


CONTRIBUTED PAPER

Conservation of vertebrates and plants in Uganda: Identifying Key Biodiversity Areas and other sites of national importance

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Funding information

Tullow Oil; United States Agency for International Development, Grant/Award Number: AID-617-LA-14_00002; Wildlife Conservation Society

Uganda is one of the most species rich countries in Africa because of the presence of several major biomes. However, it is also a country that has lost much of its natural habitat to agriculture. Uganda is a country that has been better surveyed for its biodiversity than many African countries, but despite this, there has not been a comprehensive analysis of the critical sites that contribute to biodiversity conservation at a global, as well as at a national level. We here present such an assessment using mammals, birds, reptiles, amphibians, and plants as surrogate taxa. We identified 36 terrestrial sites that are of sufficient global importance to qualify as Key Biodiversity Areas (KBAs), using the Global Standard for the Identification of KBAs, which complement an additional nine freshwater sites. National red listing of species and ecosystems was used to identify sites of national importance for conservation. We employ a conservation planning approach using Marxan to identify the minimum set of sites needed to conserve all the globally and nationally threatened species and nationally threatened habitats in Uganda. The findings show that most of the remaining natural habitat in Uganda is important for the conservation of globally and nationally threatened species and threatened habitat. Large areas of irreplaceable habitat occur outside protected areas, although more extensive surveys of these areas would likely reduce the area that is irreplaceable.

KEYWORDS

biodiversity, conservation planning, Key Biodiversity Areas, Marxan, National Red List

1 | INTRODUCTION

Under the Convention on Biological Diversity (CBD) each signatory commits to conserving biodiversity and managing

it for sustainable use. Nations are encouraged to map their biodiversity and assess which species are threatened (Secretariat of the Convention on Biological Diversity, 2005). While the emphasis is on species that are globally threatened as well as species rich ecosystems, there is an implication in the CBD that each country commits to conserving its biodiversity richness so that no species are lost at a country level.

Data accessibility statement: Data will be made available on the WCS web site and accessible by request at globaldata@wcs.org once the paper is published.

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Uganda is one of Africa's richest countries for biodiversity, ranking eighth of the 54 countries on the continent (Mongabay, 2016). However, Uganda is relatively small in area, and it contains the highest species richness per unit area of all African countries. Supporting a known 1,742 terrestrial vertebrate species (with more than half of Africa's birds), and at least 4,816 plant species (Kalema, Namaganda, Bbosa, & Ogwal-Okeng, 2016), it is an important nation for conservation on the African continent (National Biodiversity Databank [NBDB], Makerere University). Although the invertebrate fauna is less well-known, already some 1,300 species of butterflies and 260 dragonfly species have been recorded.

Uganda's human population has been growing rapidly, at 2.5–3% per year since the 1930s, and is recently estimated at about 35 million (Uganda Bureau of Statistics, 2015). Uganda is also developing rapidly as a nation and is actively encouraging mineral exploration, oil, and gas developments (Dowhaniuk, Hartter, Ryan, Palace, & Congalton, 2018), as well as expanding its power generation, supply grid, and other industries and road networks. As a result, there is a need to plan proactively for these developments and identify areas that are important for conservation as well as sites where trade-offs for development could occur.

Protected areas were established from the 1920s in Uganda; forest reserves for timber and watershed management, and game reserves for sport hunting initially. Significantly, from the earliest days, timber harvesting was planned to be sustainable. As the human population expanded and wildlife declined across the country, four of the Game Reserves were made into National Parks in the 1950s to protect large mammals and encourage the growing number of tourists that were coming to East Africa (Olupot, Parry, Guinness, & Plumptre, 2010). An assessment of the biodiversity of some of the large forest reserves (Howard, 1991) led to the creation of six forested National Parks in 1993 and 1995. In 1996, a review of the status of the national parks and game reserves led to an amalgamation of the national parks and game departments to form the Uganda Wildlife Authority (UWA) and game reserves became Wildlife Reserves (Lamprey et al., 1999; Lamprey, Buhanga, & Omoding, 2003). Around the same time, detailed biodiversity surveys of the forest reserves in Uganda by the then Uganda Forest Department, identified sites for nature reserves within the forest reserve estate for Uganda, and prioritized forests based on their conservation value (Howard et al., 2000). The current protected area estate is shown in Figure 1 and also shows that 7 of the 10 national parks, and 7 of the larger Forest Reserves occur in the biodiverse Albertine Rift region of western Uganda (Plumptre et al., 2007). In the late 1990s, Nature Uganda led an assessment of Important Bird Areas for Uganda, identifying 30 Important Bird and Biodiversity Areas (IBAs) for the country of which 10 were outside protected areas (Byaruhanga, Kasoma, & Pomeroy, 2001).

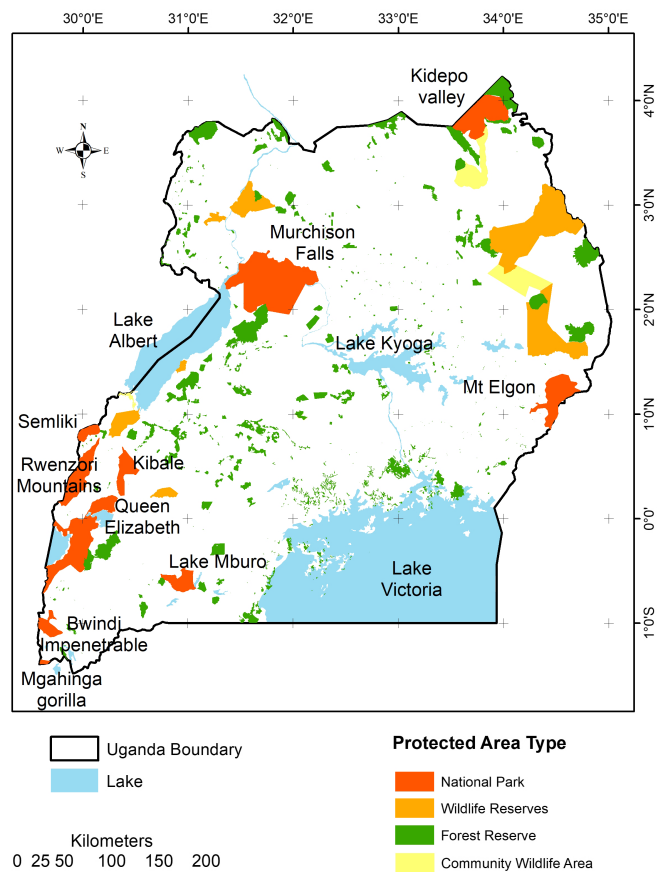


FIGURE 1 The location of protected areas in Uganda with National Parks and largest lakes named

Since then a further three sites have been added totaling 33 IBA sites.

Uganda is estimated to have lost about 50% of its biodiversity value between 1975 and 1995 due to high levels of hunting of large mammals and loss of forest, savannah, and wetland habitat to agriculture (Pomeroy, Tushabe, & Loh, 2017). While there has been some recovery in numbers of large mammals since 1996, because of populations rebuilding in the parks, much of the loss is continuing, due to habitat loss as the human population continues to expand. Some large mammals have been extirpated from the country including; black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*), oryx (*Oryx beisa*), and Bright's gazelle (*Nanger granti ssp. notata*) a subspecies of Grant's gazelle. Many other species have declined to very low population levels, particularly African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*) which are estimated to number fewer than 25 individuals each. It is unknown what smaller, undescribed species may have been lost as a result of habitat conversion, but there are several known butterfly species described from the 1930s that have not been seen since that time (P. Akite pers. comm., WCS, 2016).

Here, we identify which remaining natural habitats across Uganda are critical for the conservation of both global and nationally important vertebrates and plants. Compiling

data on globally threatened species, identifying nationally threatened species, and mapping the distributions of terrestrial vertebrates and plants, we identify which protected areas and unprotected sites are irreplaceable for the conservation of all threatened species.

2 | METHODS

2.1 | Developing a species by site matrix

We built upon surveys of biodiversity made of 65 of Uganda's forests (Howard et al., 2000; Howard, Davenport, & Kigenyi, 1997) in the mid-1990s, managed by the then Forest Department (now National Forest Authority—NFA). These surveys visited all of Uganda's forests larger than 50 km², together with 11 smaller forests in unique habitat types, and surveyed trees, small mammals, birds, butterflies, and two families of moths with the aim of establishing nature reserves within the Central Forest Reserves. Between 2000 and 2016, the Wildlife Conservation Society (WCS) surveyed many of the national parks, wildlife reserves, and forest reserves as well as sites outside these protected areas for mammals, birds, and plants. NBDB, housed at the Department of Environmental Management of Makerere University in Kampala, also compiled data from additional surveys across the country. Much of the WCS and NBDB data are georeferenced with GPS locations for each sighting. Additional literature was reviewed, such as Kingdon (1971–1982) as well as recent survey reports by other institutions, and point locations of sightings of large mammals mapped in ArcGIS 10.1. A land cover map produced by the NFA in 2010 was used to identify natural and seminatural habitats

outside protected areas. Species were allocated to protected areas, or areas of seminatural habitat outside protected areas which were identified and delimited as blocks of similar habitat. Most uncultivated land outside protected areas is grazed by livestock, and in these grazing areas the vegetation consists almost entirely of native plant species, which in turn support many native animal species except for large wild mammals, which have been replaced by livestock. However, almost all pastoral land is overgrazed. Given the limited survey data outside protected areas, these sites tended to be larger than protected areas in order to have a reasonable estimate of species composition, but could be refined with further survey effort.

We then made several assessments of these data as well as data on distribution of ecosystems in Uganda to identify sites of global and national importance for the conservation of biodiversity. Figure 2 summarizes the data that were used for each component of the methods as described in the following text.

2.2 | Globally important site assessments

2.2.1 | KBA identification

Since 2004, the conservation community has been going through a process to agree criteria to identify Key Biodiversity Areas (KBAs). These criteria build upon the IBAs Programme of BirdLife International which was initiated in the 1970s (Donald et al., 2018). KBAs are globally important sites for the persistence of biodiversity because they hold significant numbers of one or more species of conservation concern. A *Global Standard for the Identification of Key Biodiversity Areas* (henceforth Global Standard) was published after several years of consultations and details the

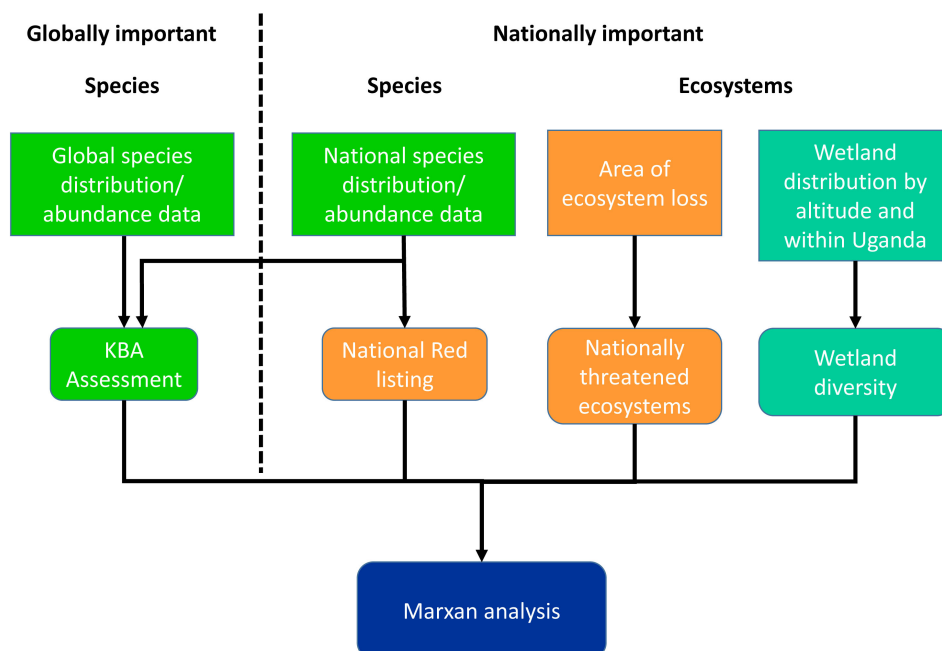


FIGURE 2 Process used to analyze data and identify sites of importance for conservation in Uganda

TABLE 1 KBA criteria applied in Uganda

KBA higher level	KBA criteria	Criteria letter code	Applied in Uganda assessment
A. Threatened biodiversity	Threatened species	A1	Applied
	Threatened ecosystem types	A2	Not applied
B. Geographically restricted biodiversity	Individually geographically restricted species	B1	Applied
	Co-occurring geographically restricted species	B2	Applied
	Geographically restricted assemblages	B3	Not applied
	Geographically restricted ecosystem types	B4	Not applied
C. Ecological integrity	Sites of ecological integrity	C	Applied but none identified
D. Biological processes	Demographic aggregations	D1	Applied
	Ecological refugia	D2	Applied
	Recruitment sources	D3	Applied
E. Irreplaceable sites	Irreplaceable sites through quantitative analysis	E	Not applied

criteria for identifying KBAs (IUCN, 2016). Eleven criteria can be used to assess whether a site is a KBA within five higher level groups (Table 1): A: Globally threatened biodiversity (Includes Criteria A1: threatened species, A2: threatened ecosystems); B: Geographically restricted biodiversity (Includes criteria B1: individual geographically restricted species, B2: co-occurring restricted range species, B3: geographically restricted assemblages, and B4: geographically restricted ecosystems); C: Intact ecological communities; D: Biological Processes (includes D1: aggregations, D2: sites of refugia D3: sources of recruitment); E: Irreplaceable sites based on conservation planning analyses. We made an assessment of Uganda's sites using Criteria A1, B1, B2, D1, D2, and D3. We assessed potential criterion C sites in Uganda but did not believe any sites met the criterion for ecological integrity. Some sites we know will be irreplaceable such as Rwenzori Mountains and Mt. Elgon National Parks, where there are species endemic to those mountains, but as these sites met KBA status for species under Criterion B1 we did not apply criterion E. Criterion B3 was not applied because standard lists of eco/bioregional species, which are required to apply the criterion, have not been developed, and we did not have the data to be able to make these global lists. We also did not assess threatened ecosystems (Criterion A2) or geographically restricted ecosystems (Criterion B4) because they require a standard list of global ecosystems which does not yet exist. Table 1 summarizes the criteria applied in this assessment.

IBAs have been migrated into the World database of KBAs but require assessing against the KBA criteria. We applied these criteria to the existing IBAs for Uganda (Birdlife International, 2017) to evaluate which would meet KBA criteria. In this case, we assessed the bird species that met IBA Criteria A1 (globally threatened species), A2 (restricted-range species), and A4 (congregations) for each site, but not the species that met A3 (biome-restricted species) as this is similar to the B3 criterion for KBAs and requires a standard list of biome-restricted species which has not been developed yet. After assessing which IBAs met at

least one of the KBA criteria we then identified additional sites that would meet the KBA criteria in Uganda.

2.3 | Nationally important sites

2.3.1 | National Red Lists of species

The IUCN Species Survival Commission guidelines for the application of IUCN red list criteria at Regional and National Levels (IUCN, 2012) were applied to eight taxa: mammals, birds, reptiles, amphibians, fish, butterflies, dragonflies, and vascular plants. Taxa were selected where there was good national expertise available, and which have been relatively well surveyed across the country. The NBDB, at Makerere University, provided species lists for Uganda for each taxon. Specialists added to these lists from their own data to provide complete species lists for Uganda. A training meeting was held in Kampala with teams of specialists for each taxon, and then species were assessed using the National Red List criteria over a 6-month period by specialist groups for each taxon (IUCN, 2012). For two taxa, with many species (butterflies and plants), it was not possible to assess all species. Instead, a shortlist of rare and restricted range species was compiled based on the expertise and knowledge of the specialists and these were assessed against the criteria. The National Red List species for each taxon should therefore be considered a minimum list. The National Red List was presented to government in 2016 and published (Ministry of Tourism, Wildlife and Antiquities, 2016). Species listed as nationally threatened (CR, EN, or VU) were entered in the Marxan conservation planning analysis (see below) together with data deficient (DD) species. DD species are often classified as such because they are very rarely seen and their distribution is poorly known, and as such are likely to also be threatened.

2.3.2 | Nationally threatened ecosystems

In the early 1960s, a phytosociological mapping of natural habitats across Uganda was made, using a combination of aerial photographs for the whole country together with ground truthing at sampling points (Langdale-Brown,

Osmaston, & Wilson, 1964). The maps produced were digitized into ArcGIS by the NBDB. A map of the extent of agriculture and natural habitats was obtained from the NFA 2010 land cover map. Nationally threatened habitats were identified using the IUCN Red Listing approach (Rodríguez et al., 2011). They were determined by calculating the percentage of natural habitat remaining by 2010 of the various habitats mapped by Langdale-Brown et al. (1964), clipping them by the 2010 map of natural habitat extent, to calculate the area lost between the 1950s and 2010 of each of the habitats. Criterion A1 from the ecosystem red list approach was then applied to the percentage of habitat lost in the past 50 years (Rodríguez et al., 2011). This approach gives a very conservative estimate of loss as it does not account for potential habitat degradation and change within the remaining natural habitat.

2.3.3 | Wetland biodiversity

Few biodiversity data were available for wetlands except for some water bird surveys. Wetlands cover 33,046 km² or 14% of the country (WCS analysis of wetland maps 2016) so are an important habitat. Wetland species will likely vary by where wetlands occur within the country, varying also with altitude and whether the wetland is seasonal or permanent. The Uganda Wetlands Division has allocated wetlands in Uganda to four geographical regions (northern, western, central, and eastern—areas that have general ecological differences in Uganda) and mapped both seasonal and permanent wetlands. In addition, we used a digital elevation model to allocate these mapped wetlands to an additional three altitude classes (less than 1,000 m, 1,000–1800 m, and greater than 1800 m). These altitude bands were selected because it was believed there were differences in wetland flora between each altitude band. In the conservation planning analysis (see below), we allocated targets for the conservation of a percentage of the area of each of these wetland classes.

2.4 | Conservation planning for global and national conservation targets

We used the conservation planning tool Marxan (Ball, Possingham, & Watts, 2009) to make an assessment of the minimum set of sites required to conserve Uganda's globally and nationally threatened species, nationally threatened habitats, and the variety of its wetland classes. Marxan is widely used for conservation planning and aims to maximize the number of species conserved across a selected set of sites while minimizing the costs of conserving the sites using a heuristic algorithm. A target amount to be conserved for each species was set as a percentage of the area of all sites where the target has been recorded to occur in Uganda for this analysis, while minimizing the cost of conservation. We used sites (protected areas and areas of natural/seminatural habitat outside protected areas) as the units of analysis. The areas of each site differ greatly, but the analysis selects the minimum number of sites required to meet the area targets for all

species. Target amounts were set for most species at 25% of the area where they have been recorded (increasing this to 50–70% for species that require large ranges—large carnivores, elephants [*Loxodonta africana*], shoebills [*Balaeniceps rex*], and apes), together with targets of 20% area for threatened habitat (25% if its total area was <1,000 km²). Targets of 10% of the habitat for each of the wetland classes were allocated, except high altitude wetlands which were assigned a target of 30% because they totaled an area less than 300 km². A cost layer was developed for the Marxan analysis that downweighted the cost of conserving sites inside protected areas, compared to sites outside the protected areas. Costs were set so that parks and wildlife reserves had lower costs (relative value of 0.3) compared with forest reserves (relative value of 1.0) which were lower than unprotected sites (relative value of 5.0). These relative costs were applied because resources for conservation are much higher for parks and wildlife reserves compared with forest reserves and the minimal budgets for anywhere outside a protected area. The 36 terrestrial KBA sites were locked into the analysis so that they were always selected but freshwater sites were not because they had not been identified at the time of the analysis. We ran the analysis 100 times to calculate the frequency of selection of each site.

The paper is based on data compiled from historical records and surveys and assessments of habitat cover. No data from individuals were collected without their consent, and most people who contributed data are coauthors on the manuscript. This information is not published elsewhere in any Journal or book chapter. The authors complied with the Wiley's Publication Ethics.

3 | RESULTS

3.1 | Globally and nationally threatened species

The number of globally listed threatened (CR, EN, and VU) terrestrial vertebrates in Uganda totaled 57 species, together with an additional 42 plant species (Table 2). While all mammals, birds, and amphibians have been assessed on the IUCN Red List, many reptiles and plants have not, so that these numbers will increase as more of these taxa are assessed. As the taxonomy of amphibians and reptiles is in flux in the region, it is also likely that more species will be identified and many of these may be threatened (Hughes et al., 2018; Hughes, Kusamba, Behangana, & Greenbaum, 2018; Portillo, Greenbaum, Menegon, Kusamna, & Dehling, 2015). The national red listing process identified 208 terrestrial vertebrates and 80 plants as threatened in Uganda (Table 2), with an additional 135 DD species.

3.2 | Nationally threatened habitats

Seven of the eighty-two phytosociological habitats (Langdale-Brown et al., 1964) were estimated as nationally

TABLE 2 Numbers of globally and nationally threatened terrestrial vertebrates and plants in Uganda

	Taxon Total species	Mammal 396	Bird 1,043	Reptile 220	Amphibian 83	Terrestrial vertebrates 1,742	Plant 3,662
Globally threatened	CR	1	4	0	1	6	3
	EN	9	8	0	1	18	4
	VU	17	11	2	3	33	35
	DD	12	2	1	7	22	3
	<i>Total global</i>	39	25	3	12	79	45
Nationally threatened	CR	14	9	4	1	28	15
	EN	25	24	8	9	66	27
	VU	38	52	17	7	114	38
	DD	40	28	48	16	132	3
	<i>Total national</i>	117	113	77	33	340	83

Note. Data deficient species are also listed because these species are rare and likely threatened but there is not enough information to make the listing.

TABLE 3 Names and remaining area of nationally threatened habitat in Uganda

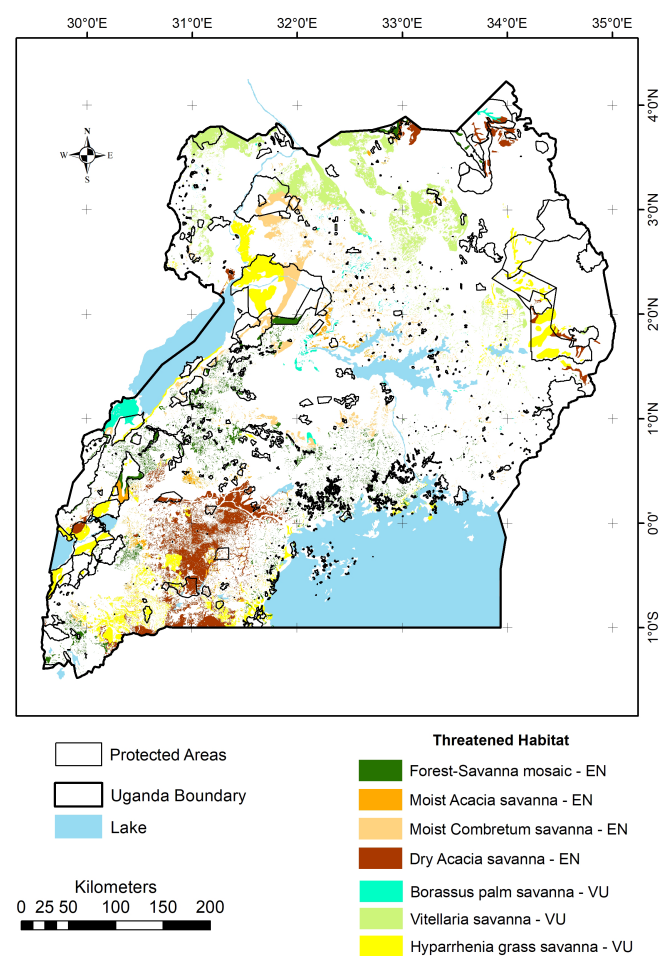
Name	Status	Criterion	Area (km ²)
Moist <i>Acacia</i> savanna	EN	A1	563
Forest-Savanna Mosaic	EN	A1	1,081
Dry <i>Acacia</i> savanna	EN	A1	2,971
Moist <i>Combretum</i> savanna	EN	A1	2,437
Open Grass savannas	VU	A1	5,010
<i>Borassus</i> Palm savannas	VU	A1	357
<i>Vitellaria</i> savanna	VU	A1	3,666

Note. These are all habitats that have lost either 50% (EN) or 30% (VU) of their original extent.

threatened (Table 3), those mostly being savannah grassland or woodland types (Figure 3). These habitats have tended to occur in areas where people readily settle and clear the habitat for agriculture. Tropical high forest was not identified as threatened, mainly because much of the forest loss occurred earlier than 50 years ago, the timeframe used in the ecosystem red listing Criterion A1. Criterion A3 uses habitat loss since 1,750 but we do not know the forest extent at that time but do know that clearance for agriculture was occurring at least 2000 years ago (Hamilton, 1984; Taylor, Robertshaw, & Marchant, 2000). Medium altitude moist evergreen and medium altitude moist semideciduous forest are also likely to qualify as threatened but we do not have the original extent to be able to measure the amount lost for these two main forest types. However, most of the remaining forest occurs within protected areas and so is captured in the conservation planning by species at those sites.

3.3 | Global sites of conservation importance

A total of 36 sites qualified as KBAs on the basis of their terrestrial vertebrate or plant species (Table 4; Table S1, Supporting Information) of which 12 were unprotected (Figure 4). These sites are in the process of being proposed to the KBA Secretariat by a Ugandan KBA National Coordination Group and should only be thought of as proposed KBA sites until confirmed. Of the 33 IBA

**FIGURE 3** Nationally threatened natural/semi-natural habitat types in Uganda

sites in Uganda, 10 did not qualify for KBA status applying the criteria in the Global Standard but these may meet the criteria for B3b of the Global Standard when bioregional bird species lists are finalized. Additionally, of those IBAs that did qualify, eight sites did not qualify for the species identified under IBA Criteria A1, A2, and A4, but required other species to trigger the KBA status. Thirteen new KBAs were identified for Uganda in this

TABLE 4 List of the 36 proposed terrestrial and 9 freshwater KBA sites listing the species that triggered KBA status

Site number	KBA site name	KBA criteria	Species that triggers KBA status	IUCN Red List
<i>IBAs that qualified</i>				
1	Budongo Forest Reserve	A1c(i)	Chimpanzee (<i>Pan troglodytes</i>)	EN
		A1a(i)	Nahan's partridge (<i>Ptilopachus nahani</i>)	EN
		B1(ii)	<i>Gomphia mildbraedii</i>	
		B1(ii)	<i>Balsamocitrus dawei</i>	
		A1b(ii)	<i>Desplatsia mildbraedii</i>	
2	Bugoma Forest Reserve	A1c(i)	Chimpanzee (<i>Pan troglodytes</i>)	EN
		B1 (iv)	Moon shrew (<i>Crocidura selina</i>)	DD
		B1 (i) ^a	Uganda Mangabey (<i>Lophocebus ugandae</i>)	
		A1a(i)	Nahan's partridge (<i>Ptilopachus nahani</i>)	EN
3	Bwindi Impenetrable National Park	A1a(i); B1 (iv)	Eastern gorilla (<i>Gorilla beringei</i>)	CR
		A1a(iv)	Narrow-headed Shrew (<i>Crocidura stenocephala</i>)	EN
		B1 (iv)	Rahm's Brush-furred Rat (<i>Lophuromys rahmi</i>)	NT
		A1b(i)	Green Broadbill (<i>Pseudocalyptomena graueri</i>)	VU
		A1a(i)	Grauer's Rush Warbler (<i>Bradypterus graueri</i>)	EN
		B1 (iv)	<i>Leptosiphos hackarsi</i>	
		B1 (ii)	<i>Ficus katendei</i>	
B1 (iv)	<i>Rytigynia ruwenzoriensis</i>			
4	Echuya Forest Reserve	A1a(iv)	Narrow-headed Shrew (<i>Crocidura stenocephala</i>)	EN
		A1b(iv)	Delany's Swamp Mouse (<i>Delanymys brooksi</i>)	VU
		A1a(i)	Grauer's Rush Warbler (<i>Bradypterus graueri</i>)	EN
5	Kasyoha-Kitomi Forest Reserve	A1c(i)	Chimpanzee (<i>Pan troglodytes</i>)	EN
		B1 (iv)	<i>Diospyros katendei</i>	
		B1 (iv)	<i>Uvariadendron magnificum</i>	
		B1 (ii)	<i>Ficus katendei</i>	
		B1(ii)	<i>Balsamocitrus dawei</i>	
6	Kibale National Park	A1c(i)	Chimpanzee (<i>Pan troglodytes</i>)	EN
		B1 (i) ^a	Uganda Mangabey (<i>Lophocebus ugandae</i>)	
		B1(ii)	<i>Balsamocitrus dawei</i>	
7	Kidepo Valley National Park	A1b(iv)	Karamoja Apalis (<i>A. karamojae</i>)	VU
8	Kyambura Wildlife Reserve	D1a(i)	Lesser Flamingo	NT
		B1 (iv)	<i>Atheris acuminata</i>	
9	Lake Bisina	B1 (iv)	Fox's weaver (<i>Ploceus spekeoides</i>)	NT
10	Lake Mburo National Park	B1 (iv)	Red-faced barbet (<i>Lybius rubrifacies</i>)	NT
11	Lake Opeta	B1 (iv)	Fox's weaver (<i>Ploceus spekeoides</i>)	NT
12	Lutembe Bay	D1a(i)	White-winged black tern (<i>Chlidonias leucopterus</i>)	LC
13	Mabira Forest Reserve	B1 (i) ^a	Uganda Mangabey (<i>Lophocebus ugandae</i>)	
		B1 (iv)	Moon shrew (<i>Crocidura selina</i>)	DD
		A1a(v)	Nahan's partridge (<i>Ptilopachus nahani</i>)	EN
		B1(ii)	<i>Balsamocitrus dawei</i>	
		B1 (iv)	<i>Vepris eggelingii</i>	
14	Virunga Volcanoes	A1a(i)	Eastern gorilla (<i>Gorilla beringei</i>)	CR
		A1a(i) ^a	Golden monkey (<i>Cercopithecus mitis kandtii</i>)	EN
		B1 (iv)	<i>Dendrosenecio erici-rosenii alticola</i>	
15	Mount Elgon National Park	A1a(iv)	Barbour's Vlei Rat (<i>Otomys barbouri</i>)	EN
		B1 (iv)	Du Toit's Torrent Frog (<i>Arthroleptides dutoi</i>)	CR
		B1 (iv)	<i>Dendrosenecio elgonensis</i>	
		B1 (iv)	<i>Hypericum bequaertii</i>	
		B1 (iv)	<i>Helichrysum amblyphyllum</i>	
16	Mount Moroto Forest Reserve	B1 (iv)	<i>Aloe wrefordii</i>	
17	Mount Otzi Forest Reserve	B1 (iv)	Moon shrew (<i>Crocidura selina</i>)	DD
18	Murchison Falls National Park	B1 (iv) ^a	Rothschild giraffe (<i>Giraffa camelopardalis rothschildii</i>)	EN

TABLE 4 (Continued)

Site number	KBA site name	KBA criteria	Species that triggers KBA status	IUCN Red List
		A1 d(i)	Elephant (<i>L. africana</i>)	VU
19	Nabugabo Wetland	B1 (i)	<i>Xyris ednae</i>	
		B1 (i)	<i>Senecio nabagubensis</i>	
20	Queen Elizabeth National Park (including Kigezi Wildlife Reserve)	A1d(i)	Elephant (<i>L. africana</i>)	VU
		B1(ii)	<i>Balsamocitrus dawei</i>	
21	Ruwenzori Mountains National Park	B1 (iv)	Ruwenzori duiker (<i>Cephalophus rubidus</i>)	EN
		B1 (iv)	Rwenzori otter shrew (<i>Micropotamogale ruwenzorii</i>)	LC
		A1a(iv)	Montane shaggy rat (<i>Dasymys montanus</i>)	EN
		A1b(iv)	Moon striped mouse (<i>Hybomys lunaris</i>)	VU
		A1a(iv)	Montane Mouse Shrew (<i>Myosorex blarina</i>)	EN
		B1 (iv)	Helmeted chamaeleon (<i>Kinyongia carpenteri</i>)	NT
		B1 (iv)	Rwenzori Plate-nosed Chameleon (<i>Kinyongia xenorhina</i>)	NT
		A1b(iv)	Ruwenzori Four Toed Skink (<i>Leptosiphos meleagris</i>)	VU
		B1 (iv)	<i>Amietia ruwenzorica</i>	DD
		B1 (iv)	<i>Dendrosenecio adnivalis</i>	
		B1 (iv)	<i>Dendrosenecio erici-rosenii</i>	
		A1a(iv) B1 (iv)	<i>Cyathia mildbraedii</i>	
		B1 (iv)	<i>Hypericum bequaertii</i>	
		B1 (iv)	<i>Rytigynia ruwenzoriensis</i>	
22	Sango Bay Area	D1 (b)	Blue swallow	VU
23	Semuliki National Park	B1 (iv)	Uganda clawed toad (<i>Xenopus ruwenzoriensis</i>)	DD
<i>Additional non-IBA sites added</i>				
24	Bugala Island—Sesse Islands	B1 (iv)	Lake Victoria swamp rat (<i>Pelomys isselii</i>)	
		B1 (iv) ^a	Sesse island Sitatunga (<i>Tragelaphus spekei sylvestris</i>)	
25	East Thruston Bay	A1a(i)	<i>Encephalartos equatorialis</i>	CR
26	Itwara Forest Reserve	B1 (iii)	<i>Telipna sheffieldi</i>	
		B1 (iv)	<i>Vepris eggelingii</i>	
27	Kalinzu	A1c(i)	Chimpanzee (<i>Pan troglodytes</i>)	EN
28	Kome Island—Sesse Islands	B1 (iii)	Lake Victoria swamp rat (<i>Pelomys isselii</i>)	
29	Kyenjojo-Mubende inselberg	B1 (iv)	<i>Sansevieria lineata</i>	
30	Mardioppei—South Moyo	A1a(i)	<i>Encephalartos macrostrobilus</i>	EN
31	Morungole FR	B1 (iv)	<i>Aloe wrefordii</i>	
32	Mpanga Falls	A1a(ii)	<i>Encephalartos whitelockii</i>	CR
33	Newtons snake tongue KBA	B1 (iv)	<i>Sansevieria newtoniana</i>	
34	Ogili Forest Reserve	B1 (iv)	<i>Sansevieria subtilis</i>	
35	Timu extension	B1(iv)	<i>Aloe ikiorum</i>	
36	Tororo Rock	A1a(i)	<i>Aloe tororoana</i>	VU
<i>IUCN Freshwater sites</i>				
37	Sio River mouth	A1a(iv); D1 a(iv)	<i>Labeo victorianus</i>	CR
38	Namasimbi	B1 (iv)	<i>Haplochromis (Paralabidochromis) victoriae</i>	DD
39	Katonga River Mouth	A1a(iv); D1a(iv)	<i>Labeo victorianus</i>	CR
40	Kagera River mouth	A1a(iv); D1 a(iv)	<i>Labeo victorianus</i>	CR
41	Lake Nabugabo wetland system	A1b(iv)	<i>Agriocnemis palaeforma</i>	VU
		A1a(iv); A1e(iv); B1 (iv)	<i>Haplochromis (Haplochromis) annectidens</i>	CR
		A1a(iv); A1e(iv); B1 (iv)	<i>Haplochromis (Paralabidochromis) beadlei</i>	CR
		A1a(iv); A1e(iv); B1 (iv)	<i>Haplochromis (Gaurochromis) simpsoni</i>	EN
		A1b(iv); B1 (iv)	<i>Haplochromis ("Astatotilapia") velifer</i>	VU
		A1a(iv); A1e(iv); B1 (iv)	<i>Haplochromis (Prognathochromis) venator</i>	EN
		A1a(iv)	<i>Labeo victorianus</i>	CR
42	Buikwe	A1 b(iv)	<i>Agriocnemis palaeforma</i>	VU
		B1 (iv)	<i>Clariallabes petricola</i>	

TABLE 4 (Continued)

Site number	KBA site name	KBA criteria	Species that triggers KBA status	IUCN Red List
		A1a(iv)	<i>Labeo victorinus</i>	CR
		A1a(iv)	<i>Oreochromis esculentus</i>	CR
		A1a(iv)	<i>Oreochromis variabilis</i>	CR
43	Lake Kijanebalola	A1b(iv); B1 (iv)	<i>Haplochromis (?) expectatus</i>	VU
44	Lake Kachila	A1b(iv); B1 (iv)	<i>Haplochromis (?) ampullarostratus</i>	VU
		A1b(iv); B1 (iv)	<i>Haplochromis (?) commutabilis</i>	VU
45	Lake Wamala catchment	A1 b(iv)	<i>Agriocnemis palaeforma</i>	VU
		A1a(iv)	<i>Labeo victorinus</i>	CR
		A1a(iv)	<i>Oreochromis esculentus</i>	CR
		A1a(iv)	<i>Oreochromis variabilis</i>	CR

Note. The site numbers here are used in Figure 3 to map the locations of the KBAs. The data from the freshwater sites were taken from Sayer, Máiz-Tomé, and Darwall (2018).

^a Species that are currently recognized as subspecies but have been proposed as full species in the literature and would trigger KBA status if recognized as such.

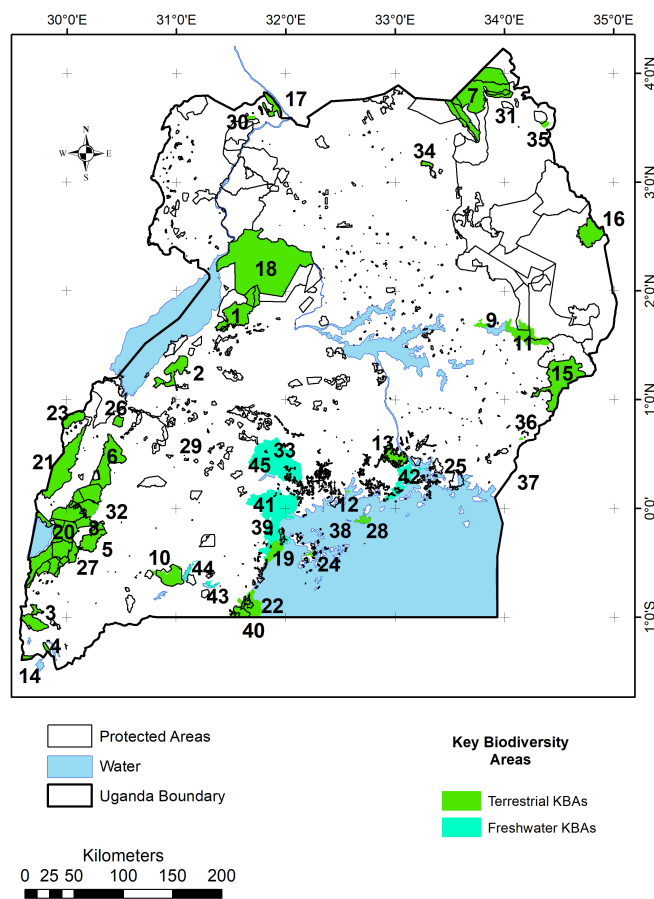


FIGURE 4 Proposed Key Biodiversity Areas (KBAs) identified in Uganda by this analysis and by an IUCN assessment of freshwater KBAs for the Lake Victoria basin (from Sayer et al., 2018). Numbers refer to the sites listed in Table 4

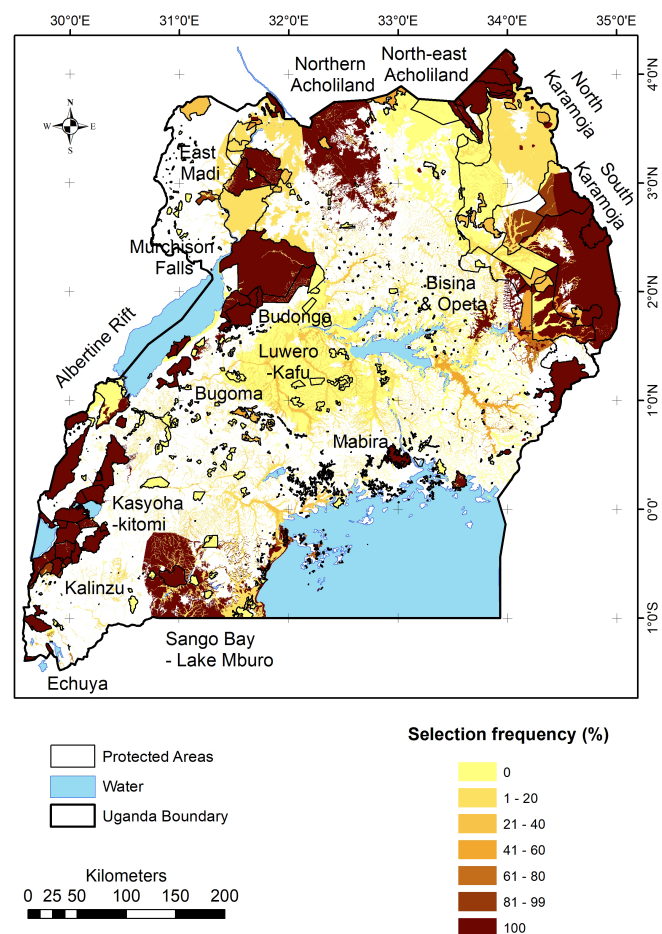


FIGURE 5 Selection frequency (%) from 100 runs of the Marxan analysis

analysis, many for species of plants, amphibians, or mammals.

IUCN made an assessment of freshwater KBAs for Lake Victoria and its catchments (Sayer et al., 2018) assessing fish, dragonflies, molluscs, freshwater crabs and crayfish, and aquatic plants. These add an additional nine KBAs for the country. Therefore, a total of 45 KBAs have been

identified and proposed for Uganda to date (Figure 4), applying the Global Standard (IUCN, 2016).

3.4 | Conservation planning for global and national conservation targets

The results of the Marxan analysis (Figure 5) show that the most irreplaceable sites for conservation in Uganda are the western protected areas, particularly the forests and

TABLE 5 The area of irreplaceable regions of Uganda, showing the area of KBAs (locked in as irreplaceable in the analysis) and those that are not KBAs, as well as areas that are currently within protected areas in Uganda (km²)

Gazetted or not	Total area	Irreplaceable		Replaceable Not KBA (km ²)
		Not KBA (km ²)	KBA site (km ²)	
Unprotected	71,494	14,811	1,329	55,354
Within protected area	34,286	4,334	15,551	14,401
Total area	105,780	19,145	16,880	69,755

Note. The area of remaining natural habitat that was replaceable and not a KBA is also given for unprotected and protected habitat.

savannahs of the Albertine Rift, but also woodlands and lowland bamboo areas of northern Acholiland, and woodland-thicket and montane forest in eastern Uganda (the protected areas of Karamoja together with Mt. Elgon National Park). Of the sites that were selected, many were selected in most runs of the analysis (80–100%) indicating that there are few alternative options to conserve all the globally and nationally threatened species and habitats at the target amounts we set. Areas of importance outside existing protected areas included the Sango bay region outside the Sango Bay Forest Reserves west of Lake Victoria, the northern woodlands in Acholiland up to the border with Southern Sudan, and the southern areas of Karamoja in the east (important for African wild dog, possibly cheetah, and Karamoja Apalis (*Apalis karamojae*)). The large area of seminatural habitat in the Luwero-Kafu flats region north of Lake Victoria, as well as north-east Acholiland are not selected often because all the species known there also occur elsewhere, but the wetlands are selected sometimes for shoebill and the papyrus gonolek (*Laniarius mufumbiri*) in these areas.

Existing protected areas cover 34,286 km² (14.2% of Uganda) but are not necessarily best located to capture all the species of conservation concern in Uganda. Terrestrial KBAs formed 16,880 km² (7.0% of Uganda) of which 15,551 km² are already within existing protected areas and only 1,329 km² is unprotected. Irreplaceable areas identified outside KBAs totaled 19,145 km² (7.9% of Uganda), of which 4,334 km² is protected (Table 5). There is a remaining area of 14,401 km² that is protected but which is not within a KBA or identified as irreplaceable. These sites will be contributing to conservation but not best located in order to maximize the outcomes for conservation of globally and nationally important species and ecosystems. The nine freshwater KBAs identified around Lake Victoria by IUCN's freshwater programme (Sayer et al., 2018) total 3,924 km², which increases the area of unprotected KBAs to 5,253 km² (2.2% of Uganda). These sites were not included in the irreplaceability analysis because these taxa were not assessed across all of Uganda but only in freshwater sites around Lake Victoria. The total area of KBAs (including Lake

Victoria freshwater sites) and irreplaceable sites is 36,025 km² (14.9% of the area of Uganda), which is well within Aichi Target 11 of 17% (Woodley et al., 2012).

3.5 | Unprotected sites of importance

Three of the areas identified as irreplaceable outside protected areas, the Sango Bay-Lake Mburo region, northern Acholi savanna, and southern Karamoja are large areas of land. These were mapped with species known to occur in these regions at a large scale because the number of surveys has been few and it was not possible to map species distributions more accurately. Further surveys are needed to identify the critical regions for species that require these three areas. In the case of the Sango Bay region, species that were limited to this region or one other site included: *Phrynobatrachus rouxi*, *Hyperolius argentovittis*, *Brazzeia longipedicellata*, *Philothamnus hughesi*, and the threatened habitat *Acacia-Cymbopogon* dry savanna. In the North Acholi region, the following species were only found here: Kori Bustard (*Ardeotis kori*), *Vitellaria-Hyparrhenia* moist savanna. Kori Bustard has only been recorded here very rarely and most records are old so surveys for this species should be made here. The Southern Karamoja region contained the following species only here or at one other site: *Heliobolus spekii*, *Crocidura macarthurii*, *Micrelaps boettgeri*, *Psammophis punctulatus*, *Laephotis wintoni*, *Taphozous perforates*, *Saccostomus mearnsi*, and *Gerrhosaurus flavigularis*. The African Wild Dog roams in this region and into Pian Upe Wildlife Reserve, where they have been observed in the recent past but likely move between Kenya and Uganda.

4 | DISCUSSION

4.1 | Critical sites for conservation in Uganda

It is clear that much of the remaining natural habitat in Uganda is important for the conservation of all the globally and nationally threatened species, as well as nationally important ecosystems. There is not much room for trade-offs, except within some of the seminatural habitats outside protected areas, because much of the natural habitat has already been converted to farmland. A total of 23 IBAs have been proposed to qualify as KBAs under the Global Standard, 13 new KBAs proposed, which with the nine freshwater KBAs totals 45 sites that meet KBA status. It is likely more KBAs will be identified with time as more taxa are assessed, and as new species are discovered for the country. It is also likely that some existing species will be split, as is occurring for amphibian species as genetic approaches are revising the taxonomy of existing species (e.g., Portillo et al., 2015), and these will all require assessing in future.

4.2 | Priority sites for conservation financing

Priority sites for funding should be the sites that are KBAs (Table 4; Table S1), and that are currently very underfunded or unprotected (A. Plumptre, personal observation, 2017). Poorly funded KBA sites include 11 forest reserves (Budongo, Bugoma, Echuya, Itwara, Kasyoha-Kitomi, Kalinzu, Mabira, Mt. Moroto, Mt. Otzi, Morungole, and Ogili) as well as several unprotected sites (Lake Bisina, Lake Opeta, Lutembe bay, Sesse island swamps, Mpanga Falls, Tororo Rock, Mardiopei-south Moyo, East Thruston Bay, Kyenjojo-Mubende inselberg and the Timu extension) with endemic aloes (Cole & Forrest, 2017), cycads, and freshwater species.

A second priority list of sites would be those that are irreplaceable (selected 100% of the time in the Marxan analyses) as they clearly support species that did not occur elsewhere in the country. These would include Pian Upe Wildlife Reserve, East Madi Wildlife Reserve, Toro-Semliki Wildlife Reserve swamps, Zulia Forest Reserve, South Busoga Forest Reserve, West Bugwe Forest Reserve, Mpanga Forest Reserve, and the Sango bay region up to Lake Mburo National Park, as well as natural habitat north of Gulu (North Acholi region) and southern Karamoja outside protected areas (Figure 5).

5 | CONCLUSION

The rapidly expanding human population, demand for land for agriculture, and the developing mining industry coupled with infrastructural development are creating huge pressures on the remaining natural habitats in Uganda, including the protected areas. The resulting loss of some protected areas in the country, and large-scale degradation of others is a major concern. Although financing is critical for many of the sites, the protection of those that are already gazetted is also a concern. East Madi Wildlife Reserve is identified as an irreplaceable site because of *Millettia lacus-alberti* as well as being important for shoebill and nationally threatened habitat. However, in the recent past, much of the site has been invaded by people (UWA aerial survey report unpublished) and it has been heavily degraded. Whether it is currently protecting the conservation targets that make it irreplaceable is uncertain. Similarly, many of the Central Forest Reserves are threatened with encroachment and several have already been lost or heavily degraded by people. Changes such as these will lead to changes in the overall configuration for the conservation plan and as such the analyses presented here will need to be updated if sites are lost. Where large-scale industry is involved in development, the mitigation hierarchy (KBA Partnership, 2018) should be adopted, avoiding natural habitat, particularly the KBAs and irreplaceable sites, and then offsetting impacts. Underfunded and unprotected KBA sites should be prime targets for offset sites.

ACKNOWLEDGMENTS

The authors are grateful to the U.S. Agency for International Development (AID-617—LA-14_00002) and Wildlife Conservation Society (WCS) for funding this analysis. We are also grateful to the support of Tullow Oil who funded the National Red List Assessment for Uganda. Eli Greenbaum (University of Texas at El Paso) and Julian Kerbis Peterhans (Chicago Field Museum) provided location data for some species and helped pull together species distribution data for reptiles/amphibians and small mammals, respectively.

CONFLICTS OF INTEREST

The authors have no conflict of interests in the publication of this paper.

AUTHOR CONTRIBUTIONS

A.P. and S.N. supported analysis of the data, raised funding for the project, and wrote the manuscript. S.A. and S.P. analyzed data and contributed to the writing of the manuscript. M.B., T.F., P.H., C.K., B.K., R.K., H.M., M.N., G.N., D.N., D.P., and H.T. contributed data, analyzed data for the national red listing, and edited the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Plumtre AJ, Ayebare S, Behangana M, et al. Conservation of vertebrates and plants in Uganda: Identifying Key Biodiversity Areas and other sites of national importance. *Conservation Science and Practice*. 2019;1:e7. <https://doi.org/10.1002/csp2.7>