weight of each mouse was recorded weekly. On average, the $Acc2^{-/-}$ mice consumed 20 to 30% more food than did the wild-type mice and attained an average body weight of 21 g per mouse compared to 23 g per wild-type mouse. The $Acc2^{-/-}$ mutant mice were generally leaner, weighing about 10% less than the wild-type mice throughout the feeding periods (Fig. 4B), and they accumulated less fat in their adipose tissues (Fig. 4, C and D). For example, the epididymal fat pad tissue in an $Acc2^{-/-}$ male weighed 0.75 g compared to 1.4 g in a wild-type male littermate (Fig. 4E). The decrease in the adipose size resulted in a decrease in the leptin release to the plasma from 53 ± 9 ng/ml in the wild type to 36 ± 3 ng/ml in the mutant mice (*30, 31*). Thus, mitochondrial oxidation of fatty acids regulates fat storage in the adipose tissue.

In conclusion, our analysis reveals that mice lacking malonyl-CoA show increased oxidation of fatty acids, decreased fat in adipose tissue and liver, and decreased storage of glycogen in the liver; however, they are still morphologically normal, grow at the expected rate, and breed normally. The $Acc2^{-/-}$ mice consumed 20 to 30% more food than did the wild type, yet lost or simply maintained body weight. In the absence of ACC2, the rate of fatty acid oxidation increased in heart and muscle, as well as the rest of the body. We speculate that adipose and liver triglycerides are mobilized, and their fatty acids are made available to the various tissues for oxidation. Hence, the reduction in fat contents and size of the adipose (Fig. 4E) led to a reduction by about 30% of leptin released to the plasma (*30, 31*), similar to that occurring in fasted mice, and signaled the hypothalamus to produce the appetite-stimulating neuropeptide Y, which promotes feeding (*32, 33*). We feel this is the most plausible explanation for the observation that $Acc2^{-/-}$ mice have smaller fat stores even as they consumed more food than did the wild type (Fig. 4). It has been suggested that malonyl-CoA may play a role in signaling the availability of physiological fuel by acting through the hypothalamic neurons (*34*). This suggestion was based on the inhibition of ACC by 5-(tetradecyloxy)-2 furoic acid that increased food intake in mice treated with fatty acid synthase inhibitors (*34*). Although this possibility could not be ruled out in the $Acc2^{-/-}$ mice, the lower leptin levels in the plasma may be sufficient to increase appetite. Moreover, the $Acc2^{-/-}$ mice appear to be normal, with no obvious neurological abnormalities.

Maintenance of high levels of fatty acid oxidation results in reduced fat accumulation and storage, a physiological state that humans try to attain through exercise. If the results shown here for mice hold true for humans, then pharmacological inhibition of ACC2 might allow individuals to lose weight while maintaining normal caloric intake.

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Conservation Conflicts Across Africa

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There is increasing evidence that areas of outstanding conservation importance may coincide with dense human settlement or impact. We tested the generality of these findings using 1°-resolution data for sub-Saharan Africa. We find that human population density is positively correlated with species richness of birds, mammals, snakes, and amphibians. This association holds for widespread, narrowly endemic, and threatened species and looks set to persist in the face of foreseeable population growth. Our results contradict earlier expectations of low conflict based on the idea that species richness decreases and human impact increases with primary productivity. We find that across Africa, both variables instead exhibit unimodal relationships with productivity. Modifying priority-setting to take account of human density shows that, at this scale, conflicts between conservation and development are not easily avoided, because many densely inhabited grid cells contain species found nowhere else.

Efforts to stem the ongoing loss of biodiversity are hampered by conflicts between conservation and development (*1–3*). Priority-setting exercises for birds have shown that such conflicts may be frequent because areas of high conservation value are often characterized by rapid habitat clearance or high human population density (*4, 5*). In contrast, Huston (*6*) has suggested that species richness generally decreases and agricultural productivity generally increases with primary productivity and that therefore conservation and development needs can be readily reconciled. Here we test these contradictory hypotheses using 1°-resolution databases summarizing the distribution of birds, mammals, snakes, amphibians, people, habitat conversion, and net primary productivity (NPP) across sub-Saharan Africa (*7*).

Our analyses (*8*) reveal that across Africa, patterns of species richness and human density exhibit marked congruence: Populations are consistently dense in areas of high species richness, and vice versa (Fig. 1A; human population density versus all species richness: $r_{s\ \mathrm{corr}} = 0.54$, $N = 1957$ grid cells). This association holds both for more widely distributed species (those in the top 75% for range size in each group: $r_{s\ \mathrm{corr}} = 0.54$, $N = 1957$; Fig. 1B) and, as reported elsewhere (*4*, *5*), for narrower endemics (those in the lower 25% for range size: $r_{s\ \mathrm{corr}} = 0.39$, $N = 1957$; Fig. 1C).

Dense human settlement is associated with high threat to biodiversity. Areas with more people have undergone greater habitat conversion (percentage of cover by converted land classes versus density: $r_{s\ \mathrm{corr}} = 0.49$, $N = 1957$). Because densely populated squares have many species overall and many narrowly distributed and therefore vulnerable endemics, it is unsurprising that they also have many threatened species (human population density versus number of threatened species: $r_{s\ \mathrm{corr}} = 0.36$, $N = 1957$). Moreover, country-specific predictions of human population densities in 2050 indicate that correlations between the distributions of people and biodiversity will persist (2050 population density versus mean species richness per grid cell: $r_{s\ \mathrm{corr}} = 0.55$, $N = 41$ countries, compared with $r_{s\ \mathrm{corr}} = 0.54$, $N = 41$ for 1998). Hence, future as well as present biodiversity losses look set to be concentrated in areas of currently dense settlement [see also (*9*)].

These findings remain qualitatively unchanged when other population data (*10*) are used and persist after controlling for latitudinal and longitudinal trends in both species richness and population density (*11*) (Fig. 1D; residual population density versus residual species richness: $r_{s\ \mathrm{corr}} = 0.64$, $N = 1957$). Moreover, all the results hold when each taxonomic group is analyzed separately ($r_{s\ \mathrm{corr}}$ values between 0.16 and 0.59). The within-taxon patterns are generally stronger for better sampled groups [e.g., correlations between human density and all species richness, in order of decreasing sampling effort (*12*): birds, $r_{s\ \mathrm{corr}} = 0.59$; mammals, 0.43; snakes, 0.43; amphibians, 0.35]. This is contrary to what one would expect if the overall population density/species richness correlation was a simple artifact of any tendency for sampling effort to be concentrated near areas of settlement (*13*).

Our results extend those of previous studies, which have concentrated on birds (*4*, *5*)

Fig. 1. Correlations between human population density (people km^{-2}) and species richness. (**A**) Density versus all species richness. (**B**) Density versus widely distributed species richness. (**C**) Density versus narrowly distributed species richness. (**D**) Residual density versus residual richness for all species. Each point represents a 1° cell; because of spatial autocorrelation, points are not fully independent of one another, but this does not affect the value of correlation coefficients (*36*).

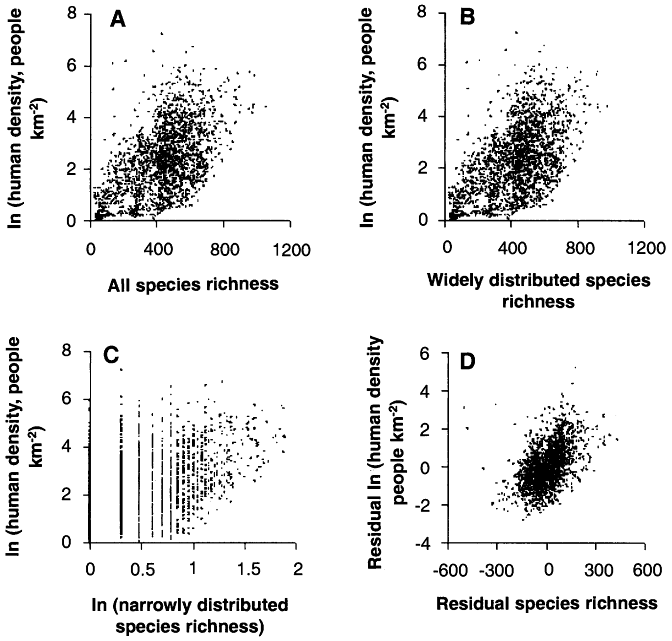

Table 1. Regression results for three components of species richness and human population density with NPP (in t C ha^{-1} year^{-1}) and altitudinal range (AltR, in m) as independent variables. We fitted a full model for each dependent variable, comprising NPP, AltR, NPP^2, AltR^2, and (NPP × AltR). We used permutation tests [999 random permutations of vectors using Permute! (*43*)] and backward elimination (with probability to reject set to 0.01) to remove nonsignificant terms; terms with very low explanatory power ($r^2 < 0.005$), which achieved conventional significance because of large sample sizes, were also removed. Only those terms still remaining are presented here.

Dependent variable	Independent variables (coefficient, r^2)				r^2
	Intercept	NPP	NPP^2	AltR	
All vertebrate species richness	127.09	86.87, 0.45	−4.68, 0.22	0.067, 0.06	0.73
Widely distributed species richness	125.09	87.17, 0.46	−4.68, 0.22	0.074, 0.05	0.73
Narrowly distributed species richness*	0.22	0.05, 0.06		0.0009, 0.33	0.41
Human population density*	0.90	0.44, 0.15	−0.026, 0.14	0.0004, 0.03	0.30

*Variables were (ln + 1) transformed.

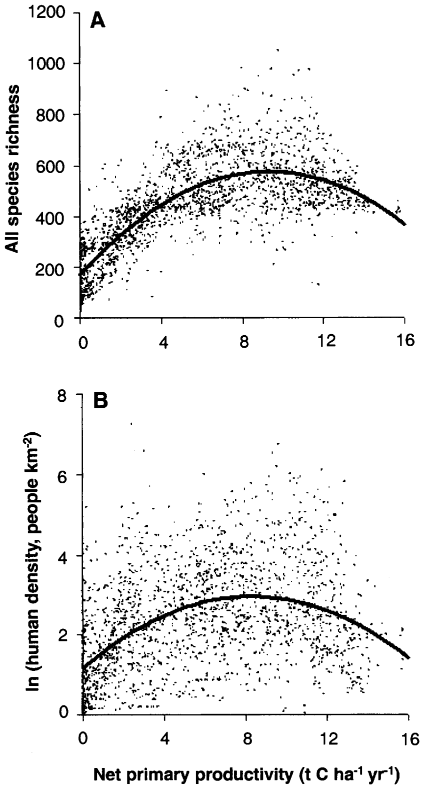

Fig. 2. Relationships between (**A**) all species richness and NPP and (**B**) human population density and NPP. For full models, see Table 1.

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or on areas defined a priori as having been already exposed to disproportionate human impacts (*14*). Taken together, these findings indicate that the tendency for human population densities to peak in or near areas of high biodiversity value may be general across the tropics. In contrast, Huston (*6*) argued that human demands on biodiverse areas need not be great, because species richness and agricultural productivity show opposing relations with primary productivity (albeit in very different data sets). We therefore examined how both species richness and human density vary as a function of NPP across Africa.

Confusion over what exactly is meant by large scale means that there is little consensus over richness/NPP relations at coarse levels (*15–18*): Here, using 1° cells spread over a very large area, we found that vertebrate species richness peaks at intermediate levels of productivity (Fig. 2A). More surprisingly, and in contrast to the prediction of monotonic increase in species abundance from the energy limitation hypothesis (*18*), we found that human population density exhibits a similar (though weaker) hump-shaped relationship with productivity (Fig. 2B; doubtless the weakness of this relationship is due in part to the importance of historical influences on human settlement). Species richness and human density both peak at intermediate levels of NPP (9.3 and 8.3 t C ha^{-1} year^{-1}, respectively). Although the mechanisms underlying these relationships are not yet clear (and may well differ), the striking similarity in patterns bears witness to the general congruence between species richness and human population density.

But although the unimodal species richness/productivity pattern holds for wider ranging species, it becomes linear and very weak for more narrowly distributed species (Table 1). One might expect endemism to be better associated with areas of high environmental heterogeneity (*19*, *20*). We tested this using the altitudinal range of each square as a measure of its heterogeneity (*20*), which (unlike scores based on current habitat types) is independent of human impacts.

For narrowly distributed species, species richness is indeed better predicted by altitudinal range than by NPP (Table 1); the reverse is true for wide-ranging species. If year-round cropping is facilitated by access to dissimilar habitats (*21*), one might also expect human densities to be linked to environmental heterogeneity. Population density and altitudinal range are positively correlated, independently of NPP (Table 1), but the relationship is very weak. We suspect that other unmeasured factors [perhaps including climatic stability (*5*, *22*)] provide a better explanation of the link between population density and endemism.

The consequences of centers of species richness and endemism being associated with dense human settlement can be visualized by expressing the performance of priority-setting exercises (*23*) in terms of the numbers of people living in areas of high conservation priority (Fig. 3). An efficient heuristic selection algorithm that identifies the near-minimum number of 1° cells capable of representing all species at least once picks 235 cells. No fewer than 110 of these belong to the 25% most densely populated squares (compared with 59 if cell priority was unrelated to population density: $G = 52.1$, $P < 0.001$). As a consequence, this near-minimum set for area (just 12% of all 1957 squares) is inhabited by a total of around 132 million people (27% of those in sub-Saharan Africa).

With the use of WORLDMAP (*24*), cell selection can be modified so that at each step, the cell chosen (after irreplaceable areas have been picked) is not simply the one with the most as yet unrepresented (complementary) rarest species, but that with the highest ratio of complementary rarest species:human population. All selected areas are then reordered picking the highest ratio of complementary richness among all species:human population at each step. This procedure identifies a set of cells that again represents all species, but at near-minimum cost in terms of total population. The resulting sequence shows that partial representation can

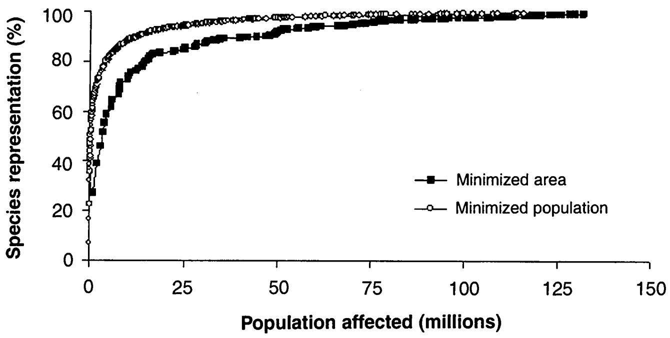

Fig. 3. Species accumulation as a function of the total number of people living in selected 1° cells, when priority selection is designed to minimize the number of cells picked (lower line) or their cumulative population (upper line; see text for further explanation).

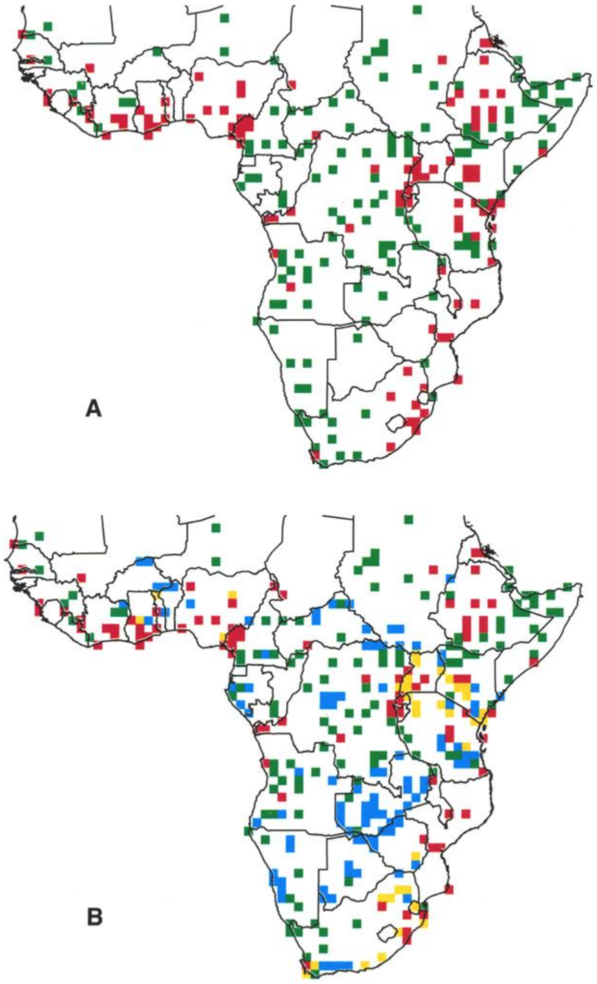

Fig. 4. (**A**) 1° cells chosen to represent all terrestrial vertebrates in a set with near-minimum total human population; grid cells are ~110 km on each side at the equator. Red cells are among the 25% most densely populated squares in Africa; green denotes the rest of the near-minimum set. (**B**) Cells chosen in an equivalent gap analysis (*27*). Cells identified as "protected" (*26*) are preselected; additional "underprotected" cells are then picked to represent all remaining species in a set with near-minimum population. Yellow and red cells are densely populated and "protected" and "underprotected," respectively; blue and green cells are less densely populated and "protected" and "underprotected," respectively. Highest priority should be attached to new conservation initiatives in red cells and maintaining existing reserves in yellow and red cells.

generally be achieved at far lower cost than with an area-minimizing algorithm (Fig. 3). However, the fully representative population-minimizing set still contains 100 high-cost cells (out of 241; $G = 31.3$, $P < 0.001$) and a total of around 116 million people (88% of those in the area-minimizing set) (*25*). This is because 79 densely settled cells are irreplaceable (containing species found nowhere else), and 21 of the remaining 31 picked before can only be replaced by higher cost alternatives. Finer scale analyses should help identify some sites within these areas (colored red in Fig. 4A) where conservation goals can be achieved without excessively compromising current or future human needs, yet the requirement for effective conservation measures in many densely populated, biodiversity-rich cells cannot be side-stepped.

One final question is how far existing protected areas might already meet conservation objectives in regions of potentially high conflict. With a broad definition of protection adequacy [which recognizes small but well-located reserves (*26*)], densely settled cells are as likely to be "protected" as other cells (34 of 137 "protected" cells are in the most heavily populated quartile; $G = 0$, NS). But even with this generous view of reserve coverage, preselection of "protected" cells in a gap analysis (*27*) does little to reduce the number or total population of additional high-cost cells required in the population-minimizing set (84 cf. 100 cells, containing $\sim$88 cf. 100 million people; Fig. 4B). In particular, the Upper Guinea forests, the Nigeria/Cameroon highlands, the Ethiopian Highlands, the Albertine Rift, the Eastern Arc, East African coastal forests, and parts of Natal all remain as areas in need of additional conservation initiatives (compare the red cells in Fig. 4, A and B). Maintaining current reserves in "protected" high-density cells, in the face of intense and growing population pressure, is an equally important challenge in ensuring the persistence of Africa's biodiversity.

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7. We used the distributional data for 1921 bird species, 940 mammal species, 406 snake species, and 618 amphibian species compiled by the Zoological Museum, University of Copenhagen, across 1° cells of mainland sub-Saharan Africa. Sources included 1115 primary publications and unpublished reports and consultation with 74 taxon specialists [for full details of sources, taxonomy, and methods, see (*12*, *28*), the supplemental data to this paper (*29*), or http://www.zmuc.dk/commonweb/research/biodata.htm]. This is the largest and most comprehensive database currently compiled for any extensive tropical region. Threatened species were taken from (*30*). Estimated human population densities for 1990 were obtained from (*31*) and degraded from a 2.5' grid to 1° resolution; country-specific population densities for 1998 and 2050 are from (*32*). To quantify land conversion, for each 1° cell, we calculated the percentage of 1-km^2 pixels in (*33*) that are covered by land classes described as cropland, cropland mosaic, secondary, degraded, or fragmented. Altitudinal range was calculated as maximum minus minimum elevation in each 1° cell, taken from (*34*). NPP values were derived from the DOLY global model (*35*) and degraded from 1/4° to 1° resolution.
8. Values for human density and richness of narrowly distributed species were transformed to ln(human density + 1) and ln(richness + 1) to achieve approximate normality. All data showed evidence of positive autocorrelation (e.g., Moran's I for autocorrelation between adjacent cells ranged from 0.32 for population density to 0.94 for NPP). Here we wish to examine patterns of association between different variables and so focus entirely on correlation coefficients and r^2 values, which are unaffected by autocorrelation (*36*). However, autocorrelation does reduce P values by overestimating degrees of freedom, increasing the risk of type I errors, and so P values are not presented for tests involving complete coverage of sub-Saharan Africa.
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23. Identifying the near-minimum set of areas capable of representing all species once was achieved with a progressive rarity algorithm in WORLDMAP (*24*). This selects first those cells containing species found nowhere else, then the cells richest in the next most narrowly distributed unrepresented species, and so on, until all species are represented at least once; sites in the resulting set are then reordered by complementary richness. The second, population-minimizing algorithm proceeds similarly but picks at each iteration the cell with the highest ratio of unrepresented rarest species:human population (*24*). For other approaches to integrating land-use conflicts into quantitative prioritization, see (*37*–*39*).
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26. Cells were defined as "protected" if they contain $\geq$three reserves or reserves cover $\geq$33% of their area or they include their biologically most important habitats (*5*). Data on reserve location were taken from (*40*). Under more demanding definitions of protection adequacy based exclusively on reserve area, proportionately fewer high-density cells are "protected" (e.g., only 17 of 162 cells that are $\geq$25% covered by reserves are high density; $G = 22$, $P < 0.001$). These findings mirror results elsewhere (*5*, *22*, *41*, *42*) and reinforce our view that conservation measures are inadequate in many high-conflict areas.
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