A Nationwide Assessment of the Biodiversity Value of Uganda's Important Bird Areas Network

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Abstract: *BirdLife International's Important Bird Areas (IBA) program is the most developed global system for identifying sites of conservation priority. There have been few assessments, however, of the conservation value of IBAs for nonavian taxa. We combined past data with extensive new survey results for Uganda's IBAs in the most comprehensive assessment to date of the wider biodiversity value of a tropical country's IBA network. The combined data set included more than 35,000 site × species records for birds, butterflies, and woody plants at 86 Ugandan sites (23,400 km^2), including 29 of the country's 30 IBAs, with data on additional taxa for many sites. Uganda's IBAs contained at least 70% of the country's butterfly and woody plant species, 86% of its dragonflies and 97% of its birds. They also included 21 of Uganda's 22 major vegetation types. For butterflies, dragonflies, and some families of plants assessed, species of high conservation concern were well represented (less so for the latter). The IBAs successfully represented wider biodiversity largely because many have distinctive avifaunas and, as shown by high cross-taxon congruence in complementarity, such sites tended to be distinctive for other groups too. Cross-taxon congruence in overall species richness was weaker and mainly associated with differences in site size. When compared with alternative sets of sites selected using complementarity-based, area-based, or random site-selection algorithms, the IBA network was efficient in terms of the number of sites required to represent species but inefficient in terms of total area. This was mainly because IBA selection considers factors other than area, however, which probably improves both the cost-effectiveness of the network and the persistence of represented species.*

Key Words: complementarity, conservation sites selection, cross-taxon congruence, IBAs

Una Evaluación Nacional del Valor de la Biodiversidad de la Red de Áreas de Importancia para Aves

Resumen: *El programa de Áreas de Importancia para las Aves (AIAs) de Birdlife International es el sistema global más desarrollado para la identificación de sitios de prioridad para la conservación. Sin embargo, ha habido pocas evaluaciones del valor de conservación de las AIAs para taxa no aviares. En la evaluación más integral, hasta la fecha, del valor de la biodiversidad en general de la red de AIAs de un país tropical, combinamos datos antiguos con los resultados de muestreos extensivos recientes de las AIAs de Uganda. El*

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conjunto de datos combinados incluyó más de 35000 registros de sitios x especies de aves, mariposas y plantas leñosas en 86 sitios en Uganda (23400 km^2), incluyendo 29 de las 30 AIAs del país, con datos sobre taxa adicionales en muchos sitios. Las AIAs de Uganda contenían por lo menos un 70% de las especies de mariposas y plantas leñosas del país, 86% de sus libélulas y 97% de sus aves. También incluyeron 21 de los 22 principales tipos de vegetación. En las mariposas, libélulas y algunas de las familias de plantas evaluadas, la representación de especies de alto interés para la conservación fue buena (menor en las plantas). Las Áreas de Importancia para las Aves representaron exitosamente a la biodiversidad en general principalmente porque muchas tienen avifaunas distintivas y, como muestra la alta congruencia trans-taxón en complementariedad, tales sitios tendieron a ser distintivos para otros grupos también. La congruencia trans-taxón en la riqueza de especies total fue más débil y se asoció principalmente con diferencias en el tamaño del sitio. Cuando se compara con conjuntos alternativos de sitios seleccionados mediante algoritmos basados en complementariedad, área o selección aleatoria de sitios, la red de AIAs fue eficiente en términos del número de sitios requeridos para representar especies, pero ineficiente en términos del área total. Sin embargo, esto se debió principalmente a que la selección de AIA considera factores distintos al área que probablemente mejoran tanto la efectividad de la red como la persistencia de las especies representadas.

Palabras Clave: AIAs, complementariedad, congruencia trans-taxón, selección de sitios de conservación

Introduction

Where should the limited resources available for biodiversity conservation be used for maximum effect? This central question for conservation science has generated several global prioritization systems, emphasizing different criteria and taxa, to identify sets of high-priority areas for conservation (Balmford 2002). They include BirdLife International's Endemic Bird Areas (Stattersfield et al. 1998), Conservation International's hotspots (Mittermeier et al. 1999; Myers et al. 2000), and the World Wide Fund for Nature (WWF) and World Conservation Union's (IUCN) Centers of Plant Diversity (WWF & IUCN 1994–1997). These examples, like most global priority-setting exercises to date, involve coarse-grained prioritization to identify large areas of global importance for biodiversity. In nearly all cases these areas are much too large to be protected in their entirety. Fine-grained prioritization that can be implemented at national or local scales and is spatially accurate enough to compare and identify specific sites for field-based initiatives is the essential next step. To date, BirdLife International's Important Bird Areas (IBA) program is the most developed of such fine-grained, site-based schemes.

The IBA program is a worldwide initiative aimed at identifying, documenting, and protecting a network of sites critical for the long-term viability of naturally occurring bird populations across the geographical range of those bird species for which a site-based approach is appropriate (Fishpool & Evans 2001). To qualify as an IBA, a site must fulfill at least one of four criteria. It should hold (1) significant numbers of one or more species of global conservation concern, (2) significant populations of one or more restricted-range species (those with global distributions of $< 50{,}000$ km^2), (3) a significant component of a group of species whose distributions are largely or wholly confined to one biome, or (4) significant numbers of one or more congregatory species. The IBA program guidelines emphasize that IBAs should complement each other and build on existing protected-area networks (Byaruhanga et al. 2001; Fishpool & Evans 2001). Programs to identify IBAs, involving BirdLife and its national partner organizations, have already been implemented in Europe, the Middle East, Asia, and Africa. In Africa 1,228 IBAs covering 7% of the region have been identified across 58 countries and territories (Fishpool & Evans 2001).

Though only bird species are considered in IBA qualification criteria, the biological rationale for IBAs includes the intention that they should also contribute to the conservation of other animal and plant taxa (Byaruhanga et al. 2001; Fishpool & Evans 2001). Two recent studies attempted to quantify how well IBAs fulfill this wider conservation role in East Africa (Brooks et al. 2001; Pain et al. 2005). Rather than assessing individual IBAs, both studies examined how well a whole set of IBAs, taken together, represent other taxa, a property that depends as much on the dissimilarity or complementarity between members of the set as on the species richness of individual sites.

Brooks et al. (2001) examined how well IBAs represent vertebrate biodiversity on a regional scale across the whole of East Africa based on distribution data for birds, mammals, snakes, and amphibians mapped on a 1° (circa 11,000 km^2) grid. The 122 grid squares with IBAs represented more than 90% of East African species for all four taxa, including regionally endemic and threatened species. These results are encouraging but the relatively coarse map grid, the assumption that all of each grid square's species occur in that square's IBAs, and the fact that only vertebrate taxa were assessed are important caveats.

More recently, an assessment based on site inventories of a more diverse mix of five taxa was carried out for 13 mainly forest IBAs in Uganda (Pain et al. 2005). The researchers used data from a major biodiversity inventory project undertaken by the National Forestry Authority, previous to 2004 the Uganda Forest Department (UFD) (Howard & Davenport 1996; Howard et al. 1997, 1998, 2000). Again the results are encouraging: the IBAs contained as many species of all taxa combined as an equal-sized set of UFD-surveyed sites selected explicitly to maximize species representation and based on all the inventory data. Because the UFD surveys did not cover most savanna and wetland IBAs, however, this analysis included less than a third of the total area of the Ugandan IBA network and so could not assess IBA performance across a full range of habitats.

Here we considered two questions: How well does an entire national IBA network represent wider biodiversity? How well do birds act as surrogates for other taxa across the represented range of forest, savanna, and wetland habitats in Uganda? For this assessment we combined the UFD data set with extensive new data sets for savanna and wetland sites and additional geographic information system (GIS) data. This combined data set covers 86 Ugandan sites, including 29 of the country's 30 IBAs. First we used it to evaluate how well Uganda's IBAs represent species in other taxa and the country's major vegetation types. We then considered the utility of birds as surrogates by analyzing cross-taxon congruence in species richness and complementarity. Finally, we examined the efficiency with which IBAs represent these taxa in terms of cumulative species richness relative to total number of sites and total area.

Study Areas and Methods

Uganda's IBAs

NatureUganda, BirdLife's national partner organization, identified 30 IBAs in Uganda (Byaruhanga et al. 2001; Fig. 1). These sites, which together represent 7% of the

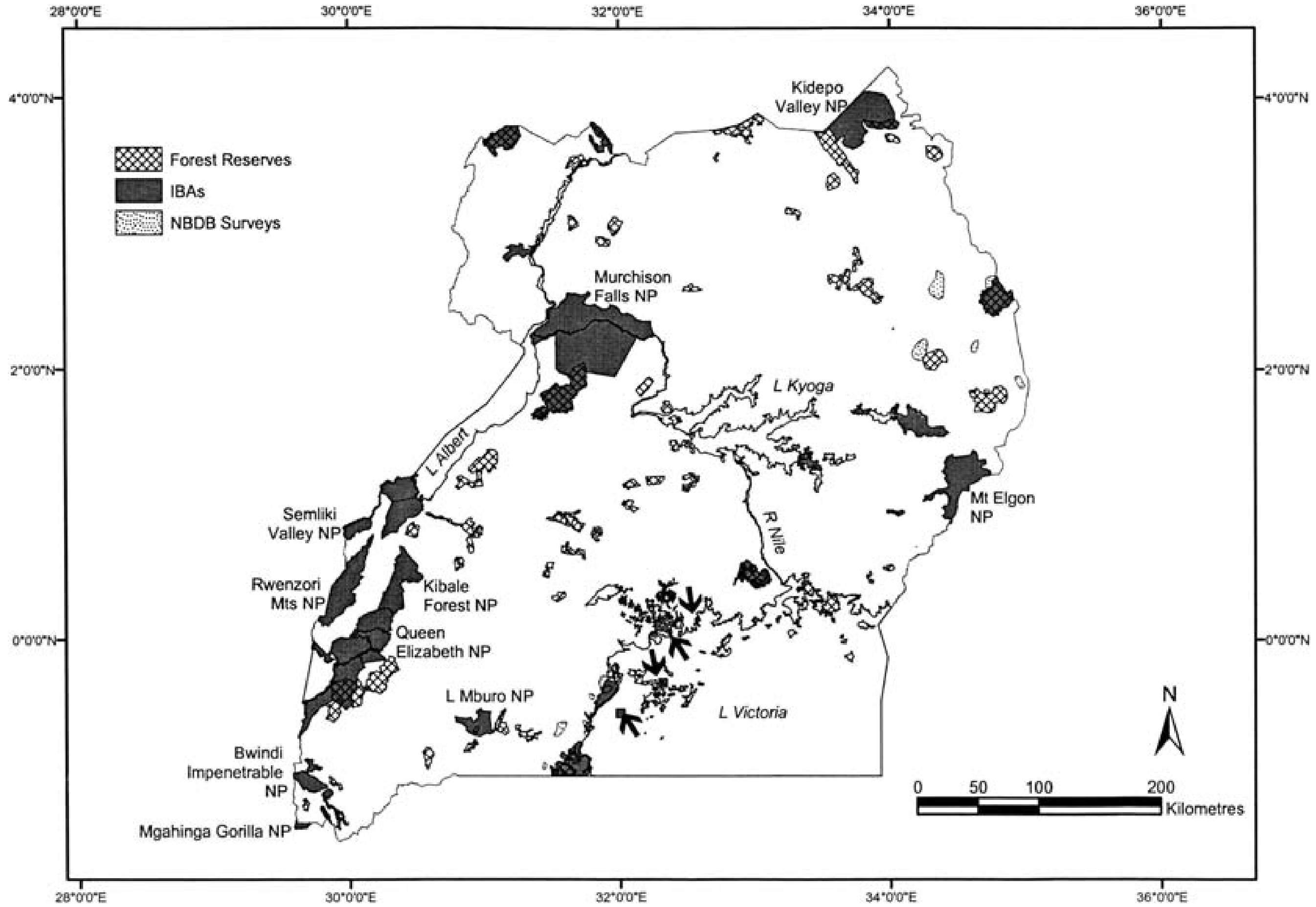

Figure 1. Map of Uganda showing all important bird areas (IBAs) and the non-IBA sites for which biodiversity survey data from Uganda Forest Department (UFD), National Biodiversity Data Bank (NBDB), or Enhancement of Research Capacity (ENRECA) project were available for birds, butterflies, and woody plants. For simplicity, only national parks (NP) and major water bodies are labeled. For one IBA, Mgahinga Gorilla National Park, survey data were not available. There are a number of smaller IBAs (indicated by arrows) and NBDB sites, especially in the Lake Victoria Basin.

country's total area, cover a wide range of forest, savanna, and wetland habitats and an elevational range from 600 to more than 5000 m. They include 10 national parks, six forest reserves, three wildlife reserves, and 11 wetland-dominated sites. Three of the wetland IBAs include some forest reserve land. The remainder are unprotected.

The Data Set

We formed our data set by combining the results of three major biodiversity surveys at 86 sites, 5 of which were covered in more than one survey. The surveys were by the UFD; Makerere University Institute for Environment and Natural Resources (MUIENR) National Biodiversity Data Bank (NBDB); and MUIENR Enhancement of Research Capacity (ENRECA) project. Between 1991 and 1995 the UFD inventoried its estate for birds, butterflies, woody plants, two families of large moths, and small mammals in 64 larger reserves (Howard & Davenport 1996; Howard et al. 1997, 1998, 2000), 5 of which are now national parks. Approximately half of the 12,000 km^2 covered is closed forest. The remainder is mainly wooded savanna. The UFD surveys covered 11 complete IBAs and important forest components of three others.

Since 1990 the NBDB has collated and computerized Uganda's biodiversity information (Reynolds et al. 1999). It has also surveyed two large areas of biodiversity interest: the mainly wetland Sango Bay area in southwestern Uganda (1994–1996) and Karamoja in the semiarid northeast (1996). Tororo Rock, a small site important as the only home to an endemic plant *Aloe tororoana* Reynolds, was surveyed in 2002. Taken together, these surveys provide data for 11 non-IBA sites and contribute to coverage of two wetland IBAs. The taxa covered vary but all these surveys included birds, butterflies, and vascular plants.

Between 2000 and 2002 the ENRECA project (a collaboration among MUIENR, the universities of Copenhagen and Cambridge and the Royal Society for the Protection of Birds [RSPB]) surveyed birds, butterflies, vascular plants, and dragonflies (Odonata) in the 17 mainly wetland and savanna IBAs not covered by the previous surveys.

Three taxa were covered in all UFD, NBDB, and ENRECA surveys, namely birds, butterflies (Rhopalocera), and woody plants. We concentrated on these three core taxa, for which we have survey data for 86 sites: 29 IBAs (total area: 16,960 km^2) and 57 non-IBA sites (total area: 6,459 km^2). For 81 sites the survey data came from a single source (UFD, NBDB, or ENRECA). For the remaining 5 sites, data from two sources were combined to cover all the habitats present. Mgahinga Gorilla National Park, a small montane forest park of 47.5 km^2, is the only Ugandan IBA that has not yet been surveyed for the three core taxa, because of security problems.

The sampling methods used for each taxon were broadly similar in the three surveys but differed in some respects, mainly because of differences in habitats covered and resources available. Observation, with sampling effort recorded in person-hours (ENRECA surveys) or person-days, was always used for birds but was supplemented by mist netting in the UFD surveys. In all surveys butterflies were sampled using a combination of netting (with sampling effort recorded in person-hours or person-days) and baited Blendon traps. Plant surveys were all based on transect sampling but the design of the transects varied, particularly between the UFD survey and other surveys. In all the surveys there were also close matches between the sampling of different taxa at each site. Although not all taxa were recorded at exactly the same sample points, taxon specialists normally worked from the same base camps for the same sampling periods and covered a very similar range of habitats.

The surveyed sites differed greatly in area, from 0.1 km^2 to 3,900 km^2 (Fig. 1). For the ENRECA surveys, which covered the largest and smallest sites, sampling effort was allocated roughly in proportion to log(site area). The UFD and NBDB surveys used different area-based rules for allocating effort, so we checked for major discrepancies between the surveys by using total person-days spent sampling the three core taxa as a common measure of effort. There was a reasonably consistent linear relationship between log(sampling effort) and log(site area) across all three surveys and for IBAs and non-IBA sites (Fig. 2). Forest sites surveyed by the UFD generally received rather more sampling effort than sites of equivalent area covered

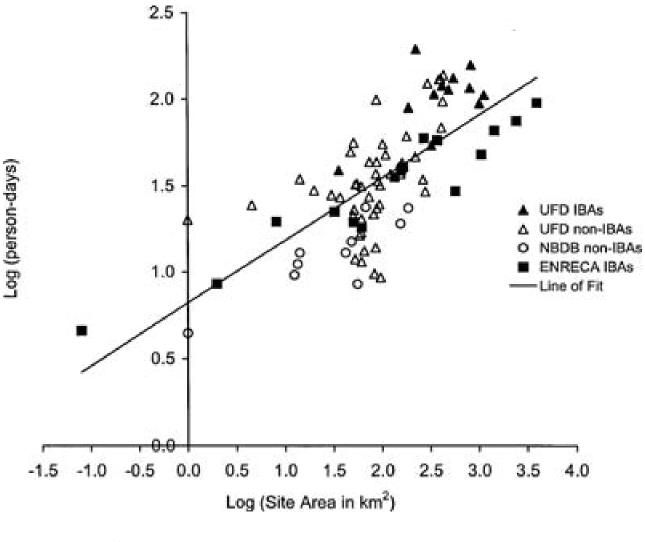

Figure 2. Total sampling effort for the three core taxa against site area for 29 important bird areas (IBAs) (solid symbols) and 57 non-IBA sites (open symbols) surveyed by the Uganda Forest Department (UFD), the National Biodiversity Data Bank (NBDB), or the Enhancement of Research Capacity (ENRECA) project. Line is the linear regression for the entire data set ($y = 0.82 + 0.36x$, Pearson's $r = 0.73$, $df = 1, 84$, $p < 0.001$).

by the NBDB or ENRECA but this mirrors the relative ease of sampling in open habitats rather than in forests.

The combined records from the UFD, NBDB, and ENRECA surveys thus provided a data set for which there was a reasonably consistent relationship between sampling effort and site area and close matching between the taxa. Therefore we used this survey-records data set for all analyses of cross-taxon congruence (see below) for which these characteristics are important. To estimate the total number of species in each taxon recorded from the IBA set, however, we created an all-records data set by adding to the survey-records data set other published and unpublished records held by NBDB or available elsewhere. For most of these additional records there was no sampling effort information. In terms of site × species records, survey records formed more than 70% of the all-records data sets for all three core taxa.

Representation of Species in the IBA Set

We determined the number of species in each taxon recorded from one or more IBAs from the all-records data set and compared these numbers with national lists to estimate the proportion of Ugandan species represented in the IBA set. In the absence of formal assessments of the conservation status of most groups, for the three core taxa we used data on species' continental or regional range sizes to examine how well IBAs represent species of varying conservation concern. Details of the national lists, important sources of records (in addition to the NBDB), and data on range size used for each taxon were as follows.

The national list of birds we used follows the *Bird Atlas of Uganda* (Carswell et al. 2005). Sources of additional records included NatureUganda surveys (Byaruhanga et al. 2001), published checklists (e.g., Carswell 1986; Wilson 1995), and unpublished records from A. Plumptre, M. Wilson, C. Schipper, and others. Categories of range size were based on species' distributions in sub-Saharan Africa (measured as number of 1° grid squares) from a database compiled by the Zoological Museum of the University of Copenhagen (ZMUC) (Burgess et al. 1998).

The national list of butterflies was based on Davenport (1996), as revised in 2001 by T. R. B. Davenport and S. Collins (unpublished data). This revision also collates many additional records. Range-size categories were based on a regional priority-scoring system developed for the UFD assessments (Howard & Davenport 1996). In the absence of detailed range-size data for butterflies, six categories were defined based on broad, regional distribution patterns in sub-Saharan Africa, from category 1 (endemic to Uganda or the Albertine Rift) to category 6 (widespread across west, central, east, and southern Africa).

In the absence of a national list of woody plants, we used the *Flora of Tropical East Africa* (Crown Agents & Balkema 1952–) as the primary source, as well as other records held in Uganda. Because of limited range data for some plant families, we analyzed species representation by range size for three families: Leguminosae, Rubiaceae, and Moraceae. In addition to data availability, other criteria considered when selecting these families were diversity of distribution, ecology, and growth form. Species' range-size categories were based on the number of eastern African floral regions (out of 21) from which the species is known, as described in the *Flora of Tropical East Africa* series. In other analyses we included woody species of all families.

Data on herbaceous plants were lacking for the 11 mainly forest IBAs surveyed only by UFD. This data gap, however, was less important for plant families with few forest species in Uganda. To provide at least a preliminary account of the representation of some herbaceous plants in IBAs, we examined species representation in the remaining predominantly savanna and wetland IBAs for two families—Graminae and Cyperaceae—which were sampled during the ENRECA and NBDB surveys. For Cyperaceae the national list was derived from Lye (2001). For grasses, the *Flora of Tropical East Africa* and Phillips et al. (2003) were used for both the national list and additional distribution records.

Odonata were not recorded by UFD, but data from the ENRECA and NBDB surveys and site lists provided by other entomologists allowed us to assess the representation of the taxon in 24 IBAs. The national list was based on K. D. Dijkstra and V. Clausnitzer (unpublished data). Main sources of additional records were J. J. Kisakye, K. D. Dijkstra, V. Clausnitzer, and N. Donnelly (unpublished data); Etyang (1996); Miller (1993); and Miller and Miller (2003).

Representation of Vegetation Types in the IBA Set

We used digital maps of Uganda's major vegetation types (based on extensive surveys undertaken in the early 1960s and aerial photographs, Langdale-Brown et al. 1964) and IBA boundaries to assess representation of vegetation types. We used GIS technology to determine the areas covered by each of the 22 major vegetation types within the IBA set and in the country as a whole.

Cross-Taxon Congruence in Species Richness and Complementarity

To explore various aspects of cross-taxon agreement in species' distribution patterns, we used the survey-records data set to construct a site × species presence or absence data matrix for the 86 sites and three core taxa. We then used scatter plots and Pearson's correlation coefficients between pairs of taxa to examine cross-taxon congruence in species richness. Recorded species richness depends to some extent on site area, with more extensive sites likely to show higher species richness because of the greater variety of habitats and elevational ranges they contain and/or the greater sampling effort that they receive (Rosenzweig 1995; Hubbell 2001). To correct for this, we used residuals from linear regressions for each taxon of log(species richness) on log(site area in square kilometers) to reexamine congruence in richness. We also repeated all these analyses excluding the UFD-surveyed sites—which have been the subject of previous studies (Howard et al. 1998)—to determine whether the remaining 27 mainly savanna and wetland sites showed patterns of congruence similar to those shown by the whole data set.

Because the conservation value of a site depends, among other things, on how fully its biota complements that of other sites, we also examined cross-taxon congruence in complementarity between pairs of sites, quantifying complementarity as

$$\text{complementarity score} = \frac{A + C}{A + C + B},$$

where A is the number of species at site 1 only, B is the number of species common to both sites, and C is the number of species at site 2 only.

This value, known as the Marczewski-Steinhaus distance, is the complement of the Jaccard index of similarity (Colwell & Coddington 1994). It increases as species' dissimilarity between sites increases and can vary from 0 (all species recorded from both sites) to 1 (no species in common).

Comparing a pair of sites that differ greatly in area and/or sampling effort can produce an artificially high complementarity score because of the effects of area or sampling effort on observed species richness. To reduce this bias we arranged sites in order of descending area and, for each taxon, calculated complementarity scores only between each site and the next smallest. We then examined cross-taxon congruence in paired sites' complementarity scores, as measured using different taxa, by means of scatter plots and Pearson's correlation coefficients. We repeated the analysis with sites ordered by sampling effort rather than area and with UFD sites excluded. Lastly, for each taxon, we checked for remaining bias in complementarity scores due to differences in area between sites by testing the significance of regressions of complementarity score on the difference in area between paired sites, expressed as a proportion of the area of the larger site. We also carried out the equivalent analyses for differences in sampling effort.

Efficiency of Species Representation in the IBA Set versus Efficiency in Alternative Sets

We considered the efficiency (sensu Pressey & Nicholls 1989) with which species of the three core taxa (birds, butterflies, and woody plants) are represented in a set of sites in relation to the total number of sites or the total area required. Using the survey-records data set and considering all three core taxa together, we compared the total number of these species represented in the IBA set with the number represented in alternative sets of sites selected by four other methods: (1) random selection; (2) with optimization for number of sites, complementarity-based selection of a near-minimum set of sites based on a progressive rarity algorithm; (3) as in (2) but with optimization for area; and (4) selection of sites in order of decreasing area.

For random selection, we used an algorithm that randomly selects sets containing a specified number of sites and calculates the total number of species represented in each set and the total area it covers. For each possible number of sites (1 to 86) we ran 500 simulations and calculated the mean number of species represented (with lower and upper 5% confidence intervals) and the mean area.

Complementarity-based selection of a near-minimum set using a progressive rarity algorithm while optimizing for the number of sites is a method available in the WORLDMAP software package (Williams 2000). It employs an algorithm based on Margules et al. (1988) and discussed by Williams (1998). We used it to select a near-optimal set of sites representing all species at least once in as few sites as possible and to reorder the selected sites by complementary species richness (i.e., in decreasing order of the number of new species they added to the selected set).

Complementarity-based selection of a near-minimum set while optimizing for area is similar, except that site areas (square kilometers) are entered as costs to select a near-optimal set representing all species in as small a total area as possible. After selection, sites were reordered by their ratio of complementary richness to area (i.e., in decreasing order of the number of new species they added to the selected set per square kilometer added).

Selecting sites in order of decreasing site area is a simple method that takes advantage of the general tendency for larger sites to have greater species richness but uses no biological information.

We plotted species accumulation curves for these four selection methods against the number of sites selected and the total area selected and then compared their efficiency with that of the IBA set.

We did not analyze multiple representations of species in different sets of selected sites because the very wide range of site areas (over three orders of magnitude) made meaningful interpretation difficult.

Results

Representation of Species in the IBA Set

For all three core taxa a high proportion of Ugandan species has been recorded from one IBA or more (Table 1). As

Table 1. Numbers and percentages of Ugandan species in different taxa recorded from one or more important bird areas (IBAs) in the all-records and survey-records data sets.

Taxon	*Ugandan species total*	*All records from IBAs (%)*	*Survey records from IBAs (%)*
Birds	1013	987 (97)	780 (77)
Butterflies[a]	1249	917 (73)	698 (56)
Woody plants	1566	1136 (73)	1064 (68)
Graminae	475	212 (45)	212[b]
Cyperaceae	234	133 (57)	133[b]
Dragonflies[c]	231	199 (86)	na

[a] *Two groups of very similar congeneric species are combined as* Ypthima *sp. (7 species) and* Leptotes *sp. (5 species).*

[b] *Existing records for these families are all from surveys of 18 IBAs.*

[c] *All-records species lists for 24 IBAs were analyzed; na, not applicable.*

expected, the proportion was highest for birds but, when all records were considered, more than 70% of Ugandan butterflies and woody plants were also represented.

For birds, representation in IBAs remained close to 100% across six range-size categories (Fig. 3a). Proportional representation dropped slightly, from 100% to 95%, between the most wide-ranging species and those with Africa-wide range sizes of 51 to 150 1° grid squares. However 97% of species in the most restricted-range category (1 to 50 grid squares) were represented in IBAs.

A similar analysis for butterflies based on less accurate range information showed much greater variation across range-size categories in the proportion of species represented in IBAs (Fig. 3b). Representation decreased more sharply from very widespread species of generally low conservation priority to those with less extensive ranges but, as with birds, increased for the most restricted-range category: 82% of species in this category (Ugandan endemics and Albertine Rift endemics) are known from one or more IBAs.

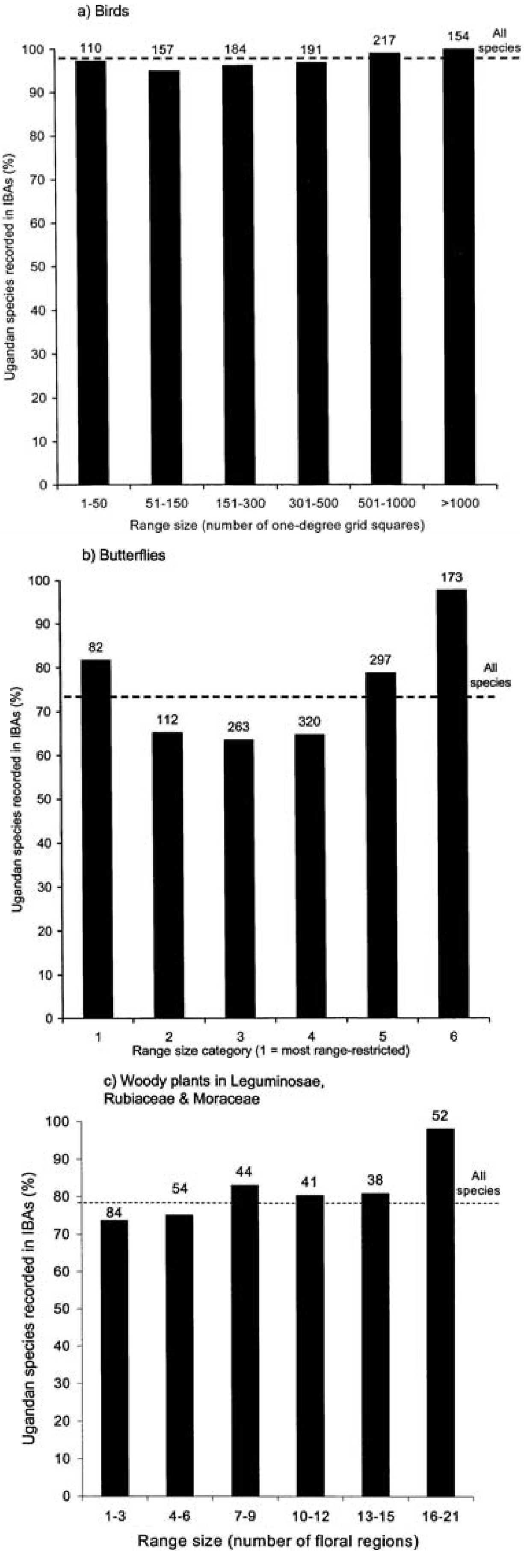

Figure 3. Percentages of Ugandan species in different range-size categories recorded from important bird areas for (a) birds, (b) butterflies, and (c) woody plants in the families Leguminosae, Rubiaceae, and Moraceae. Categories are based on the following criteria: birds, occurrence in 1° grid squares in sub-Saharan Africa, data compiled by the Zoological Museum of the University of Copenhagen (ZMUC); butterflies, broad regional distribution pattern in sub-Saharan Africa, categories as defined by Howard and Davenport (1996), varying from 1 (endemic to Uganda or the Albertine Rift) to 6 (widespread across eastern, central, western, and southern Africa); woody plants, occurrence in eastern African floral regions, data from the Flora of Tropical East Africa series (Crown Agents and Balkema 1952). Numbers above columns are the total numbers of species in each range-size category.

The equivalent analysis for woody plants in three families, with range-size categories based on East African floral regions, showed a somewhat different pattern (Fig. 3c). Only 74% of species in the most range-restricted category (those known from three or fewer floral regions) have been recorded from IBAs, a lower proportion than for any other range-size category.

For other taxa, assessments of species representation in the IBA set were inevitably less complete because species lists were lacking for several IBAs. Nevertheless, for dragonflies, grasses, and sedges, the data gaps were small enough to make a provisional assessment worthwhile. Although dragonfly species lists were lacking for six IBAs, 86% of the 231 species on the national list have already been recorded from IBAs (Table 1), including 11 of the 13 Ugandan species recently assessed as threatened or near threatened in a provisional red list of East African dragonflies (assessment by V. Clausnitzer, K. D. B. Dijkstra, and F. Suhling, personal communication).

Data on herbaceous plants were lacking for the 11 forest IBAs surveyed by UFD. However, the 18 IBAs for which we had survey data held 133 Cyperaceae species and 212 Graminae species, representing 57% and 45%, respectively, of the Ugandan totals for these families.

Representation of Vegetation Types in the IBA Set

All but one of the major Ugandan vegetation types defined by Langdale-Brown et al. (1964) were represented within IBAs. The exception was grass steppe, which is confined in Uganda to small parts of Karamoja. Although our analysis was based on vegetation mapping carried out in the early 1960s, the areas of each major vegetation type within IBAs (Fig. 4a) are probably broadly similar today. This is because in the IBA network the most vulnerable vegetation types occur mainly in national parks and forest or wildlife reserves and so have not been converted extensively (although limited changes could have occurred because of natural processes such as ecological succession). For two rare vegetation types—swamp forest and high-altitude moorland and heath—the IBA set holds nearly 100% of the total area in Uganda, as estimated in the 1960s (Fig. 4b). For some of the other types, in particular forest, the total area in Uganda has declined markedly since the 1960s because of widespread conversion in unprotected areas. For these, proportions of the national total area within IBAs estimated using 1960s data considerably underestimated the current situation. From Langdale-Brown et al. (1964), closed forest covered roughly 5.8% of Uganda's land area in the early 1960s, but by 2000 this had declined to about 3.6% (Arinaitwe et al. 2000). Based on this recent estimate, the combined area of all closed forest types within IBAs represented more than 50% of the total for the whole country.

Cross-Taxon Congruence in Species Richness

Analyzing data for all surveyed sites, all three pairwise comparisons between the core taxa showed significant positive correlations in species richness, which were stronger for birds versus butterflies and butterflies versus woody plants than for birds versus woody plants (Table 2, Figs. 5a, 5b, & 5c). When the effects of site area were corrected for by using residuals from log(richness) on log(area) regressions, however, all the correlations were weakened and that between birds and woody plants was not significant (Table 2). With exclusion of UFD-surveyed sites, the results were similar but congruence between birds and butterflies and between birds and woody plants was strengthened, whereas that between butterflies and woody plants was weakened. For this smaller data set, only congruence between birds and butterflies remained significant after correction for area effects (Table 2).

Cross-Taxon Congruence in Complementarity

All three pairwise comparisons between the core taxa showed strong cross-taxon congruence in site complementarity scores (comparing each site with the next smallest) (Figs. 5d, 5e, & 5f). Ranking sites by sampling effort rather than area changed their order to some extent, and hence the pairs of sites that were compared, but had very little effect on correlation coefficients (Table 2). Reanalysis excluding UFD sites strengthened congruence between birds and butterflies but weakened that between woody plants and both the other taxa (Table 2). The lower congruence for birds versus woody plants and butterflies versus woody plants, however, was largely the result of a single outlier. When this outlier was excluded correlation coefficients for these comparisons increased to 0.66 and 0.79, respectively ($\mathrm{df} = 1{,}23$, $p < 0.001$ in both cases).

Our checks for biases in the above results due to difference-in-area effects suggested such biases were small or absent. For all three taxa, regression analyses showed no significant relationship between complementarity scores and the differences in area of the paired sites being compared, expressed as a proportion of the area of the larger site ($F < 2.76$, $\mathrm{df} = 1{,}83$, $p > 0.1$ in all cases). The equivalent analyses for differences in sampling effort gave very similar results.

Efficiency of Species Representation in the IBA Set versus Efficiency in Alternative Sets

When we compared the total number of species from core taxa represented in IBAs with the numbers in alternative sets of sites selected using four other methods, their relative efficiency depended largely on whether this was measured in terms of the number of sites or the total

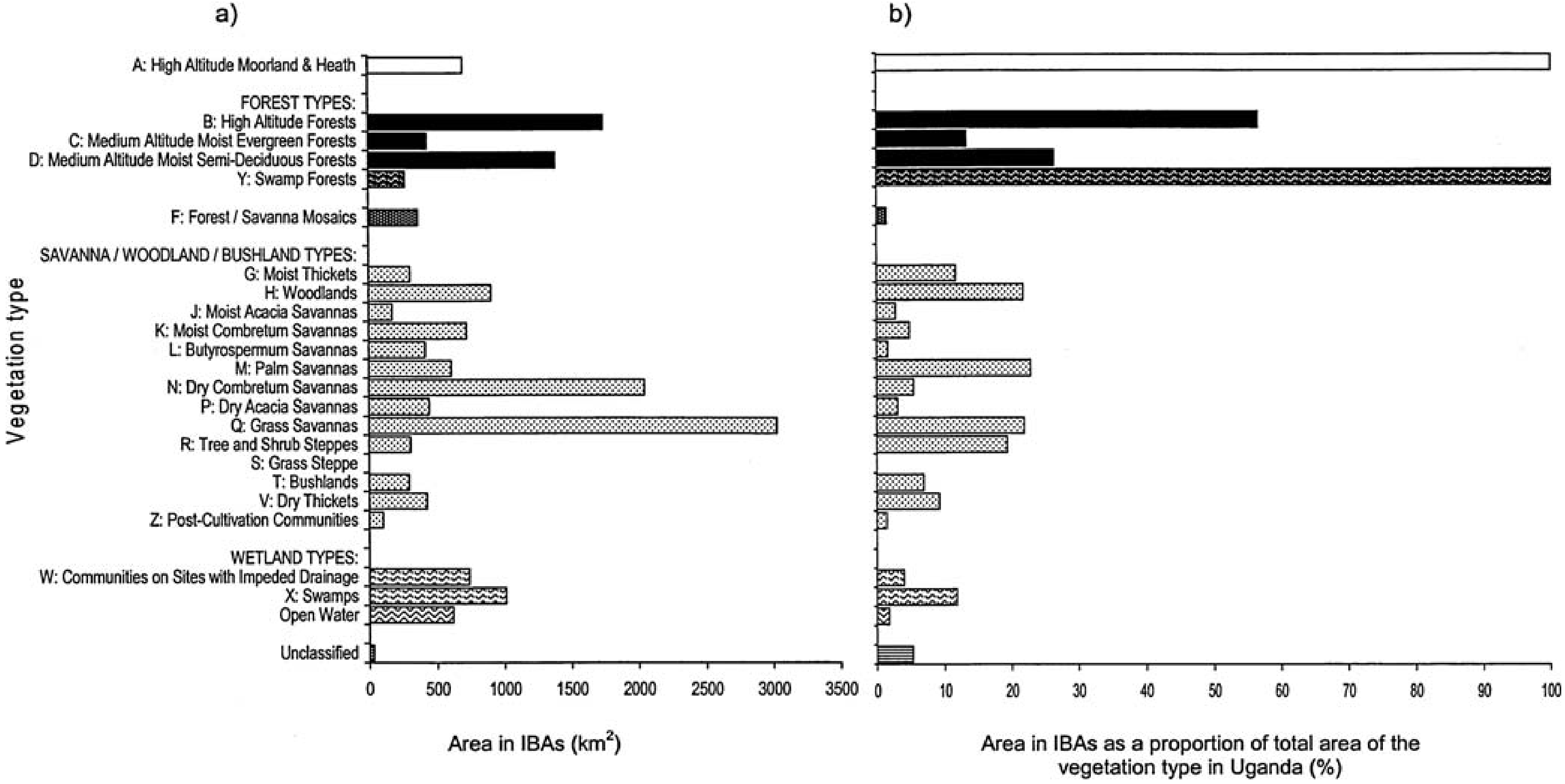

Figure 4. Representation in Ugandan important bird areas (IBAs) of the major vegetation types defined and mapped by Langdale-Brown et al. (1964), expressed as (a) area and (b) percentage of total area in Uganda, as assessed in the early 1960s. The code letters are as used in Langdale-Brown et al. (1964).

Table 2. Pearson's correlation coefficients and their significance levels for cross-taxon congruence in log(species richness) before or after correcting for the effect of site area and for complementarity scores between pairs of sites, with sites ordered by area or sampling effort.

	Species richness		*Complementarity*	
	all sites (n = 86)	excluding UFD* sites (n = 27)	all sites (n = 85)	excluding UFD* sites (n = 26)
	log(richness), uncorrected for area effects		*complementarity score with sites ordered by area*	
Birds vs. butterflies	0.57, $p < 0.001$	0.80, $p < 0.001$	0.80, $p < 0.001$	0.84, $p < 0.001$
Birds vs. woody plants	0.29, $p < 0.01$	0.62, $p < 0.001$	0.71, $p < 0.001$	0.53, $p < 0.01$
Butterflies vs. woody plants	0.58, $p < 0.001$	0.51, $p < 0.01$	0.72, $p < 0.001$	0.51, $p < 0.01$
	residual from regression of log(richness) on log(area), correcting for area effects		*complementarity score with sites ordered by sampling effort*	
Birds vs. butterflies	0.34, $p < 0.001$	0.52, $p < 0.01$	0.80, $p < 0.001$	0.85, $p < 0.001$
Birds vs. woody plants	−0.08, $p > 0.05$	0.08, $p > 0.05$	0.73, $p < 0.001$	0.49, $p < 0.01$
Butterflies vs. woody plants	0.31, $p < 0.01$	-0.11, $p > 0.05$	0.72, $p < 0.001$	0.50, $p < 0.01$

[*] *Uganda Forest Department.*

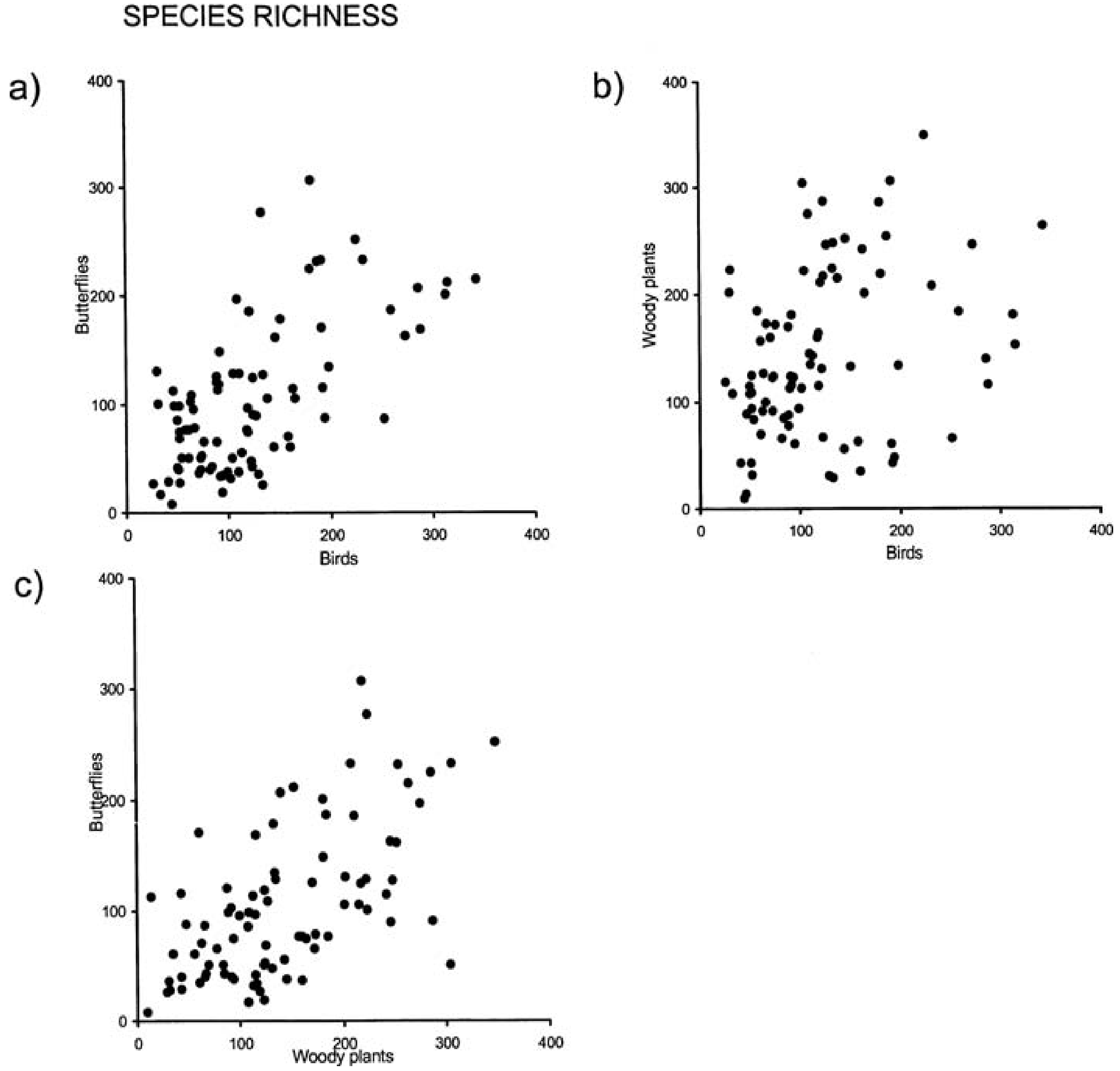

Figure 5. Cross-taxon congruence between pairs of taxa for (a, b, c) species richness at 86 sites and (d, e, f) complementarity scores between 85 pairs of sites, each site compared with the next smallest.

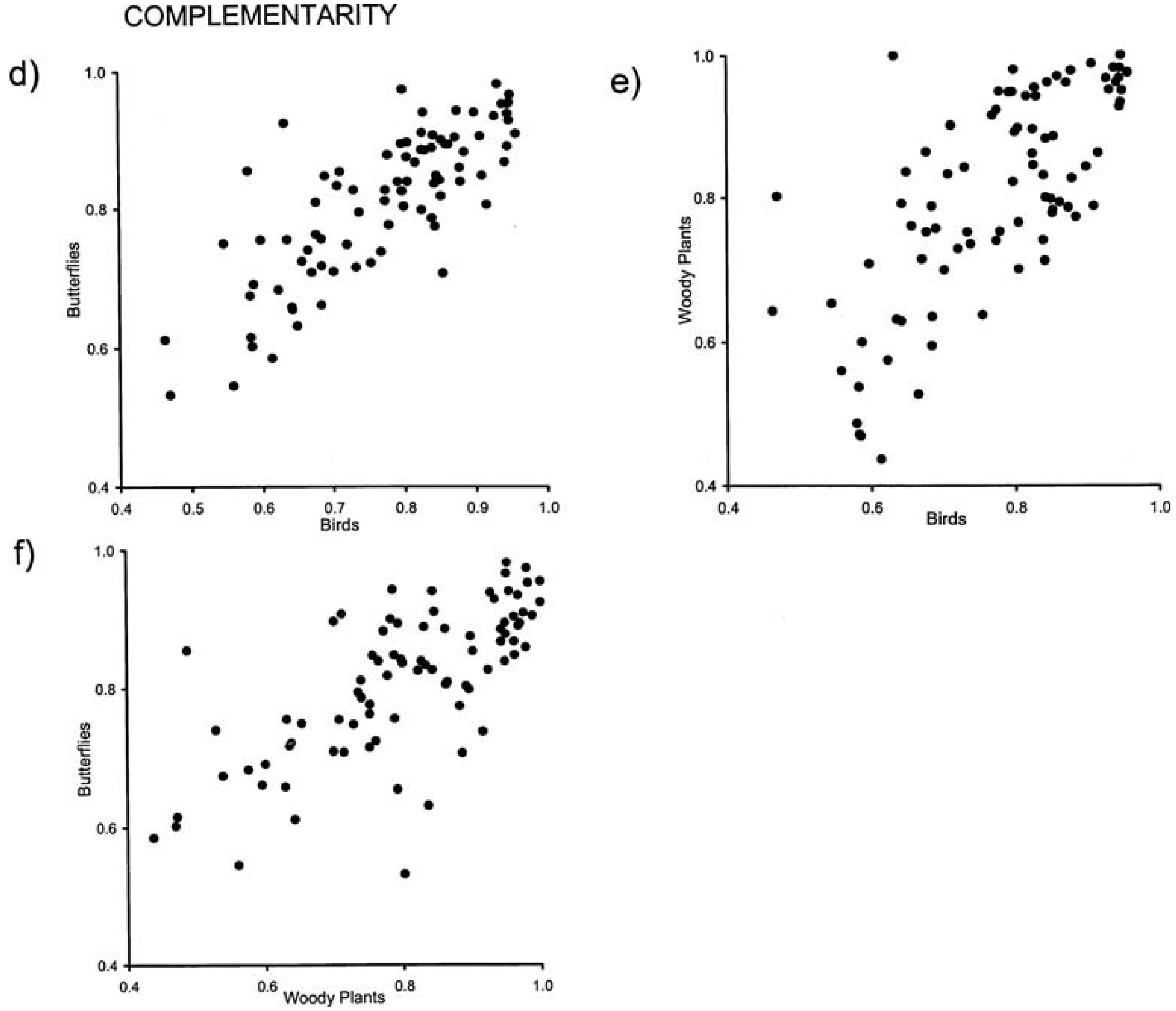

Figure 5. continued

area required. When efficiency was considered in terms of the number of sites selected (Fig. 6a), the progressive-rarity algorithm optimizing for number of sites outperformed other selection methods and the IBA set. Ordered by complementary richness, the first 29 sites selected represented 2,589 species, compared with 2,492 in the 29 IBAs for which we had survey data. The IBA set performed considerably better than random selection. None of 500 randomly generated sets of 29 sites contained as many species, and the mean number in these random sets was only 2,159. This difference, however, was partly due to the larger average size of IBAs compared with non-IBA sites in our survey data set (Fig. 2). When sites were selected simply in order of size, the 29 largest contained 29 more species than the IBA set, but in an area 2650 km^2 (16%) larger.

Considering the efficiency of species representation in terms of total area selected (Fig. 6b), the progressive-rarity algorithm optimizing for area and reordering sites by the ratio of complementary richness to area performed considerably better than the other selection methods and the IBA set. Selecting sites in order of decreasing size was consistently the least area-efficient method, but the IBA set also performed poorly, even in comparison with random selection. Randomly selected sets of the same total area as the IBAs (16,960 km^2) represented approximately 2,558 species on average (2.6% more than in the IBA set) and 95% of randomly selected sets of this size contained more than the 2,492 species in the IBAs. To represent this many species, however, random selection required an average of 55 sites, nearly double the number in the IBA set. Even the area-optimizing algorithm used 47. Only the algorithm optimizing for number of sites outperformed the IBA set in terms of both area and number of sites simultaneously. The first 29 sites it selected represented 97 (4%) more species than the IBA set in an area 0.6% smaller.

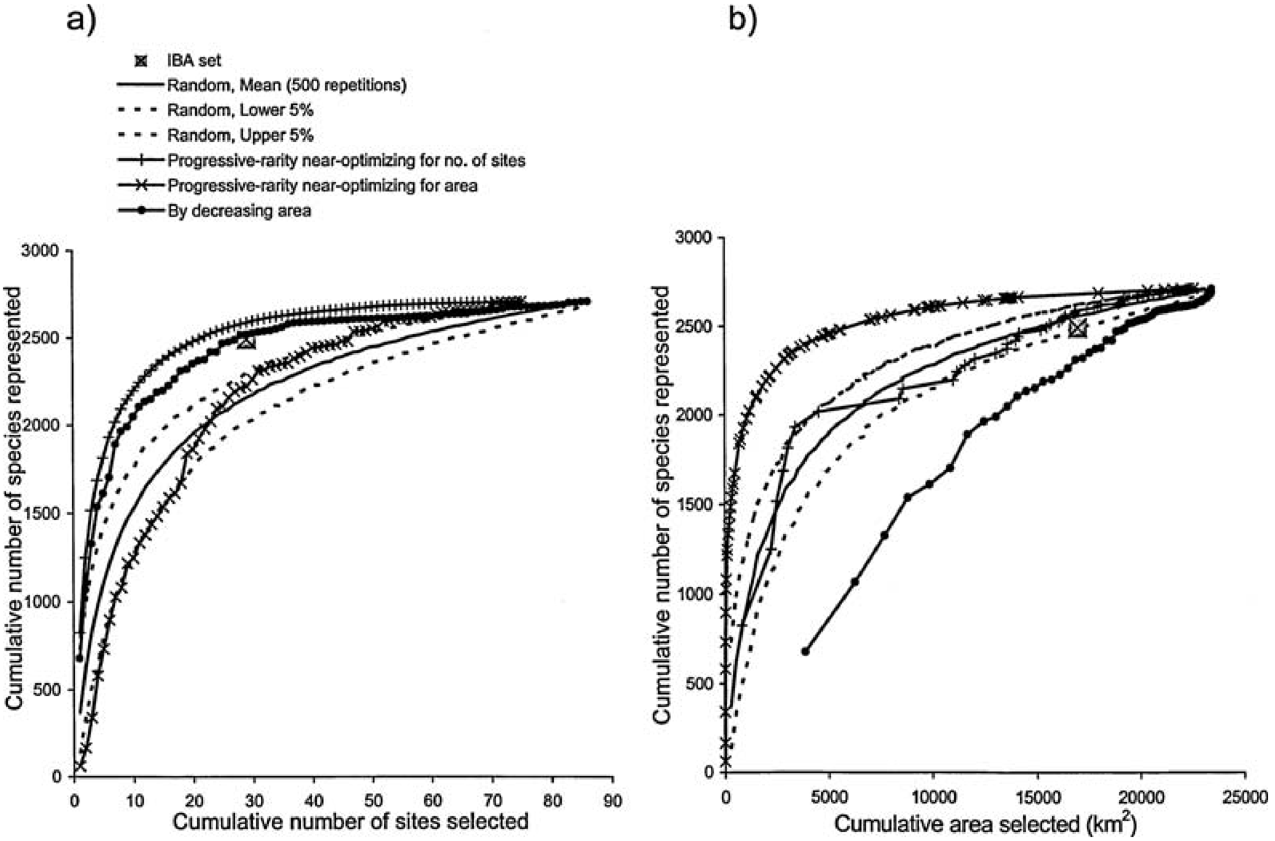

Figure 6. Cumulative curves for total number of species represented on (a) total number of sites selected or (b) total area selected for four stepwise site-selection methods, with species representation in the 29 surveyed important bird areas (IBAs) plotted on the same axes for comparison.

Discussion

Representation of Species and Vegetation Types in the IBA Set

Although sites qualify as IBAs only on the basis of their bird fauna, the Ugandan IBA network contained a high proportion of species in all four taxa for which we had reasonably complete data sets. More than 70% of Uganda's woody plant and butterfly species, at least 86% of dragonfly species, and 97% of the country's birds have been recorded from at least one IBA. Nevertheless, levels of representation of the nonavian taxa are somewhat lower than those for three vertebrate groups in the regional study of East African IBAs by Brooks et al. (2001). This is probably in part because we assessed nonvertebrate taxa and restricted our IBA species lists to proven records (rather than assuming that all species in an IBA's 1° grid square occur within the IBA).

The kinds of Ugandan species that have not been recorded from IBAs appear to vary between taxa. For birds there were a few missing species, and most of these have reasonably large African ranges, which only just extend into Uganda. Butterfly species in the most restricted range category were disproportionately well represented in the IBA set. This is largely due to the high proportion of Albertine Rift endemic butterflies represented—a direct result of the fact that the Albertine Rift is a major area of endemism for both birds and butterflies (Plumptre et al. 2003).

Although the number of species involved was smaller and the criteria used to identify potential priority species were different, good representation of species of high conservation priority also occurred for dragonflies, mainly because of the large proportion of forest species recorded from IBAs. For woody plants, representation in IBAs of high priority, range-restricted species in the families Leguminosae, Rubiaceae and Moraceae was not as good. However, 74% of the Ugandan species restricted in eastern Africa to three or fewer floral regions have been recorded from IBAs, with 79% of the total species from these families recorded within the IBAs. An analysis of the most range-restricted species that have not been recorded from IBAs indicates that these are generally very rare plants (62%) or species for which Uganda lies at the margin of their ranges within the eastern Africa region (38%).

The 22 major Ugandan vegetation types defined by Langdale-Brown et al. (1964) were well represented in

IBAs across the full range of forest, savanna, and wetland types. Only one (grass steppe) was unrepresented, although analyses based on more detailed vegetation classifications may reveal other gaps. The IBAs represented distinctive high-elevation habitats very well and, based on a recent estimate (Arinaitwe et al. 2000), include more than 50% of all the forest remaining in Uganda. Wetland habitats are reasonably well represented but are still vulnerable because most of the IBAs with substantial wetland components have little or no statutory protection. Swamp forest and high-altitude moorland and heath are almost exclusively found in IBAs.

Cross-Taxon Congruence in Species Richness and Complementarity

The good representation of butterflies and woody plants in the IBA set was at least partly the result of the cross-taxon congruence in species richness and complementarity between the three core taxa. Congruence was particularly high in terms of patterns of complementarity. Congruence in species richness, though good overall, was greatly reduced once the effect of site area was taken into account. These findings held when the UFD sites previously analyzed by Howard et al. (1998) were excluded from analyses. They were consistent with the results of that and other fine-scale studies that have found strong congruence in complementarity (Oliver et al. 1998; Su et al. 2004) but weak or nonsignificant congruence in species richness when this is not conflated with site area or sampling effort effects (Prendergast et al. 1993; Pomeroy 2000; Su et al. 2004).

Efficiency of Species Representation in the IBA Set

Comparison of the total number of species from core taxa represented in IBAs with the numbers in alternative sets of sites selected using other methods (Fig. 6) showed that the IBA set was relatively efficient in terms of representing many species in relatively few sites but inefficient in terms of the total area required—which is not surprising because area efficiency is not the major objective in IBA selection. The relative inefficiency of the IBA set in area terms needs to be considered in the light of the following points: (1) Because IBA criteria require sites to hold significant numbers or populations of one or more criteria species and because IBA guidelines recommend that IBAs should coincide, where possible, with existing protected areas (Fishpool & Evans 2001), IBAs tend to be big. Uganda's IBAs are no exception. (2) Although it leads to apparent inefficiency in terms of species representation for a given area, the emphasis on large sites will undoubtedly increase the viability of populations (for birds and also other taxa). The IBAs may thus be relatively efficient in terms of species persistence. (3) Although area-minimized and randomly selected sets of sites contained more species in a given total area, this was at the expense of including many more sites. Economic and political costs of managing protected areas increase with their number and, per unit area, are lower in bigger reserves (Balmford et al. 2003). Therefore these more area-efficient networks may not be as cost-efficient as they appear at first.

In our analyses, the area inefficiency of the Ugandan IBA network may appear exaggerated for two reasons. First, the 57 non-IBA sites in our data set were not a random selection of Ugandan locations. All were surveyed because of their potential value for biodiversity conservation or their designation as protected areas. Second, the Ugandan avifauna has many open-habitat species and more than 160 wetland specialists (Wilson 1995), several of which are IBA-criteria species, so much of the IBA network is savanna and wetland. In contrast, Uganda's butterflies and woody plants have few wetland specialists and proportionately more species restricted to forest. Therefore wetland, and to a lesser extent savanna IBAs reduce the area efficiency of the IBA network for these particular taxa. Paradoxically, this demonstrates how birds' wide distribution (as a group) across a broad range of habitats makes them particularly suitable as surrogates (Bibby 1999; Balmford 2002). Fish in Uganda show high levels of endemism, with an estimated 500 species endemic to Lake Victoria alone and high richness or endemism in most of the other large Ugandan lakes (Snoeks 2000). Several wetland IBAs cover parts of these hotspots and include large areas of habitat important for fish. Sets of "important biodiversity areas" selected using butterflies or woody plants as surrogates would include far less wetland and so would represent the country's globally important fish biodiversity much less well.

Taken together, our results suggest that Uganda's IBA network, although not capturing all aspects of the nation's biodiversity, does represent a large and extremely important component and a central core of sites on which to build. In future we will develop our evaluations of the IBA network and other Ugandan sites of conservation interest by examining individual taxa in more detail, comparing cross-taxon congruence at different spatial scales, exploring site prioritization and threats, and incorporating additional sites, taxa, and GIS data.

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