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River birds as potential indicators of local- and catchment-scale influences on Himalayan river ecosystems

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ABSTRACT

Rivers are affected by changes in catchment land-use and other modifications to their channel, floodplains and riparian zones. Such changes can affect biodiversity downstream, and specialist river birds might indicate the effects across multiple scales and through different ecological pathways. The risks of catchment-scale effects on rivers are especially acute in the Himalayan mountains, where the world's greatest diversity of river birds occupies one of the most rapidly changing riverine environments on Earth. Here, we use multivariate analysis on data collected over two years to investigate the distribution of this group of birds in relation to natural and anthropogenic variations in riverine habitats along one of the major headwaters of the Ganges. River bird distribution was linked to channel character, bank morphology, aspects of river flow and land use. Riverine specialists were associated significantly with the least modified reaches characterised by faster flows, exposed bedrocks, banks with pebbles, boulders with more intact riverine forests. Our data provide evidence from which to develop specialist river birds as cost-effective indicators of human impacts on river ecosystems, but further work is needed to separate the effects of natural and anthropogenic influences. Such work could also guide conservation action to help balance the exploitation of catchment ecosystem services with the protection of river biodiversity.

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Ganges; principal component analysis; river conservation; species habitat relationship; stream ecology

1. Introduction

Although they occupy less than 1% of the Earth's surface, river ecosystems support a disproportionately large fraction of its biodiversity, while acting also as significant corridors for the movement of plants, animals and nutrients (Naiman et al. 1993; Strayer and Dudgeon 2010). Rivers also represent extensive ecotones where energy flux, complex physical structure and flow dynamics have combined to shape the life history traits of many species (Townsend and Hildrew 1994; Robinson et al. 2002). Rivers, however, are also hotspots for human activity and resource exploitation which now drive rates of extinction and impairment more rapid than in other ecosystems, yet freshwaters in general are rarely incorporated into conservation planning (Paukert et al. 2011). At its core, this is an expression of a widespread issue in river management in which the downstream effects of the exploitation of ecosystem goods and services in river catchments is not always well balanced with biodiversity protection (Maltby & Ormerod 2011).

Among all riverine organisms, birds are the most conspicuous, with specialized traits evolved to exploit the energetic resources and habitat conditions provided by rivers (Ormerod and Tyler 1993; Buckton and Ormerod 2002). Since their ecology is relatively well

known, the effects of environmental change on the distribution, abundance and range of river birds are often readily interpreted (Ormerod et al. 1986; Ormerod and Tyler 1993; Colombari and Cordiner 1999; Ormerod et al. 2000). Moreover, river birds along montane rivers are easily identified and reliably surveyed by both professionals and citizen scientists creating an opportunity for cost-effective assessment at a range of scales from catchment to regional (D'Amico 2002; D'Amico and Hemery 2003; Vaughan et al. 2007). As well as potentially reflecting wider ecosystem integrity and the status of other organisms (Ormerod and Tyler 1993), birds have particular conservation appeal that could help to communicate the importance of river biodiversity more widely (Vaughan et al. 2007).

The world's piedmont and mountain rivers hold a particularly specialized array of river birds formed from around 60 species representing 16 different families (Buckton and Ormerod 2002). These species range from those totally reliant upon the river channel (e.g. dippers and forktails) to those which occupy and use riparian habitats more opportunistically (e.g. *Motacilla* spp. and *Myophonus* spp.). This obligate group of riverine birds is most diverse in areas of the world with large productivity and high topographic variation and is richest of all in the

Himalayan mountains, where 13 species have overlapping ranges (Buckton and Ormerod 2002). Complex structural habitats and distinct resource partitioning allow several of these species to coexist, for example through associations among piscivores and aquatic, aerial or ground-gleaning insectivores (Buckton and Ormerod 2008). As a result, river birds are affected by both terrestrial and aquatic processes over multiple scales, making them potentially useful indicators of both catchment and river quality (Larsen et al. 2010). In such a speciose bird community as that in the Himalayan mountains, however, there is still only limited information on factors affecting distribution and abundance.

As well as being biologically diverse, the Himalayan mountains are among the most geomorphically dynamic regions of the world characterized by high levels of erosion and dynamism. Furthermore, a wide range of global change effects now impact Himalayan rivers, including glacial retreat, increasing modification of catchments and riparian zones, diffuse pollution, urban encroachment, impoundment and abstraction (Manel et al. 2000). These changes are so extensive that the Ganges is now listed among the world's top ten rivers at risk from over-exploitation (Wong et al. 2007). So far, however, the ecological consequences of these modifications, including the impact on river birds, are poorly known. Nor are there any conservation monitoring and assessment programmes.

Our aims in this paper were two-fold. First, we assessed the distribution of river birds in the upper Gangetic river system in relation to river habitat structure. Second, we wished to make an initial appraisal of whether river birds might be candidate indicators for monitoring and assessing the status of Himalayan rivers to help balance the use of ecosystem services with biodiversity protection in river catchments. We tested two hypotheses:

- (I) River bird assemblage composition reflects variation in habitat features associated with natural altitudinal variation
- (II) Natural patterns in the composition of river bird assemblages are modified by habitat features related to land use practice and water resources development

2. Methods

2.1. Study area

The study was conducted in the Bhagirathi basin, the principle headstream of the Upper Ganges in the state of Uttarakhand in the western Indian Himalaya, and in six first order streams. The main river runs for 217 km along an elevational gradient, between 3100 m a.s.l. (30°59'39.1"N, 78°56'38.7"E)

and 330 m a.s.l. (30°07′03.9" N, 78°18′26.0" E) (Figure 1). The catchment of 8847 km² has mean summer temperatures of around 1 to 40°C and mean winter temperatures of -27 to 8°C, while annual precipitation ranges from 533 to 2284 mm.

The river flows through deep gorges and narrow valleys where the major tree species include broadleaves, conifers and some riverine specialists (Picea smithiana, Cedrus deodara, Pinus wallichiana, Populus ciliata, Alnus nepalensis, Pinus roxburghii, Acacia catechu, Bauhinia variegata, Celtis australis, Mallotus philippensis, Toona ciliata, Adena cordifolia and Holoptelea integrefolia) (Rajvanshi et al. 2012). Elsewhere, as in other areas of the Himalayan mountains and Middle Hills, extensive landscape areas have been cleared for agriculture, including pasture land and terracing for root crops or arable production (Manel et al. 2000).

Himalayan rivers are mostly perennial, but discharge patterns are strongly seasonal as a result of monsoonal precipitation and snow-melt (Brewin et al. 2000). While large discharge volumes from the Himalaya provide major potential for hydroelectric power development (Rees and Collins 2006), such seasonality means that power can only be harnessed reliably using impoundments. Already, the Bhagirathi has multiple operational dams and impoundments along its length, creating extensive backwaters and leading to the development of towns and villages.

2.2. Bird surveys

Forty-one river reaches (500 m each) were surveyed (Figure 1) along an altitudinal gradient (300-3100 m a. s.l.) following a widely used model for assessing river bird distribution (Buckton 1998). Surveys were carried out in the pre-monsoon (April–June, breeding season) and post-monsoon periods (October-December, wintering season) in the years 2014 and 2015, with timings consistent across all river reaches and sufficient to detect altitudinal migrant species that move between elevations in winter (Grimmett et al. 1999).

In each of the two seasons, three visits were made to each river segment (500 m) to increase the detection probability of all species (McCarthy et al. 2013). This visit frequency is considered appropriate for species that occupy linear territories along rivers (D'Amico and Hemery 2003). The banks were walked always by the same observer (AS) and surveys were carried out during early morning (06.00 to ± 10.00) and late afternoon (15.00 to \pm 18.00) using 8 \times 42 binoculars. All birds seen or heard were identified by sound or sight and recorded by distance category from the channel: 0-25 m, 25-100 m, >100 m or 'inflight' (Marchant et al. 2002). A species was recorded as present if it was observed during surveys on any occasion and considered absent otherwise.

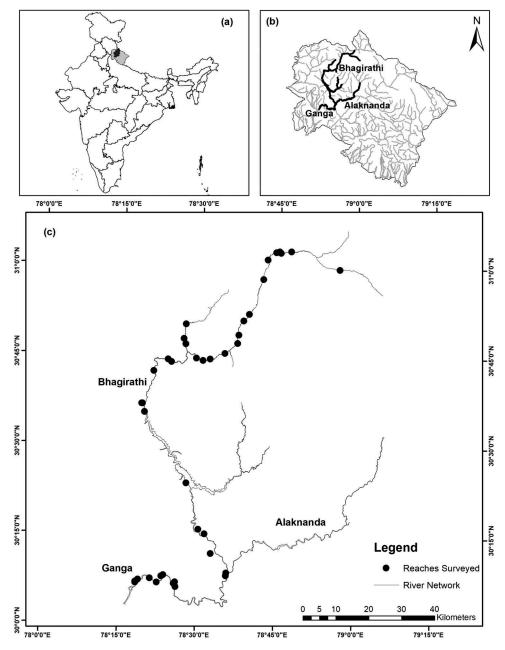


Figure 1. Map showing the (a) Bhagirathi basin (shaded black) in the state of Uttarakhand (shaded grey) India; (b) the river network in the state of Uttarakhand; and (c) the intensive study site showing the 41 river reaches surveyed.

Birds were grouped into two categories (river obligates and non-obligates) depending on their dependence on river production. River obligates were defined as species that (i) occur exclusively along streams or river channels during a significant part of their breeding or nonbreeding life cycle; and (ii) depend on production wholly or partly originating from the river channel (Buckton and Ormerod 2002). Species feeding and roosting on habitats such as wet woodlands, inland waters, ponds and lakes besides inhabiting river banks were described as nonobligate species.

2.3. River habitat survey

Variables describing the river channel (the central element of the river corridor), flow character, bank structural composition were recorded along with information on adjacent land use following the methodology detailed in Raven et al. (1997) and subsequently applied to Himalayan rivers (Manel et al. 2000). Observations were conducted at two different scales: (i) perpendicular transects or 'spot checks' at 10 points every 50 m along the 500 m reach and (ii) 'sweep up' assessments of features over the whole 500 m survey site following Raven et al. (1997) (see Table 1 supplementary material for details). Spot checks recorded features over given bank widths on either side of the observer while sweepup variables recorded the extent of features over the entire 500 m reach, describing them either as absent, present (<33% of the survey reach) or extensive (>33%). The physical structure of the river and its bank was recorded on a six-point scale ranging across absent or

Table 1. Bird species encountered during field surveys in the years 2014–2015 along the Bhagirathi river (list contains species which were recorded at least once every year). Obligate and non-obligate river birds are indicated by symbols α by β , respectively.

Bird species	Family	Number of sites recorded
Ruddy Shelduck (<i>Tadorna ferruginea</i>) β	Anatidae	2
Gadwall (Mareca strepera) β	Anatidae	1
Mallard (Anas platyrynchos) B	Anatidae	1
Indian Spot-billed Duck (Anas poecilorhyncha) β	Anatidae	1
Northern Shoveler (Anas clypeata) B	Anatidae	1
Common Teal (Anas crecca) β	Anatidae	1
Red-crested Pochard (Netta rufina) β	Anatidae	1
Tufted Duck (Aythya fuligula) β	Anatidae	1
Striated Heron (Butorides striata) B	Ardeidae	1
Indian Pond Heron (<i>Ardeola grayii</i>) β	Ardeidae	2
Gray Heron (<i>Ardea cinerea</i>) β	Ardeidae	2
Little Cormorant (Microcarbo niger) β	Phalacrocoracidae	6
Great Cormorant (Phalacrocorax fuscicollis) β	Phalacrocoracidae	3
Indian Thick-knee (Burhinus oedicnemus) β	Burhinidae	1
Great Thick-knee (Esacus recurvirostris) β	Burhinidae	1
River Lapwing (Vanellus duvaucelii) β	Charadriidae	4
Ibisbill (<i>Ibidoryncha struthersii</i>) a	lbidorynchidae	2
Common Sandpiper (Actitis hypoleucos) β	Scolopacidae	7
Pallas's Gull (Ichthyaetus ichthyaetus) β	Laridae	1
White-throated Kingfisher (Halcyon smyrnensis) B	Alcedinidae	13
Common Kingfisher (Alcedo atthis) β	Alcedinidae	5
Crested Kingfisher (Megaceryle lugubris) a	Alcedinidae	18
Pied Kingfisher (Ceryle rudis) β	Alcedinidae	1
Brown Dipper (Cinclus pallassi) a	Cinclidae	23
Blue Whistling Thrush (Myophonus caelereus) β	Muscicapidae	33
Plumbeous Water Redstart (<i>Phoenicurus fuliginosus</i>) a	Muscicapidae	33
White-capped Redstart (Phoenicurus leucocephalus) a	Muscicapidae	27
Little Forktail (Enicurus scouleri) a	Muscicapidae	12
Spotted Forktail (Enicurus macultus) a	Muscicapidae	8
Grey Wagtail (Motacilla cinerea) β	Muscicapidae	22
White Wagtail (Motacilla alba) β	Motacillidae	5
White-browed Wagtail (Motacilla maderaspatensis) B	Motacillidae	24

rare (1-20% cover); occasional (21-40% cover); frequent (41-60% cover); abundant (61-80% cover); and dominant (81-100% cover). The bank substratum composition was recorded according to the previously defined scale with respect to percentage of boulders, cobbles, pebbles, gravel and sand. The lotic zone of the river was classified as cascades, riffles, runs, glides and dam backwaters. Cascades were defined as white waters falling from a height of more than 1 m, riffles as shallow, fast flowing discrete sections and runs as reaches more than 30 m of shallow fast flowing sections. Riverine vegetation was recorded as extent of grasses, shrubs and trees in the 500 m section. Trees were recorded as absent, isolated and scattered, occasional clumps or semi-continuous and continuous. Canopy structure of the adjacent riverine vegetation was measured using a densitometer and was ranked as 0, 1 or 2 based on the percentage of the canopy cover for <20%, 20-50% and >50%, respectively. Bank profile was described as natural/unmodified, steep (>45° slope). Presence and absence of settlements along the banks were recorded alongside dominant human activities, such as fishing, sand-mining, road construction, water extraction for domestic use, recreational camping that were noted separately as categorical or ordinal variables. Altitude was recorded for all the river reaches sampled and was also used in the analysis.

2.4. Statistical analysis

Data for abundance counts of individual bird species were pooled for the two years of survey; to understand the relative abundance of different species, we calculated the encounter rate, i.e. number of individuals of each species encountered for every 500 m of river segment. Quantitative relationships between river bird species, assemblage composition and habitat features were modelled empirically using multivariate techniques in which assemblages and habitat characteristics were reduced to simplified axes using ordination-type methods (Rotenberry and Weins 1980; Hill et al. 1990, 1991). Ordination is an exploratory analytical method of ordering of species along some ecological gradients. Any species occurring in less than two river reaches were not considered for further analysis.

Habitat variables from river habitat survey that included categorical (n = 14), ordinal (n = 4) and continuous (n = 5) variables were reduced by principal components analysis (PCA) (Abdi and Williams 2010). The principal components (PCs) were used further to understand the possible importance of habitat structure to different bird species. We used variables that expressed the habitat character of the site location; channel properties (e.g. river flow type, channel width and presence of characteristic features like cascades and riffles), bank features (e.g. width of the bank), bank

material (e.g. pebbles, boulders, sand), riverine vegetation canopy structure and distance of vegetation from the bank. We used Canonical correspondence analysis (CCA) to examine bird assemblage composition in relation to habitat characters using the R 3.1 (R Core development team 2014) package 'vegan' (Oksanen et al. 2016). CCA is a multivariate extension of weighted averaging ordination, which effectively arranges species occurrence and co-occurrence along putative predictor vectors that are a combination of best-fitting environmental variables (Ter Braak 1987). The presence/ absence of 14 bird species figured in this analysis, and the untransformed PCs were used as potential predictors. We did not weigh these analyses by abundance, using only presence-absence data.

To assess which variables best explained the presence of each species, we used logistic regression to relate the presence/absence of the six most widespread river bird species to the highest ranking PCs that described habitat character. Intercept terms were ignored as we were interested in the incremental effect of habitat change. Using the sign of the coefficient term in the regression model, we identified the most significant habitat variables in the PC separately for presence and absence of the bird species.

3. Results

3.1. River birds and encounter rates

A total of 32 river bird species from 13 families was recorded during this two-year survey, of which 14 species qualified for further analysis (Table 1). Amongst this group, species richness ranged from 0 to 11 species for a single river segment (Supplementary Material). No duck species (family Anatidae) were recorded from more than one site and were excluded from further analysis. The major contribution to the river bird community along the river Bhagirathi was from the family Musicapidae and Alcedinidae, each represented by four species, and subsequently by three species of wagtails, two cormorants, three waders and one species of gull. Obligate river birds belonged to the families Muscicapidae, Cinclidae, Alcedinidae, Ibidorynchidae and Charadriidae.

The obligate species were mostly passerines, with Plumbeous Water Redstart and White-capped Water Redstart the most frequent species followed by Brown Dipper (Figure 2(a)), while Ibisbills were recorded only from two river reaches (Table 1). Non-obligate river species included Blue Whistling Thrush and Whitebrowed Wagtail as the most encountered species (Figure 2(b)). Grey Wagtails occurred singly or in pairs while White Wagtails and White-browed Wagtails were seen in flocks of 4-12 individuals. River Lapwings occurred in four river reaches (Table 1) in

flocks sometimes exceeding 50 individuals during communal winter roosts.

3.2. River habitat characteristics

Four PCs explained over 60% of the variance in habitat character in the 41 river reaches sampled (Table 2), and there was marked heterogeneity. Intercorrelation between variables prevented clear identification of natural versus human influences on habitat features, but PC1 (26.5% of explained variance) described a trend from narrower, faster, tree-lined river reaches at higher elevation to lower reaches with modified banks lined by urban settlements. PC2 (15.4%) largely reflected trends in substratum character from river reaches with boulders and pools to those with pebble islands and bars in the river channel. PC3 (10.5%) increased where midsized river reaches had boulder-strewn banks, while PC4 (9.0%) increased in wider, lower reaches with pools, mid-channel bars, agriculture and trees along the banks.

3.3. Bird distribution and habitat structure

In ordination, four constrained habitat axes explained 32% of the total inertia in the bird species data, with CCA1 (17.7%) and CCA2 (9.6%) explaining most variation (Figure 3). Taken individually, habitat PC1 $(F_{1,36} = 5.11, p = 0.001), PC2 (F_{1,36} = 3.84, p = 0.002)$ and PC4 ($F_{1,36} = 2.89$, p = 0.006), all explained significant aspects of assemblage composition and reflected the habitat requirements of each species.

Among bird species, Spotted Forktail, Brown Dipper, Plumbeous Water Redstart, Grey Wagtail and White-capped Redstart all had higher scores on CCA1 reflecting affinities for higher altitude, narrower channels, faster flows and more intact riparian vegetation. In contrast, River Lapwing, Blue Whistling Thrush, White-throated Kingfisher, White-browed Wagtail and Little Cormorant scored negatively on CCA1, reflecting their downstream distribution and tolerance of human activities. On CCA2, White Wagtail, White-browed Wagtail and Little Cormorant scored positively, reflecting their occurrence at slower flow, broader channels and banks with agriculture, while Spotted Forktail, White-throated Kingfisher and Blue-whistling Thrush scored negatively. In combination, these effects meant that the ordination broadly separated two species groups respectively of riverine obligates (Figure 3, grey circle) and nonobligates (Figure 3, black circle), with a large part of this division occurring on habitat PC1 ($F_{1,36} = 5.11$, p = 0.001). Preference for higher altitude reaches was stronger among passerines than non-passerines as reflected by their positive values on CCA axis 1.

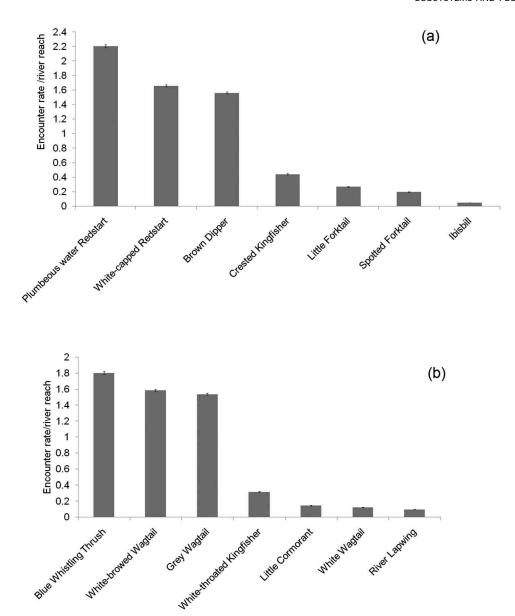


Figure 2. Encounter rate of river bird species recorded in various river reaches sampled across the two years. (a) Obligate riverine species; and (b) non-obligate riverine species.

Error bars were plotted with the standard error values which were calculated for temporal replicates of the 41 river reaches sampled along the Bhagirathi river.

Table 2. Trends in habitat characters shown by PCA from river habitat surveys of 41 sites in Upper Ganges (Bhagirathi river) in 2014–15. The percentage of variance explained by each PC (principal component) is shown in parentheses.

PC1 (26.1%)	PC2 (15.5%)	PC3 (9.8%)	PC4 (8.8%)
Altitude (+)	Boulders (+)	Channel width 10-30 m (+)	Pool (+)
Riffles (+)	Trees (+)	Boulders (+)	Agriculture (+)
Cascades (+)	Shrubs (+)	Channel width <10 m (-)	Mid channel bars (+)
Logs in river channel (+)	Pool (+)	Cascades (–)	Trees (+)
Shrubs (+)	Agriculture (–)	Trees (–)	Cascades (–)
Trees (+)	Pebble island in river channel (–)	Channel width more than 30 m (-)	Boulders (–)
Channel width <10 m (+)	Log in river channel (–)	Log in river channel (–)	Pebble island in river channel (-)
Urban settlements (-)	Mid-channel bars (–)		
Modified river banks (-)	Altitude (–)		
channel width more than 30 m (-)			

Logistic regression confirmed relationships between the presence/absence of each of the six most widespread river birds and river habitat character (Table 3; Figure 4). Specifically, the regressions confirmed how Plumbeous Water Redstart occurred mostly on moderately wide (10-30 m) river segments with pebble banks, faster flow and pebble island; Brown Dipper and White-capped Redstart preferred narrower, tree-lined river reaches at higher elevations with cascades while avoiding wider river segments

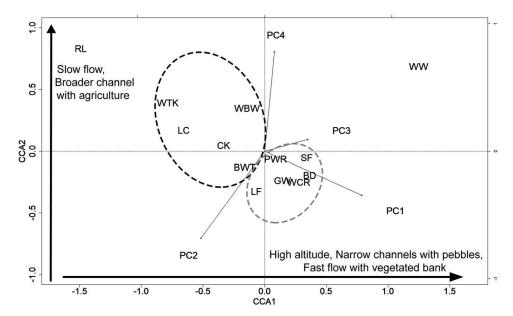


Figure 3. Biplot of the first two CCA axes showing the positions of 14 river bird species and the associated principal components describing river habitats in the upper Ganges; riverine obligates are encircled by grey dotted lines and non-obligates by black dotted lines. PWR –Plumbeous Water Redstart; WCR – White-capped Redstart; BD – Brown Dipper; GW – Grey Wagtail; WBW – White-browed Wagtail; WW – White Wagtail; CK – Crested Kingfisher; WTK – White-throated Kingfisher; BWT – Blue Whistling Thrush; SF – Spotted Forktail; LF – Little Forktail; LC – Little Cormorant; RL – River Lapwing.

with settlements, urban land-use and modified river banks; Blue Whistling Thrush and Grey Wagtail were positively associated with boulder-strewn banks, cascades and pebble islands, while being absent from river reaches with slow flow and agricultural land use (Table 3; Figure 4).

4. Discussion

Our broad aims in this paper were to assess factors affecting the distribution of Himalayan river birds and to appraise whether this group might be candidates for indicating river quality, particularly in catchments being modified to meet human needs. We tested two specific hypotheses to support these aims: that the assemblage composition of river birds reflected natural altitudinal variation, and that natural patterns in composition would be modified by land use practice and water resource development.

Table 3. Results of logistic regression representing the presence/absence of six most widespread river bird species in relation to the highest ranking principal components describing habitat character. PCs with a significance value above 0.001 are listed.

Bird species	Significant PCs	Regression coefficient	Pr(> z)
Plumbeous Water Redstart	PC4	1.87	0.004
White-capped Redstart	PC2	-1.06	0.006
Brown Dipper	PC1	0.79	0.003
Blue Whistling Thrush	PC1	0.70	0.003
Crested Kingfisher	PC4	0.72	0.041
Grey Wagtail	PC2	0.14	0.475
	PC4	2.01	0.006

There was support for both hypotheses, with individual species and assemblage composition changing with river flow, riparian vegetation, and river or bank morphology. At the same time, however, natural and anthropogenic links with river bird distribution were confounded by downstream progression.

Detailed, fine-scale assessments of habitat character coupled with information on bird distribution can reveal the habitat preferences of different bird species (e.g. Rushton et al. 2004, Pearce-Higgins and Grant 2006). Riverine landscapes are well suited to studies of this type of analysis because bird distribution and environmental variations are both relatively easy to quantify (Ward et al. 2002; Vaughan et al. 2007). So far, however, despite previous broad-scale work (Manel et al. 2000; Buckton and Ormerod 2008), no previous study has used detailed standardized habitat data from river systems in the Himalayan region to understand the distribution of specialist river birds in relation to natural and anthropogenic aspects of catchment character. This is despite the Himalayan Mountains having more specialist river birds than anywhere on earth (Buckton and Ormerod 2002) and, for the Indian Himalaya and headwaters of the Ganges, our study is the most detailed assessment to date of factors potentially affecting this group (Table 2). As well as assessing the ecology of several species already linked strongly to river ecosystems (e.g. dippers and grey wagtails) (Ormerod et al. 1986; Ormerod and Tyler 1986), our data augment understanding of the ecology of several species that are restricted to South-East Asia in general, and Himalayan river

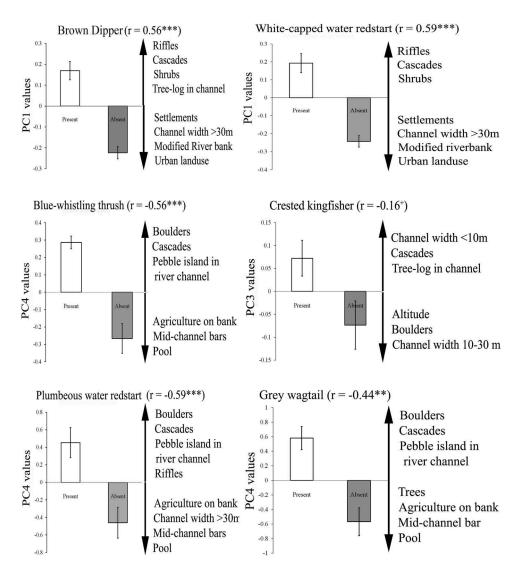


Figure 4. Plots depicting correlation between the principal components of the river-habitat variables across the sampled (41) river reaches along the Upper Ganges and the presence/absence of six species of river birds. The most significant variables of the PC are shown in the vertical axis of individual plots. Error bars indicate \pm 1 SE.

systems in particular (Buckton and Ormerod 2008). The data also provides further insight into the extent to which human resource exploitation for ecosystem goods and services in the Himalayan mountains might now be affecting the distribution of river birds.

As with other survey methods used to understand bird distribution, especially in complex environments, our study has some inevitable limitations. While the selection of environmental variables investigated was based on recognised approaches (Raven et al. 1998; Vaughan et al. 2007), data collection was limited to a single river basin, and inter-correlation between natural downstream changes and indicators of anthropogenic modification was inevitable. The overall bird patterns in relation to river habitat character might therefore best be regarded as responses to synoptic, multi-variate habitat change that reflects a combination of natural and anthropogenic change. Moreover, climatic factors like temperature and rainfall patterns were not considered, which in

Himalayan regions are marked by major seasonal influences on river systems (Brewin et al. 2000). The focus on dynamic river channels in the higher altitudes meant that floodplains were not investigated, where terrestrial bird species would be encountered and would have confounded the results. Also important, despite some initial data (Buckton and Ormerod 2008), we are not yet in a position to quantify accurately either the diets of the target species, nor, as a result, factors affecting the prey available to them. Finally, there was no measured water quality in the analysis, though there are marked natural and anthropogenic influences on the chemistry of Himalayan rivers that might affect river birds indirectly (Manel et al. 2000).

Notwithstanding these caveats, several important results about Himalayan river birds and catchment character emerged from this study. Specifically, the clear separation of different species along major variates describing habitat character (Figure 2) revealed how smaller, passerine and river-obligate species

preferred high altitude river reaches with faster flows as distinct from larger, non-obligate bird species that apparently preferred wider channels with slow flow and more urban land-use. The riverine obligates avoided urban land-use habitats which are characterized by paved banks and river banks clear of riverine vegetation, a pattern observed in other parts of the world (Larsen et al. 2010; McClure et al. 2015). These observations suggest that the river obligate species offer the best potential indicators of human impact, and we expand this theme below. This separation between obligate and non-obligate species concur with well-known ecological principles where sympatric species at the risk of overlapping resources differ along key dimensions that ensure either niche complementarity or resource partitioning (Schoener 1974). In bird communities, niche separation reflects differences in feeding behaviour (Buckton and Ormerod 2002; Cody 1968), dietary specialization (Nudds and Bowlby 1984), habitat use and morphology (Miles and Ricklefs 1984). Passeriformes are morphologically pre-adapted to diverse techniques, which include fly catching, ground gleaning and aquatic foraging in stream or bankside habitats. In turn, these behaviours provide scope for different members to exploit the three main sections of the riverine environment, i.e. the channel, the bankside and the riparian zone. This group has members from different genera, including Cinclus, Enicurus, Phoenicurus and Myophonus, which vary in morphology (body size), habitat use and foraging techniques despite similarities in overall food spectra. Even with similar body sizes, Plumbeous Water Redstart and Little Forktail have different foraging techniques in which the former feeds more frequently by aerial fly-catching, while the latter feeds from spray-drenched exposed boulders and wetted bankside pebbles and rocks. Within the obligate group, there was separation in the utilization of the water channel and banksides by individual species, ranging from predominantly aquatic habitat use in the Brown Dipper and Little Forktail, ground-gleaning or flycatching over the channel or riparian zone in the Plumbeous and White-capped Water Redstart, and foraging or near the riparian margin in the Spotted Forktail (Buckton and Ormerod 2008). These contrasting patterns of microhabitat use illustrate how different species can partition physical habitat space and foraging niches in riverine environments.

The occurrence of species from 13 families, varying markedly in their basic ecology, results from the high species richness of Himalayan river birds, in turn reflecting the physiographic complexity, marked altitudinal relief and high primary production in this near-tropical region (Buckton and Ormerod 2002). The importance of the pronounced altitudinal range of the Himalaya was illustrated here in the altitudinal distributions and habitat associations of individual species. While altitude per se can affect bird distribution, associated factors such as temperature, atmospheric oxygen concentrations, nutrients, slope or flow velocity also reflect elevational change. Changes in the spatio-temporal heterogeneity of river flows can alter the distribution and abundance of certain fish and aquatic invertebrates (Bunn and Arthington 2002) which are important dietary components for several of the bird species studied.

Pivotal to the use of river birds as indicator organisms, there is a major question about the extent to which human activities in the Himalayan region have modified river bird distribution either (i) because some species occupy altitudinal ranges where human activities are now intense and widespread, such as the agricultural conversion of natural environments with subsequent downstream effects (Manel et al. 2000); or (ii) because human activities have altered the nature of altitudinal gradients - for example by modifying river flow regimes. Factors such as land use, urbanisation and habitat modification contributed to some of the variates that explained river bird distribution. Investigators increasingly recognize that human actions at the landscape scale can affect the ecological integrity of river ecosystems, impacting habitat, water quality and the biota via numerous and complex pathways (Allan et al. 1997; Ward 1998; Strayer et al. 2003). Modification of natural banks to concrete embankments and removal of natural bank vegetation alters habitat structure in the channel and riparian zone with potential consequences for prey abundance. Additionally, the removal of natural riverine forest to enhance opportunities for agriculture alters allochthonous litter input to the channel, modifying nutrient cycling and food web character (Murakami and Nakano 2001). Long-standing evidence shows how river birds can integrate these effects, reflecting for example the effects of chemical pollution, contaminants, habitat modification, prey abundance or changing flow pattern (Ormerod & Tyler 1993). Such indicator effects can extend beyond the wetted perimeter of the river to the riparian zone (Larsen et al. 2010) through prey subsidies across the riparian - aquatic interface, or because riparian forests influence the abundances of aquatic invertebrates by contributing to the in-stream physical habitat, by stabilizing stream banks or by contributing allochthonous input (Osborne and Kovacic 1993; Lowrance et al. 1997). Our data revealed outcomes consistent with all these indicator effects - and for example Brown Dipper and White-capped Redstart avoided river banks with intensive urban land-use and settlements while Plumbeous human Water Redstart, Blue Whistling Thrush and Grey Wagtail avoided river reaches with intensive agriculture. As noted above, however, more specific studies are

required to develop these indicator effects more precisely.

Potentially more important in the region of our study are extensive changes in river networks that remove whole river sections or modify flow patterns fundamentally where rivers are impounded for water supply or hydro-power. Both can be regarded as important ecosystem services, but their exploitation may come at a cost to biodiversity. Work elsewhere has shown how river regulation affects river birds adapted to feeding on emergent aquatic invertebrates (Jonsson et al. 2012; Strasevicius et al. 2013) while river-obligates are the most vulnerable to considerable shifts in surface flows due to their specialized foraging techniques. In India, the location of most dams overlap with the most species rich areas in the Himalaya (Pandit and Grumbine 2012). Specifically in our study area, the development of Tehri dam, Koteshwar hydropower plant and Kotli-Bhel hydropower project (under development in Bhagirathi basin) has led to the diversion of approximately 68 km (31%) of the river Bhagirathi, while 85 km (39%) of the riverine buffer zone has been submerged to a width of 1 km (Rajvanshi et al. 2012). Dams alter the natural flow regime of the channel downstream creating pools that are deeper and wider and are avoided by all the obligate river bird species which showed preference for river reaches with cascades (Figure 3). Bank-nesting species - including several of those considered here - are vulnerable to both loss of riparian habitat, as well as flow variability and nest flooding during sensitive periods of their annual cycles, such as breeding (Chiu et al. 2008, 2013; Roche et al. 2012; Strasevicius et al. 2013). Modified river flow regimes are postulated to affect species at higher trophic levels whose life cycles are often matched closely to specific flow conditions and food web character (Nakano and Murakami 2001; Jonsson et al. 2012, 2013; Royan et al. 2013; Strasevicius et al. 2013). As well as feeding on specific prey types, Himalayan river birds use heterogeneous habitat features in complex ways that are involved in resource partitioning among this group (Buckton and Ormerod 2008). However, alterations in habitat structure in modified rivers are likely to arise through human activity both directly and where altered hydrological and hydraulic pattern leads to inundation, flow variability or micro-habitat loss (Nilsson and Bergrren 2000). Variability in flow conditions, especially large fluctuations in water velocity and depth caused by impoundment, affects the availability of foraging habitats which is liable to disrupt riverbird community structure (Cumming et al. 2012).

In combination, the response of river birds to landscape scale change, resource exploitation and potential response to water resource developments in our study support the concept that river birds are

capable of indicating the effects of wider landscape changes on river processes. As highly conspicuous indicators of habitat quality, birds are particularly suitable and charismatic subjects for biological monitoring (Ormerod and Tyler 1993; Feck and Hall 2004; Mattsson and Cooper 2006). Our work contributes to the development of river birds as indicators by helping to understand how bird communities might respond to a range of anthropogenic activities along Himalayan rivers. Birds could then be used to convey the importance of trading-off the protection of ecological integrity, biological production and conservation value of river systems with the resource values of rivers and their catchment for people in India and beyond. Although further work is required for the full appraisal and use of river birds for ecological monitoring, this work suggests that by synthesizing the population and distribution data for a range of river bird species, it may be possible to detect a wide range of changes in river environments and thus can provide scientific basis for river resource management in the Himalayan region.

Disclosure statement

No potential conflict of interest was reported by the authors.

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