relationships among the variables included in the model to identify possible redundancies. Subsequently, we fitted two separate SEMs for lake productivity and waterbirds functional diversity, and an integrated SEM revealing the correlation between the two factors. The significance of each path-coefficient was tested 1000 bootstrapped resamples. We reported the standardized coefficients that can be directly compared to make inferences about the relative strength of relationships (Grace & Bollen, 2005). The structural equation analyses were performed using R version 3.6.1 (R Development Core Team, 2019) with package “*Lavaan*” version 3.1-3 (Rosseel et al., 2015).

Results

A total of 148 species, belonging to six orders and 19 families were recorded in this study (Appendix S1). The highest number of species was from the family Scolopacidae (37 species), followed by Anatidae (34 species). Some families such as Phalacrocoracidae, Threskiornithidae and Rostratulidae only had one species each. In addition, among the 35 lakes and reservoirs surveyed, number of species ranged from four to 113 species, with the highest species richness recorded in lakes and reservoirs located in Hubei Province and Beijing (eastern China), and lowest species richness recorded in lakes and reservoirs located in Inner Mongolia and Qinghai Province (western China) (Appendix S2).

Geographical patterns of waterbirds species richness and functional diversity

Waterbirds species richness showed remarkable geographical distribution gradients (Figure 3a). Generally, higher waterbirds species richness was found in lakes of the northern and eastern part of China. Lower species richness was found at higher altitude in the west. Similar pattern was found in waterbirds FRic (Figure 3b). Linear regression showed that FRic increased with latitude and longitude (Figure 4a, 3b), but decreased with altitude (Figure 4c). Furthermore, multiple regression analysis showed that lake area, mean temperature of the wettest quarter, annual total precipitation, and precipitation of the warmest quarter had significant effects on waterbirds FRic, explaining greater than 71% of the total variation in the dataset (Table 1). More specifically, FRic increased with lake area, mean temperature of the wettest quarter, and annual total precipitation, but decreased with precipitation of the warmest quarter.

Site-specific environmental variables including lake productivity, mean diurnal range, mean temperature of the wettest quarter, mean temperature of the warmest quarter, annual total precipitation, precipitation of the driest month, precipitation of the warmest quarter and precipitation of the coldest quarter showed large-scale variation across the landscape of north China. For example, lake productivity decreased with altitude; mean diurnal range, mean temperature of the wettest quarter, and mean temperature of the warmest quarter decreased with latitude, longitude and altitude; while annual total precipitation of the driest month, precipitation of the warmest quarter and precipitation of the coldest quarter increased with longitude (Table 2).

Final structural equation models

Three SEMs were fitted: one for lake productivity, one for waterbirds FD, and an integrated one that included both lake productivity and waterbirds FD to explicitly test the causal link between them. All three models converged successfully (Figure 5-7), and achieved adequate fit with CFI (Comparative fit index) of 0.90, 0.98 and 0.90 for the productivity SEM, waterbird FD SEM and integrated SEM, respectively (Hu & Bentler, 1999). These models had similar hierarchical structure, in which the responsible variable (lake productivity or waterbirds FD) was modelled by a few latent factors. These latent factors were in term defined by the observed variables. In all models, two latent factors were common: geographic position and climate. The geographic position was measured by the latitude and longitude of the central point of the lake and its average elevation. The climate was defined by using spatial mean of seven bioclimatic variables with

low correlation (checked using VIF). In addition, a causality from geographic position to climate condition was specified in all SEMs.

Determinates of Lake Productivity

The three latent factors (i.e. geographic position, climate, and nutrient in the lake) were all included in the SEM. The three factors collectively explained 93% of the variation in lake productivity (Figure 5). Lake nutrient level, which was defined by water TP and TN concentration, had the largest effects on productivity, followed by climate (standardized path coefficient = 0.93 and 0.77 for nutrient and climate, respectively, Figure 5). The effects of geographic position on lake productivity was indirect and realized through its influence on climatic condition; and had a standardized path coefficient of 0.16 (0.77×0.21).

Lake productivity decreased with elevation (path coefficient = $-0.93 \times 0.77 \times 0.07 = -0.19$) and increased with both latitude and longitude with comparable path coefficient (0.12 and 0.13 for latitude and longitude, respectively, Figure 5). For the measured bioclimatic variables, while all variables related to precipitation as well as T2 and T3 had positive effect on lake productivity, the impact of temperature diurnal range was negative with a path coefficient of -0.22 (-0.83×0.27). Lake productivity was positively related with nutrient; and the effect of TP level was slightly larger than that of TN (standardized path coefficient 0.52 and 0.40 for TP and TN, respectively, Figure 5).

Determinates of waterbirds functional diversity

Similar to the lake productivity model, the three latent factors (geographic position, climate, and lake morphology in the lake) were all included in the SEM, collectively explaining 52% of the variation in waterbirds FD (Figure 6). In comparison with lake morphology, climate had higher effects on waterbirds FD (path coefficient = 0.69 and 0.21 for climate and morphology, respectively, Figure 6). The effects of geographic position on waterbirds distribution was indirect through climate with an effect of 0.57 ($0.82 \times 0.69 = 0.56$). Based on the standardized model coefficients, climate condition had the strongest effects on waterbirds FD, followed by geographic position and lake morphology (the coefficients are 0.69, 0.57, and 0.21 for climate, geographic position and lake morphology, respectively, Figure 6).

Waterbirds FD decreased with elevation (path coefficient = $-0.59 \times 0.82 \times 0.69 = -0.33$), and increased with both latitude and longitude, with longitude showing much stronger effect than latitude (path coefficients were 0.61 and 0.23 respectively, Figure 6). For the measured bioclimatic variables, similar to the productivity model, while all precipitation variables as well as T2 and T3 had positive effect on waterbirds FD, the impact of temperature diurnal range was negative. In addition, the four precipitation variables had comparable effects on FD (Figure 6). The model also indicated a positive effect of lake area (standardized path coefficient is 0.21, Figure 6).

Relationship between waterbirds functional diversity and lake productivity

The final integrated SEM combined lake productivity and waterbirds FD together and included an explicit pathway from productivity to waterbirds FD (Figure 7). The model had reasonably adequate explanation power for the three key latent variables (R^2 for climate, waterbirds FD and lake productivity was 0.73, 0.56 and 0.96, respectively, Figure 7). From the fitted path coefficients, climate had the greatest effect on waterbirds FD (0.65), which were similar to that of the waterbirds FD model (Figure 6). The effects of geographic position (0.60) was relatively strong, while the effects of other variables, including lake morphology (0.21), lake productivity (0.17) and nutrient (0.16, indirectly via its effect on lake productivity) were relatively weak.

Discussion

In this study, we applied integrated modelling procedures (SEM) to productivity and waterbirds functional diversity data collected from lakes and reservoirs in the arid and semi-arid northern China covering over 5 million km² with the aim to explore macroecological pattern involving geographic gradients in inland aquatic systems. Both lake productivity and waterbirds FD displayed strong geographical variations across northern China (Figure 3). We found that the geographic position exerted effects on lake productivity and waterbirds FD in a similar way, i.e. through its influences on climatic conditions, which was defined by seven bioclimatic variables in this study. This causality from geographic position to climatic conditions was significant and consistent in all three SEMs. Specifically, our analyses showed an unambiguous decreasing elevational gradient for both lake productivity and waterbirds FD (Herzog, Kessler, & Bach, 2005; Rahbek, 1995). An increasing gradient with location coordinates was also obvious; and the effects of latitude (through its effects on climate) on both lake productivity and waterbirds FD were relatively weaker than those of longitude. Moreover, the “latitudinal gradient”, which predicts species diversity decreases when moving away from the equator towards northern latitudes (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012), was not supported. Instead, we found evidence of a reverse trend in our analyses (Figure 4a). The opposite latitudinal gradient in this study should be treated with cautions as the study focused on the temperate zone that have a rather narrow latitudinal range and strong negative effects of elevation might obscure the real latitudinal pattern. Nevertheless, our analysis results supported a number of hypotheses underlying the geographic gradients by Field et al. (2009): 1) Climate; 2) Productivity; and 3) Size of ecosystem. More importantly, our results revealed a hierarchical structure of drivers that regulate the observed biodiversity and productivity patterns (Macneil et al., 2009).

Drivers of geographic and elevational patterns of lake productivity

The lake productivity model had relatively high performance in explaining the observed geographic and elevational gradients (R^2 for separated and integrated models was 0.93 and 0.96, respectively, Figure 5 and 7). Both linear regression analysis (Figure 4d, 4e) and structural equation modeling (Figure 5 and 7) showed that lake productivity was positively related with water TN and TP concentration. Moreover, the results from the integrated SEM indicated that the effect of nutrient, which was defined by TN and TP concentrations in water, was much stronger than that of climate. The close relationship between nutrient, lake chlorophyll *a* concentration, and lake productivity (Jeppesen et al., 2005; Smith, 1979) was expected because nitrogen and phosphorus are important limiting nutrients in freshwater ecosystems (Elser et al., 2007; Schindler, 1974). Lake ecosystem productivity depends on the supply of nutrients, especially phosphorus (Wetzel, 2001). According to previous studies, phosphorus loading alone could explain 79-95% of the variances in lake chlorophyll *a* concentration (Schindler, 1978).

Climatic conditions, measured mainly by temperature and precipitation variables including mean temperature of the wettest quarter, mean temperature of the warmest quarter, annual total precipitation, precipitation of driest month, and precipitation of the warmest quarter also had positive effects on lake productivity, except for mean diurnal range which showed the opposite trend (Figure 5 and 7). Climatic variation has been found to influence the magnitude of chlorophyll *a* concentration (O'Reilly, Alin, Plisnier, Cohen, & McKee, 2003). Lake productivity increased with air temperature, which is the function of solar energy input. (Warner & Lesht, 2015) reported that air temperature and precipitation were identified as important predictors, which had positive effects on chlorophyll *a*. Our results are consistent with those studies, although the mechanisms are not clear. One possibility is that higher air temperature reduces ice cover, which facilitates wind-induced mixing and nutrient resuspension (Nicholls, 1998; Schwab, Eadie, Assel, & Roebber, 2009). And increases in the form of rain would cause increased run-off, which could bring more nutrients to the lakes from non-monitored or diffuse non-point sources. However, these hypotheses were not fully explored in our study, and further researches are needed to understand the mechanisms on how climate influences lake productivity. In addition, in our study, it was mean diurnal range, mean temperature of the wettest quarter, mean temperature of the warmest quarter showed significant effects on lake productivity. For which, it may due to the sampling time (i.e. we monitored lake chl-*a* in summer).

Drivers of geographic and elevational patterns of waterbirds functional diversity

The waterbirds FD SEMs achieved sufficient performance in explaining the spatial variations in waterbirds FD (R^2 for both separated and integrated models were 0.52 and 0.56 respectively, Figure 6 and 7). Geographic position, defined by latitude, longitude and altitude, had dominating effect on waterbirds FD through its influence on climate. Climate is typically a strong descriptor of broad-scale richness patterns (Hawkins et al., 2003), and the theory that climate's control of energy drives the global richness gradient has generated an extensive literature quantifying the relationship between species richness and climatic variables (Whittaker et al., 2007). Our results demonstrated that waterbirds FD increased with temperature, giving empirical affirmation to the species-energy hypothesis in that species diversity increases with environmental temperature (Allen, Brown, & Gillooly, 2002). Temperature is one of major determinants of latitudinal and altitudinal gradients in animal diversity (Allen et al., 2002; Rohde, 1992), which may be explained by energy hypothesis, although the underlying mechanism remains unknown (Hawkins et al., 2003). The model results also showed that waterbirds FD increased significantly with precipitation. Furthermore, the modelled path coefficients indicated that precipitation was more important than that of temperature in our system. Precipitation is one of the resource-based estimates of available energy, especially in arid and semi-arid ecosystems (Brown & Davidson, 1977), where biodiversity patterns are strongly related to precipitation amount (Waide et al., 1999). This is particularly true for waterbirds, whose distribution is generally determined by rainfall (Wen et al., 2016) through changing habitat availability, like water depth, habitat area and habitat diversity (Canepuccia, Isacch, Gagliardini, Escalante, & Iribarne, 2007). As most of the lakes included in our study are located in the arid and semi-arid region of China, precipitation is critical to maintain enough habitat area for waterbirds.

Lake morphology, which was defined solely by lake area in this study, had positive effect on waterbirds FD. This pattern resembles the common species-area relationship observed in many ecosystems (Arrhenius, 1921; Guadagnin, Maltchik, & Fonseca, 2009; Keil, Storch, & Jetz, 2015; MacArthur & Wilson, 1967; Nogues-Bravo & Araujo, 2006; Rosenzweig, 1995). According to the theory of island biogeography (MacArthur & Wilson, 1967), large and more diverse ecosystems are likely to harbor more species due to higher immigration rates and lower extinction rates. Indeed, lakes in arid and semi-arid zones can be regarded as aquatic islands in a terrestrial world, offering an explanation for the positive species-area relation in our analysis. This finding is consistent with Suter (Suter, 1994), who reported species-area relationship for waterfowl assemblages on the 20 major Swiss lakes north of the Alps. Likewise, Froneman et al. (2001) described a positive species-area relationship in waterbirds communities in farm ponds, South Africa, and Guadagnin et al. (2009) also described that the number of waterbirds species in wetlands from the Atlantic coastal zone of Brazil showed a positive relationship with their size.

Relationship between waterbirds species richness and lake productivity

Many studies revealed that productivity affects diversity (Carpenter et al., 1987; Dodson et al., 2000; Mittelbach et al., 2001), especially for plants (Chase & Leibold, 2002). Nonetheless, no general consensus concerning the form of the pattern has emerged based on theoretical considerations or empirical findings (Waide et al., 1999). And positive, negative, and hump-shaped patterns were common at most spatial scales and no one pattern predominated (Mittelbach et al., 2001). For avian species, particularly waterbirds, there are only a few studies presented the relationship between diversity and productivity (Hawkins et al., 2003; Hurlbert & Allen, 2004). Results of our integrated SEM gave evidence to support the causality from lake productivity to waterbirds FD albeit the relationship was weak in comparison to other factors. As the majority of waterbirds forage on the riparian zone of lakes (mean trait value of foraging at ground was greater than 55% for all lakes, Appendix A1) and have plants as their major diets (Appendix A2), this weak causality is expected.

Conclusions and caveats

A major contribution of this study is that our findings reveal the key environmental drivers of large-scale patterns in lake productivity and functional diversity using advanced statistical techniques (i.e. SEM). This approach showed that the observed geographical and altitudinal gradients in lake productivity and waterbirds FD (Figure 3) can be partly explicated by the gradients in climatic conditions, which is in turn significantly related to the geographic position of the lakes on the earth surface. As the relationship between productivity and species diversity in arid and semi-arid ecosystems has not been addressed, our study could contribute to the mechanistic explanations underlying the observed broad – scale biodiversity gradients in arid and semi-arid region. However, site-specific factors, such as lake morphology (for waterbirds) and nutrients (for productivity) impose their effects independently (Figure 5-7), and their effects could be more important than climatic variables (e.g. for lake productivity). These results, although supporting some primary macroecological biodiversity theories such as species–energy and species–resource hypothesis, could not lead to a mechanism that unifies these theories (McGill, 2010), exemplifying one key limitation of statistical analyses: statistical relationships do not necessarily reveal the underlying mechanisms regulating waterbirds biodiversity (Stomp et al., 2011). For example, the SEM indicates that altitude has a strong negative effect (indirectly through climate and lake productivity, Figure 7) on waterbirds FD. However, these causal paths could be driven by other environmental variables that co-vary with altitude but were not measured in our study. For instance, seasonal variation in environmental conditions increases at higher elevation, which could reduce species diversity by excluding sensitive species with a narrow tolerance range (Currie et al., 2004). Nevertheless, through articulating the dominant processes, our results could contribute to future studies seeking mechanistic explanations underlying the observed macroecological phenomena.

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Conflict of Interest

None declared.

Authors' Contributions

LGC provided funds, LGC, WL and ZYM originally formulated the idea, WL and ZYM developed methodology, ZYM, TWZ, ZQ, THT and JYF conducted fieldwork and data collection, WL and ZYM performed statistical analyses, ZYM wrote the first version of the manuscript, WL and LGC revised the manuscript. All authors contributed to the final version of the manuscript.

Data Availability Statement

The data used in this study have been archived through Dryad online data repository and are publically available at <https://doi.org/10.5061/dryad.mpg4f4qwd>.

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Table 1 The five trait types and 16 specific traits used to characterize waterbirds functional diversity in lakes and reservoirs located in North China.

Type	Trait	Mean	SD	Sources
Resource Quantity	Size (cm)	48.48	31.65	a and b
	Mass (g)	1078.07	1912.80	a and b
	Wingspan (cm)	89.86	52.22	a
	Migration	-	-	b
	Pelagic	-	-	b
	Breeding range (km ² , log transformed)	7.24	0.71	b
Life history	Generation (year)	8.07	2.85	a
Reproduction	Clutch size (no. of eggs)	4.55	2.17	a and b
	Incubation (day)	24.89	4.63	c
Diet	Diet-Inv (% of invertebrate)	49.53	31.84	c
	Diet-V (% of vertebrate)	22.84	28.17	c
	Diet-Scav (% of scavenger)	0.88	3.84	c
	Diet-Plant (% of plant materials)	26.76	31.97	c
	Hab-W (% of time on water surface)	15.20	30.87	c
Habitat	Hab-Rip (% of time on riparian area)	40.34	28.88	c
	Hab-G (% of time on ground)	41.91	32.51	c

1. Planet of Birds, website visited 23 Jun 2016:<http://www.planetofbirds.com/>
2. BirdLife International, website visited 28 Jun 2016:<http://datazone.birdlife.org/>
3. Wilman et al., 2014

Table 2 Multiple regression analysis of waterbirds functional diversity (dependent variable) as a function of environmental variables. Only significant variables were reported ($P < 0.05$).

Regression variables	Partial regression coefficients	Standard error	Standardized coefficients	p
Constant	-1.246	0.246		<0.001
Lake area	0.425	0.073	0.561	<0.001
Mean temperature of wettest quarter	0.050	0.035	1.128	<0.001
Annual total precipitation	0.065	0.019	1.739	<0.001
Precipitation of the warmest quarter	-0.062	0.026	-1.237	<0.001
Model summary	$R^2=0.710$, $P<0.001$	$R^2=0.710$, $P<0.001$	$R^2=0.710$, $P<0.001$	$R^2=0.710$, $P<0.001$

Table 3 Multiple regression analysis of each environmental variables as function of geographical location. Only significant variables were reported ($P < 0.05$).

Variables	Partial regression coefficients
Lake productivity (model $R^2=0.527$, $P<0.001$)	Lake productivity (model $R^2=0.527$, $P<0.001$)
Constant	3.335

Variables	Partial regression coefficients
Altitude	-0.001
Mean diurnal range (model $R^2=0.983$, $P<0.001$)	Mean diurnal range (model $R^2=0.983$, $P<0.001$)
Constant	679.672
Latitude	-8.563
Longitude	-1.886
Altitude	-0.054
Mean temperature of the wettest quarter (model $R^2=0.985$, $P<0.001$)	Mean temperature of the wettest quarter (model $R^2=0.985$, $P<0.001$)
Constant	555.232
Latitude	-2.335
Longitude	-1.811
Altitude	-0.055
Mean temperature of the warmest quarter (model $R^2=0.989$, $P<0.001$)	Mean temperature of the warmest quarter (model $R^2=0.989$, $P<0.001$)
Constant	614.684
Latitude	-4.048
Longitude	-1.628
Altitude	-0.058
Annual total precipitation (model $R^2=0.655$, $P<0.001$)	Annual total precipitation (model $R^2=0.655$, $P<0.001$)
Latitude	-13.296
Longitude	12.088
Precipitation of the driest month (model $R^2=0.508$, $P<0.001$)	Precipitation of the driest month (model $R^2=0.508$, $P<0.001$)
Constant	-6.546
Longitude	0.077
Precipitation of the warmest quarter (model $R^2=0.508$, $P<0.001$)	Precipitation of the warmest quarter (model $R^2=0.508$, $P<0.001$)
Constant	-398.625
Longitude	8.540
Precipitation of the coldest quarter (model $R^2=0.502$, $P<0.001$)	Precipitation of the coldest quarter (model $R^2=0.502$, $P<0.001$)
Constant	-18.736
Longitude	0.236

Figure 1. A pair of Mute Swans (*Cygnus olor*) inhabits at Wuliangsu Lake, Inner Mongolia

Figure 2. Locations of the 35 surveyed lakes and reservoirs in North China. Elevation gradient is used as background

Figure 3. Map of the 35 surveyed lakes and reservoirs in North China showing (a) waterbirds species richness, (b) functional richness, and (c) lake productivity ($\text{mg}\cdot\text{m}^{-3}$)

Figure 4. Patterns of species richness and lake productivity with environmental variables. Species richness of waterbirds as a function of (a) latitude, (b) longitude, and (c) altitude. Lake productivity (measured as chlorophyll *a*) as a function of (d) total nitrogen, (e) total phosphorus. Data points correspond to individual lakes. Regression lines show best linear fits. All regression lines are significant ($P < 0.05$)

Figure 5. SEM for lake productivity. Latent variables are in ovals and measured variables in rectangles. The strength of the causality (standardized path coefficient) is indicated by the width of the line. Black lines indicate positive effects while red lines mean negative impacts. T1: mean diurnal range, T2: mean temperature of the wettest quarter, T3: mean temperature of the warmest quarter, P1: annual total precipitation, P2: precipitation of the driest month, P3: precipitation of the warmest quarter, and P4: precipitation of the coldest quarter

Figure 6. SEM model for waterbirds functional diversity. Latent variables in ovals and measured variables

in rectangles. The strength of the causality (standardized path coefficient for direct comparison) was indicated by the width of the link. Black lines indicate positive effects while red lines mean negative impacts. T1: mean diurnal range, T2: mean temperature of the wettest quarter, T3: mean temperature of the warmest quarter, P1: annual total precipitation, P2: precipitation of the driest month, P3: precipitation of the warmest quarter, and P4: precipitation of the coldest quarter

Figure 7. Integrated SEM model in which waterbirds functional diversity is linked with lake productivity. Latent variables are in ovals and measured variables in rectangles. The strength of the causality (standardized path coefficient) was indicated by the width of the link. Black lines indicate positive effects while red lines mean negative impacts. T1: mean diurnal range, T2: mean temperature of the wettest quarter, T3: mean temperature of the warmest quarter, P1: annual total precipitation, P2: precipitation of the driest month, P3: precipitation of the warmest quarter, and P4: precipitation of the coldest quarter

Appendices

Appendix S1 Biometric trait data of for all 148 waterbird species recorded in this study.

Waterbirds	Generation	Clutch	Incubation	Migratory	Size	Mass	DietV	DietInv	DietS
<i>Actitis hypoleucos</i>	6.8	4	21.5	A	20	48	40	50	0
<i>Aix galericulata</i>	7.4	10.4	30.5	A	46	567.04	10	20	0
<i>Amaurornis phoenicurus</i>	3.7	6	20	A	30.5	180	20	40	0
<i>Anas acuta</i>	6.8	7.9	23	A	58	944.62	10	20	0
<i>Anas clypeata</i>	6.5	9.9	22	A	49.5	612.56	0	60	0
<i>Anas crecca</i>	6.3	9.4	22	A	36	341.89	0	30	0
<i>Anas falcata</i>	6.6	7.3	25	A	46	645.83	0	10	0
<i>Anas formosa</i>	6.6	7.3	24.5	A	41	433.98	0	10	0
<i>Anas penelope</i>	6.4	8.5	24.5	A	48	770.03	0	0	0
<i>Anas platyrhynchos</i>	6.6	10.8	27	A	58.75	843.42	20	40	0
<i>Anas poecilorhyncha</i>	6.6	7.9	26	A	60.5	999.96	0	10	0
<i>Anas querquedula</i>	6.5	8.5	22	A	39	325.6	20	40	0
<i>Anas strepera</i>	6.6	9.8	24	A	46	915.58	0	0	0
<i>Anser albifrons</i>	11.3	5.5	25	A	75.5	2506.39	0	0	0
<i>Anser anser</i>	11.6	4.9	27.5	A	82.5	3302.41	0	0	0
<i>Anser cygnoides</i>	11.4	5.5	28	A	87	3511.94	0	0	0
<i>Anser erythropus</i>	11.4	4.9	26.5	A	59.5	1755.5	0	0	0
<i>Anser fabalis</i>	11.4	4.9	27	A	77.5	2754.73	0	0	0
<i>Anser indicus</i>	11.4	4.9	28.5	A	73.5	2212.55	0	0	0
<i>Ardea cinerea</i>	10.3	3.9	25.5	A	94	1443	80	20	0
<i>Ardea purpurea</i>	10.5	4	27.5	A	84	1064.48	70	30	0
<i>Ardeola bacchus</i>	6.7	4	20	A	47	304.89	30	70	0
<i>Arenaria interpres</i>	7.3	4	23	A	23.5	135.98	0	80	0
<i>Aythya baeri</i>	7.6	7.7	27	A	44	681.23	20	20	0
<i>Aythya ferina</i>	7.6	8.9	52.5	A	45.5	822.99	20	10	0
<i>Aythya fuligula</i>	7.3	9.4	25.5	A	43.5	701.17	0	50	10
<i>Aythya marila</i>	8.2	9.4	27	A	45.5	1005.37	0	80	0
<i>Aythya nyroca</i>	7.6	8.9	26.5	A	40	574	20	10	0
<i>Botaurus stellaris</i>	5.5	4.6	25.5	A	72	1319.45	90	10	0
<i>Bubulcus ibis</i>	8.1	3.9	23.5	A	51	365.95	30	60	10
<i>Bucephala clangula</i>	8	9.4	30	A	46	918.56	10	70	0
<i>Butorides virescens</i>	5.1	3.9	19	A	41.5	201.5	70	30	0
<i>Calidris acuminata</i>	7.4	4		A	19.5	66.08	0	80	0
<i>Calidris alpina</i>	8.1	4	22	A	19	51.89	0	80	0
<i>Calidris canutus</i>	6.8	3.5	21.5	A	24	141.87	10	80	0

Waterbirds	Generation	Clutch	Incubation	Migratory	Size	Mass	DietV	DietInv	DietS
<i>Calidris_ferruginea</i>	7.6	3.8	19.5	A	20.5	58.08	0	80	0
<i>Calidris_melanotos</i>	7.4	4	22	A	21	79.73	0	80	0
<i>Calidris_minuta</i>	6.8	4	20.5	A	13	21.1	0	70	0
<i>Calidris_ruficollis</i>	7.5	4	22	A	14.5	26.79	0	60	0
<i>Calidris_subminuta</i>	7.4	4		A	14.5	30.2	0	70	0
<i>Calidris_temminckii</i>	6.5	4	21.5	A	14	23	0	90	0
<i>Calidris_tenuirostris</i>	7.4	4	21	A	27	192	0	50	0
<i>Casmerodius_albus</i>	9.1	3.9	26	A	92	871.33	60	40	0
<i>Charadrius_alexandrinus</i>	5	3	26	A	15	42.3	0	100	0
<i>Charadrius_asiaticus</i>	5.8	3		A	19	77.09	0	80	0
<i>Charadrius_dubius</i>	5	4	25	A	15.5	38.7	0	100	0
<i>Charadrius_hiaticula</i>	5.1	3.5	24	A	19	64.04	0	100	0
<i>Charadrius_leschenaultii</i>	5.8	3	24	A	22.5	74.8	10	90	0
<i>Charadrius_mongolus</i>	5.2	3	23	A	19.5	64	0	100	0
<i>Charadrius_veredus</i>	5.2	3		A	22	95	0	80	0
<i>Chlidonias_hybrida</i>	9.9	2.5	19	A	26	83.67	60	40	0
<i>Chlidonias_leucopterus</i>	9.9	2.5	20	A	25	54.2	20	80	0
<i>Chlidonias_niger</i>	8.8	2.5	21.5	A	25.5	65.3	60	40	0
<i>Ciconia_boycciana</i>	16.1	3.5	33	A	112.5	4847.74	90	10	0
<i>Ciconia_nigra</i>	15.9	3.5	35	A	97.5	2926	90	10	0
<i>Clangula_hyemalis</i>	9	6.3	26.5	A	48.75	871	0	80	0
<i>Cygnus_columbianus</i>	12.7	3.9	31.5	A	135	6377.96	0	0	0
<i>Cygnus_cygnus</i>	12.3	4.5	35	A	152.5	9349.99	0	0	0
<i>Cygnus_olor</i>	12.2	5.9	38	A	142.5	10682.04	10	10	0
<i>Egretta_eulophotes</i>	6.6	3.2	23.5	A	66.5	461.83	40	60	0
<i>Egretta_garzetta</i>	6.6	3.5	23	A	60	312	40	60	0
<i>Eudromias_morinellus</i>	6.9	3	25	A	21	108.16	0	70	0
<i>Fulica_atra</i>	7	7.7	23.5	A	37.5	717.12	30	10	0
<i>Gallicrex_cinerea</i>	4.4	4.2	24	A	39.25	390.39	0	30	0
<i>Gallinago_gallinago</i>	4.8	4	19	A	26	112.94	0	80	0
<i>Gallinago_megala</i>	4.8	4		A	28	121	0	80	0
<i>Gallinago_solitaria</i>	4.8	4		A	30	140.11	0	100	0
<i>Gallinago_stenura</i>	4.8	4	20	A	26	113	0	80	0
<i>Gallinula_chloropus</i>	5.9	5.8	19.5	A	34	339.63	20	20	0
<i>Gelochelidon_nilotica</i>	11.7	2.5		A	38	218.25	50	50	0
<i>Glareola_maldivarum</i>	7.3	2.4		A	24	75.2	0	100	0
<i>Grus_grus</i>	13.4	2	29.5	A	107.5	5499.99	20	10	0
<i>Grus_japonensis</i>	12.3	2	31.5	A	145	8785.99	40	20	0
<i>Grus_leucogeranus</i>	13	2	28	A	140	5913.44	30	10	0
<i>Grus_monacha</i>	12	2	28.5	A	95.5	3729.9	20	10	0
<i>Grus_nigricollis</i>	13	2	32	B	115	5999.99	40	20	0
<i>Grus_vipio</i>	13	2	30	A	125	4662.99	10	20	0
<i>Grus_virgo</i>	11.2	2	25	A	95	1500	10	20	0
<i>Haematopus_ostralegus</i>	13.7	3	30	A	40	526	10	90	0
<i>Heteroscelus_incanus</i>	5.7	4	24	A	27.5	108.24	20	80	0
<i>Himantopus_himantopus</i>	7.3	3.2	25.5	A	37.5	176.82	0	100	0
<i>Hydrophasianus_chirurgus</i>	4.8	4		A	48.5	160.03	0	60	0
<i>Hydroprogne_caspia</i>	12.2	2	26.5	A	50.5	655	90	0	10
<i>Ibidorhyncha_struthersii</i>	9.6	4		B	40	294	10	90	0
<i>Ixobrychus_cinnamomeus</i>	4.1	3.9		A	40.5	126.49	70	30	0

Waterbirds	Generation	Clutch	Incubation	Migratory	Size	Mass	DietV	DietInv	DietS
<i>Ixobrychus_eurhythmus</i>	4.1	4.2	17	A	37.5	139	70	30	0
<i>Ixobrychus_minutus</i>	4.1	4.2	18.5	A	32.5	99.49	30	70	0
<i>Ixobrychus_sinensis</i>	4.1	4.6	18.5	A	35	94.29	20	80	0
<i>Larus_argentatus</i>	13	2.5	29	A	61	1090.99	50	30	20
<i>Larus_brunnicephalus</i>	11.5	3	24	A	43	569.29	50	30	10
<i>Larus_canus</i>	9.8	3	25	A	43	412.53	40	40	10
<i>Larus_crassirostris</i>	11.5	2.5	24.5	A	47	561	40	30	30
<i>Larus_ichthyaetus</i>	12.4	2	25	A	66	1378.84	70	20	0
<i>Larus_minutus</i>	10.5	2.4	24	A	27.5	118	20	80	0
<i>Larus_relictus</i>	6	2.4	25	A	44	490.2	60	40	0
<i>Larus_ridibundus</i>	9.6	1.7	24	A	40	284	20	70	0
<i>Larus_saundersi</i>	11.5	3		A	30.5	198	40	60	0
<i>Larus_schistisagus</i>	11.5	3	29	A	61	1323	40	30	20
<i>Limicola_falcinellus</i>	4.8	4	21.5	A	17	37.1	0	80	0
<i>Limnodromus_semipalmatus</i>	5.8	2	22	A	34.5	212	40	60	0
<i>Limosa_lapponica</i>	8.9	4	20.5	A	39	291.65	0	80	0
<i>Limosa_limosa</i>	8.6	4	23	A	40	288.37	20	60	0
<i>Lymnocryptes_minimus</i>	5.4	4	22.5	A	18	50.07	0	80	0
<i>Melanitta_fusca</i>	7.5	7.9	27.5	A	54.5	1800.17	10	80	0
<i>Mergellus_albellus</i>	5.7	7.9	27	A	39.5	608.55	20	70	0
<i>Mergus_merganser</i>	7.3	9.8	31	A	65	1451.02	90	10	0
<i>Mergus_serrator</i>	7.3	8.9	31.5	A	55	1015.17	70	20	0
<i>Mesophoyx_intermedia</i>	5.6	3.5	21	A	64	458.83	80	20	0
<i>Netta_rufina</i>	7	8.9	27	A	55.5	1118	0	0	0
<i>Numenius_arquata</i>	5	4	28	A	55	802.99	0	40	0
<i>Numenius_madagascariensis</i>	10.1	4	16	A	59.5	792	0	90	0
<i>Numenius_minutus</i>	10.1	4	22.5	A	31	173	0	80	0
<i>Numenius_phaeopus</i>	9.1	4	25	A	43	364.57	0	60	0
<i>Nycticorax_nycticorax</i>	8.8	3.9	22.5	A	60.5	810	70	30	0
<i>Pelecanus_crispus</i>	11	2	32	A	170	9512.09	100	0	0
<i>Pelecanus_philippensis</i>	15.4	3.5	30	A	139.5	5010.98	100	0	0
<i>Phalacrocorax_carbo</i>	11.3	3.5	29	A	90	2528.97	90	10	0
<i>Phalaropus_fulicarius</i>	9.9	4		A	38.5	308	0	100	0
<i>Phalaropus_lobatus</i>	4.9	4	21.5	A	21	36.68	0	80	0
<i>Philomachus_pugnax</i>	4.9	4	19	A	18.5	35.5	0	80	0
<i>Platalea_leucorodia</i>	7.2	3.5	24.5	A	82.5	1228	20	70	0
<i>Pluvialis_fulva</i>	5.6	4	23.5	A	24.5	250	0	70	0
<i>Pluvialis_squatarola</i>	6	4	26.5	A	29	84.11	0	70	0
<i>Podiceps_auritus</i>	7.1	4.5	23.5	A	34.5	730.96	60	40	0
<i>Podiceps_cristatus</i>	7.1	3.9	28	A	53.5	575	70	30	0
<i>Podiceps_grisegena</i>	7.1	4.5	22.5	A	45	1646	50	50	0
<i>Podiceps_nigricollis</i>	7.1	3.5	22	A	31	320.69	20	80	0
<i>Porzana_fusca</i>	2.7	5.2	20	A	22	49.7	0	40	0
<i>Porzana_pusilla</i>	2.7	6.6	18	A	18	61.06	10	70	0
<i>Rallus_aquaticus</i>	4.6	8.1	22	A	26.5	162.11	40	20	0
<i>Recurvirostra_avosetta</i>	8.7	3.5	24	A	43.5	325	10	80	0
<i>Rissa_tridactyla</i>	12.9	2	26	A	39	706	50	30	0
<i>Rostratula_benghalensis</i>	8.6	3.2	18	C	25.5	76.6	0	60	0
<i>Scolopax_rusticola</i>	6.3	4	17.5	A	34	205	0	70	0
<i>Sterna_albifrons</i>	10.9	2.5	22.5	A	25	94.69	60	40	0

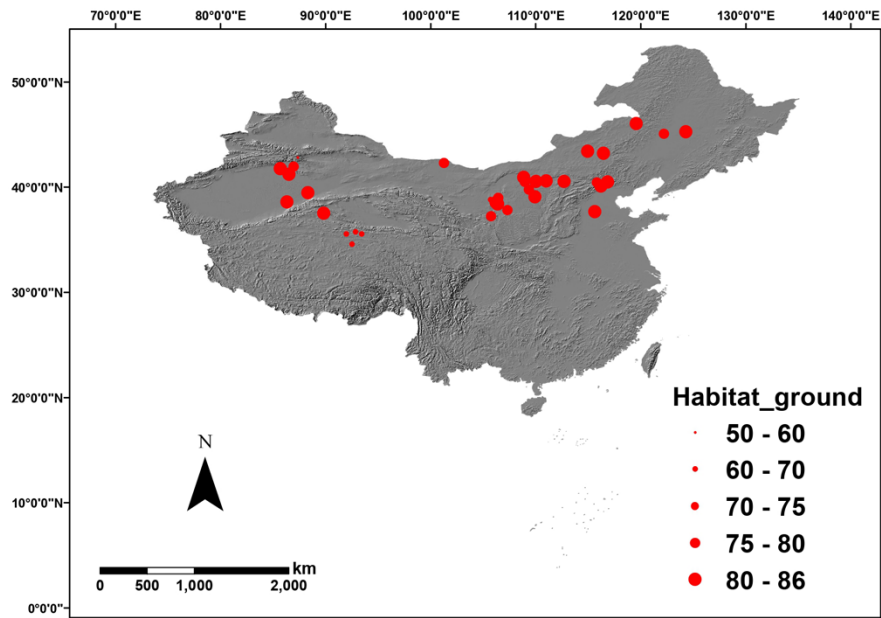
Waterbirds	Generation	Clutch	Incubation	Migratory	Size	Mass	DietV	DietInv	DietS
<i>Sterna.hirundo</i>	11.5	2	25	A	35.5	53.8	80	10	10
<i>Tachybaptus.ruficollis</i>	5.4	3.7	22.5	A	27	3450	20	80	0
<i>Tadorna.ferruginea</i>	10.9	8.5	28.5	A	66	885.22	10	10	0
<i>Tadorna.tadorna</i>	10.9	8.9	29.5	A	62.5	1418.68	20	70	0
<i>Tringa.erythropus</i>	5.6	4		A	30.5	77.5	20	80	0
<i>Tringa.glareola</i>	5.2	4	22.5	A	21	158	0	100	0
<i>Tringa.nebularia</i>	6.3	4	24	A	32.5	71.4	20	80	0
<i>Tringa.ochropus</i>	5.6	4	21.5	A	22.5	48.4	20	70	0
<i>Tringa.stagnatilis</i>	5.6	4		A	24	129	20	60	0
<i>Tringa.totanus</i>	6.2	4	25.5	A	28	62.1	20	80	0
<i>Vanellus.cinereus</i>	8.9	4	28.5	A	35.5	165	0	100	0
<i>Vanellus.vanellus</i>	9	4	25.5	A	29.5	198	0	100	0
<i>Xenus.cinereus</i>	6.4	4	23.5	A	23.5	123	0	60	0

Appendix S2 Data of the 35 lakes and reservoirs used in this study.

lake name	No. of waterbirds species	Productivity (mg.m ⁻³)	FRic	Latitude	Longitude	Lake area (ha)
Wuliangsu hai	96	11.36	0.096254	40.93	108.83	29300.00
Hasu hai	51	8.36	0.055521	40.6	110.98	4161.54
Dalinuo er	99	3.30	0.104735	43.25	116.42	38536.07
Erdos	72	10.13	0.092827	36.71	109.31	1717.43
Chagannao er	72	72.92	0.089553	43.43	114.92	3300.00
Wulagai	103	4.62	0.097590	46.06	119.57	22600.00
Juyan hai	40	2.62	0.064184	42.33	101.25	4000.00
Dai hai	43	25.35	0.063914	40.55	112.66	2420.00
Khorchin	66	69.42	0.082376	45.08	122.18	18047.04
Hangjinnao er	55	18.32	0.072142	40.5	108.96	1600.00
Nai hai Wetland	55	96.95	0.073630	40.53	110.01	1308.25
Honggou reservoir	4	14.60	0.000051	38.84	105.67	160.00
Sand Lake	74	11.43	0.079616	38.62	106.33	8602.23
Habahu	45	10.07	0.067270	37.83	107.28	240.00
Mingcui hu	74	14.85	0.083680	38.38	106.37	492.00
Yue hai	37	39.34	0.060880	38.57	106.21	1070.37
Xinghai hu	24	55.21	0.037125	38.99	106.41	3283.91
Tian hu	24	6.65	0.037125	38.02	105.74	591.00
Hongjiannao	74	1.75	0.082940	39.1	109.88	3330.00
Kusai hu	9	0.41	0.017198	35.73	92.83	32600.00
Goulucuohu	9	0.49	0.022734	34.6	92.47	2350.00
Zhuonai hu	8	0.51	0.012421	35.55	91.95	16300.00
Yan hu	9	0.51	0.018675	35.53	93.42	1120.00
Chagan hu	94	40.00	0.089094	45.26	124.29	51936.54
Hengshui hu	113	16.30	0.100239	37.69	115.58	18787.00
Cui hu	56	15.00	0.068850	40.08	116.17	166.00
Alagou	8	1.06	0.008048	42.85	87.36	94.00
Bosten Lake	58	8.98	0.082285	41.67	86.9	94529.19
Heshilike	17	51.07	0.017170	41.75	85.69	525.00
Kongquehe	17	39.62	0.017170	41.25	86.5	79.25
Kenadaliya	17	5.76	0.017170	38.61	86.29	69.90
Taitemahu Lake	31	6.65	0.051730	39.48	88.29	26930.42

lake name	No. of waterbirds species	Productivity (mg.m ⁻³)	FRic	Latitude	Longitude	Lake area (ha)
Ayakekumuhu Lake	21	2.74	0.046644	37.52	89.79	98800.00
Miyun Reservior	113	3.55	0.102017	40.48	116.83	18800.00
Yehahu Lake	105	5.79	0.089492	40.46	115.84	441.00

Appendix A1 Map of the CMW (the community-level weighted means of trait values) for the percentage of foraging on ground in the 35 surveyed lakes. Background is the 3D representation of the surface (hillshade).



Appendix A2 Map of the CMW (the community-level weighted means of trait values) of percent use of plant materials. Background is the 3D representation of the surface (hillshade).

