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Subsistence use of papyrus is compatible with wetland bird conservation

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ABSTRACT

Conservationists have historically advocated measures that limit human disturbance. Nevertheless, natural disturbances are important components of many ecosystems and their associated species are often adapted to such regimes. In consequence, conservation managers frequently simulate natural disturbance, particularly in temperate forest systems. This practice is less widespread and seldom studied in tropical regions, where biodiversity conservation and human activities are often thought to conflict. However, many tropical systems have been subject to natural and anthropogenic disturbance over evolutionary timescales, and disturbance may therefore benefit the species they host. Determining whether this is true is especially important in tropical wetlands, where human activities are essential for sustaining local livelihoods. Here we investigate the impacts of disturbance from human resource use on habitat-specialist bird species endemic to papyrus swamps in East and Central Africa. Bird densities were estimated using point counts and related to levels of human activity using physical characteristics of wetland vegetation as a proxy for disturbance. All species were tolerant to some degree of disturbance, with particular species occurring at highest density in intensely disturbed habitat. Species were generally more tolerant to disturbance in larger swamps. Our results suggest that low-intensity use of papyrus wetlands by people is compatible with the conservation of specialist bird species, and highlight the potential benefits of traditional human activities to conserve biodiversity in the tropics.

1. Introduction

Habitat degradation is one of the greatest threats to biodiversity (WWF, 2014) and restoring habitat is frequently the focus of conservation management (Hodgson et al., 2011). To this end, conservationists have advocated measures that limit disturbances caused by human activity, adopting the view that the needs and actions of people often conflict with the objectives of biological conservation (Brown, 2002). The classic "fences and fines" approach dominated much of the 20th century but has been criticized for its failure to account for the interests of communities by impeding the use of natural resources (Hutton et al., 2005). This is particularly problematic in developing countries (Barrett et al., 2001), where people's livelihoods are closely linked to natural resource use (Khadka and Nepal, 2010). In consequence, conservation now often adopts a more community-based approach, which strengthens the link between conservation and human needs (Adams and Infield, 2003). These participatory methods incorporate a variety of incentives to make conservation more favourable to local communities (Spiteri and Nepalz, 2006). Nevertheless, community-based conservation schemes often restrict resource use (Lele et al., 2010), commonly with financial incentives (Barrett et al., 2001) and as such, maintain the premise that human activities are detrimental to biodiversity.

Many ecosystems have, however, been modified over very long periods of time. Thus, human disturbances potentially play a role in maintaining biodiversity (Hobbs and Huenneke, 1992), with many species having evolved under natural disturbance regimes prior to the influence of humans (Lindenmayer et al., 2008). The role of disturbance is recognised and incorporated into management programmes in various temperate systems (Bengtsson et al., 2000; Seymour et al., 2002). Forests, for example, were prehistorically grazed by megaherbivores, and subsequently by domestic animals following the regional extinction of large grazers (Bengtsson et al., 2000). Human-based disturbances which create early successional habitat, are used by forest managers to simulate natural forms of disturbance (Bengtsson et al., 2000; Lashley et al., 2014; Seymour et al., 2002). The extent to which disturbance is important for maintaining biodiversity has seldom been studied or considered in tropical areas; home to high levels of global biodiversity (Hillebrand, 2004), yet a rapidly growing human population and extreme poverty place increasing pressures on tropical societies, habitats and species (Hutton and Leader-Williams, 2003; Spiteri and Nepalz, 2006). Therefore, it is crucial to understand the extent to which populations of species can be sustained in human-modified landscapes and how specific land-use practices influence biodiversity (Chazdon et al., 2009).

Tropical wetland systems encapsulate the potential conflicts and synergies between human exploitation of natural resources and conservation; vital for human wellbeing (Senaratna Sellamuttu et al., 2011)

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and the alleviation of poverty, as well as hosting a rich biodiversity (Russi et al., 2013). In East Africa, papyrus (*Cyperus papyrus*) swamps support the livelihoods of millions of people through the provision of ecosystem goods and services (van Dam et al., 2014) including water, food, medicinal herbs, fishing and grazing habitat for livestock (Terer et al., 2012b). Papyrus is frequently harvested and used for roof and fence construction, and to craft items such as baskets, trays, sleeping mats and ropes, which provide basic resources and a vital source of income for rural poor communities living in close proximity to swamps (Maclean et al., 2003b). These swamps also host a unique biodiversity including a suite of generalist species of birds (Maclean et al., 2003a), alongside several species of specialist passerines (Britton, 1978; Vande weghe, 1981). In common with wetlands worldwide, papyrus swamps are increasingly threatened by habitat loss from drainage and encroachment for agriculture (Maclean et al., 2011b). As a result, population estimates of papyrus passerines suggest that they are decreasing in numbers, undergoing even greater declines than the habitat on which they depend (Maclean et al., 2013).

Disturbance from human activities in papyrus swamps has been considered detrimental to biodiversity and, in consequence, legislation in East Africa tends to impose restrictions on harvesting by local people (Hartter and Ryan, 2010; Wetlands Inspectorate Division, 2001). However, these restrictions can alienate local stakeholders and risk the success of further conservation efforts (Terer et al., 2012a). Disturbance from subsistence use, including harvesting for materials and burning from smoking bees out of hives or hunting game or fish (Maclean et al., 2006), has been ongoing for over a millennium (Terer et al., 2012b), and papyrus swamps have been exposed to natural forms of disturbance from fire and large herbivore grazing prior to human settlement (Taylor, 1990). Following the regional extinction of large herbivores, people are likely to have replaced the role of these natural forms of disturbance in maintaining a more open habitat through harvesting and burning (Maclean et al., 2006). As with forest systems, this history of disturbance could have implications for the way wetlands in sub-Saharan Africa should be managed.

Here, we investigate the effects of disturbance on a suite of habitat–specialist species as an exemplar of the potential impacts of subsistence resource use, from direct cutting and burning, by local people on biodiversity in the tropics. Specifically, we quantify the effects of varying levels of disturbance on the relative densities of specialist bird species in an area of south west Uganda. Habitat specialists are typically more sensitive to disturbance (Devictor et al., 2008). In consequence, if the densities of these birds are not negatively affected by disturbance, resource extraction to support local livelihoods is unlikely to be detrimental to birdlife, potentially to wildlife in general, and the long-term provision of ecosystem services. We conclude by discussing the implications of our findings for the conservation management of tropical wetlands and other habitats.

2. Material and methods

2.1. Study site

The study was conducted between May and June 2014 at Lake Bunyonyi, south west Uganda (01°17′S 29°55′E), to coincide with post-rainy season breeding (Britton, 1978). In this area, papyrus swamps persist along the lake shore and in valley bottoms, surrounded by heavily cultivated land. This region is subject to particularly high levels of disturbance from harvesting and burning as a result of increasingly high human populations (Maclean et al., 2011b) and levels of poverty (Gable et al., 2015), as well as hosting among the highest densities of papyrus endemic passerines (Maclean et al., 2011b). At Lake Bunyonyi, papyrus is most commonly harvested and sold in bundles to use as a source of fuel, for thatching roofs, constructing fences and occasionally creating small out-buildings (see Maclean et al., 2003b). Thin strips of papyrus are also cut and used on a smaller scale to make a variety of handcrafts used for domestic purposes, or sold locally, increasingly to tourists (Maclean et al., 2003b). Small-scale burning in this area is largely caused by fishermen in an attempt to catch eels, which are marketed locally or used to feed families (J. Ruhakana *pers. comm*). Occasionally, burning can be initiated accidently in an attempt to smoke bees out of hives while harvesting honey, often situated in the swamp interior distant from local communities (Maclean et al., 2006). These subsistence-based activities are more frequent during the dry season in Uganda, when income from crop production declines (Maclean et al., 2003b).

2.2. Study species

Research concentrated on five specialist species of passerines most closely associated with papyrus in the study area, which have global distributions centred around East and Central Africa (Maclean et al., 2013). White-winged scrub-warbler (*Bradypterus carpalis*), greater swamp warbler (*Acrocephalus rufescens*) and papyrus canary (*Serinus koliensis*) are entirely confined to papyrus, although papyrus canary often forages in adjacent cropland (Vande weghe, 1981). Papyrus yellow warbler (*Chloropeta gracilirostris*) and Carruthers's cisticola (*Cisticola carruthersi*) are primarily confined to papyrus, but can inhabit wetlands dominated by other types of vegetation, namely *Typha* and *Miscanthidium* spp. (Vande weghe, 1981). Carruthers's cisticola was also found to inhabit wetland recently converted to agriculture in this study. All species are currently listed as Least Concern on the International Union for Conservation of Nature (IUCN) Red List, with the exception of papyrus yellow warbler, which is classified as Vulnerable due to a small and fragmented population, suspected to be in decline owing to the exploitation of its habitat (IUCN, 2015).

2.3. Point count survey

105 point count surveys were conducted by the same observer between 7 am and 11:30 am, when the birds were most vocal. Swamps surveyed ranged in size from approximately 0.01 ha to 996 ha and covered the length of the lake (~35.6 km) (Fig. 1). A 1- to 2-min adjustment time was used prior to survey to minimise disturbance caused by arrival on-site. Numbers of focal bird species were identified visually or aurally within a 15-min period and the distance of each individual from the point of survey recorded within distance bands (0–19 m, 20–49 m, 50–99 m, 100–199 m). Each point covered a circular area with a 200 m radius, the location of which was recorded on GPS in the UTM (Universal Transverse Mercator) projection system. Counts were conducted from the edge of swamps often on higher land, offering an effective vantage point of both the edge and interior. Wetlands surveyed varied in size (mean size: papyrus swamp = 6.3 ha; broad wetland = 30.8 ha), thus multiple counts were conducted at opposing sides of large wetlands (diameter > 400 m^2). Given the length of survey period and variation in area of swamp surveyed, data collected per count represent a relative, not absolute, indicator of species' abundance at each point (see Maclean et al., 2013, Maclean et al., 2011b, for population assessments across the region).

2.4. Disturbance estimation

For the purpose of this study, we concentrate on human disturbance from recent and past harvesting of papyrus wetlands, together with occasional recent burning. As stands of papyrus first regrow following disturbance, culm width decreases and density increases (Maclean et al., 2006; Muthuri et al., 1989; Terer et al., 2012b). Thus, disturbance can be efficiently measured visually, using physical characteristics as a reliable indicator of disturbance levels. Based on this, five vegetation categories were created and used as proxies for disturbance (Table 1). The dominant form of disturbance in our study area was harvesting. A small amount of recent burning was also recorded (within ~5% of point counts), which was combined with harvesting to represent high

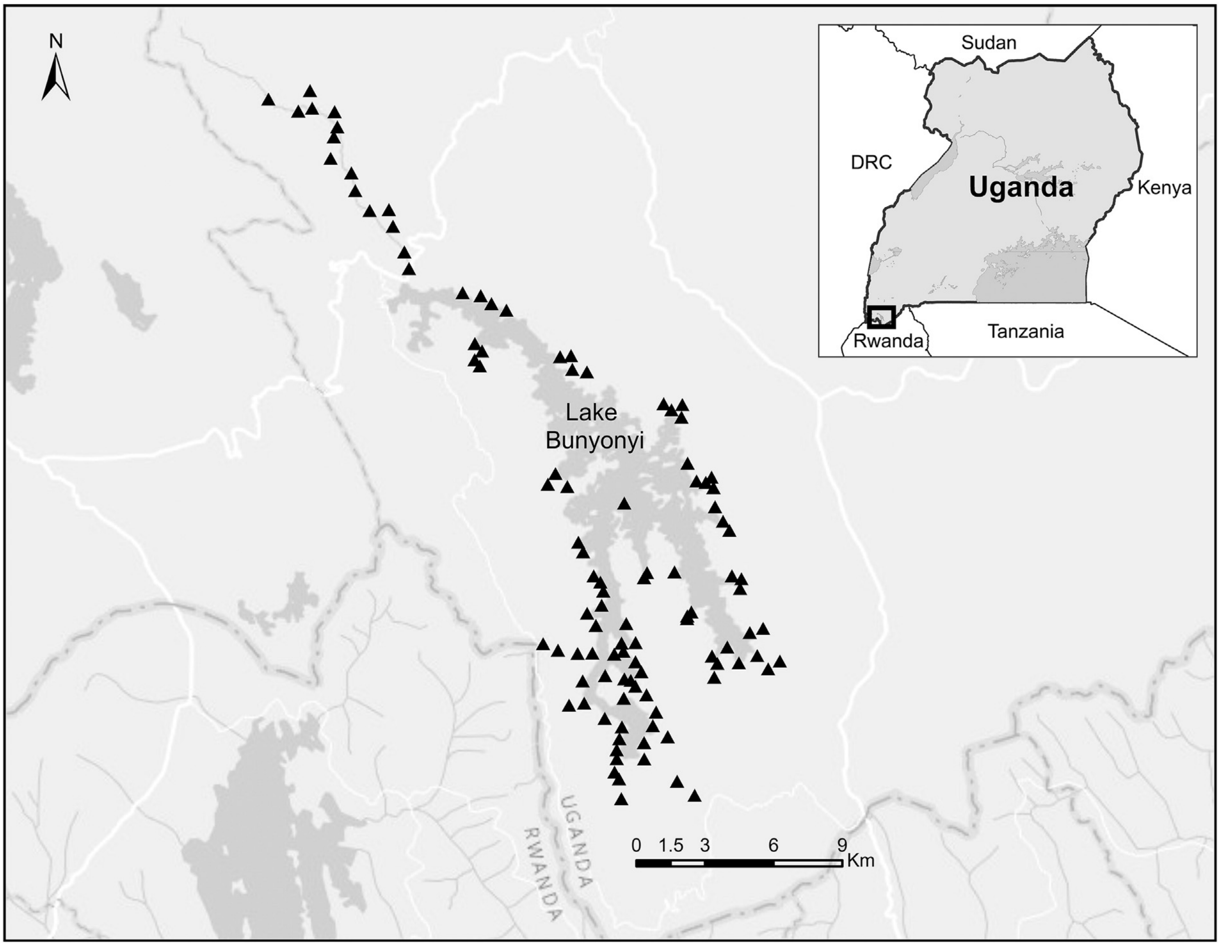

Fig. 1. Point count locations (▲) around Lake Bunyonyi (lake shaded dark grey). Inset: location of the study site (◘) in south west Uganda. Basemap credit: Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community.

intensity disturbance. Regeneration is similar following each of these disturbances within our study site, since the water level remains relatively stable at Lake Bunyonyi (Denny, 1972) and regrowth occurs primarily from rhizomes rather than seeds (Terer et al., 2012b). Some areas consisted of very low densities of papyrus mixed among other types of vegetation, largely due to water levels and soil conditions at particular sites (see Kansiime et al., 2007; Lind and Visser, 1962). These areas were taken to represent undisturbed but suitable habitat, and allowed us to explore aspects associated with physical habitat characteristics. Sketch maps were drawn to scale on the day of survey, noting the proportion of vegetation types within the survey area. GPS readings and satellite imagery were used to record vegetation boundaries and approximate coverage of each vegetation type. Maps were later digitized in ESRI ArcGIS v 10.1 and R v 3.0.2 (R Development Core Team, 2014) was used to calculate the proportion of each vegetation type surveyed per point count. The perimeter and area of each swamp surveyed were obtained using ArcGIS 10.1, and circularity calculated (4πarea/perimeter^2) to provide an indication of patch shape.

2.5. Data analyses

2.5.1. Detectability functions

Measures of abundance obtained from point count sampling depend on the detectability of species within the radius surveyed; accounted for using distance sampling techniques. As most counts were conducted from the edge of swamps, the area surveyed and distance of swamp from the observer within the circular radius differed between counts. In effect, this alters the assumption that detectability from the observer will be equal across all point counts (Thomas et al., 2010). To combat this, detectability functions for each species were calculated in Distance 6.2 (Thomas et al., 2010), using the distance of each individual recorded from the observer, and these functions used to provide weighted estimates of the swamp surveyed by each point count. Ultimately this provided a “detectability-weighted” area surveyed, which was included in subsequent analysis as a measure of sampling effort per point count.

To confirm that detection ability did not vary between vegetation types, we ensured that the distance from the observer did not differ among habitat types, then included habitat types as covariates in Distance 6.2 using the Multiple Covariate Distance Sampling (MCDS) extension (Marques and Buckland, 2003). The inclusion of these effects consistently resulted in a less parsimonious model, indicating that height and density of vegetation was unimportant for the detection of the focal species, likely because most birds were recorded aurally rather than visually.

2.5.2. Statistical analyses

Generalized linear mixed effects models (GLMMs) were used to determine the effect of disturbance and vegetation type on species' density. Models were fitted using the “glmmADMB” package in R (Bolker et al., 2012) with a negative binomial error structure and log link function. The proportions of four distinct categories of disturbance within the survey area were included as fixed-effects; RD (recently disturbed), PD (past disturbance), ND (non-disturbed), MP (mixed papyrus/vegetation) (Table 1). To reduce multicollinearity (Dormann et al., 2013), MD (moderately disturbed) was removed due to correlation with ND for papyrus vegetation (Spearman coefficient = −0.67) and broader

Table 1
Vegetation classifications and physical characteristics used to indicate disturbance.

Vegetation category and symbol	Description	History of disturbance	Age	Typical height (cm)	Density	Culm thickness	Senescence?	Intensity of disturbance
Recently disturbed (RD)	Cleared (harvested), burnt, regrown immature papyrus[a], agricultural wetland[b]	Recent (weeks–months)	0–6 months	0–200	None/very low	None/very thin	No	High
Past disturbance (PD)	Mature papyrus regrown following disturbance	Past (>6 months)	>6 months–1 year	>200	High	Thin	No	Intermediate
Mature moderately disturbed (MD)	Mature papyrus previously disturbed and fully regrown to maturity	Past (1–1.5 years)	>1 year	>200	Moderate	Thick	Some	Moderate/low
Mature undisturbed (ND)	Mature papyrus, not likely to be disturbed, any disturbance over 1.5 years ago	None/>1.5 years	>1.5 years	>200	Low	Thick	Yes	Low
Mixed vegetation papyrus (MP)	Mixed wetland vegetation containing >40% papyrus[a], poor growing conditions for papyrus	None	>1 year	50–200	Low	Thin	Some	Low

[a] Includes wetland dominated by other wetland types for two of the study species also found in these areas (Carruthers's cisticola and papyrus yellow warbler) (Vande weghe, 1981; Maclean et al., 2006).
[b] Applicable to Carruthers's cisticola only.

wetland categories (Spearman coefficient = −0.50 (PYW); −0.45 (CC)). As MD is intermediate between mature undisturbed papyrus and papyrus intensely disturbed in the past, removing this category enabled us to closely examine the effect of intense compared to no disturbance and explore our research aim. Prior to doing so, we ran additional models including this term, confirming that this intermediate category of disturbance was not important. Squared terms for each disturbance category were included as explanatory variables to account for the possibility of non-linear responses. Interactions of each disturbance category with the overall area of the wetland (log-transformed to improve normality) and wetland shape (circularity) were included as the study species are known to respond to patch area and edge (Maclean et al., 2006) and may, therefore, be more tolerant of disturbance in larger and/or more circular swamps. To account for the possibility of spatial autocorrelation and pseudoreplication, two random effects (region and wetland) were included in the models. A cluster analysis was performed on the location of point counts, and used to designate each point count to one of seven "regions" of the lake. All except two of the study species were found in all regions. To ensure the results obtained were not attributable to differences between regions, we repeated analysis including only those regions where the species were found. In each case, the results were qualitatively similar. Wetland ID was included as a second nested random effect, as repeated point counts were conducted in separate parts of some larger wetlands.

Effects were analysed using multi-model inference (Burnham and Anderson, 2002). A global model containing the four disturbance categories, their interactions with area and circularity and squared terms as explanatory variables, was created for each species. Abundance was included as the response variable and the detectability-weighted area used as an offset in each model, allowing us to explore the effects of vegetation type on species density as opposed to abundance. All variables were zero-centred and z-score standardised prior to inclusion in models. The "MuMIn" package (Barton, 2014) was used to produce all possible combinations of the global model, ranked by their Akaike Information Criterion adjusted for small sample size (AICc). A set of best models was created for each species, consisting of all those with ΔAICc ≤ 2 from the top-ranked model (Burnham and Anderson, 2002). Model averaging was used to identify key variables likely to be affecting relative abundance and account for model uncertainty (Burnham and Anderson, 2002; Johnson and Omland, 2004). The relative importance (RI) of each parameter was calculated as the proportion of models in the top model set with that term included. Since the interactions between patch geometry and vegetation type within the top model set may alter the strength and directional effects of terms alone, analysis was repeated with full models excluding the interactions, and confirmed that the overall qualitative conclusions held regardless of the inclusion of two-way interactions.

3. Results

3.1. Survey data

A total of 105 point count surveys were conducted from 80 papyrus and 57 broad wetland swamps (Table 2). The number of point counts in which each species was recorded ranged from 22 (21%) in 12 patches for papyrus yellow warbler, to 87 (82.9%) in 69 patches for greater swamp warbler. Although greater swamp warbler was the most frequently encountered species, Carruthers's cisticola was the most abundant, with a total of 198 individuals recorded. Papyrus yellow warbler was the least common, with 28 individual observations.

3.2. Factors affecting population density

The number of plausible models (ΔAICc ≤ 2) ranged from two for Carruthers's cisticola, to five for papyrus yellow warbler (Table A1). All species showed effects of patch geometry, habitat requirements and disturbance on population density, though the direction and magnitude of their response differed between species.

3.2.1. Patch geometry

Patch area was contained in the top model set for all species (Table A2). Averaging of the top model set showed that the density of all but one species was positively affected by the overall size of the wetland, with higher densities in larger patches (Fig. 2a). Only the greater swamp warbler was negatively influenced by area, occurring at higher densities in smaller swamps (Fig. 2a).

Wetland shape was also important for the majority of the study species. Patch circularity was in the top model set for all species, excluding papyrus canary (Table A2). Model averaging the top model set revealed that patch shape was most important for white-winged scrub-warbler

Table 2
Summary of point count data collected (n = 105). Greater swamp warbler (GSW), white-winged scrub-warbler (WWW) and papyrus canary (PC) are entirely confined to papyrus, thus wetland patches for these species consist only of papyrus swamps. Carruthers's cisticola (CC) and papyrus yellow warbler (PYW) occupy wetlands dominated by both papyrus and other types of vegetation.

Species	Total wetland patches surveyed	Point counts with species present	Wetland patches with species present	Highest count per survey	Total individuals recorded
GSW	80	87 (82.9%)	69 (86.3%)	9	187
WWW	80	47 (44.8%)	33 (41.3%)	10	121
PC	80	25 (23.8%)	22 (27.5%)	7	69
CC	57	48 (45.7%)	19 (33.3%)	19	198
PYW	57	22 (21.0%)	12 (21.1%)	3	28

and the broad wetland species (papyrus yellow warbler and Carruthers's cisticola), with these species occurring at higher densities in patches with a higher area:edge ratio (Fig. 2a).

3.2.2. Habitat requirements

Wetland composition was an important habitat requirement for all of the study species, for which papyrus mixed with other wetland vegetation (MP) was contained in the top model set (Table A2). MP negatively affected the density of all three papyrus-restricted passerines (Fig. 2b). This effect was non-linear for white-winged scrub-warbler for which densities were only adversely affected when swamps contained high proportions of this category. The effect of MP interacted with circularity for greater swamp warbler, with effects reversed in more circular swamps (Fig. 2b), and interacted with patch size for papyrus canary, where the effect was only apparent in smaller swamps (Fig. 2b). The density of Carruthers's cisticola, a broader wetland species, was slightly higher in swamps dominated by MP, particularly in more circular swamps (Fig. 2b). Papyrus yellow warbler was the least affected by

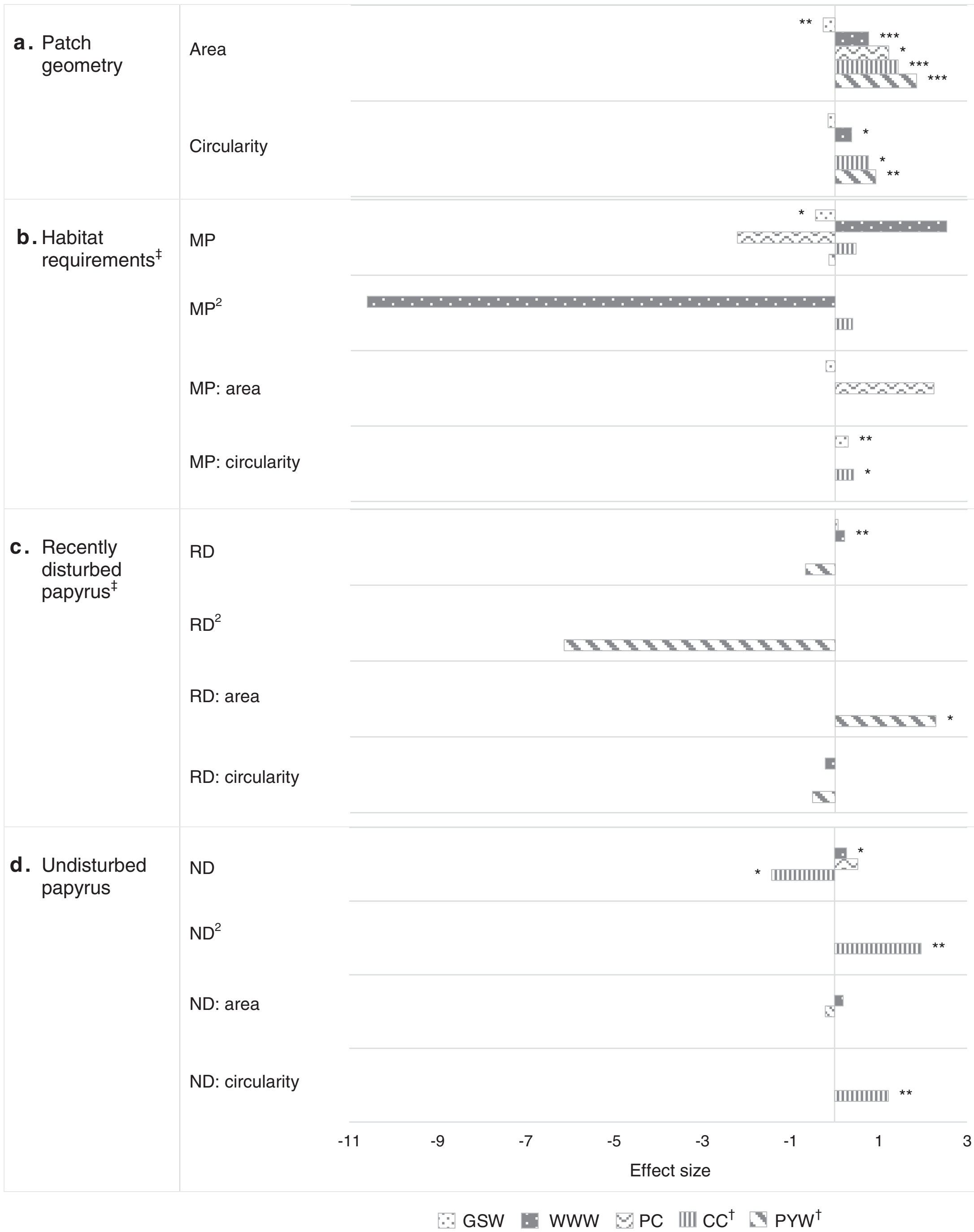

Fig. 2. Effect sizes of model averaged coefficients (ΔAICc ≤ 2) of explanatory variables from analysis of varying vegetation types on density for each species, displayed by category of interest: MP (mixed papyrus/vegetation), RD (recently disturbed papyrus/vegetation), ND (undisturbed papyrus); terms marked with "2" represent squared term of that variable; GSW (greater swamp warbler), WWW (white-winged scrub-warbler), PC (papyrus canary), CC (Carruthers's cisticola), PYW (papyrus yellow warbler). Bars represent the magnitude and direction of coefficients; area = log area of swamp; * significant effects where confidence intervals do not overlap with 0 ($P < 0.05$, 0.01, 0.001 represented by 1, 2 and 3 asterisks, respectively); ":" interactions with geometric variables; ‡ contains wetland dominated by other types of wetland vegetation for species which also inhabit this habitat type; † species also found in wetlands dominated by other vegetation types. See Table A2 for full model averaged output. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

this category, occurring at only slightly higher densities in areas with low amounts of MP (Fig. 2b) with an RI of 0.13 (Table A2).

3.2.3. Effects of disturbance

Most species were positively affected by the amount of intensely disturbed habitat within the survey area and were largely unaffected by the presence of large proportions of intermediate disturbance (Fig. A1). Low intensity disturbance within the survey area also did not strongly influence the density of most species, and those showing a positive relationship to undisturbed papyrus displayed a relatively weak response (Fig. A1). Considering all factors together, the overall importance of disturbance differed between species, often influenced by interactions with patch geometry:

i. *High intensity*

The amount of recently disturbed wetland (RD) within the survey area appeared in the top model set for three of the study species (Table A2). This effect was positive for greater swamp warbler and white-winged scrub-warbler, but with an RI of 0.24 and 1, respectively. Model-averaged results suggested that white-winged scrub-warbler occurred at significantly higher densities in areas with a high proportion of RD (Fig. 2c). Papyrus yellow warbler showed a slight negative response to the amount of RD (Fig. 2c). However, this effect was non-linear due to the presence of the squared term within the top model set (Table A2), thus RD only began to negatively affect this species when there were large proportions of it within the survey area. Moreover, the direction of this effect depended on the size of the wetland (Fig. 2c); in large swamps, large proportions of RD increased the density of papyrus yellow warbler.

ii. *Intermediate intensity*

The proportion of wetland disturbed in the past and regrown (PD) was the least important variable considered; only included in the top model set for papyrus yellow warbler (Table A2). Nevertheless, this term had an RI of 0.21 and was not found to be important when averaging across all models in the top model set (Table A2). As a result, all species tended to be relatively unaffected by intermediate intensities of disturbance.

iii. *Low intensity*

Undisturbed papyrus (ND) was in the top model set for three of the species, but unimportant for the two remaining species (Table A2). Model averaged results showed that the proportion of this category marginally influenced the number of papyrus canary (Fig. 2d; Table A2), and had a weak positive effect on the number of white-winged scrub-warbler within the survey area (Fig. 2d), with slightly higher densities in areas with large amounts of ND. This effect was negative for the density of Carruthers's cisticola, but as the squared term was also found to be important (Table A2), the effect was non-linear, with lower densities of this species in areas with intermediate levels of ND. Nevertheless, the direction of this effect depended on the circularity of the patch (Fig. 2d); higher densities of Carruthers's cisticola occurred in areas with large proportions of ND in more circular patches.

4. Discussion

Restricting disturbance from human activities is problematic in tropical areas where people rely heavily on natural resources for their livelihoods (Hutton and Leader-Williams, 2003), and fails to consider the potential role of disturbance in maintaining biodiversity. Investigating the effects of disturbance from habitat use on papyrus-restricted avifauna, we have shown that this group of species is tolerant to some degree of disturbance and some species even benefit from it. Demonstrating that subsistence resource use can be compatible with conservation in wetland systems has the potential to increase the capacity of biodiversity conservation in tropical regions to meet the needs of both people and wildlife.

4.1. Impacts of disturbance in tropical wetlands

Habitat specialist species are thought to be the most sensitive to changes in their habitat (Ntongani and Andrew, 2013), and thus papyrus-specialist passerines have been considered vulnerable to disturbance from human use (see Maclean et al., 2003a). However, the relative density of papyrus passerines within the survey area was most affected by the composition of wetland and overall size of swamps, as opposed to the level of disturbance. Should these species be adversely affected by disturbance, densities would be negatively impacted by recently disturbed and/or papyrus regrown following disturbance and positively affected by the presence of undisturbed habitat. On the contrary, papyrus disturbed in the past and regrown was not important for the density of any of the study species, highlighting that none of the species has a preference for or against papyrus that has been cut and regrown. Meanwhile, only two species (papyrus yellow warbler and white-winged scrub-warbler) responded to the amount of wetland that had been recently disturbed by cutting or burning and, consistent with occurrence data collected from large swamps across the south west of Uganda (Maclean et al., 2006), actually appeared to benefit from cleared areas of papyrus. Given that these species are insectivorous (Britton, 1978), creating open cut areas allows insects to thrive and enhances the availability of foraging for these birds. These two species also tended to prefer more circular swamps, favouring the swamp interior over the swamp edge. Open areas within the swamp could offer foraging sites that are sheltered and more secure from predators (Britton, 1978). On the other hand, greater swamp warbler preferred smaller swamps with more edge, potentially as a result of interspecific competition from the higher densities of the other species within larger swamps, and papyrus canary is known to feed on nearby crops (Britton, 1971), perhaps explaining why these species appeared largely unaffected by foraging opportunities created by disturbance within swamps.

Allowing some undisturbed papyrus to remain is, however, evidently important. Papyrus yellow warbler only benefitted from intensely disturbed papyrus within larger swamps, which typically had higher proportions of undisturbed wetland, with a negative effect of intense disturbance in smaller swamps. Similarly, the density of white-winged scrub-warbler was higher in areas with large proportions of recently disturbed and undisturbed papyrus, suggesting it preferred areas with a mixture of both. The species' that appeared to benefit from the presence of large proportions of undisturbed papyrus, Carruthers's cisticola and papyrus canary, were arguably the most sensitive to disturbance. Owino and Oyugi (2008) reported that papyrus canary was sensitive to disturbance in a sample of swamps in western Kenya. Yet in the current study, each of these species were largely unaffected by both disturbed categories, suggesting that they do tolerate disturbance, providing there is some undisturbed habitat within which to nest (Britton, 1978).

Species residing within papyrus swamps are likely to have evolved under a long history of disturbance and therefore, in common with temperate forest species, may have adapted to such pressures over time (Bengtsson et al., 2000; Hobbs and Huenneke, 1992; O'Reilly et al., 2006). Alternatively, those most resilient to disturbance pressures remain in wetlands today (Balmford, 1996). Swamps were prehistorically grazed by large herbivores such as hippopotamus (*Hippopotamus amphibious*) and exposed to natural fires (Maclean et al., 2006). Consistent with ideas from the Vera hypothesis (Vera, 2000) and in common with temperate forests (see Bengtsson et al., 2000), these herbivores are likely to have maintained a more open landscape and prevented swamps from being closed, dense habitat. While the history of swamp use is undocumented in Uganda, pollen data from wetlands in the west of the country reveal evidence of human activity dating back to ca. 2200 years B.P. (Hamilton et al., 1986; Taylor, 1990). By creating large open cut areas of papyrus within the swamp, traditional human activities such as harvesting essentially mimic the disturbance caused by large herbivores while grazing. Although most large herbivores have been lost from the region over the last 70 years, human activities ultimately replace the role of these animals in creating early successional habitat. Adopting ideas from the management of temperate systems, this has strong implications for the conservation management of wetlands in tropical East Africa.

Contrary to traditional assumptions, the results of our study suggest that the conservation of papyrus-dwelling passerines need not involve the complete restriction of natural resource use by local communities. Though our study employed proxy measures of disturbance, previous studies investigating the effects of intense forms of disturbance on papyrus birds elsewhere in East Africa also suggested levels of tolerance to low-intensity disturbance (e.g. Maclean et al., 2006; Owino and Oyugi, 2008). Policy guidelines in Uganda largely recognise that papyrus extraction is a traditional activity important for the livelihoods of local people (Wetlands Inspectorate Division, 2001). Yet where conservation is concerned, the principles from the "fences and fines" approach still prevail (Barrett et al., 2001), advocating that use should be restricted or prohibited (Hartter and Ryan, 2010). However, providing swamps remain large and some undisturbed wetland remains, low intensity subsistence use can continue without detriment to the species dependent on it. Wetland size is often not considered within existing legislation, yet the number of interactions between vegetation category and geometry in our study highlight the need to factor wetland size or shape into policy guidelines, with evidence for greater avian tolerance to swamp structure or disturbance in larger swamps. When swamps are smaller in size, simply maintaining broad types of wetland vegetation will not suffice. Pure papyrus, as opposed to papyrus mixed among broader wetland vegetation, is important for maintaining densities of these study species, who likely require the relatively taller stands of papyrus for feeding and nesting (Owino and Oyugi, 2008).

Taken together, our results support the annual rotational harvesting recommendation of Terer et al. (2012b) to maintain the biomass regeneration of papyrus following repeated destruction (Owino and Ryan, 2007), ensure its availability for subsequent generations and enable sections of undisturbed papyrus to persist year-round for biodiversity. Papyrus has an exceptionally fast regeneration time, with complete regrowth within approximately 6 months of disturbance (Muthuri et al., 1989). In turn, the species dependent on this habitat need only tolerate a short period of time when sections of their habitat have been cleared. Governance in Uganda has taken a decentralized approach whereby wetland management is often controlled in a hierarchy from district to village level (Maclean et al., 2011a) which, within our study area, allows swamp users to cooperate to ensure sufficient resources remain for others nearby (Maclean et al., 2003b) and permits regrowth of alternate harvested areas between years. Application of these self-regulation methods across East Africa could be key both for continued subsistence resource use and the persistence of wetland specialist birds (Maclean et al., 2011a; Shiferaw, 2006).

Habitat loss is currently one of the main threats to papyrus in south west Uganda (Maclean et al., 2013) leading to the removal of swamps, the reduced overall size of wetlands and an increased level of fragmentation across the landscape (Fahrig, 2003; Owino and Ryan, 2007). We have highlighted that densities of each species, with one exception, are higher within larger swamps and, in consequence, the drainage of larger swamps will have a disproportionately adverse effect on regional populations. Low intensity subsistence use of papyrus, on the other hand, results in temporary disturbance to the swamp as opposed to permanent removal following reclamation for crop production (Boar, 2006). While swamp drainage for agriculture will continue to have a damaging effect on biodiversity, resource extraction is less problematic and can even be beneficial. Thus, subsistence harvesting can persist within larger swamps where species are tolerant of such disturbances, while use should be discouraged from smaller swamps where the impacts have the potential to be more detrimental. Previous work demonstrates that sustainable use of this kind can be more profitable for people, since the net present value of harvested papyrus and fish far exceeds that of crops obtained from drained swamp land (Maclean et al., 2003c).

4.2. Implications for conservation

Conservation in the tropics often views the needs of people as a trade-off with those of biodiversity. Although it is now generally accepted that conservation should involve communities, with the Convention on Biological Diversity (CBD) encouraging this approach (Berkes, 2007), restrictions on natural resource use still prevail. The United Nations (UN) recognises the need to achieve a balance between poverty reduction and ecosystem conservation (Senaratna Sellamuttu et al., 2011), yet managing systems to meet demand without detriment to biodiversity conservation is a challenge (Senaratna Sellamuttu et al., 2011) that has been the focus of little investigation.

Using evidence from papyrus avifauna, we have shown that conservation in tropical wetlands need not require complete exclusion of human resource use. As with temperate forest systems, traditional human activities can mimic former natural forms of disturbance, creating open areas of habitat which may benefit biodiversity. Future work is needed to establish the applicability of this conclusion to other wetlands in East Africa and more widely. The productivity and regrowth of other wetland vegetation can be similar to that of papyrus (Muthuri et al., 1989) and other macrophytes experience comparable forms of disturbance because of the socio-economic uses they provide (Terer et al., 2012b). Hence, the possible effects of disturbance on both local livelihoods and conservation in other wetlands merits further research.

The long history of human activity is well-documented across Africa (Hamilton et al., 1986) and other tropical regions (e.g. Heckenberger et al., 2003). Given the potential to mimic decreasing natural disturbances, conservation in the tropics, particularly of other wetlands, will benefit from acknowledging that human activities can play a role in maintaining biodiversity. Rather than promoting alternative livelihoods as a means to promote biodiversity conservation (Brown, 2002), emphasis could be placed on understanding and documenting the past history of disturbance in tropical habitats and the impacts of low-intensity natural resource use on biodiversity, without the a priori assumption that all disturbance is detrimental. Due to the need to support rural livelihoods, "conservation through use" (Brown, 2002) may in some instances prove to be of direct benefit to biodiversity, rather than a separate poverty-alleviation objective. Strong consideration for local livelihoods is also likely to lead to greater support for conservation (Spiteri and Nepalz, 2006), helping to minimise conflict between people and biodiversity conservation (Senaratna Sellamuttu et al., 2011).

5. Conclusion

This study highlights the potential to combine subsistence resource use and conservation management in tropical wetland systems. Using papyrus swamps as a case study, we demonstrate that specialist species can tolerate disturbance, possibly as a result of the historic disturbance of papyrus, even prior to inhabitation by humans. Striving to conserve wetlands and the biodiversity dependent on them does not necessarily involve the complete restriction of people who rely on the resources they provide. Instead, the disturbance that results from such activities may be of benefit to biodiversity and can be incorporated into the conservation management of tropical systems such as wetlands, creating a win–win situation for both wildlife and people.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.07.036.

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