Causality between abundance and diversity is weak for wintering migratory waterbirds

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SUMMARY

1. The species–area relationship, which is closely linked with the more general species–energy theory, is one of the most well-known patterns in geographical ecology, but the underlying causes remain contentious. The more individuals hypothesis (MIH) articulates a causal path from resource availability to population abundance to species richness. The MIH has been tested with a range of taxa including plants, invertebrates and land birds but never with migratory waterbirds.

2. Using multiyear simultaneous survey data of wintering waterbirds in 10 lakes at Poyang Lake, China, and remotely sensed habitat condition measurements, we applied structural equation modelling (SEM) to test three causal paths: (A) good habitat conditions (e.g. habitat availability and heterogeneity) attract more species (high richness); (B) habitat conditions promote abundance (more individuals); and (C) habitat conditions promote abundance, which in turn increases richness.

3. We also modelled responses of species richness and abundance to habitat conditions using generalised additive mixed modelling (GAMM) to assess their co-variation.

4. While our analysis confirmed the first two paths, we found no support for the third, which is the central postulate of the MIH. In addition, in agreement with GAMM, SEM indicated that species richness was more closely related to habitat quality than to abundance. Our findings suggest that wintering waterbird species richness and abundance are two intrinsic community indices that covary with environmental variables.

Keywords: habitat quality, migratory waterbird, more individuals hypothesis, Poyang Lake, species–area relationship

Introduction

One of the most well-known patterns in geographical ecology is the species–area relationship (SAR), which describes a general positive relationship between area and species richness (Preston, 1948, 1960; MacArthur, 1972; Simberloff, 1976). As an extension to SAR (Wright, 1983), the species–energy theory (Gaston, 2000; Storch, Evans & Gaston, 2005) suggests that the potential or available energy of the environment may play the pri-

mary role in determining species richness over broad geographical extents (Hurlbert, 2006), in that sites with a greater resource flux have more species (Currie, 1991; Wright, Currie & Maurer, 1993). Richness–energy relationships vary considerably among habitats (Waide *et al.*, 1999; Mittelbach *et al.*, 2001), with scale of the observation (Weiher, 1999; Chase & Leibold, 2002; Belmarker and Jetz, 2011) and with estimates of energy flux (Groner & Novoplansky, 2003), such as net primary productivity, biomass or their surrogates (e.g. NDVI – nor-

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malised difference vegetation index) (Hurlbert, 2004; Phillips, Hansen & Flather, 2008; Hurlbert & Jetz, 2010). Nevertheless, the species–energy (productivity) relationship is one of the best documented macro-ecological phenomena (Hutchinson, 1959; Brown, 1981).

One of the underpinning explanations of the positive species–energy relationship is the more individuals hypothesis (MIH) (Wright, 1983; Srivastava & Lawton, 1998). The MIH postulates a causal path from resource availability to population abundance to species richness in that 1) areas with greater food resources support more individuals and 2) communities with more individuals support more species. This increase in persistence enhances diversity. Studies that have examined the MIH for several groups including plants (O'Brien, 1993; Stevens & Carson, 1999; Šimová *et al.*, 2011), forest birds (Currie *et al.*, 2004; Hurlbert, 2004; Evans, James & Gaston, 2006; Mönkkönen, Forsman & Bokma, 2006; Hurlbert & Jetz, 2010), ants (Srivastava & Lawton, 1998; McGlynn, Weiser & Dunn, 2010), macroinvertebrates (Mori, Murakami & Saitoh, 2010), fish (Mason *et al.*, 2008) and lizards (Buckley & Jetz, 2010) by relating resource availability to total abundance or richness have found mixed support. For example, Currie *et al.* (2004) showed that species richness was more closely correlated with energy availability than with total number of individuals. In examining the global richness–energy relationship in forests, Šimová *et al.* (2011) found no evidence to support the MIH and limited evidence for a prominent role of productivity in species richness patterns. Nevertheless, most of the studies fall short of totally rejecting MIH, and each study increases the complexity of the MIH by pointing to different aspects moderating the relationship, such as habitat heterogeneity (Hurlbert, 2004), seasonality (Yee & Juliano, 2007), disturbance (Drever, Goheen & Martin, 2009) and community structure (Mönkkönen *et al.*, 2006; Evans, Greenwood & Gaston, 2007). Therefore, the key issue for MIH is whether there exists a causal link between abundance and species richness. If causality does exist, is it direct or indirect, how strong is the association and how does environmental variability affect abundance–richness relationships? Structural equation modelling (SEM) is increasingly used in ecological studies to investigate complex relationships and causality (Laughlin *et al.*, 2007; Menezes *et al.*, 2013; Kissling, Field & Gaese, 2008; Grace *et al.*, 2010, 2012; Sandom *et al.*, 2013), and might provide a framework to disentangle the direct and indirect effects of abundance on species diversity.

To our knowledge, there has been no reported test of MIH for waterbirds, although there are several studies

for land birds (e.g. Hurlbert, 2004; Hurlbert & Jetz, 2010). Species richness and abundance of wintering waterbirds, especially migratory species, are affected by environmental factors that might not be experienced by other biota. For example, the regional species pool at the wintering site might be dependent on the conditions at breeding sites several thousand kilometres away (Hobson & Wassenaar, 1996). In addition, the appropriate proxy for energy flux in aquatic systems is rather difficult to measure compared with terrestrial ecosystems (e.g. biomass, NDVI and potential evapotranspiration are readily available and are used as a proxy for energy flux in terrestrial systems). Ecosystem size, covarying with resource concentration or productivity (MacArthur & Wilson, 1967; Yee & Juliano, 2006), could provide an alternative proxy for energy flux when studying regional biodiversity patterns (Blakely & Didham, 2010).

The Poyang Lake system in China is the largest freshwater wetland complex in East Asia (Shankman, Keim & Song, 2006), and provides one of the most important wintering sites for migratory waterbirds in the East Asian–Australasian Flyway (Ji *et al.*, 2007). During the low water period in winter, an array of sublakes, hydraulically connected or isolated, emerge as water level withdraws. These lakes provide a range of foraging habitats for hundreds of thousands of migratory waterbirds from different guilds (Wang *et al.*, 2013). The mosaic of lakes of varying sizes and environmental properties within the Poyang system provides a good opportunity to test relationships among the species richness, abundance and environmental factors, and makes possible the testing of MIH.

In this study, we used a multiyear wintering waterbird census data set from the Poyang Lake region, including remotely sensed habitat size and rugosity, to test the causality implied by MIH. We tested for differences in richness, abundance and community composition in different lakes. We also predicted that increasing habitat size and heterogeneity (Honkanen *et al.*, 2010) would support greater species richness and abundance of wintering waterbirds. Finally, we tested the following three causal paths: (A) richness increases with habitat availability and heterogeneity, in that species number would increase with increasing habitat condition. As a special case of the species–energy theory, Wright (1983) proposed a general model linking SARs with positive productivity–species richness relationships. (B) Abundance increases with habitat availability and heterogeneity, that is total number of individuals would increase with increasing habitat condition; (C) habitat availability and heterogeneity promote abundance, which in turn

supports high richness. The third causal path is the central postulate of the MIH: that increasing habitat size would lead to an increase in abundance, which, in turn, would result in increased richness. According to MIH, all three causal paths are testable, and the model for path C should increase the prediction power.

Methods

Study site

This study focuses on the main extent of Poyang Lake located at the middle Yangtze River basin of China (28°22'–29°45'N, 115°47'–116°45'E; Fig. 1). With an area of approximately 4000 km² during summer high water (Shankman *et al.*, 2006), Poyang Lake is the largest freshwater wetland system in South-Eastern Asia. The lake is freely connected with Yangtze River (Fig. 1), and is a

seasonally dynamic system with inundation regimes and water level fluctuations largely controlled by the hydraulic balance of the five major tributaries (Fig. 1) and the Yangtze River, which in turn responds to the subtropical monsoonal climate. This seasonally inundated wetland area is a unique biodiversity hotspot hosting hundreds of thousands of wintering migratory waterbirds from the East Asian Flyway (Ji *et al.*, 2007; Wang *et al.*, 2013). Historically, there were 159 waterbird species recorded in Poyang Lake, half of which belong to wintering migrants (Wang, 2004).

During the low water winter season, the area becomes a system of sublakes interspersed with mudflats and grasslands (Dronova, Gong & Wang, 2011) (Fig. 1). These sublakes and the associated mudflats are the primary habitats for wintering waterbirds. Sublakes range in size from 310 to 8580 ha, and habitat heterogeneity varies in relation to the differing size, shape and configuration of shallow waters, mudflats and wet meadows. This spatial heterogeneity provides diverse habitats with rich food resources to accommodate the specific requirements of a range of waterfowl species. The hydrological regimes, especially the timing of water recession, affect vegetation development and composition (Guan *et al.*, 2014), thus exhibiting strong effluence on habitat quality. Under natural conditions, the low water period at Poyang Lake lasts approximately from November to late February–early March, although the exact timing varies among years (Shankman *et al.*, 2006; Wang *et al.*, 2012). Generally, during the period of low water, the overall reduction in the waterbody area is expected to continue until the next rain season; however, winter precipitation events and the irregular operations of the river regulators (especially the Three Gorges Dam) can produce more complex dynamics.

Wintering waterbird survey

We compiled annual field waterbird census data set from 2006 to 2012 for 10 sublakes in the Poyang Lake area (Fig. 1). To avoid repeated counting, the waterbird surveys were conducted simultaneously, that is waterbirds were counted on the same date by a number of teams from fixed observation points/routines. We used survey data in January or February when the waterbird community (both abundance and richness) is most stable (i.e. all wintering birds had arrived and departure does not start until March). Depending on the size and visibility of each sublake, one, two or three permanent observation locations (fixed points) were established. The observation sites were located on high ground such

Fig. 1 A habitat distribution map of Poyang derived from a satellite image taken on 29 December 2006. The 10 sublakes with simultaneous waterbird survey data are marked. Inset shows the location of Poyang Lake in China, and the lake is directly connected with the Yangtze.

that the entire sublake was visible to maximise detectability so that all birds on the lake could be counted. All birds were identified to species level.

Habitat mapping

We used the Landsat TM5 or TM7 satellite images (from <http://www.usgs.gov/>) from December to January to map the distribution of shallow waters, wet meadows and mudflats in the Poyang Lake region. We used mid-winter images based on the following: (1) the period is consistent with the time of bird surveys; (2) water level in Poyang Lake is the lowest; therefore, the size of exposed lake bed is maximum; and (3) the size and distribution of the three types of habitat are relatively stable due to low rainfall and evaporation. All requested images had high quality and low cloud cover (<5%) in study area.

After geo-referencing (root mean squared error <30 m), we used a standard automated algorithm, the unsupervised ISODATA clustering method for image classification (Lillesand, Kiefer & Chipman, 2008), and all satellite images were segmented into three habitat classes, that is water area, grassland and mudflat. The performance of image classification was assessed for the 2011 habitat distribution map using field transection surveys, with an overall accuracy >95%. The three habitat classes used here comprise the major habitats for wintering waterbirds in Poyang. In shallow water and mudflats, buried tubers of submerged plants, *Vallisneria spiralis* in particular, become accessible to foraging cranes (Jia *et al.*, 2013, 2014). In addition to plant food resources, stranded fish, shellfish and shrimps are scattered across the small ponds on the mudflats attracting large numbers of fish-eating species such as storks, herons and egrets. At a slightly higher elevation (often <1 m difference), vegetation develops into wet meadow, where *Carex* spp., *Potentilla limprichtii* and other wetland plants are abundant, providing quality food for geese (Wang *et al.*, 2013; Guan *et al.*, 2014). The 10 selected sublakes have clear boundaries, visible from satellite images taken during the low water period (i.e. there are elevated banks formed either naturally or artificially, Fig. 1). For each sublake, we calculated the size (total area in ha) and the number of habitat patches. In addition, the rugosity of the largest patch of shallow water, wet meadow and mudflat was computed as follows:

$$SI = \text{Perimeter} / 2\sqrt{\pi \times \text{Area}},$$

where Perimeter and Area are in m and m² at 30 m × 30 m resolution, respectively.

Data analysis

Generalised additive mixed models (GAMM). Before modelling, we tested for correlation between variables using Spearman's rank correlation (Table 1). We avoided including variables with strong correlation (i.e. Spearman's $\rho > 0.60$) in the same model (i.e. if two variables were strongly correlated, two separate models with each of the correlated variables and other variables were fitted and evaluated with the adj. R^2 and deviance explained, see below).

We used GAMM to explore the relationship between species richness and abundance, and how these changed with availability and distribution of habitats, while accounting for variability among survey years. Before building GAMMs, we specified the best probability distribution function (PDF) for each of the responsive variables by fitting null models, and selected the PDF with lowest Akaike's information criterion (AIC). To identify the optimal GAMMs, we adopted a six-step protocol following the recommendation of Zuur *et al.* (2009):

1. Specify the fixed model structure: start with the best possible model in terms of all explanatory variables subjected to Table 1;
2. Determine whether a smoothing function should be kept for each explanatory variable;
3. Determine whether adding interaction terms of the explanatory variables improves the model;
4. Model validation: examine whether the model residuals are normally distributed and homogeneous;

Table 1 Spearman's ρ of the candidate variables

	A2	A3	H1	H2	H3	R1	R2	R3
A1	0.25	0.34	0.47	0.49	0.48	0.23	0.61	0.18
A2		0.74	0.61	0.36	0.65	0.35	0.60	0.54
A3			0.36	0.25	0.42	0.14	0.47	0.63
H1				0.62	0.86	0.30	0.54	0.48
H2					0.73	0.33	0.37	0.46
H3						0.35	0.56	0.56
R1							0.33	−0.05
R2								0.34

Bold number indicates strong correlation, and corresponding variables will not be included in the same model.

A1, A2 and A3 = log-transformed total area (ha) of shallow waters, wet meadow and mudflat, respectively; H1, H2 and H3 = number of shallow water bodies, wet meadow and mudflat, respectively;

R1, R2 and R3 = shape index defined by

$R = \text{Perimeter} / 2\sqrt{\pi \times \text{Area}}$.

Fig. 2 Structural equation model used to describe the full covariance matrix among habitat condition (i.e. availability, heterogeneity and irregularity), waterbird diversity (square root transformed) and abundance (natural log density). Variables within a rectangle are observed, while those within an ellipse are latent. Line with a single arrowhead hypothesizes direct effect (causality), and curved line with two arrowheads represents error covariance. The correlations between observed variables are omitted for simplicity. Habitat availability and heterogeneity are latent variables measured by A1, A2 and A3 = log-transformed total area (ha) of shallow waters, wet meadow and mudflat, respectively; H1, H2 and H3 = square root transformed number of shallow water bodies, wet meadow and mudflat, respectively; and R1, R2 and R3 = shape index defined by $R = \text{Perimeter} / 2\sqrt{\pi \times \text{Area}}$. Richness and abundance are latent variables measured by number of recorded species and total counts, respectively. Paths 1 and 3 represent the effects of habitat conditions on waterbird richness; paths 2 and 4 represent the effect of habitat conditions on waterbird abundance; path 5 represents the effect of abundance on richness; and path 6 represents the effects of richness on abundance. Four alternative models were developed: (i) without paths 5 and 6; (ii) with path 5; (iii) with path 6; and (iv) with paths 5 and 6 and evaluated to investigate the causality between abundance and richness.

5. Determine whether random variables (i.e. site and year) are necessary to improve the model;

6. For the optimal random structure in (5), re-evaluate the fixed structure in step (1).

To identify the best model among competing GAMMs for each of the biodiversity indices (step 1), we used the 'MuMIn' in R (Barton, 2012) for model averaging. Function 'dredge' in the MuMIn package can perform an exhaustive screen of all the candidate models, and rank and weigh them based on the AIC_c (the small sample correction AIC). The relative importance of explanatory variables (including interactions) was calculated as a sum of the Akaike weights over all of the models with a $\Delta AIC < 4$ (Burnham & Anderson, 2002; Grueber *et al.*, 2011). The explanatory variables with >50% relative importance were reported.

Structural equation modelling (SEMs). Structural equation modelling (SEM) is a multivariate method increas-

ingly used by researchers in the natural sciences to address questions about complex systems (Grace *et al.*, 2012). SEM allows explicit testing of these direct and indirect dependencies, providing a framework for learning about causal processes. Thus, it is well suited to assess the relative support for our hypotheses linking habitat conditions to species richness and abundance (Fig. 2). A general conceptual model (Fig. 2) provides a basic outline of the hypothesised relationships between different components of the lake ecosystem. Habitat availability and heterogeneity, which are latent variables measured by the size, number and rugosity of shallow waters, wet meadows and mudflats, are both thought to be important drivers of species richness and population abundance (Wen *et al.*, 2011; Wang *et al.*, 2013). Other environmental variables, such as hydrology and climate, likely affect the primary productivity of a lake system through temperature and light conditions, but due to a lack of site-specific data, none of these factors were considered in this analysis. In addition, anthropogenic disturbance, such as elevated levels of recreational activities (e.g. fishing, boating and bird watching), may cause short- and/or longer-term stress in wildlife (Tavares *et al.*, 2015). As a large part of our study area is within the boundary of National Nature Reserves, where human activities are proscribed by the *China Nature Reserve Regulation* and hence were relatively low (Yifei, Guan and Guanhua, field observations), such activities have not been included in our analysis.

We used both absolute fit indices (model chi-squared test – χ^2 test and root mean square error of approximation – RMSEA) and incremental fit indices (such as comparative fit index – CFI) to evaluate model fit. Model χ^2 test and RMSEA evaluate the overall model fit assessing the magnitude of discrepancy between the sample and fitted covariance matrices, while CFI compares the χ^2 test to a baseline model.

All analyses were conducted using R (version 3.1.1) (R Development Core Team, 2013) with packages mgcv version 1.7.27 (Wood, 2001), MuMIn version 1.9.11 (Barton, 2012) and lavaan version 0.5.14 (Rosseel, 2012).

Results

Response of abundance and species richness to habitat variables

The GAMMs for abundance and richness are summarised in Table 2. Although the models have their own set of predictors, both indices responded positively to the size of shallow waters in the sublakes (Fig. 3), and the partial response curves was similar for richness and

Table 2 Summary of the final models for biodiversity indices

Response	Predictor*	Importance†	Best model		Deviance explained
			AICc‡	Adj-R ²	
Richness	A1	1.00	418.90	0.60	64.6%
	R1	0.51			
	A3	0.29			
Abundance (counts ha ⁻¹)	A1	1.00	476.14	0.51	55.5%
	A3	0.51			
	H2	0.38			

Both 'Site' and 'Year' were specified as random effects in the final models.

*See Table 1 for the definition of other variables.

†Relative importance of the predictor variable, calculated as a sum of the Akaike weights over all of the models in which the parameter of interest appears.

‡Small sample corrected Akaike information criteria (AIC).

abundance (Fig. 4). Furthermore, the size of shallow water-habitats has relatively high importance in both models. In both cases, 'Site' and 'Year' were selected as random effects in the model structure, indicating the spatial and temporal variations in species richness and abundance.

Three habitat condition variables were considered to be important for wintering waterbird abundance: the size of shallow waters, size of the mudflat and the number of wet meadows, of which the size of shallow water had the highest importance according to the weighted AICc (Table 2). With a relative importance value of 0.51, the size of mudflats also made a significant contribution to waterbird abundance (Table 2). Relationships between waterbird abundance and mudflats and shallow waters were largely linear, especially for the size of mudflats. In addition, waterbird abundance responded positively to both size of shallow waters and mudflats (Fig. 3a).

The size of shallow waters, size of mudflat and rugosity of the waterbody were included in the species richness model, and the size of shallow waters was the most important variable followed by the rugosity of waterbody (Table 2). Unlike the response of abundance, species richness increased with the size of shallow waters but decreased with the size of mudflats, although the impact of the size of shallow water was much stronger (Fig. 3b).

Fig. 3 The response surface of waterbird abundance (count/1000) (a) and species richness (b) to the logarithmic transformed size (m²) of shallow waters and mudflats associated with sublakes within the Poyang area

Fig. 4 Partial response of richness (a) and abundance (b) of wintering waterbird to area of shallow water bodies.

Correlation between species richness and abundance

The relationship between species richness and abundance was positive, although the relationship was non-linear (Fig. 5). The modelling process suggested that no smoothing parameter was needed (i.e. generalised linear model was sufficient to fit the data). The resultant model had an adjusted R^2 of 0.35, and 31.5% of the deviance in data was explained by the model.

Structural equation models: causality between abundance and richness

Goodness-of-fit indices suggested that the model without a direct or indirect effect between abundance and richness best fits the data (i.e. M1 in Table 3). In

Fig. 5 The relationship between species richness and abundance. Cycles are the raw records, and red line is the fitted GLM with reverse link function (i.e. Gamma distribution).

contrast, the model with a two-way direct effect (the reciprocal effect model, M4) was the worst performing. Both the absolute fit indices and incremental fit indices of the models with casual links between abundance and richness (either from abundance to richness M2 or from richness to abundance M3) were identical to those of the model with no direct effect but correlated error (M5).

The best fitted model (Fig. 6), that is M1 without direct effect between richness and abundance, was found to be adequate based on both the absolute fit indices (model χ^2 test and root mean square error of approximation – RMSEA) and incremental fit indices. The χ^2 test suggested that M1 was the only model with no significant deviation between the observed covariance matrix and that of the specified SEM ($\chi^2(3) = 9.463$, $P = 0.051$, Table 3). Furthermore, M1 was the only model with a RMSEA below 0.08, showing a good fit; RMSEA for other models was >0.10 . In addition, the CFI for M1 was also highest among the candidate models although CFI was >0.95 for all models.

The effects of habitat availability and heterogeneity on wintering waterbird community richness and abundance estimated from the best SEM are summarised in Table 4. The total effects of habitat availability and heterogeneity were comparable for both species richness and abundance. Nevertheless, the habitat conditions had slightly stronger effects on waterbird richness than on abundance (Table 4 and Fig. 6).

Even though the model without direct and indirect link between abundance and species richness ranked highest, three alternative models (M2, M3 and M5 in Table) were plausible and could not be totally rejected. This is also reflected in that the difference of AIC was <4 (Table 3), suggesting that the alternative models were also supported. The alternative models can be found in supplementary information.

	BIC	χ^2	d.f.	P	RMSEA	SRMR	CFI	GFI
No direct effect (M1)	1899.70	9.46	3	0.051	0.08	0.03	0.99	0.98
Abundance richness (M2)	1903.93	9.46	2	0.038	0.13	0.03	0.98	0.98
Richness abundance (M3)	1903.93	9.46	2	0.038	0.13	0.03	0.98	0.98
Richness abundance (M4)	1908.16	9.46	1	0.021	0.19	0.03	0.98	0.98
No direct effect with correlated error (M5)	1903.93	9.46	2	0.038	0.13	0.03	0.98	0.98

Table 3 Goodness-of-fit statistics comparing the five models specified in Fig. 2

BIC, sample size-adjusted Bayesian information criteria; d.f., degree of freedom; RMSEA, root mean square error of approximation; SRMR, standardized root mean square residual; CFI, comparative fit index; GFI, goodness-of-fit index. Best model, which meets all criteria, is indicated in bold.

Table 4 The estimates of direct, indirect and total effects of habitat availability and heterogeneity on wintering waterbird species richness and abundance based on Fig. 6

	Habitat availability			Habitat heterogeneity		
	Direct	Indirect	Total	Direct	Indirect	Total
Richness	0.74	0.18	0.92	0.17	0.79	0.96
Abundance	-0.56	1.43	0.87	1.34	-0.60	0.74

Fig. 6 The best structural equation model for the wintering waterbird abundance and species richness. The standardized path coefficients are shown with statistical significance (***) $P < 0.001$; ** $P < 0.01$ and NS, $P > 0.05$). The thickness of the line indicates the strength of the effect. Dashed lines indicate negative effect. The covariations between observed variables are omitted for simplicity. Goodness of fit: $\chi^2 = 9.46$, d.f. = 4, $P = 0.05$, RMSEA = 0.08, CFI = 0.99. CFI, comparative fit index; RMSEA, root mean square error of approximation.

As the two latent variables (i.e. availability and heterogeneity) were significantly correlated ($P < 0.01$, path coefficient = 1.07, Fig. 6), and the difference of their effects on the community indices were negligible (Table 4), they were combined into one variable and referred to as habitat quality. With this newly defined variable, we fitted a set of models using the same general conceptual model (Fig. 2). The goodness-of-fit statistics of all candidate models were summarised in Table 5, and the best fitted model (M6 in Table 5) was presented in Fig. 7. The reduced models were superior to their more complicated counterparts with smaller Bayesian information criteria (BIC), RMSEA and standardized root mean square residual (SRMR), and higher CFI and goodness-of-fit index (GFI) (Tables 3 & 5). Similar results were achieved with the simplified models: both richness and abundance were significantly

positively affected by habitat quality, and the influences of habitat quality on richness and abundance were comparable (i.e. 0.90 and 0.86). The best fitted model had relatively high predictive power (R^2 was 0.81 and 0.73 for richness and abundance, respectively, Fig. 7), which was higher than individual GAMMs (Table 2). In addition, the relative importance (i.e. path coefficient) of the measured environmental variables in defining habitat quality was similar in the two models (i.e. Figs 6 & 7).

Discussion

Our analysis found no evidence supporting a causal link between abundance and richness for migratory waterbirds in the Poyang region, although we did find a positive correlation between species richness and abundance, which is consistent with previous studies on plants (Currie, 1991; Stevens & Carson, 1999; Šimová *et al.*, 2011), land birds (Currie *et al.*, 2004; Evans *et al.*, 2007; Chiari *et al.*, 2010), invertebrates (Yee & Juliano, 2007) and bacteria (Jankowski, Schindler & Horner-Devine, 2014). In addition, and in concordance with many previous studies (e.g. Hurlbert & Jetz, 2010; McGlynn *et al.*, 2010; Šimová *et al.*, 2011), we found that richness and abundance responded to habitat conditions differently when analysed using generalised additive models, although relationships with the most important variable (i.e. size of shallow waters) were generally positive.

The positive relationship between species richness and abundance seemingly confirmed the MIH: communities with more waterbirds tended to have more species. However, the often reported unimodal relationship (Waide *et al.*, 1999; Cardinale *et al.*, 2009) was not observed in our data, which might indicate that resource availability is not a limiting factor for wintering waterbird communities in the Poyang region. In addition, the positive correlation is probably not a causal relationship (cf. Cardinale *et al.*, 2009), rather both abundance and richness are responding to habitat size and/or other habitat characteristics in a similar way (as below).

Environmental determinants of the wintering waterbird community

As the largest freshwater wetland system in East Asian–Australasian Flyway, Poyang Lake accommodates hundreds of thousands of migratory waterbirds every winter (Ji *et al.*, 2007; Wang *et al.*, 2013). The majority of wintering birds, such as waders, cranes and storks, use shallow waters and mudflats as their primary foraging ground (Wang *et al.*, 2013; Jia *et al.*, 2014). The GAMMs and SEMs

Table 5 Goodness-of-fit statistics comparing the five simplified models specified in Fig. 2

	BIC	χ^2	d.f.	P	RMSEA	SRMR	CFI	GFI
No direct effect (M6)	1886.15	12.86	7	0.082	0.051	0.02	0.99	0.97
Abundance richness (M7)	1890.39	12.86	6	0.053	0.110	0.02	0.99	0.97
Richness abundance (M8)	1890.39	12.86	6	0.053	0.110	0.02	0.99	0.97
Richness abundance (M9)	1894.62	12.86	5	0.032	0.140	0.02	0.98	0.97
No direct effect with correlated error (M10)	1890.39	12.86	6	0.053	0.110	0.02	0.99	0.97

CFI, comparative fit index; RMSEA, root mean square error of approximation; GFI, goodness-of-fit index; BIC, Bayesian information criteria; SRMR, standardized root mean square residual.

Best fitted model in bold (see Table 3 for term definition).

Fig. 7 The simplified SEM for the wintering waterbird abundance and species richness. The standardized path coefficients are shown with statistical significance (*** $P < 0.001$; ** $P < 0.01$; and NS, $P > 0.05$). The thickness of the line indicates the strength of the effect. Dashed lines indicate negative effect. The co-variations between observed variables are omitted for simplicity. Goodness of fit: $\chi^2 = 11.86$, d.f. = 6, $P = 0.05$, RMSEA = 0.10, CFI = 0.99. CFI, comparative fit index; RMSEA, root mean square error of approximation.

confirmed the importance of area and number of shallow waters for waterbird richness and abundance. The unique hydrological regimes in Poyang Lake determine the size, distribution and quality of various wintering habitats through the control of variation in water depth (Wang *et al.*, 2012) and vegetation (Guan *et al.*, 2014). Although both GAMM and SEM demonstrated the importance of variables derived from interpretation of satellite images, SEM suggested that they might not be suitable to define habitat availability and heterogeneity due to the high correlation between these two variables. Habitat availability and heterogeneity are conceptually convenient but might be difficult to define quantitatively using field measurements (Tews *et al.*, 2004), as demonstrated in this study. In recognising this, we defined a single latent variable,

termed 'habitat quality', comprised of all remotely sensed variables for the SEM. The simplified SEM fitted the data better with significant information gain (AIC was 1899.70 and 1886.15 for the first and simplified SEM, respectively). The standardised path coefficients indicated that the total area of shallow waters within a lake was the most important environmental factor for wintering waterbird community, followed by the number of mudflat patches, which was generally in agreement with the GAMMs fitted separately for species richness and abundance. Furthermore, in line with other studies (e.g. Currie *et al.*, 2004), we found that waterbird species richness was more closely related to environmental factors than abundance, although the difference was small. This pattern was evident according to GAMMs and integrated modelling using SEM. One plausible explanation is that richness was measured more accurately than abundance in survey data sets.

The causality between abundance and species richness

Biological diversity comprises both species richness, that is the number of species in a community, and their abundance. Although our data confirmed the generally positive correlation between wintering waterbird abundance and species richness, there was insufficient support of the causality between the two community indices implied by the MIH. Out of all candidate SEMs, the models without direct effect between richness and abundance were the only ones with a RMSEA below 0.08, and RMSEA of the other models with a direct link indicated poor fit (>0.10) (MacCallum, Browne & Sugawara, 1996). Furthermore, the incremental fit indices also showed that models without link between richness and abundance performed better (Hu & Bentler, 1999).

As demonstrated by other studies, a relationship could be spurious if two variables respond in a similar way to exogenous factors such as productivity (Srivas-

tava & Lawton, 1998). Using GAMM, in which temporal and site variations were accounted for, we showed that species richness of wintering waterbirds was positively related to the logarithm of the total area of shallow waters, and the relationship was linear. Although we did not measure resource directly, the size of habitat could be used as a proxy of available resources as the spatial variation of resource density might not be small in shallow waters (i.e. the linear relationship between habitat size and available resource). This finding fits well with the SAR (Arrhenius, 1921; Gleason, 1922; Schoener, 1976; Simberloff, 1976), a special case of the energy-species theory (Hurlbert, 2006), which states that along a gradient of ecosystems of increasing size, the numbers of species inhabiting those ecosystems increase, rapidly at first, but then more slowly for larger ecosystems. For abundance, however, the relationship deviated slightly from linearity but was still positive. The partial response curves clearly showed similar but not identical relationships. Moreover, we found that the area of mudflats had opposite effects on abundance and richness, although its importance for both richness and abundance was lower than water area. These divergences in the responses of richness and abundance to environmental conditions provided complementary evidence of the weak causality between abundance and richness.

Unlike typical regression techniques, structural equation modelling enables researchers to test specific predictions about the importance of causal pathways (Mitchell, 1992; Grace *et al.*, 2010). In a study of invertebrates in natural tree holes, Yee & Juliano (2007) found the direct and indirect (via abundance) effects of productivity on the species richness, and confirmed the MIH. In contrast, we did not find clear evidence to support the causal link between abundance and richness for wintering waterbirds in Poyang Lake, even though we could not reject causality unequivocally [the ΔAIC was <4 , suggesting that the alternative models were also supported (Burnham & Anderson, 2004)]. The model with no direct and indirect link between abundance and species richness had the most support from data, and was clearly better than the alternatives. Furthermore, the three plausible alternative models (with direct link either from abundance to richness or from richness to abundance, or no direct links but with correlated error) had similar path coefficients (Supporting information) and support from the data. This gave further evidence that wintering waterbird species richness and abundance are two intrinsic community indices, which indeed covary with environmental variables, and could be independent of each other.

The lack of causality between abundance and richness in our study may be due to the group of organisms analysed. In a review on diversity patterns in the freshwater realm, Heino (2011) found that there was no clear geographical diversity gradient for freshwater birds, which was contrary to their terrestrial counterparts. Furthermore, in a study of forest bird communities in Europe and North America, Mönkkönen *et al.* (2006) found a linear relationship between bird density and annual productivity, and that increased density and energy use resulted in more species. However, the link of energy use–density–species richness was weaker for migrants than for residents. Migratory species, especially long-distance migrants, spend different periods of their annual cycles in different parts of the world; therefore, the regional species pool and population are affected by broad-scale adverse changes in breeding and wintering areas, as well as stopover sites during migration (Newton, 2008). Thus, locally measured habitat quality (i.e. at their wintering grounds in this study) could only partially explain the observed temporal and spatial variations, and a larger scale study combining breeding and wintering habitats might improve our understanding of regional diversity patterns. Furthermore, Poyang Lake is located at the subtropical monsoon zone, and displays strong annual wet–dry cycles. Hence, inundation patterns in previous years may also be important drivers (Jia *et al.*, 2014), through impacts on lake productivity. The temporal correlation in waterbird community metrics may be potentially important, and weaken the modelled causality.

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References

- Arrhenius O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.

- Barton K. (2012) MuMIn: Multi-model inference. R package version 1.7.7.
- Belmaker J. & Jetz W. (2011) Cross-scale variation in species richness–environment associations. *Global Ecology and Biogeography*, **20**, 464–474.
- Blakely T.J. & Didham R.K. (2010) Disentangling the mechanistic drivers of ecosystem-size effects on species diversity. *Journal of Animal Ecology*, **79**, 1204–1214.
- Brown J.H. (1981) Two decades of homage to Santa Rosalia: toward a general theory of diversity. *Animal Zoology*, **21**, 877–888.
- Buckley L.B. & Jetz W. (2010) Lizard community structure along environmental gradients. *Journal of Animal Ecology*, **79**, 358–365.
- Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.
- Burnham K.P. & Anderson D.R. (2004) Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods & Research*, **33**, 261–304.
- Cardinale B.J., Hillebrand H., Harpole W.S., Gross K. & Ptnick R. (2009) Separating the influence of resource ‘availability’ from resource ‘imbalance’ on productivity–diversity relationships. *Ecology Letters*, **12**, 475–487.
- Chase J.M. & Leibold M.A. (2002) Spatial scale dictates the productivity–biodiversity relationship. *Nature*, **416**, 427–430.
- Chiari C., Dinetti M., Licciardello C., Licitra G. & Pautasso M. (2010) Urbanization and the more-individuals hypothesis. *Journal of Animal Ecology*, **79**, 366–371.
- Currie D.J. (1991) Energy and large-scale patterns of animal-and plant-species richness. *The American Naturalist*, **137**, 27–49.
- Currie D.J., Mittelbach G.G., Cornell H.V., Field R., Guégan J.F., Hawkins B.A. *et al.* (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology letters*, **7**, 1121–1134.
- Drever M.C., Goheen J.R. & Martin K. (2009) Species-energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. *Ecology*, **90**, 1095–1105.
- Dronova I., Gong P. & Wang L. (2011) Object-based analysis and change detection of major wetland cover types and their classification uncertainty during the low water period at Poyang Lake, China. *Remote Sensing of Environment*, **115**, 3220–3236.
- Evans K.L., Greenwood J.J. & Gaston K.J. (2007) The positive correlation between avian species richness and human population density in Britain is not attributable to sampling bias. *Global Ecology and Biogeography*, **16**, 300–304.
- Evans K.L., James N.A. & Gaston K.J. (2006) Abundance, species richness and energy availability in the North American avifauna. *Global Ecology and Biogeography*, **15**, 372–385.
- Gaston K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gleason H.A. (1922) On the relation between species and area. *Ecology*, **3**, 158–162.
- Grace J.B., Anderson T.M., Olff H. & Scheiner S.M. (2010) On the specification of structural equation models for ecological systems. *Ecological Monographs*, **80**, 67–87.
- Grace J.B., Schoolmaster D.R. Jr, Guntenspergen G.R., Little A.M., Mitchell B.R., Miller K.M. *et al.* (2012) Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere*, **3**, art73.
- Groner E. & Novoplansky A. (2003) Reconsidering diversity–productivity relationships: directness of productivity estimates matters. *Ecology Letters*, **6**, 695–699.
- Grueber C.E., Nakagawa S., Laws R.J. & Jamieson I.G. (2011) Multimodel inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, **24**, 699–711.
- Guan L., Wen L., Feng D., Zhang H. & Lei G.C. (2014) Delayed flood recession in central Yangtze floodplains can cause significant food shortages for wintering geese: results of inundation experiment. *Environmental management*, **54**, 1331–1341.
- Heino J. (2011) A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, **56**, 1703–1722.
- Hobson K.A. & Wassenaar L.I. (1996) Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia*, **109**, 142–148.
- Honkanen M., Roberge J.M., Rajasärkkä A. & Mönkkönen M. (2010) Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. *Global Ecology and Biogeography*, **19**, 61–71.
- Hu L.T. & Bentler P.M. (1999) Cut off criteria for fit indexes in covariance structure analysis: conventional criteria versus new alternatives. *Structural Equation Modeling*, **6**, 1–55.
- Hurlbert A.H. (2004) Species–energy relationships and habitat complexity in bird communities. *Ecology Letters*, **7**, 714–720.
- Hurlbert A.H. (2006) Linking species–area and species–energy relationships in *Drosophila* microcosms. *Ecology Letters*, **9**, 287–294.
- Hurlbert A.H. & Jetz W. (2010) More than “more individuals”: the nonequivalence of area and energy in the scaling of species richness. *The American Naturalist*, **176**, E50–E65.
- Hutchinson G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals. *The American Naturalist*, **93**, 145–159.
- Jankowski K., Schindler D.E. & Horner-Devine M.C. (2014) Resource availability and spatial heterogeneity control bacterial community response to nutrient enrichment in lakes. *PLoS ONE*, **9**, e86991.
- Ji W.T., Zeng N.J., Wang Y.B., Gong P., Xu B. & Bao S. (2007) Analysis on the waterbirds community survey of

- Poyang Lake in winter. *Geographic Information Sciences*, **13**, 51–64.
- Jia Y.F., Guan L., Wang Y.Y., Liu G.H., Lei G.C. & Wen L. (2014) Combining population growth model and generalized additive model to determine optimal water level for waterbird conservation: a case study of Siberian crane (*leucogeranus leucogeranus*) in Poyang Lake, China. *River Research and Applications*, doi: 10.1002/rra.2840.
- Jia Y.F., Jiao S.W., Zhang Y.M., Zhou Y., Lei G. & Liu G.H. (2013) Diet shift and its impact on foraging behaviour of Siberian Crane (*Grus leucogeranus*) in Poyang Lake. *PLoS ONE*, **8**, e65843.
- Kissling W.D., Field R. & Gaese K.B. (2008) Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects? *Global Ecology and Biogeography*, **17**, 327–339.
- Laughlin D.C., Abella S.R., Covington W.W. & Grace J.B. (2007) Species richness and soil properties in *Pinus ponderosa* forests: a structural equation modelling analysis. *Journal of Vegetation Science*, **18**, 231–242.
- Lillesand T.M., Kiefer R.W. & Chipman J.W. (2008) Digital image interpretation and analysis. *Remote Sensing and Image Interpretation* **6**, 585–592.
- MacArthur R.H. (1972) *Geographical Ecology*. Princeton University Press, Princeton, NJ.
- MacArthur R.H. & Wilson E.O. (1967) *The Theory of Island Biogeography*. Monographs in Population Biology. Princeton University Press, Princeton, New Jersey.
- MacCallum R.C., Browne M.W. & Sugawara H.M. (1996) Power analysis and determination of sample size for covariance structure modelling. *Psychological Methods* **1**, 130–149.
- Mason N.W., Irz P., Lanoiselée C., Mouillot D. & Argillier C. (2008) Evidence that niche specialization explains species–energy relationships in lake fish communities. *Journal of Animal Ecology*, **77**, 285–296.
- McGlynn T.P., Weiser M.D. & Dunn R.R. (2010) More individuals but fewer species: testing the ‘more individuals hypothesis’ in a diverse tropical fauna. *Biology Letters*, **6**, 490–493.
- Menezes R.F., Borchsenius F., Svenning J.C., Søndergaard M., Lauridsen T.L., Landkildehus F. & Jeppesen E. (2013) Variation in fish community structure, richness, and diversity in 56 Danish lakes with contrasting depth, size, and trophic state: does the method matter? *Hydrobiologia*, **710**, 47–59.
- Mitchell R.J. (1992) Testing evolutionary and ecological hypotheses using path analysis and structural equation modelling. *Functional Ecology* **6**, 123–129.
- Mittelbach G.G., Steiner C.F., Scheiner S.M., Gross K.L., Reynolds H.L., Waide R.B. *et al.* (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381–2396.
- Mönkkönen M., Forsman J.T. & Bokma F. (2006) Energy availability, abundance, energy-use and species richness in forest bird communities: a test of the species–energy theory. *Global Ecology and Biogeography*, **15**, 290–302.
- Mori T., Murakami M. & Saitoh T. (2010) Latitudinal gradients in stream invertebrate assemblages at a regional scale on Hokkaido Island, Japan. *Freshwater Biology*, **55**, 1520–1532.
- Newton I. (2008) *The Ecology of Bird Migration*. Academic Press, London.
- O’Brien E.M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa’s woody flora. *Journal of Biogeography*, **20**, 181–198.
- Phillips L.B., Hansen A.J. & Flather C.H. (2008) Evaluating the species energy relationship with the newest measures of ecosystem energy: NDVI versus MODIS primary production. *Remote Sensing of Environment*, **112**, 4381–4392.
- Preston F.W. (1948) The commonness, and rarity, of species. *Ecology*, **2**, 254–283.
- Preston F.W. (1960) Time and space and the variation of species. *Ecology*, **4**, 611–627.
- R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*, Reference Index Version 3.1.1. R Foundation for Statistical Computing: Vienna, Austria; ISBN 3-900051-07-0, Available at: <http://www.R-project.org>.
- Rosseel Y. (2012) lavaan: an R package for structural equation modelling. *Journal of Statistical Software*, **48**, 1–36.
- Sandom C., Dalby L., Fløjgaard C., Kissling W.D., Lenoir J., Sandel B. *et al.* (2013) Mammal predator and prey species richness are strongly linked at macroscales. *Ecology*, **94**, 1112–1122.
- Schoener T.W. (1976) The species–area relationship within archipelagos: models and evidence from island birds. *Proceedings of XVI International Ornithological Congress*, Vol. 6, pp. 629–642.
- Shankman D., Keim B.D. & Song J. (2006) Flood frequency in China’s Poyang Lake region: trends and teleconnections. *International Journal of Climatology*, **26**, 1255–1266.
- Simberloff D. (1976) Experimental zoogeography of islands: effects of island size. *Ecology*, **57**, 629–648.
- Šimová I., Storch D., Keil P., Boyle B., Phillips O.L. & Enquist B.J. (2011) Global species–energy relationship in forest plots: role of abundance, temperature and species climatic tolerances. *Global Ecology and Biogeography*, **20**, 842–856.
- Srivastava D.S. & Lawton J.H. (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. *The American Naturalist*, **152**, 510–529.
- Stevens M.H.H. & Carson W.P. (1999) Plant density determines species richness along an experimental fertility gradient. *Ecology*, **80**, 455–465.

- Storch D., Evans K.L. & Gaston K.J. (2005) The species–area–energy relationship. *Ecology Letters*, **8**, 487–492.
- Tavares D.C., Guadagnin D.L., de Moura J.F., Siciliano S. & Merico A. (2015) Environmental and anthropogenic factors structuring waterbird habitats of tropical coastal lagoons: implications for management. *Biological Conservation*, **186**, 12–21.
- Tews J., Brose U., Grimm V., Tielbörger K., Wichmann M.C., Schwager M. *et al.* (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.
- Waide R.B., Willig M.R., Steiner C.F., Mittelbach G., Gough L., Dodson S.I. *et al.* (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, **30**, 257–300.
- Wang X.H. (2004) *Poyang Lake Wetland Ecosystem Assessment*. Science Press, Beijing.
- Wang L., Dronova I., Gong P., Yang W.B., Li Y.G. & Liu Q. (2012) A new time series vegetation–water index of phenological–hydrological trait across species and functional types for Poyang Lake wetland ecosystem. *Remote Sensing of Environment*, **125**, 49–63.
- Wang Y.Y., Jia Y.F., Guan L., Lu C., Lei G., Wen L. *et al.* (2013) Optimising hydrological conditions to sustain wintering waterbird populations in Poyang Lake National Natural Reserve: implications for dam operations. *Freshwater Biology*, **58**, 2366–2379.
- Weiher E. (1999) The combined effects of scale and productivity on species richness. *Journal of Ecology*, **87**, 1005–1011.
- Wen L., Rogers K., Saintilan N. & Ling J. (2011) The influences of climate and hydrology on population dynamics of waterbirds in the lower Murrumbidgee River floodplains in Southeast Australia: implications for environmental water management. *Ecological Modelling*, **222**, 154–163.
- Wood S.N. (2001) mgcv: GAMs and generalized ridge regression for R. *R News*, **1**, 20–25.
- Wright D.H. (1983) Species-energy theory: an extension of species area-theory. *Oikos*, **41**, 496–506.
- Wright D.H., Currie D.J. & Maurer B.D. (1993) Energy supply and patterns of species richness on local and regional scales in R. In: *Species Diversity in Ecological Communities* (Eds E. Ricklefs & D. Schluter), pp. 66–74. University of Chicago Press, Chicago, IL, U.S.A.
- Yee D.A. & Juliano S.A. (2006) Consequences of detritus type in an aquatic microsystem: effects on water quality, micro-organisms and performance of the dominant consumer. *Freshwater Biology*, **51**, 448–459.
- Yee D.A. & Juliano S.A. (2007) Abundance matters: a field experiment testing the more individuals' hypothesis for richness–productivity relationships. *Oecologia*, **153**, 153–162.
- Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A. & Springer G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The three alternative SEMs.

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