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Can wetlands maintained for human use also help conserve biodiversity? Landscape-scale patterns of bird use of wetlands in an agricultural landscape in north India

K.S. Gopi Sundar [a,b,*], Swati Kittur [b]

[a] International Crane Foundation, E11376, Shady Lane Road, Baraboo, WI 53913, USA
[b] Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, Mysore 570 002, India

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ABSTRACT

Wetlands in tropical agricultural landscapes are maintained largely by local institutions explicitly for human use, which is assumed to deter biodiversity. Conservation efforts have been biased towards protecting large wetlands that are assumed to be adequate to conserve the majority of species of focal taxa, usually birds. These assumptions remain untested, and landscape-scale conservation planning for wetlands is largely absent, as is a generalised understanding of wetland use by focal taxa. We designed a landscape-scale survey to understand patterns and processes determining beta diversity of birds using agricultural wetlands in south-western Uttar Pradesh, India where wetlands have experienced prolonged and intensive human use for several centuries. Observed bird species richness (99 species in 28 wetlands) is the highest known for any agricultural landscape in south Asia signifying that even intensive human use of wetlands does not necessarily deter their ability to retain biodiversity. Birds exhibited strong scale dependent wetland use underscoring the need to conserve wetlands of varying sizes and at varying densities on the landscape. Beta diversity was due largely to species turnover (0.877) with minimal effect due to nestedness (0.055) suggesting that conserving a few large wetlands will not adequately meet goals of conserving the majority of wetland bird species. Prevailing assumptions regarding biodiversity conservation in tropical agricultural wetlands require being revised, and a landscape-scale approach that incorporates ecological realities is needed. Incorporating local institutions alongside formal protectionist methods offer a potential win–win situation to maximise conservation of biodiversity in tropical agricultural wetlands.

1. Introduction

Inland wetlands amid croplands, or agricultural wetlands (not including croplands such as flooded rice paddies, but only discrete wetlands recognised as lakes, ponds, and oxbow lakes), tend to be small and isolated but can provide a range of ecological services such as groundwater recharge, and also ensure the preservation of biodiversity (Semlitsch and Bodie, 1998; Leibowitz, 2003). Scientific attention on agricultural wetlands has been minimal, and practically all the attention has been on wetlands located in temperate regions (Finlayson and Spiers, 1999; Zedler and Kercher, 2005). The vast majority of studies have focused on wetlands that are maintained on the landscape as part of national networks of protected areas or via payments to farmers (Davies et al., 2009; Thiere et al., 2009; Fennessey and Craft, 2011). Biodiversity conservation and ecological services, particularly water retention for agriculture, are the primary impetus to conserving the majority of these wetlands. Human use of these wetlands is either limited or absent to help maximise conservation of focal taxa and to improve water quality (Zedler and Kercher, 2005; Fennessey and Craft, 2011).

The situation in most tropical countries that have much higher human densities and species richness is starkly differently. The majority of freshwater inland wetlands in the tropics are agricultural wetlands which experience intensive, sustained, and multiple human uses including cattle grazing, harvest of multiple wetland products (e.g. reeds, fish, silt), and water for agricultural and domestic purposes (Adger and Luttrell, 2000; Silvius et al., 2000; Dixon and Wood, 2003; Gopal, 2005; personal observations). A miniscule proportion of such wetlands are protected for biodiversity conservation in most tropical countries, and there is growing interest in enhancing persistence of agricultural wetlands for their various ecological services, including as habitat for biodiversity conservation (Zedler and Kercher, 2005; Brander et al., 2006;

* Corresponding author at: International Crane Foundation, E11376, Shady Lane Road, Baraboo, WI 53913, USA.
E-mail address: gopi@savingcranes.org (K.S.G. Sundar).

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Verhoeven and Setter, 2010). It is widely assumed that removal of human use from wetlands is necessary to maximise biodiversity conservation (Gopal, 1999; Middleton, 2013). Increasing attention is being directed at ascertaining the value of large wetlands already assumed to be important, and towards wetlands that are part of national protected area networks. As a result, an unbiased understanding of how agricultural wetlands in general may be contributing towards conserving and maintaining biodiversity is missing.

Landscape-scale effects have been documented for several taxa species that use agricultural wetlands. It is becoming increasingly evident that landscape-scale characteristics interact with site-level habitat characteristics to affect species densities and life histories (Naugle et al., 1999; Albanese and Davis, 2013). Additionally, the value of understanding processes contributing to landscape-scale diversity, or β-diversity, of focal taxa is gaining in importance, especially since this understanding can aid in conservation planning greatly (Paracuellos, 2006; Baselga, 2010). The two processes that drive β-diversity are nestedness and species turnover (Baselga, 2010). Nestedness occurs when the full complement of species are found in few sites on the landscape, with assemblages in other sites being subsets of the ones found in the few sites. Alternatively, landscapes where species turnover is dominant has sites with dissimilar species assemblages requiring a large number of sites to ensure that the full complement of species is accounted for. If nestedness is dominant, efficient conservation can be achieved by identification and protection of the few sites to ensure that at least some populations of all species are conserved. Conversely, if species turnover is the dominant process, effective conservation for the full complement of species of the focal taxa can be achieved only by retaining a large number of sites on the landscape (see Baselga, 2010). Landscape-scale understanding of patterns and processes driving wetland use by taxa can therefore be invaluable to help plan wetland conservation, but is rare in most regions of the world.

The lack of attention to wetland ecology is readily apparent in south Asia (Dudgeon, 2003; Zedler and Kercher, 2005). This region has among the highest human densities in the world with also the highest level of agricultural intensification spanning several centuries (Ellis et al., 2010). Despite these pressures, a relatively large number of agricultural wetlands remain as flooded natural depressions as well as water storage structures maintained for irrigation (Space Application Centre, 2010; Panigrahy et al., 2012). Wetlands are maintained here as part of a long-standing tradition explicitly for human use (Ambastha et al., 2007; Sundar, 2011). Growing demand for drained agricultural land has lead to widespread illegal conversions of wetlands, but strong dependence on wetland resources (e.g. for grazing, cattle collection of wetland products such as lotus stems for food) have prompted farmers to acquire legal grounds for their preservation as common lands (Singh, J. versus State of Punjab, 2011). An understanding of ecological values of these wetlands, however, has been minimal. Even basic aspects such as mapping using robust, repeatable methods have been achieved relatively recently (Space Application Centre, 2010; Panigrahy et al., 2012). Wetland conservation focuses on single, large wetland sites with large number of wintering waterfowl, and discussions on landscape-scale approaches are negligible (Ambastha et al., 2007; Nagabhatla et al., 2010). Conservation discussions also continue to repeat assumptions regarding the deterrence of biodiversity due to human use. Converting a large number of common use wetlands to reserves seems practically implausible given the millions of people currently dependent on the wetlands, and the costs involved in acquiring so much land. In addition, conversions of common use wetlands to reserves is seldom without political consequences, and reserves experience significant ecological changes that do not always fulfill the goals of species conservation (Gopal, 1999; Lewis, 2003). Additionally, the focus is entirely on conserving large wetlands with the implicit assumption that this approach will conserve the majority of focal wetland species (Nagabhatla et al., 2010; Space Application Centre, 2010). This approach assumes therefore that β-diversity follows a strong nested pattern, but it is not known if this is indeed the case. Can wetlands maintained explicitly for human use, and experiencing intensive, sustained use also be useful for biodiversity conservation, and are there landscape-scale patterns of wetland use by focal taxa that require consideration while considering agricultural wetlands as repositories for biodiversity?

To answer these questions we conducted a landscape-scale study of winter wetland use by birds in seven districts of south-western Uttar Pradesh in the Gangetic flood-plains focusing on wetlands not protected as bird reserves. This region is listed as an internationally important landscape for wetland birds (BirdLife International, 2003), but surveys of wetland use by birds using robust field designs are absent. Recent work focusing on the landscape as a whole has documented persistence of a surprisingly high bird diversity, including the majority of the global populations of several bird species of global conservation concern (Sundar, 2011; Sundar and Kittur, 2012). The seven districts have >10,000 persisting wetlands of vastly varying sizes (see Section 2), of which only four are protected as bird sanctuaries (R. De, Uttar Pradesh Forest Department, pers. comm.). Wetland distribution is irregular varying spatially in extent and density (Fig. 1c and d) providing an excellent opportunity to assess if bird use of wetlands varies due to these two landscape-scale metrics of wetland distribution. In this study, we specifically assess: (i) whether birds exhibit variation in wetland use due to two landscape-scale metrics (size and density) of wetland distribution (or scale dependent wetland use), and (ii) the dominant processes determining β-diversity of birds (nestedness or species turnover) using these agricultural wetlands.

2. Methods

2.1. Study area

South-western Uttar Pradesh is located in the north Indian Gangetic floodplains, and has been almost entirely converted to non-woody cereal agriculture for at least three centuries with human population densities currently ranging from 500 to 3000 people km^2 (Ellis et al., 2010). Agricultural wetlands comprise <1% of the landscape with the majority being small and isolated (Anonymous, 2007). The primary crops here are rice during the rainy season or monsoon (June–October) and wheat during the winter (November–February), with fields largely left fallow during the summer. We focused on seven districts in south-western Uttar Pradesh bounded by the Ganges and Yamuna rivers (Fig. 1a and b). Monsoonal rainfall in 2012 was delayed starting in mid-August against the normal start in July. Also, the total volume of rainfall (460 mm) was well below normal in south-west Uttar Pradesh (annual mean for 2000–2009: 1300 mm; District Magistrate Office, Etawah, pers. comm.). The survey therefore assessed wetland use by birds during a below-normal rainfall year when the landscape was water stressed. Additional details of land use and bird diversity on the landscape are available elsewhere (Sundar, 2011; Sundar and Kittur, 2012).

Our personal observations have shown that wetlands experience year-round use by people. The most common uses included grazing a variety of livestock (cattle, pigs, sheep, goat), water extraction for domestic and agricultural use, harvest of several natural resources including vegetation and aquatic fauna, removal of dried soil in the summer to strengthen walls and agricultural dykes, cultivation of water chestnut in the monsoon, and illegal hunting of waterfowl using both guns and poisons. The over-

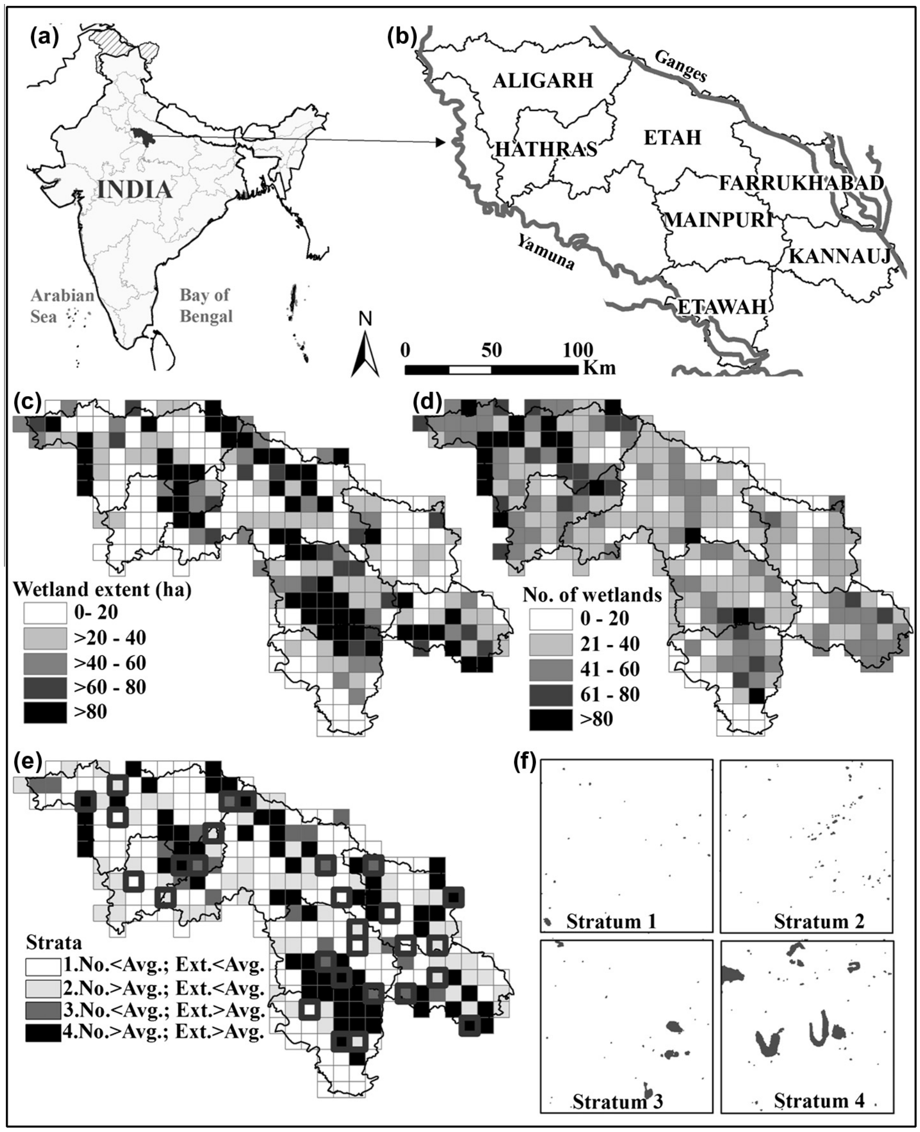

Fig. 1. Location of the survey area in India (a; hatched areas are internationally disputed boundaries), and the focal districts in the state of Uttar Pradesh with major rivers marked (b). The *a priori* stratification using extent (c) and density of wetlands (d) in each 5′ × 5′ grid cell into four strata and the randomly chosen grids (in bold, e) are shown. Representative grids of each of the four strata showing the variation in the extent and density of wetlands are also shown (f).

whelming majority of wetlands are common lands maintained by democratically elected village councils. A few wetlands are privately owned and many have mixed ownership with multiple governmental departments and private farmers. Though several wetlands are labelled as perennial on older official maps, field observations showed that the vast majority are now seasonal. There is no systematic documentation of ownership, history and intensity of human use, or hydrology of agricultural wetlands in this region making it impossible to consider these variables *a priori* to design a field study. These aspects could affect bird use of wetlands, but could not be taken into consideration while designing this study. All the wetlands had agriculture up to their edge with wheat being the primary crop during the survey in the focal landscape.

2.2. Wetland mapping

We used LISS-III satellite imageries from the winter of 2009–10 (a near-normal rainfall year) to identify and map wetlands in the focal districts. The imageries provided a pixel resolution of 23.5 × 23.5 m. We used a combination of unsupervised classification (in ERDAS Imagine 8.5), and visual reclassification using onscreen digitization, Area of Interest and recode functionality to identify wetlands (see Sundar and Kittur, 2012). The final wetland layer was verified using Google Earth and during field visits between August and October 2012. The final wetland map had 93% accuracy (see Appendix S1). We identified 11,793 discrete wetlands; mean size of wetlands was 1.25 ha (±7.79 SD; range: 0.06–338). We used a two-stage stratified random procedure to identify focal wetlands and also ensuring our ability to assess scale dependent wetland use. First, we overlaid the wetland map with a 5′ × 5′ grid corresponding roughly to 10 × 10 km, and ascertained the density and extent of wetlands in each grid (Fig. 1c and d) using ArcGIS10.1. The overall mean number of wetlands per grid was 37 (±13 SD), and extent was 50 (±21SD) ha. Number and extent of wetlands varied at the district level (see Appendix S2). This likely represented a combination of district-level variations in geography, historical land use management styles and decisions regarding cropping patterns. We therefore used mean values in each district and classified grids into one of four strata ranging from grids with <mean number and extent of wetlands (stratum 1), to grids with >mean number and extent of wetlands (stratum 4, Fig. 1e). One grid of each stratum was randomly chosen within each district (Fig. 1e, bold squares). In each chosen grid, we randomized the choice of focal wetland for survey (Fig. 1f). For strata with >mean values of wetland extent, we biased the choice towards larger wetlands (>1 ha). For this, we eliminated all wetlands ⩽1 ha from the sample, and randomly picked the focal wetland from the remaining wetlands. Since small wetlands dominated the landscape (see Fig. 1) this ensured the representation of wetlands of all potential sizes in the final sample. Randomly selected focal wetlands covered a large variation in size (range: 0.05–32.77 ha; mean = 6.029 ± 8.9 SD ha; see Appendix S3).

2.3. Bird use of wetlands

We counted birds at focal wetlands during January and February 2013. This period is after the completion of inward migration and before the return migration of migratory birds ensuring minimal variation due to season. At each wetland, two observers identified and counted all birds simultaneously using the double-observer method that enables estimation of detection probability with which to obtain robust abundance estimates (Nichols et al., 2000). We used the method to estimate and correct for potential detection bias due to the two observers as well as wetland size (see Analyses below). At small wetlands, both observers counted from one or two locations from where the entire wetland was visible. At larger wetlands, observers walked the periphery covering parts of the wetland together. At wetlands with large concentrations of waterbirds, double-observer estimates were derived in a sub-section of the wetland using a spotting scope, and counts for the rest of the wetland were conducted by any one observer. Emergent vegetation along the periphery or in the wetlands that could reduce visibility was absent in all but three wetlands due to agriculture spread up to the water's edge, intensive human use of wetlands, and likely due to low rainfall. Both observers meandered through larger wetland to flush skulking species and to ensure coverage of the entire wetland.

2.4. Analyses

2.4.1. Bird use of wetlands: species richness and abundance

We computed sample based rarefaction curves using presence/absence of species across visited wetlands to assess sampling adequacy using EstimateS (Colwell et al., 2012). We computed the Chao 2 estimator to assess the total number of species occurring in agricultural wetlands in the focal study area. Bird nomenclature follows Gill and Donsker (2013).

Detection of animals in a habitat is seldom perfect, and can be affected by a variety of variables (Nichols et al., 2000). The more prominent variables affecting detection in wetlands are observer bias, vegetation height, size of habitat patch, weather conditions, season, and species behaviour. We controlled for several of these by surveying within the same season, and only counting on days without rain or winds. Since emergent vegetation was absent in most wetlands, we focused on estimating bias due to observers, p_{Obs}, using the double-observer method (see Appendix S4). We also assumed *a priori* that detection probability varies due to wetland size. Since the median size of focal wetlands was ~2.5 ha, we separated wetlands as small (<2.5 ha, $n = 14$) and large (>2.5 ha, $n = 14$), and estimated detection probability separately for each. To overcome small sample sizes, we followed Nichols et al. (2000), and clumped species with similar natural history, size, visibility and behaviour to estimate a common p_{Obs} (see Appendix S4 and S5). The combined estimate computed for each clumped class was used as common estimate for each species within that class. Raw counts of birds were divided by p_{Obs} to obtain corrected abundance estimates. Most analyses required that the numbers were rounded off, and we used only whole numbers in the analyses.

2.4.2. Bird use of wetlands: spatial patterns

All subsequent analyses were carried out in R (R Development Core Team, 2011). To test if species assemblages differed between each of the four *a priori* strata, we used the multi-response permutation procedure (MRPP). The MRPP statistic δ is a weighted mean of within-group means of pair-wise dissimilarities among bird communities in each stratum. The algorithm first computes all pair-wise distances, then computes δ. It then permutates the sampling units and their associated pair-wise distances, and recalculates a δ based on the permuted data. This step is repeated for a desired number of times, and the significance test is the fraction of permuted δs < observed δ, corrected for small sample size. This test requires far fewer assumptions relative to parametric tests (Cai, 2006). We used Bray-Curtis distance to compute dissimilarity matrices using the package "vegan" in R. This analysis is useful to understand if the overall species composition varies on the landscape as a function of wetland size and density (or scale dependent wetland use). A significant value would indicate that wetlands of varied sizes and occurring at different densities on the landscape are necessary to help maintain the overall species richness of birds using agricultural wetlands.

Species that exhibited very strong scale dependence would be found in only one strata. Those that did not would be found in >1 strata, and could either show a preference for one or >1 strata, or be distributed across all strata with no preference for any strata. We identified such species and species assemblages by employing the "indicator species" analyses that uses both abundance and frequency of occurrence to identify species associated with a particular stratum significantly more than by chance (Dufrêne and Legendre, 1997). Species that were sparse in abundance and distribution across strata would not feature in the list of indicator species. Apart from the traditional one species: one stratum association, individual species may be associated more than by chance with >1 strata (De Cáceres et al., 2012). Additionally, a small set of species may occur together in a stratum significantly more than by chance collectively helping to "indicate" the preferred stratum for them (De Cáceres et al., 2012). We therefore also computed indicator values of both individual species and bird assemblages (up to a total of three species) with one and >1 strata. Indicator species analyses were executed using package "indicspecies" in R. The associations of one species: ⩾1 strata associations are identified as $\mathrm{IndVal}_{ij} = A_{ij} + B_{ij} * 100$, where A_{ij} is the proportion of individuals of species i that are in strata j (or fidelity); and B_{ij} is the proportion of sites in strata j that contain species i (or specificity). P-values are computed by permutations, and we limited the number of indicator species by retaining only those with $p \leqslant 0.05$. For >1 species: one stratum associations, we used the function "pruneindicators" with the values $A = 0.8$ and $B = 0.2$ to help limit the candidate set of indicator assemblages given the relatively large data set we were working with. This function discards those indicators whose abundance patterns are nested within valid indicator assemblages. This function also explores the coverage (% sites within a stratum) of the remaining number of indicators, and explores subsets of increasing number of indicators until the same coverage as that of the complete set is recovered. Individual species identified as indicators in the one species: one stratum associations may therefore not be part of identified indicator assemblages. Indicator species can be identified using either abundance or presence–absence matrices. The vast majority of the species in our data set (>60%) were restricted to one or two strata (see Results). We therefore only used abundance matrices.

We determine the contribution of two processes leading to observed β-diversity: species turnover and nestedness (Baselga, 2010). Currently, nestedness is assumed to be the dominant process driving landscape level β-diversity of birds whereby conserving a few large wetlands would be adequate to conserve the full complement of species. Conversely, β-diversity could also be due to species turnover, or when assemblages in individual wetlands differ considerably from those in other wetlands and the full complement of species was covered only by the inclusion of a large number of sites (Baselga, 2010). We computed the overall dissimilarity measure of β-diversity (using the Sørensen dissimilarity equivalent), β_{SOR}, additively partitioned into two components accounting for only nestedness, β_{NES}, and only spatial turnover, β_{SIM} (the Simpson dissimilarity, or similarity independent of species richness; see Baselga, 2010): $\beta_{SOR} = \beta_{NES} + \beta_{SIM}$. We use package "betapart" in R for the analysis.

3. Results

Ninety-nine species of birds were identified in the 28 focal wetlands (see Appendix S5). Chao 2 indicated that this was 86% of the total potential species richness (Fig. 2a; mean Chao 2 = 115, 95% CI: 105–139). Species richness was similar across strata (Fig. 2b). Detection probability varied with observer, across species groups, and with wetland size (see Appendix S4). A total of 4315 (corrected abundance) birds were counted with abundances being several magnitudes higher in strata with larger wetlands (strata 3 and 4; Fig. 2c).

A majority of the species (63.6%) were found only in one (36.3%) or two strata (27.3%). Species assemblages across the four *a priori* strata were significantly different (Significance of δ = 0.048; chance corrected within-group agreement A = 0.019; 999 permutations).

Six species exhibited strong preference when considered individually using either a single or multiple strata (Table 1a and b). All six species preferred only strata in which the extent of wetlands > mean (strata 3 and 4 in Fig. 1f). The list included two near-threatened species (Oriental Darter *Anhinga melanogaster*, Black-headed Ibis *Threskiornis melanocephala*), one globally-threatened species (Sarus Crane *Grus antigone*), and three common species (Woolly-necked Stork *Ciconia episcopus*, Grey Heron, *Ardea cinerea*, Pied Starling *Gracupica contra*). Only the Grey Heron exhibited preference due to both single and multiple strata (see Table 1a and b). Six species were distributed across all strata showing evidence of lack of scale dependence or preference for strata, but of these only the Black-winged Stilt *Himantopus himantopus* and the Red-wattled Lapwing *Vanellus indicus* had relatively high indicator values (IndVal > 0.7; Table 1c). Indicator species analyses using species assemblages produced species combinations that exhibited weak levels of preference showing associations with stratum 1 and stratum 2 (IndVal < 0.6, Table 1d). Indicator assemblages comprised of 17 species of which 13 did not feature in associations of single species with single and multiple strata, and only the Grey Heron featured in all the results (associated with stratum 3 and 4 in all analyses). Assemblages showed stronger preferences relative to single species associations only for associations with stratum 4 (Table 1d).

More than half the species (52.5%) were seen in only one or two wetlands. Species richness of birds using agricultural wetlands was due almost entirely to species turnover (β_{SIM} = 0.877) with negligible effect due to nestedness (β_{NES} = 0.055).

4. Discussion

A relatively large number of species were documented using agricultural wetlands in south-western Uttar Pradesh. Scale

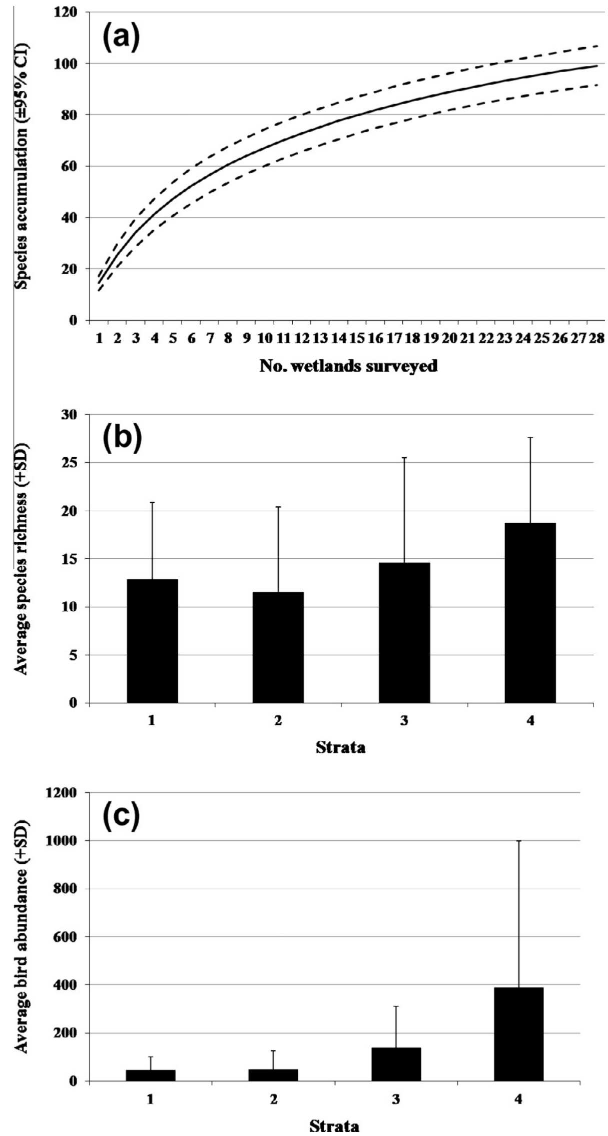

Fig. 2. Descriptive statistics of bird species richness and abundance in 28 focal wetlands in Uttar Pradesh, India: (a) Species-rarefaction curve using a presence-absence matrix to show sampling adequacy; (b) mean (+SD) species richness in focal wetlands of each of four strata; and (c) mean (+SD) abundance of birds in focal wetlands of each of four strata.

dependent wetland use was apparent for the full species assemblage. Nineteen individual species showed strong preference for one or two strata, and always with strata that had > mean wetland size. Six species showed evidence of using wetlands on the landscape independent of wetland density and extent. The β-diversity of birds using agricultural wetlands was due almost entirely due to species turnover with a negligible effect due to nestedness.

Comparable robust surveys of bird use of agricultural wetlands using *a-piori* designs that incorporate both detection bias and landscape-scale elements are lacking in south Asia. Some surveys that covered multiple large agricultural wetlands using the one-visit method are available, and help provide crude comparisons of bird species richness with this study. A survey in and around Bengaluru, Karnataka identified 78 species across 155 wetlands (survey period: 1987–96; M.B. Krishna, pers. comm.); 86 species were located across 69 wetlands in a survey in Tamil Nadu (survey period: 2006; Guptha et al., 2011); 84 species were located across 280 wetlands in another survey in Tamil Nadu (survey period: 2008–11; Abhisheka et al., 2013); and a survey in Andhra Pradesh identified

Table 1
List of species identified to be associated significantly more than by chance with single and multiple stratum using the indicator species analyses. Numbers are indicator values (generated by the package "indicspecies" in R) and *p*-values (in parenthesis).

Species	Stratum 1	Stratum 2	Stratum 3	Stratum 4
(a) Single species : single strata				
Oriental Darter				0.655 (0.05)
Grey Heron				0.674 (0.03)
Woolly-necked Stork			0.655 (0.04)	
Pied Starling			0.721 (0.03)	

Species	Ind Val (*p*)	Stratum 1	Stratum 2	Stratum 3	Stratum 4
(b) Single species: multiple strata					
Grey Heron	0.674 (0.044)			+	+
Sarus Crane	0.741 (0.008)			+	+
Black-headed Ibis	0.694 (0.058)			+	+

Species	Ind Val
(c) Single species: all strata (p-values cannot be computed for species occurring evenly across all strata)	
Red-wattled Lapwing	0.802
Black-winged Stilt	0.707
White-throated Kingfisher	0.598
Temminck's Stint	0.535
Green Sandpiper	0.535
Common Moorhen	0.423

Strata, coverage, and species	Ind Val
(d) Multiple species: single strata (p-values cannot be computed for this analysis). See Methods for an explanation of "Coverage"	
Strata 1:	
Coverage: 57.1%	
Little Egret + Ruff + Green Sandpiper	0.535
Common Sandpiper + White-throated Kingfisher	0.478
Strata 2:	
Coverage: 85.7%	
White Wagtail + Green Sandpiper	0.586
Common Sandpiper + White Wagtail + Common Greenshank	0.535
Little Stint + Bronze-winged Jacana + Little Cormorant	0.535
Strata 3:	
Coverage: 100%	
Pied Starling	0.721
Woolly-necked Stork	0.655
Strata 4:	
Coverage: 71.4%	
Grey Heron + Black-headed Ibis	0.791
Bronze-winged Jacana + Painted Stork + Black-headed Ibis	0.756

55 species across 21 wetlands (survey period: 2012; Chimalakonda, 2012). We avoid comparing species checklists available from individual wetlands since multiple observers and visits were used to enumerate those. We enumerated 99 bird species despite very small wetlands constituting half of the total sample of 28 focal wetlands (see Appendix S3). In addition, Chao 2 estimates indicated a total species richness of 105–139 indicating that despite prolonged and very high human pressure on the wetlands, Uttar Pradesh's agricultural wetlands support a high number of bird species. The observed species richness is the highest known for agricultural wetlands in any landscape in south Asia.

Though larger wetlands had much higher abundances of birds, clear evidence for scale dependent wetland use due to wetland size and density was evident. In addition, species turnover was largely responsible for the β-diversity of birds. In our study, we deliberately attempt a generalised understanding of use of wetlands of all types by birds, and are not able to incorporate site-level characteristics such as the kind of wetland, site-level characteristics such as water depth and hydrology, proximity to vegetation, and as well as ownership. These characteristics can differ with wetland type (e.g. ponds, marshes, lakes), as can varying human use of the wetland. The strong results we obtain with respect to scale-dependent wetland use and species turnover being the dominant process is therefore likely representative of the diversity of conditions at individual wetlands. The results are nonetheless useful to help underscore (1) the need to conserve wetlands of all sizes since species show strong scale dependence, (2) the need to understand the effects of differing densities of wetlands, and (3) the need to conserve a large number of wetland sites on this landscape to ensure conservation of the full complement of bird species since species turnover is the dominant process on the landscape. Focusing on a large number of small wetland sites may therefore be an efficient conservation strategy on this and similar landscapes given the relative ease in conserving smaller sites as also increased feasibility of the conservation of such sites. However, the inclusion of large wetlands in the full complement of conserved sites on the landscape is necessary given the preference of several birds of conservation importance to >mean sized wetlands.

The landscape-scale patterns and processes we document have not previously been demonstrated in tropical agricultural landscapes (Dudgeon, 2003; Zedler and Kercher, 2005). High species turnover, however, have been noted for invertebrates using agricultural wetlands (Céréghino et al., 2008). This suggests that turnover and not nestedness is the dominant process driving β-diversity of wetland biodiversity in agricultural wetlands. Small wetlands on the landscape are recognised to be invaluable for a range of resident taxa including amphibians, turtles, small birds and small mammals (Gibbs, 1993). The importance of factors other than just wetland size is also known to be important for wetland taxa. For example, hydroperiodicity is far more important for amphibian conservation relative to wetland size (Babbitt, 2005). Clearly, the majority of discussions that implicitly assume species nestedness, and assume the adequacy of conserving only large wetlands, require being updated. Wetland surveys require the incorporation of more robust field designs that can assist in understanding the requirements of wetland-dependent species in a more objective manner and not driven by untested assumptions.

Observed patterns in this study may have been accentuated due to the lower than mean rainfall year. The differing degrees of intensity and kinds of uses of wetlands by humans may also play a strong role in the observed pattern (scale dependence) and process (species turnover) affecting bird use of wetlands. Varying site conditions is well documented to alter use of individual wetlands by species and also to affect landscape-scale patterns such as scale dependence and nestedness (Naugle et al., 1999; Paracuellos, 2006; Céréghino et al., 2008; Albanese and Davis, 2013). The lack of detailed information on the variety and intensity of human use of wetlands is a deterrent to the understanding of specific uses that may be useful to maximise bird use of wetlands in tropical agricultural landscapes. During our visits, we documented several uses that were detrimental to both wetland quality and extent. Several of these activities were also illegal including pumping out water, encroachment, and hunting birds using poisons and guns suggesting that not all forms of human use would be useful to sustain birds in wetlands (unpublished information). Hydroperiodicity is documented to be important for wetland taxa (Babbitt, 2005), and draining water from wetlands to water crop fields will likely reduce bird use of the wetlands. Many of the uses that would be detrimental to bird use were, however, illegal suggesting that conditions for bird use of agricultural wetlands in Uttar Pradesh's landscape can be further enhanced merely by enforcing existing legal and institutional policies.

Identifying species that exhibited preference for specific strata was useful since it helps underscore the importance of larger wetlands for species of global conservation significance (e.g. Sarus Crane), while also helping identify common species that can be used to monitor landscape-level wetland use over the long term (e.g. Bronze-winged Jacana *Metopidius indicus*, White-throated Kingfisher *Halcyon smyrnensis*; Table 1). These species also use the agricultural parts of the landscape suggesting that the prevailing crops (rice and wheat) are conducive to the persistence of these species (see Sundar and Kittur, 2012). Other crops like sugarcane or soy bean may not be as conducive to persistence of birds in remnant wetlands on the landscape. Comparative studies from landscapes with different crops are however absent, and will aid greatly to understand if tropical agricultural wetlands elsewhere exhibit similar levels of use by birds, and if landscape-scale patterns are similar when the dominant crops are different.

Findings were contrary to the implicit assumption of species nestedness that exist in literature which in turn lead to a focus on only large wetlands. Such a focus will assist few species that showed clear preferences for larger wetlands (e.g. Woolly-necked Stork), but will not help achieve conservation of the majority of the species on the landscape. However, it is not known if patterns change after human use is removed from large wetlands that are included in protected area networks. Landscape-scale effects will be very difficult to understand in such protected wetlands since the number of protected wetlands is very small. For example, in the focal study area, only four of the >10,000 wetlands are protected as bird reserves (R. De, Uttar Pradesh Forest Department, pers. comm.). Studies that can help evaluate the efficacy of formal protection mechanisms for large wetlands are needed to understand if such protection is helping to achieve intended targets of conserving most of the species on the landscape.

4.1. Conservation implications

Current thinking in the tropics that individual, large, undisturbed wetlands are needed or are adequate to conserve overall bird diversity on a landscape is not accurate. Conservation planning needs to move from a single-site approach to an approach that is able to incorporate processes affected at landscape scales. Such an approach will also assist to understand the need to spread out sites identified for protection taking into account landscape-scale effects such as scale dependence. Planning discussions also require reducing reliance on untested assumptions instead increasing reliance on science-based evidence. This will also help improve the science of wetland ecology and conservation in regions like south Asia where objective, robust information is currently sparse. Also, agricultural wetlands that experience intensive and sustained human use also harbour substantial bird species richness. This suggests that incorporating formal protection of wetlands as reserves is not the only mechanism available to conserve wetland biodiversity. Local institutions require being incorporated and strengthened to help retain wetlands on agricultural landscapes. Incorporating local practices, such as the maintenance of common use wetlands, alongside formal conservation strategies, such as improving the coverage of wetlands in national protected area networks, are rarely considered and are urgently needed to help reconcile the challenges of biodiversity conservation alongside food production for humans (Fisher et al., 2008; Tcharntke et al., 2012). This combination can provide a win–win situation when humans subsist on natural resources that provides crucial habitat for biodiversity in a landscape otherwise converted entirely to crops. However, wetlands cover <1% of the landscape in areas like south-western Uttar Pradesh, the vast majority of which are tiny and isolated. Such wetlands tend to be converted relatively rapidly, and require urgent conservation attention. Wetland restoration on landscapes such as Uttar Pradesh is also needed to help improve the overall extent of wetlands on the landscape. Supporting local institutions and explicitly allowing continued human use of wetlands can aid to gain local participation in restoration plans, and achieve global goals of biodiversity conservation.

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Appendix A. Supplementary material

Accuracy assessment of classified imagery (Appendix S1), descriptive metrics providing the number, extent and mean size of wetlands in the 7 focal districts of Uttar Pradesh (Appendix S2), details of the 28 focal randomly selected wetlands (Appendix S3), estimated p_{Obs} values for different bird groups (Appendix S4), and bird species enumerated in the study (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of material) should be directed to the corresponding author.

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.09.016.

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