within the KRB was calculated from the total set of pixels in each class in Fig. 1.

Flux measurements. Short-term flux measurements were made simultaneously at sites 3 and 4 from 19 Jun to 29 Jun 1995, using four heat-flux plates and four temperature probes. Evapotranspiration and CO_2 flux were measured using the eddy-covariance method with an Applied Technologies sonic anemometer and LI-COR 6262 infrared gas analyser mounted on 2-m towers[25]. The mean and standard error for energy flux, gross primary production and evapotranspiration at sites 3 and 4 were calculated on the basis of 30-min averages. CO_2 fluxes at sites 11, 17 and 21 were determined using eddy-covariance methods and 2.5-m towers[26]. Mean values and standard errors at these sites were calculated using the daily mean CO_2 fluxes. The daily methane fluxes were integrated over the thaw period to obtain annual emission. Winter methane fluxes were assumed to be zero. CH_4 flux was measured during the thaw season, Jun–Aug, at 27 MNT and MAT sites along the Dalton Highway in 1996 using a static chamber method[30]. Air samples were taken over periods of 30–45 min and were analysed on a gas chromatograph equipped with a flame ionization detector.

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Complementarity and the use of indicator groups for reserve selection in Uganda

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A major obstacle to conserving tropical biodiversity is the lack of information as to where efforts should be concentrated. One potential solution is to focus on readily assessed indicator groups, whose distribution predicts the overall importance of the biodiversity of candidate areas[1,2]. Here we test this idea, using the most extensive data set on patterns of diversity assembled so far for any part of the tropics. As in studies of temperate regions[2–8], we found little spatial congruence in the species richness of woody plants, large moths, butterflies, birds and small mammals across 50 Ugandan forests. Despite this lack of congruence, sets of priority forests selected using data on single taxa only often captured species richness in other groups with the same efficiency as using information on all taxa at once. This is because efficient conservation networks incorporate not only species-rich sites, but also those whose biotas best complement those of other areas[9–11]. In Uganda, different taxa exhibit similar biogeography, so priority forests for one taxon collectively represent the important forest types for other taxa as well. Our results highlight the need, when evaluating potential indicators for reserve selection, to consider cross-taxon congruence in complementarity as well as species richness.

By containing elements of both East African savannas and Central African rain forests, Uganda boasts more species for its size than almost any other country in Africa[12]. Much of this diversity is restricted to 15,000 km^2 of forest reserves (which also contain non-forest habitats) under the jurisdiction of the Uganda Forest Department[13]. The aim of a five-year inventory of the woody plants, large moths (saturnids and sphingids), butterflies, birds, and small mammals (rodents and insectivores) of all of the principal forest reserves was to provide information to the government regarding a plan to protect ~3,000 km^2 (20%) of the remaining forest estate as a strict nature reserve[14,15]. Forests were surveyed in proportion to their area (see Methods). In total, nearly 100 man-years of survey effort yielded records of 2,452 species.

Constraints on funding and expertise mean that surveys of this magnitude will rarely be undertaken elsewhere in the tropics. However, the size and taxonomic breadth of the Uganda data set mean that it provides an exceptional opportunity to test ways in which future priority-setting exercises could be conducted more quickly and at lower cost. Here we focus on one widely proposed short cut to establishing priorities for biodiversity conservation, and determine whether survey data on just one or two putative indicator groups can identify robust reserve networks capable of conserving biodiversity as a whole[1,2].

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Table 1 Cross-taxon congruence

	Large moths	Butterflies	Birds	Small mammals
Total recorded species richness				
Woody plants	0.68 $P < 0.001$	0.72 $P < 0.001$	0.69 $P < 0.001$	0.53 $P < 0.001$
Large moths		0.76 $P < 0.001$	0.75 $P < 0.001$	0.53 $P < 0.001$
Butterflies			0.68 $P < 0.001$	0.49 $P < 0.001$
Birds				0.66 $P < 0.001$
Residual species richness				
Woody plants	0.13 NS	0.14 NS	0.07 NS	0.12 NS
Large moths		0.55 $P < 0.001$	0.32 $P < 0.05$	0.22 NS
Butterflies			0.34 $P < 0.05$	0.04 NS
Birds				0.25 $P < 0.10$
Complementarity scores				
Woody plants	0.77 $P < 0.001$	0.74 $P < 0.001$	0.85 $P < 0.001$	0.51 $P < 0.001$
Large moths		0.68 $P < 0.001$	0.71 $P < 0.001$	0.52 $P < 0.001$
Butterflies			0.75 $P < 0.001$	0.58 $P < 0.001$
Birds				0.52 $P < 0.001$

Cross-taxon congruence in total recorded species richness ($N = 50$ forests), residual species richness after controlling for sampling effort ($N = 50$ forests), and complementary scores ($N = 49$ pairs of forests). Values are Pearson correlation coefficients. NS, not significant.

One simple route to identifying possible indicator taxa is to quantify how far spatial patterns of species richness coincide across different groups[2,3,5,6,16–19]. High congruence would be extremely interesting from an evolutionary perspective, and encouraging in terms of rapid assessment of biodiversity, but so far studies of temperate areas have revealed rather low congruence in species richness[3,4,7,8]. Because of increased endemism, there might not be such low congruence in the tropics, where high biological diversity coupled with very limited resources for its assessment mean that the benefits of using indicators would be greatest. However, no equivalent analyses at scales appropriate for reserve planning have been conducted yet anywhere in the tropics (but see ref. 18).

In practice, our data from Uganda at first suggest high congruence: there is a good match across taxa in the total numbers of species recorded from each forest (Table 1). But this apparent congruence is driven largely by differences in forest area and hence sampling effort, rather than congruence in species richness per unit area. Because of survey design, sampling effort per forest was closely correlated across taxa ($P < 0.001$ for all ten Pearson correlations), with larger, more extensively sampled forests generally appearing species-rich and smaller forests appearing species-poor as a result. Controlling for differences in sampling effort by first taking residuals from regressions of total species richness on the number of days spent sampling a taxon, and then comparing these residual scores across pairs of taxa, shows that there is low underlying congruence in species richness (only 3 out of 10 cross-taxon correlations are significant at $P < 0.05$; Table 1). Controlling for variation in forest size and sampling effort in other ways (such as taking residuals about forest area, or calculating relative species richness after conducting rarefaction[20]) confirmed that congruence in underlying species richness is very low. Our results thus mirror earlier findings, and, taken in isolation, indicate that concentrating on one or a few groups may be of limited utility in setting site-based priorities for conserving biodiversity as a whole.

However, looking at congruence in species richness is not a sufficient test of the ability of one taxon to indicate the overall conservation value of different sites[2,5,21–23]. A more appropriate test is to see how well sets of priority sites chosen using information from just that group capture diversity in other taxa as well. We used a simple but powerful complementarity-based algorithm to identify networks of forests containing near-maximum numbers of species in a fixed area (nominally 20% of the total forest estate; see Methods). We ran this algorithm using data either from single groups or from all taxa at once. For each of the resulting site-selection sequences, we examined the manner in which the cumulative number of species in all survey groups increased as a function of the combined area of the sites selected.

The top 20% of forest area picked using only the data on butterflies or birds contained as many or more species overall as the equivalent set of sites identified using data on all groups together (whether measured as the mean percentage representation of all five groups (Fig. 1), or as a cumulative representation of all species (not shown)). The data on moths also performed well, although using data on the poorest-performing group (which, at the 20% threshold, is the plants) resulted in the loss of ~10% of species, compared to using data on all taxa.

One explanation for these results could be that nearly any selection sequence simply reflects forest area (with the biggest forests being chosen first), indicating that priority sets of forests could perhaps be identified using information on forest size alone. But when we tested this by selecting sites simply in order of decreasing area, the resulting networks were very inefficient: choosing the top 20% of the forest estate this way resulted in the loss of 400 or more species, compared with using data on birds or butterflies. One last, important check is to examine the efficiency of picking sites entirely at random. On average (across 100 runs each for networks of 1, 2, 3 … 50 sites), randomly selected networks contained two to three times more sites, of smaller average size, than systematically picked networks of the same total area. Despite this, random selection captured fewer species per unit area than using data on birds, butterflies or all groups of taxa (Fig. 1). Moreover, such piecemeal networks would cost far more to establish and maintain, and presumably lose many more of their species through isolation and edge effects. Studies of both area-based and random selection therefore confirm that gathering at least some biological information is well worthwhile.

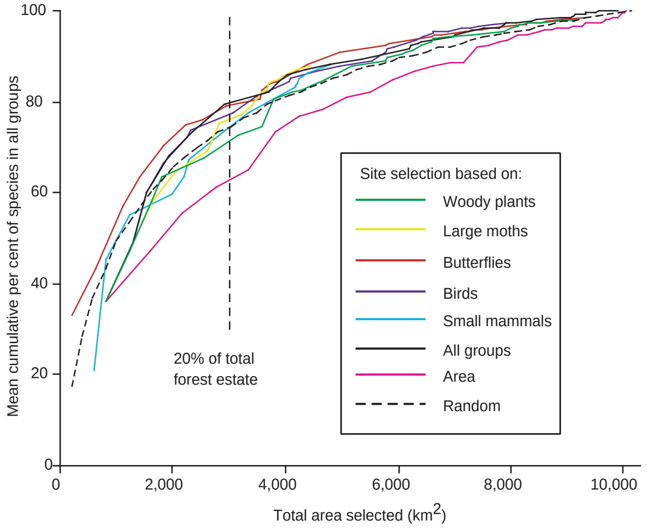

Figure 1 Mean cumulative representation of species across all five groups (woody plants, large moths, butterflies, birds and small mammals) as a function of cumulative area, when sites are picked on the basis of data on single taxa, on all groups, on forest area, or at random. Relatively few forests were picked using data on large moths or small mammals because all of the relatively few species in these groups could be captured in quite small networks of sites. The 20% threshold is drawn for illustrative purposes only. In reality, the Forest Department selected parts of (as well as whole) forests[15], but, for simplicity, we compare algorithm performance when only whole reserves are chosen.

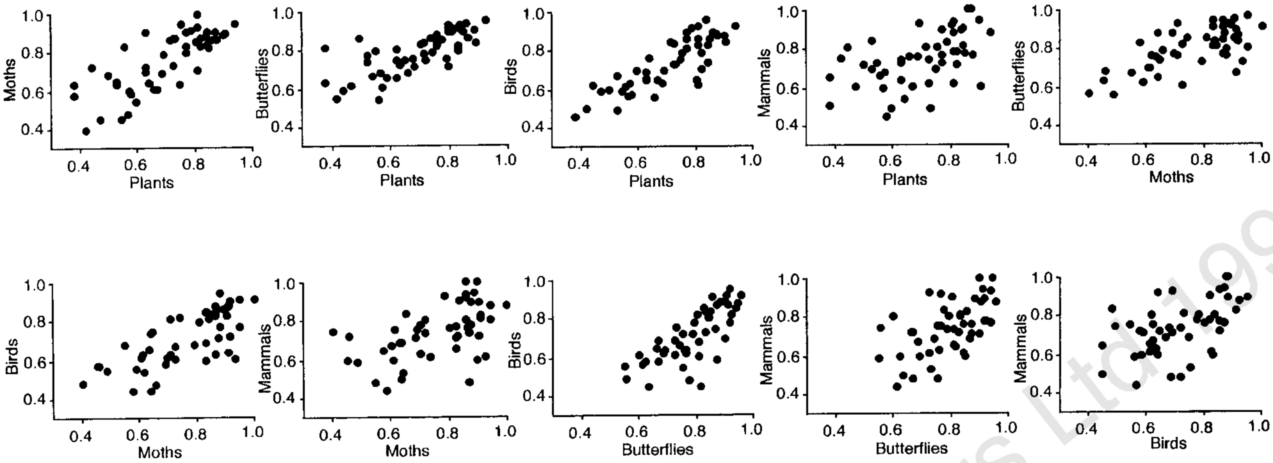

Figure 2 Cross-taxon congruence in complementarity scores[27] between 49 pairs of forests.

Why, in this case, are data on butterflies or birds alone just as useful for priority-setting as information on an entire suite of taxa, given that congruence in species richness is so strikingly low? The answer lies in the key issue of complementarity. The overall efficiency of a network of sites depends not just on their species richness but also on how well they complement one another biologically[9,10]. In the same way, the extent to which data on a single taxon can be used to establish an efficient network of sites for conserving all groups depends on the extent not just of congruence in species richness, but also of cross-taxon congruence in patterns of complementarity. This point has been recognized only recently[1,24–26], and remains almost completely untested.

We studied this overlooked yet critical issue directly by calculating standardized complementarity scores[27] for pairs of forests; we then compared these scores across different groups. Cross-taxon congruence in these scores was consistently high (Fig. 2; Table 1). Pairs of forests with high complementarity for one taxon generally exhibited correspondingly high complementarity for all other taxa, and *vice versa*. This was not due to any confounding effect of differences between forests in sampling effort or area (see Methods).

Instead, cross-taxon congruence in complementarity arose because all the groups examined showed fundamentally similar patterns of biogeography. Modified TWINSPAN analyses[28] of the biogeographical affinities of the forest reserves consistently identified six major groups (montane forests, western mid-altitude forests, lakeshore forests, savanna/forest mosaics, moist savannas and dry northern savannas), regardless of which taxon's distribution was assessed. Forests of different types exhibited high complementarity. Thus the top sites picked in any run of the priority-setting algorithm typically represented several forest types, and so collectively contained a broad set of species from each of our focal taxa.

These results, from the most detailed assessment of the performance of indicators for reserve selection anywhere in the tropics, show that in Uganda cross-taxon congruence in biogeography (and hence in between-site complementarity) is high enough to overwhelm low congruence in species richness. As a result, some groups can, by themselves, reliably indicate the overall conservation importance of forests. Thus similar priority-setting surveys in the region could in future be carried out more cheaply, without compromising their value, by focusing on just one or two taxa. As was the case here, exactly which groups perform best as indicator taxa will probably depend as much on the availability of local expertise as on the biology of the groups.

Our results also indicate that previous assessments of cross-taxon surrogacy in priority-setting, based on quantifying congruence in species richness, may have been inadequate. Certain groups may function as good indicators for reserve selection in other areas that, like Uganda, are characterized by high biogeographical heterogeneity. More appropriate analyses of putative indicators that examine congruence in complementarity and assess the overall value of the networks of sites identified by those groups are now needed for other parts of the tropics. □

Methods

Surveys. Surveys were carried out by teams of biologists and specially trained forest rangers using established techniques (described in ref. 14). Forest reserves differed considerably in area; to ensure that roughly constant fractions of the individuals in a forest were sampled, survey effort was spread in proportion to forest size (regressions of number of days of inventory versus forest area were significant at $P < 0.001$ for all five groups).

Reserve-selection algorithm. This algorithm selected first the forest with the most species, then that with the biggest complement of species (that is, the most species not represented in the selected site), and so on, until all species were represented at least once. In the event of ties, the smaller of the tied forests was picked. By incorporating both between-site complementarity and species richness, this sort of algorithm has higher efficiency (that is, it captures more species in a given area[9]) than site selection based solely on species richness[9,10,29,30]. Moreover, for the type of problem tackled here, where we aimed to select as priorities a substantial minority of a relatively small number of sites, this 'simple greedy' algorithm has similar power to more sophisticated techniques[11,24]. Our results deal with species accumulation as a function of total area of sites selected, but our conclusions were unchanged when we examined species accumulation versus number of sites selected.

Cross-taxon congruence in complementarity. Complementarity scores were calculated as the sum of the number of species found at just one or the other of a pair of sites, divided by the combined total found at either or both sites[27]. To avoid cross-taxon correlations being inflated by pseudoreplication or driven by marked differences in area between paired forests, we calculated complementarity scores only between each site and the next smallest forest in our study (yielding $N = 49$ scores from 50 forests). High cross-taxon congruence in complementarity was not driven by potentially confounding effects of forest size or sampling effort: residual complementarity scores (controlling for significant relationships between complementarity and forest area, sampling effort, and the difference in these values between forests) remained highly intercorrelated across taxa ($P < 0.001$ for all cross-taxon correlations using residual values).

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Membrane potential synchrony of simultaneously recorded striatal spiny neurons *in vivo*

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The basal ganglia are an interconnected set of subcortical regions whose established role in cognition and motor control remains poorly understood. An important nucleus within the basal ganglia, the striatum, receives cortical afferents that convey sensorimotor, limbic and cognitive information[1]. The activity of medium-sized spiny neurons in the striatum seems to depend on convergent input within these information channels[2]. To determine the degree of correlated input, both below and at threshold for the generation of action potentials, we recorded intracellularly from pairs of spiny neurons *in vivo*. Here we report that the transitions between depolarized and hyperpolarized states were highly correlated among neurons. Within individual depolarized states, some significant synchronous fluctuations in membrane potential occurred, but action potentials were not synchronized. Therefore, although the mean afferent signal across fibres is highly correlated among striatal neurons, the moment-to-moment variations around the mean, which determine the timing of action potentials, are not. We propose that the precisely timed, synchronous component of the membrane potential signals activation of cell assemblies and enables firing to occur. The asynchronous component, with low redundancy, determines the fine temporal pattern of spikes.

The membrane potential of striatal spiny projection neurons recorded in anaesthetized animals *in vivo* fluctuates between two subthreshold states[3–5]. The quiescent, hyperpolarized 'down' state, and the noisier, depolarized 'up' state, are separated by 15–30 mV. Spike threshold is usually 3–5 mV above the mean potential of the 'up' state[6]. The 'up' state is caused by synchronous synaptic input from a large number of corticostriatal afferents interacting with nonlinear membrane conductances in the striatal spiny neurons[4]. Because individual corticostriatal synapses are relatively weak[7], many afferents must be activated to cause a striatal neuron to fire[8]. Neurons within functionally related striatal microzones receive similar sets of afferents, which arise from spatially distributed, but functionally related, cortical areas[9,10]. Although the neurons within a microzone respond to behavioural events in a time-locked manner[11], their responses are asynchronous[12]. We recorded intracellularly from 23 pairs of striatal neurons in rats anaesthetized with urethane and ketamine/xylazine to measure the amount of synchrony of the shared corticostriatal afferents.

The membrane potentials of all the neurons in our sample showed distinct 'up' and 'down' states. Membrane potential traces of a pair of simultaneously recorded spiny neurons are shown in Fig. 1a. All-points histograms of 10-s samples demonstrate the bimodality of the membrane potentials (Fig. 1b). Cross-correlograms of the times of the transitions from the 'down' state to the 'up' state ('up' transitions) and transitions from the 'up' state to the 'down' state ('down' transitions) were constructed to measure the synchrony of the subthreshold membrane-potential state transitions (Fig. 2). All cross-correlograms showed significant central peaks (outside the 95% confidence intervals of the correlogram), indicating synchrony of both 'up' and 'down' state transitions. No further significant peaks were found in our correlograms, indicating that the state transitions are not due to a single oscillatory process[5].

We tested the hypothesis that synchrony of the state transitions of spiny neurons is dependent on the distance between them. The synchrony of the state transitions was weakly anticorrelated with distance ($r = -0.40$, $t = 3.14$, $P < 0.05$). The correlations found between the neurons in all the pairs of our sample showed that a large proportion of the state transitions of the striatal population are synchronized even over distances of a millimetre or more.

We calculated cross-correlations of the membrane potentials within individual 'up' states of simultaneously recorded spiny cells to see whether correlations on the time scale of individual synaptic inputs could be detected. The membrane potentials within the 'up' states of the spiny neurons were variable, reflecting the incoming corticostriatal synaptic activity[5]. The cross-correlations of the individual 'up' states were also variable. For each pair, we averaged the cross-correlations over several 'up' states. In 30% (7 of 23 cells) of our sample, a large central peak (outside the 95% confidence limits[13,14]) was evident. The central peaks had half-widths varying from 5 to 10 ms, which is the same time scale as corticostriatal