

Energy and trace-gas fluxes across a soil pH boundary in the Arctic

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Studies and models of trace-gas flux in the Arctic consider temperature and moisture to be the dominant controls over land–atmosphere exchange^{1,2}, with little attention having been paid to the effects of different substrates. Likewise, current Arctic vegetation maps for models of vegetation change recognize one or two tundra types^{3,4} and do not portray the extensive regions with different soils within the Arctic. Here we show that rapid changes to ecosystem processes (such as photosynthesis and respiration) that are related to changes in climate and land usage will be superimposed upon and modulated by differences in substrate pH. A sharp soil pH boundary along the northern front of the Arctic Foothills in Alaska separates non-acidic (pH > 6.5) ecosystems to the north from predominantly acidic (pH < 5.5) ecosystems to the south. Moist non-acidic tundra has greater heat flux, deeper summer thaw (active layer), is less of a carbon sink, and is a smaller source of methane than moist acidic tundra.

In 1995 and 1996, we studied the ecosystem properties on either side of a prominent pH boundary within the Kuparuk River basin (KRB) in Alaska, the primary study area of the Arctic System Science Land–Atmosphere–Ice Interactions (ARCSS–LAII) Flux Study⁵ (Fig. 1). We characterized moist non-acidic tundra (MNT) and moist acidic tundra (MAT) ecosystems at two intensive study sites about 7 km apart on either side of the boundary (Fig. 1b, sites 3 and 4). We also collected soil and vegetation data from numerous other MNT and MAT sites within the KRB during an accuracy assessment of the landcover map in Fig. 1b (ref. 6). This adds to earlier information from Toolik Lake, Happy Valley and Prudhoe Bay, Alaska^{7–11}.

The vegetation and soil properties on either side of the boundary are similar to those described for MNT and MAT in other studies^{8,12}. Site 3 has MNT with 36% cover of non-sorted circles¹³. The non-sorted circles are partly vegetated patches of highly frost-active soils that are about 1–2 m in diameter and spaced at intervals of 2–3 m; bare soil covers about 4% of site 3. The vegetation community between the circles is *Dryado integrifoliae-Caricetum bielowii*⁸, which is dominated by non-tussock sedges (*Carex bigelowii*, *C. membranacea* and *Eriophorum triste*), prostrate shrubs (*Dryas integrifolia*, *Salix arctica*, *S. reticulata* and *Arctous rubra*) and minerotrophic mosses (*Tomentypnum nitens*, *Hylocomium splendens* and *Ditrichum flexicaule*). Soils of MNT have a broken organic layer over a dark-coloured A horizon (a mineral horizon containing

organic-matter accumulation) with high base saturation, over a gleyed C horizon (a subsoil mineral horizon relatively unaffected by soil-formation processes except for the presence of grey colours resulting from poor drainage and reduction of iron)^{11,14}. All soil horizons have consistently high pH (>6.5) and are highly frost stirred (cryoturbated).

Site 4 is covered by tussock tundra (*Sphagno-Eriophoretum*⁸) with few (<1% cover) non-sorted circles. This vegetation type is dominated by dwarf shrubs (*Betula nana*, *Ledum palustre* ssp. *decumbens*, *Salix planifolia pulchra*), tussock sedges (*Eriophorum vaginatum*) and acidophilous mosses (*Sphagnum* spp., *Aulacomnium* spp., *Polytrichum* spp. and *Dicranum* spp.). Soils of MAT have a thick continuous organic horizon over gleyed subsoil material and contain cryoturbated organic material in the lower part. Both sites 3 and 4 are on silty loess deposits¹¹. Soil pH of MAT sites tends to increase with depth from about 4.0 at the surface to 6.5 in the frozen C horizons.

The pH boundary extends at least 300 km to the east and west of the study area^{15,16}. Loess blankets much of the Arctic Coastal Plain and Arctic Foothills, and both MAT and MNT occur on these extensive deposits, so it is difficult to explain the sharp vegetation boundary solely by differences in surface deposits¹⁷. The boundary may be partly due to a stronger winter Arctic climate north of the topographic barrier of the Arctic Foothills¹⁸. A colder, windier climate with shallower snowpack would promote the formation of non-sorted circles¹² and cause the continual stirring of non-acidic subsoils to the surface^{11,14}. The abundance of non-sorted circles and relatively low shrub biomass (85 versus 202 g m⁻²) north of the boundary results in the greyer tones on the false-colour infrared image (Fig. 1a). Lower shrub biomass, lower leaf-area index (LAI) and lower normalized difference vegetation index (NDVI) of MNT at site 3 is consistent with previous studies^{9,19} (Table 1).

South of the boundary, MNT is found only in relatively small areas on limestone bedrock and in naturally disturbed systems, such as river floodplains, snowbeds, windy hill crests and recently glaciated areas. In most of the Arctic Foothills, vegetation succession and peat formation (paludification) during the Holocene have converted formerly dry vegetation on mineral-rich loess and till deposits to MAT. Paludification is enhanced toward the south as a result of increased temperature and precipitation. Mosses, particularly *Sphagnum*, are important to this conversion. It is abundant in MAT but not MNT, and has numerous unique properties that strongly promote waterlogging and cold acidic soils^{20–23}.

The vegetation and soil differences between MAT and MNT have important consequences for land–atmosphere exchanges. Site 3 (MNT) had 28% more soil heat flux during 10 days of observation and 54% deeper end-of-summer thaw than site 4 (MAT). Summer thaws of MNT are consistently deeper than those of MAT throughout the KRB, despite MNT being dominant in the northern, colder portion of the study area²⁴, because the MNT has shorter, more open plant canopies (less shading by vascular-plant leaf area), less continuous moss cover and thinner organic horizons (Table 1). In a related study, evapotranspiration, soil heat flux and sensible heat flux (heat exchange between the atmosphere and the land surface) showed a similar relationship with net radiation at two acidic tundra sites (sites 4 and 6; Fig. 1b) despite latitudinal and elevation differences in climate, indicating that the energy budgets are more strongly correlated with vegetation type than with climate²⁵.

Site 4 also had about twice the gross photosynthesis and three times the respiration of the MNT site, as well as a greater net carbon gain, during the same 10-day measurement period (Table 1), despite the close proximity of the two sites and nearly identical temperature, net radiation and relative humidity²⁵. These results are consistent with CO₂-flux data from two other sites (11 and 21; Fig. 1b) during the same period in 1995. Site 11 (MAT) had similar summer climate and CO₂ flux to that at site 4, whereas site 21 (MNT) had a lower flux than site 3, probably owing to the colder early summer climate near the coast²⁶. Integrated fluxes from sites 11 and 21

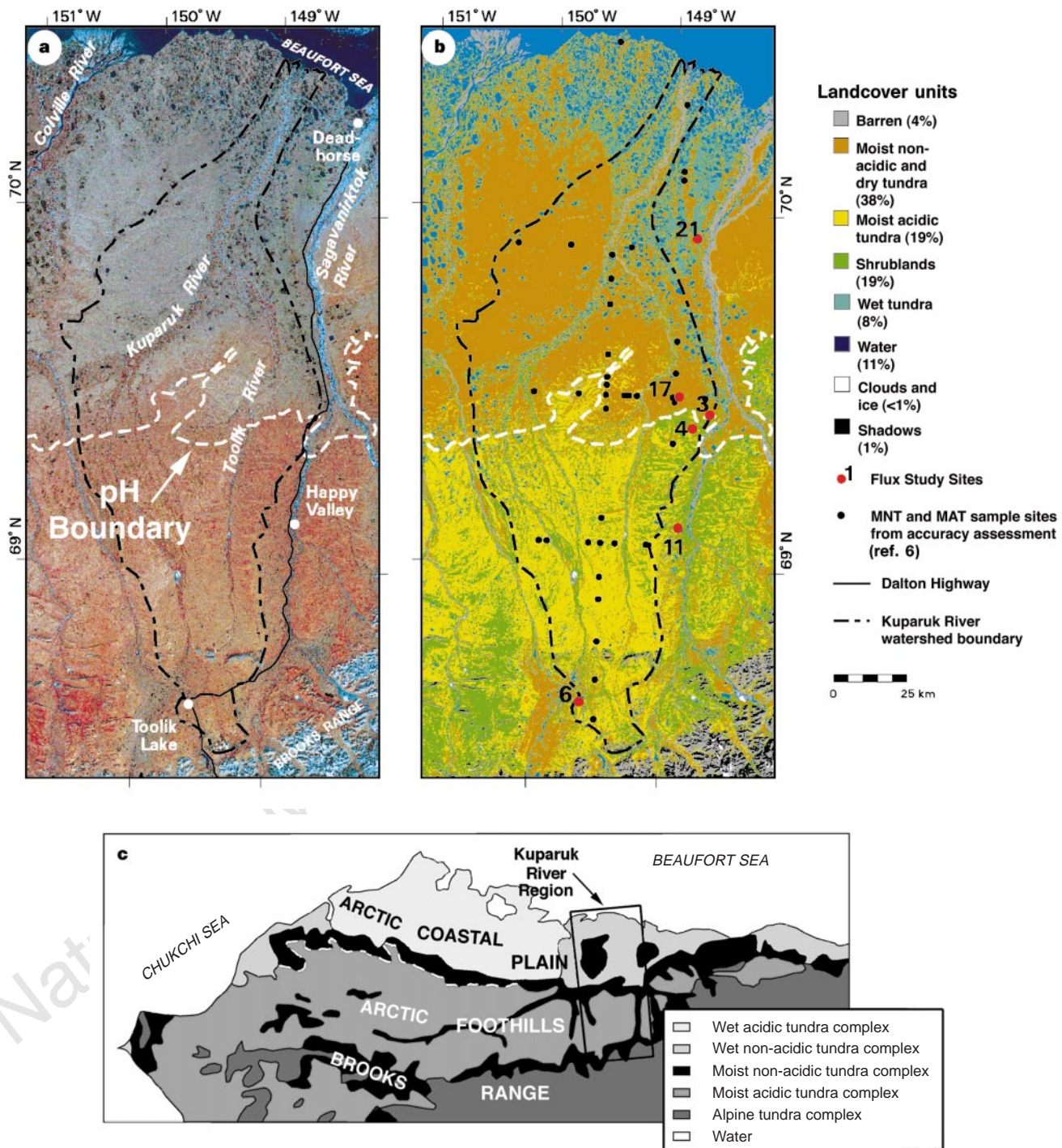


Figure 1 Maps of the study area. **a**, Landsat MSS false-colour infrared mosaic of the Kuparuk River Basin (dashed line), northern Alaska. A broad band of foothills occurs between the mountains and the Arctic Coastal Plain with many lakes. The pH boundary separating the redder tones to the south from the greyer tones to the north corresponds to soils that are acidic and non-acidic, respectively. Landsat data are courtesy of the US Geological Survey Alaska Data Center. **b**, Land-cover map. Red circles indicate intensive study sites. Black dots are other sites visited

during the accuracy assessment of the map⁶. **c**, The map shows a generalized distribution of acidic and non-acidic vegetation types in northern Alaska, prepared from an integration of information from several sources including AVHRR (Advanced Very-High Resolution) satellite images, soil maps, vegetation maps and surface-geology maps. The location of the pH boundary west of the Colville River (white dashed line) is less distinct and unstudied.

throughout the summer of 1995 showed that the MAT site was a much greater carbon sink than the MNT site (55.2 versus 27.6 g C m⁻² per season). In 1996, an even larger difference was observed between site 11 and site 17, an MNT site close to site 3 that has a summer climate very similar to sites 3 and 11. Site 11 (MAT) gained 52.5 g C m⁻² per season compared with 3.3 g C m⁻² per season at site 17 (MNT) (Table 1). Taken together, our data demonstrate a consistent spatial and temporal pattern of a much larger carbon sink

in MAT than in MNT. Methane flux showed a pattern opposite to that of CO₂, with the wetter, more anaerobic soils of MAT effluxing over six times the methane of MNT (Table 1).

Greater carbon accumulation in the vegetation has also led to twice as much organic carbon in both the active layer and the permafrost in the soils at site 4 than site 3 (Table 1). The basal ¹⁴C date from the frozen C horizon at site 4 was 8,500 years BP compared to 12,500 years BP in the same horizon at site 3, demonstrating the

Table 1 Comparison of ecosystem properties of MNT and MAT at sites in the Kuparuk River Basin

Ecosystem property	Sites 3 and 4			Other sites			Reference
	MNT	MAT	Significance	MNT	MAT	Significance	
Soil							
pH of top mineral horizon	7.6 [1]	5.5 [1]	n.a.	7.0 ± 0.16 [20] 6.3 ± 0.1 [14]	5.3 ± 0.13 [10] 4.6 ± 0.1 [33]	***	Ref. 14 Ref. 8†
O-horizon thickness (cm)	9 ± 1 [71]	15 ± 1 [71]	**	11 ± 1.9 [21]	21 ± 1.8 [15]	***	This study‡ This study§
Soil moisture of top mineral horizon (cm ³ cm ⁻³ , Jul 95)	0.37 [1]	0.40 [1]	n.a.				
Bare soil (% cover)	4.4 ± 1.6 [6]	0.2 ± 0.0 [6]	***	8 ± 1 [140]	1 ± 0.2 [121]	***	This study§
Vegetation							
Height of plant canopy (cm)	3.9 ± 0.3 [340]	6.5 ± 0.4 [340]	***				This study
Leaf area index	0.50 ± 0.03 [66]	0.84 ± 0.05 [66]	***	0.57 ± 0.06 [7]	0.81 ± 0.08 [11]	**	Ref. 19
NDVI (MSS)	0.23 [1]	0.32 [1]	n.a.	0.28 ± 0.00 [4 × 10 ⁶]	0.41 ± 0.00 [2 × 10 ⁶]	n.a.	This study¶
NDVI (Hand-held)				0.62 ± 0.02 [7]	0.71 ± 0.01 [11]	**	Ref. 19
Moss cover (%)	65 ± 4 [12]	79 ± 4 [12]	**				This study
Above ground biomass (g m ⁻²)							
Shrubs	85 ± 18 [10]	202 ± 22 [10]	***	127 ± 19 [7]	270 ± 19 [11]	***	Ref. 19
Graminoids	124 ± 12 [10]	112 ± 15 [10]	n.s.	118 ± 22 [7]	118 ± 24 [11]	n.s.	Ref. 19
Forbs	40 ± 22 [10]	10 ± 2 [10]	***	12 ± 4 [7]	12 ± 2 [11]	n.s.	Ref. 19
Mosses, lichens, litter	504	460	n.a.	221 ± 85 [7]	207 ± 33 [11]	n.s.	Ref. 19
Total	753 ± 60 [10]	784 ± 139 [10]	n.s.	447 ± 23 [7]	607 ± 27 [11]	***	Ref. 19
Energy and trace-gas flux							
Soil heat flux (19–30 Jun 1995, MJ m ⁻² d ⁻¹)	1.39 ± 0.21 [331]	1.09 ± 0.16 [275]	***				This study
Thaw depth (cm)	57 ± 1 [71]	37 ± 1 [71]	***	52 ± 2 [20] 57 ± 5 [14]	39 ± 2 [14] 36 ± 3 [33]	***	This study§ Ref. 8
Evapotranspiration (19–30 Jun 1995, mm d ⁻¹)	1.16 ± 0.17 [331]	1.06 ± 0.16 [275]	n.a.				This study
10-d gross primary production (19–30 Jun 1995 g CO ₂ -C m ⁻² d ⁻¹)	0.94 ± 0.14 [331]	1.82 ± 0.27 [275]	n.a.				This study
10-d net CO ₂ uptake (g CO ₂ -C m ⁻² d ⁻¹)	0.67 ± 0.10 [331]	0.95 ± 0.27 [275]	n.a.	0.27 ± 0.41 [12]	1.02 ± 0.33 [12]	n.a.	This study¶
10-d respiration loss (g CO ₂ -C m ⁻² d ⁻¹)	0.27 ± 0.04 [331]	0.87 ± 0.13 [275]	n.a.				This study
1995 net CO ₂ uptake (g CO ₂ -C m ⁻² per season)				27.6 [77]	55.2 [90]	n.a.	This study#
1996 net CO ₂ uptake (g CO ₂ -C m ⁻² per season)				3.3 [31]	52.5 [73]	n.a.	This study ^{††}
Methane emission (mg CH ₄ cm ⁻² yr ⁻¹)				69 ± 33 [12]	449 ± 301 [15]	*	This study†††
Soil organic carbon (kg C m ⁻³)	40 [1]	88 [1]	n.a.	56 ± 5 [5] 55 ± 5 [16]	44 ± 11 [6] 49 ± 4 [7]	n.s.	Ref. 11 Ref. 10

Standard error of the mean and number of samples [in brackets] are given for most variables. Probability of significance in all cases was based on two-sample *t*-test. Significance levels:

P* ≤ 0.1; *P* ≤ 0.05; ****P* ≤ 0.01; n.s., non-significant; n.a., non-applicable.

† Data are from 47 permanent plots in the Toolik Lake region.

‡ Measurements at 36 random points within the Kuparuk River basin during accuracy assessment of the land-cover map.

§ Estimates obtained from aerial surveys at 361 sites within the Kuparuk River basin during accuracy assessment of the land-cover map.

¶ Mean MSS NDVI values for the land-cover map.

Sites 11 (MAT) and 24 (MNT).

† Sites 11 (MAT) and 24 (MNT). Time intervals for measurements: site 11, 1 Jun–31 Aug 1995; site 24, 16 Jun–31 Aug 1995.

†† Sites 11 (MAT) and 17 (MNT). Time intervals for measurements: site 11, 6 Jun–31 Aug 1996; site 17, 15 Jun–19 Aug 1996.

††† Methane measurements at 37 plots at Toolik Lake region, Happy Valley and Deadhorse.

faster accumulation rate at the acidic site. Other soil data from MAT and MNT sites throughout the basin do not show a similar consistent trend of more carbon in the MAT soils (Table 1), presumably because there is a wide diversity of genetic environments, including MNT fen and fluvial sites, and MAT sites on a variety of surface ages. Other studies, however, show that MNT soils have consistently lower C:N ratios (15 versus 20)¹¹, greater microbial activity and more highly decomposed organic fraction²⁷. The relative winter CO₂ flux rates of MNT and MAT remain unresolved²⁸.

Extrapolations of trace-gas fluxes and soil carbon based solely on numbers from the more extensively studied MAT, as has been done in all previous high-latitude extrapolations, results in large errors. For example, in the map area of Fig. 1, this would overestimate gross photosynthesis by at least 35%, respiration by 140%, net CO₂ uptake by at least 15%, and methane flux by 140%. Similar, but more diffuse, pH boundaries separate worldwide zonal tundra types. MNT corresponds to the sedge-dominated 'typical tundra' of Russian authors, whereas MAT corresponds to shrubby 'southern tundra'¹². Over century to millennium time scales, we expect that zonal soil pH boundaries will shift northwards in response to climate warming, deeper winter snowpacks and reduction of loess sources. Regions with declining soil pH will show a decrease in soil heat flux and large increases in methane flux and carbon storage in the plant canopy. □

Methods

Site selection. In the summers of 1995 and 1996, several sites were monitored

to characterize the energy and trace-gas fluxes of arctic tundra⁵. Sites 3, 17 and 24 have MNT and sites 4, 6 and 11 have MAT vegetation. To compare MNT and MAT fluxes under nearly identical summer climates, we chose two sites about 7 km apart (sites 3 and 4; Fig. 1b) on opposite sides of the pH boundary on hilltops (224 and 332 m, respectively) with similar topography. The sites were accessible by helicopter from Happy Valley and were as similar and homogeneous as possible, and were far enough from the Dalton Highway to eliminate the effects of road dust.

Soils. Percentages of soil types and O-horizon thickness at sites 2 and 4 were determined from 71 random points at each site. Soil classification is according to the Gelisol Order in US soil taxonomy²⁹. The pH values at all sites are from surface samples collected at 39 random MNT and 24 MAT points within the KRB basin. The mean O-horizon thickness for the same sites was determined from 10 samples at each site. Bare-soil values for the KRB are visual estimates from 261 sites visited during accuracy assessment of the land-cover map⁶. Soil organic carbon was analysed on acid-treated samples using a Leco CHN-1000 analyser¹¹.

Vegetation. The land-cover map of the KRB was derived from a mosaic of Landsat Multispectral Scanner (MSS) images provided by the USGS EROS Alaska Data Center⁶. The height of the plant canopy was determined from 340 random points each at sites 3 and 4. Percentage cover of moss and bare soil was determined from four 50-m and two 70-m line transects at each site. Vascular plant leaf-area index was measured with a LI-COR PCA 2000 plant canopy analyser¹⁹ at 66 points at each site. Biomass is the mean dry mass of 10 random 20 × 50-cm clip harvest plots within sites 3 and 4. The normalized difference vegetation index (NDVI) at sites 3 and 4 was determined from the pixel of the Landsat MSS image centred on the sample sites. Mean NDVI for MNT and MAT

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 CO₂ 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 towers²⁵. 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. CO₂ fluxes at sites 11, 17 and 21 were determined using eddy-covariance methods and 2.5-m towers²⁶. Mean values and standard errors at these sites were calculated using the daily mean CO₂ fluxes. The daily methane fluxes were integrated over the thaw period to obtain annual emission. Winter methane fluxes were assumed to be zero. CH₄ 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 method³⁰. 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 Africa¹². Much of this diversity is restricted to 15,000 km² of forest reserves (which also contain non-forest habitats) under the jurisdiction of the Uganda Forest Department¹³. 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 km² (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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