# Economic benefits of biodiversity exceed costs of conservation at an African rainforest reserve

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**Economic research on biodiversity conservation has focused on the costs of conservation reserves and the benefits of intact ecosystems; however, no study has simultaneously considered the costs and benefits of species diversity, a fundamental component of biodiversity. We quantified the costs and benefits of avian biodiversity at a rainforest reserve in Uganda through a combination of economic surveys of tourists, spatial land-use analyses, and species–area relationships. Our results show that revising entrance fees and redistributing ecotourism revenues would protect 114 of 143 forest bird species (80%) under current market conditions. This total would increase to 131 species (≈90%) if entrance fees were optimized to capture the tourist's willingness to pay for forest visits and the chance of seeing increased numbers of bird species. In contrast, the cost of purchasing agricultural land for ecological rehabilitation of the avian habitat would be economically prohibitive. These results suggest that local biodiversity markets could play a positive role in tropical conservation strategies if the appropriate institutions for redistribution can be developed.**

choice experiment | cost–benefit | deforestation | land value | Uganda

As part of an expanding response to declining global biodiversity (1), interdisciplinary research teams of economists and ecologists have conducted valuation exercises designed to estimate the costs (2–4) and benefits (5–7) of biodiversity preservation. The cost–benefit approach is essential for determining economically optimal conservation levels, yet there are few examples of studies that have simultaneously examined both the costs and benefits of conservation (6). We are unaware of any studies that have examined both the costs and benefits of biodiversity at the level of species diversity. The results of such an analysis would be particularly important for biodiversity conservation in tropical areas. Compared with the developed world, species diversity in the tropics is extraordinarily high, and conservation costs are relatively inexpensive. Funding for tropical conservation is limited, however, and economic opportunities for impoverished human populations are often hindered by conservation actions.

We conducted a study to address these issues at the Mabira Forest Reserve in southern Uganda. The Mabira Forest is a 300-km$^2$ remnant of tropical lowland forest that is surrounded by agricultural lands and located ≈50 km from Uganda's capital, Kampala. Pressure on the forest is intense, with harvesting timber, making charcoal, collecting fuelwood, and encroaching agricultural development competing with forest conservation as land-use activities. In 1996, a donor-funded initiative established an ecotourism center at the forest, and since then, small but growing numbers of tourists have visited the reserve (3,842 foreign nationals in 2000). A portion of the proceeds from the ecotourism center has been distributed to surrounding communities in an ad hoc manner with the hope of increasing awareness of the potential economic benefits of preserving the forest. This study was based on the philosophy that the local community should be compensated for the opportunity costs of not converting the forest to agricultural lands. We assumed a goal of conserving the maximum number of forest bird species, subject to the constraint that the opportunity costs of conservation cannot exceed the benefits from tourism. We assumed that subsistence farmers in this area are the dominant agents of land-use change because such farmers often are in other tropical countries (8–10) and that the transfer of benefits from tourists to these agents is a desirable mechanism to fund sustainable development (11).

## Methods

**Benefits of Avian Species Diversity.** We used a choice experiment to calculate the economic benefits of avian species diversity through tourist revenue at the Mabira Forest Reserve (12). Choice experiments give respondents a number of options that are described by various attributes and ask which option is preferable. By varying the attribute levels according to experimental design rules, a model for choice based on attributes can be developed.

Random utility theory, in which consumers make discrete choices from a set of alternatives, underpins the choice experiment approach. The utilitarian approach to economic valuation assumes that individuals maximize their own utility, or personal satisfaction, by choosing to consume (in the broadest sense) that set of goods and services that gives them the most satisfaction. In random utility theory, the consumer is said to obtain utility $U$ (conditional on their choice) from an alternative $i$ by $U_i = v_i + \varepsilon_i$. This conditional indirect utility function is composed of a systematic indirect utility component ($v_i$) and a random error component ($\varepsilon_i$). An alternative $i$ will be chosen if it has a greater utility than the alternative $j$. Thus, the probability of choosing $i$ over $j$ is $p(i)$ = probability ($v_i + \varepsilon_i \geq v_j + \varepsilon_j$), where $i$ and $j$ are elements of the choice set.

Utility in this case is considered "indirect" because it is not based on the quantities of goods or services consumed but rather on the prices of services and products like entrance fees and on the attributes of alternatives available. In the context of choice experiments, the standard multinomial choice model applies when indirect utility $v_i$ is defined as $v_i = \Sigma_j B_k X_i^k$, where $B_k$ is the coefficient on the attribute $X^k$ and when the distribution of $\varepsilon_i$ is assumed to be Gumbel or type I extreme value. This model can be estimated by maximum-likelihood techniques and can be extended to a random parameters logit model (13) by assuming that an individual's utility $i$ for an alternative $k$ is described by $U_{ik} = BX_{ik} + B^v X_{ik}$, such that each person's utility deviates from the population mean $B$ by the vector $B^v$. Unlike the standard multinomial model, estimating the coefficients on $X$ requires estimating the distribution from which these $B$s arise; this method is similar to a Bayesian statistical approach. The result is a more realistic model of behavior that accounts for heterogeneity among individual respondents.

We modeled the propensity of tourists to visit the Mabira Forest

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Reserve by asking respondents to choose between Mabira and two other forest reserves (Budongo Forest Reserve and Kibale National Park) that could act as substitutes for a tropical forest visit in Uganda. Site attributes and their levels were based on reviews of the literature, personal observations, communications with relevant Ugandan authorities, and potential policy implications of the results. Before surveying began, we pretested the surveys to ensure their clarity and intelligibility to respondents. Two Ugandan assistants administered the survey in the departure lounge at Entebbe International Airport (Uganda) during July and August 2001. Eight hundred sixty-one surveys containing usable responses were collected, mostly from tourists (80.1%) and foreign residents of Uganda (16.5%). Comparison of the resulting random parameters logit model with actual tourist visitation data revealed close concordance between actual and predicted proportions of tourists visiting the Mabira Forest Reserve (12). By assuming policy-relevant values for entrance fees and tourist numbers, the effects of changes in forest attributes (such as avian diversity) on tourism revenue can be modeled.

**Costs of Avian Species Diversity.** Our first step in modeling the costs of avian biodiversity was to model land values on the basis of relationships between land-use categories and biophysical/economic variables. Data on land-use categories were obtained from two Landsat satellite images (Earth Satellite Corp., Rockville, MD) of the Mabira Forest and the surrounding area. The first of these images was taken in December 1986 [Thematic Mapper (TM) sensor], and the second was taken in December 2001 [Enhanced Thematic Mapper (ETM) sensor]. We estimated the rate and spatial location of deforestation from 1986 to 2001 by digitizing land-use at a 1:50,000 scale from these two images. Land-use types were classified as intact forest, smallholder agriculture, and forest regeneration from pre-1986 deforestation. All three land-use classes were clearly differentiable on the basis of a real-color image by using TM/ETM sensor bands 1, 2, and 3 and a false-composite color image by using bands 3, 4, and 5. A geographic information system coverage of land-use from the National Biomass Project of the Uganda Forest Department, derived from SPOT satellite imagery (1989–1992), aerial photography (1995), and extensive ground truthing (1993–1995), facilitated the interpretation of the Landsat images. After digitizing polygons of the three land-use types, we converted the coverage into a grid of one-hectare cells ($100 \times 100$ m) and did not consider the regenerating forest class further.

We assumed that the annual economic rent $R_i$ of an agricultural plot of land $i$ is equivalent to the private benefits a farmer derives from agriculture ($P_iQ_i$) minus the cost of production ($C_iI_i$). Therefore, a forest plot will be converted to agricultural land when the benefits of conversion outweigh the costs, which is represented by the following equation: $R_i = P_iQ_i - C_iI_i$, $A_i = 1$ if $R_i > 0$, and $A_i = 0$ if $R_i < 0$, where $P$ are output prices, $Q$ are quantity of outputs, $C$ are input prices, and $I$ are quantity of inputs. $A_i = 1$ when a plot is converted to agriculture (deforested), and $A_i = 0$ when left as standing forest. Because spatially referenced data for the above parameters were unavailable, we assumed $Q$ to be a function of biophysical variables that influence crop productivity and $P$ and $C$ to be functions of transportation costs. Furthermore, we assumed that population density affects $P$, $C$, $Q$, and $I$ through the size of the labor pool, the size of output markets, and the demand for agricultural land (8–10). $Q$ was modeled as a function of the slope, elevation, and soil type, the distance to the nearest river, and the distance to the geographical center of the forest. Transportation costs were a function of distances to the nearest town, market town, road, paved road, and nearest agricultural plot.

We assumed that standing forest had no other economic benefit aside from providing habitat for forest birds and, therefore, that there were no additional costs to clearing forest other than those we modeled. Because we defined two states for each plot, the probability $A_i$ that a plot has been deforested can be estimated by the following logistic regression model that includes the variables described above: $\text{logit}[A_i\ (1, 0)] = \exp(BX_i + B_0)$, where logit refers to the log odds transformation of $A_i$, $B$ is a vector of coefficients on the $X$ explanatory variables, and $B_0$ is an intercept term. The resultant probabilities of deforestation for spatially referenced plots are relative measures of the net economic rent per hectare (i.e., plots having a greater probability of deforestation have relatively higher agricultural profitability than those having lower probabilities of deforestation).

To move to an absolute measure of rent (and hence a measure of the cost of supplying avian habitat), we multiplied relative rents by the value of an average hectare of land in the Mabira Forest area ($114.00). The figure of $114.00 was arrived at by calculating the product of the relative abundance, productivity, and farm-gate price of seven main crops grown by farmers in areas surrounding the Mabira Forest Reserve (14) and subtracting the average input costs associated with each crop (15). We assumed that the rates of return for each main crop, which were calculated by using Uganda-wide data from ref. 15, are representative of the input costs in the Mabira Forest region. See ref. 16 for a more detailed investigation of this method at a different study site.

The methods described above resulted in a spatial map of land values per hectare at the Mabira Forest Reserve. By assuming that conservation efforts would proceed by protecting the cheapest land plots first, we calculated a total cost curve for the provision of the forest area by summing sequentially the lowest to the highest valued 1-hectare plots. Our "conservation currency" was bird species, however, not forest area. We therefore used data on the richness of bird species and forest area from 66 forests in Uganda (17) to construct a species–area relationship using linear regression methods. We obtained the following species–area regression from this analysis: $\ln(\text{species}) = 2.42 + 0.46 \cdot \ln(\text{area})$, $n = 59$, $R_2 = 0.48$, $P < 0.0001$. By then substituting bird species for area in the regression equation, this model was used to convert the total conservation cost curve from a denomination of forest area to one of bird species. Note that this simple species–area relationship ignores potential effects of forest heterogeneity on species richness.

## Results

Our model of rainforest reserve selection showed that the number of bird species likely to be seen at a reserve was a strong predictor of tourist visitation, second only to wildlife viewing in its significance (Table 1, in bold). Because raising entrance fees to protected areas will result in fewer tourist visits but more revenue (our choice model suggests demand is inelastic), we simulated fee increases and calculated associated changes in revenue levels to determine the entrance fee at which the maximum amount of revenue is delivered to the forest reserve (12). An entrance fee of ≈$47.00 (all monetary values have been converted to U.S. dollars, year 2001) was found to maximize tourism revenue. In contrast, international tourists and foreign residents of Uganda are currently charged <$5.00 to visit the Mabira Forest Reserve. This dramatic undervaluation of the willingness to pay of tourist visitors is consistent with results from other tropical areas (18, 19) and suggests much room for improvement in entrance fee policy. Increasing entrance fees would not only provide greater amounts of revenue for protected area management, but also by concomitantly reducing tourist numbers, it may help alleviate some of the negative ecological and cultural effects of international tourism (20, 21).

Economically valuable land for agriculture was concentrated mostly in the southwestern portion of the Mabira Forest Reserve and along the southern margins (Fig. 1). Much of the interior of the reserve was of little economic value, however, which suggests

**Table 1. Parameter means for random parameters logit regression model of international tourist and foreign resident visitation rates to forest reserves in Uganda**

| Attribute | Coefficient (SE) | *t* value |
|---|---|---|
| **ln(Birds)** | **0.5216 (0.0301)** | **17.3** |
| Entrance fee | −0.0295 (0.0021) | −14.2 |
| Travel time | 0.5306 (0.0719) | 7.4 |
| (Travel time)$^2$ | −0.0504 (0.0176) | −8.2 |
| Part of tour | −0.0364 (0.0328) | −1.9 |
| Tents | −0.0657 (0.0348) | −1.9 |
| Cabin | 0.3480 (0.0328) | 10.6 |
| Luxury lodge | 0.2551 (0.0326) | 7.8 |
| Primary forest | −0.0378 (0.0321) | −1.2 |
| Secondary forest | −0.1920 (0.0341) | −5.6 |
| Both forest types | 0.1798 (0.0315) | 5.7 |
| Chance of wildlife | 0.7143 (0.0199) | 35.8 |
| Log-likelihood | −11549.4 | |
| Pseudo $R^2$ | 0.388 | |
| No. of observations | 13,623 | |

Bold shows that the number of bird species likely to be seen at a reserve was a strong predictor of tourist visitation, second only to wildlife viewing in its significance.

that a biologically valuable core area could be preserved at a relatively low cost. Most of the predictor variables for deforestation were significant and in the expected direction; only distance to the town of Lugazi and distance to the nearest river were not significant predictors at the 5% level (Table 2). Both measures of market connectedness (the distance to the nearest town/village, to Jinja market town, and to the nearest road of any kind) and biophysical features (elevation, slope, and proximity to rivers) were important predictors of deforestation (see ref. 22 for more details).

Using our model of rainforest reserve selection to calculate the total benefit curve and the methods described above to calculate the total cost curve, we fixed the entrance fee and the number of tourists who visited the reserve at 2001 levels and simulated total revenue as the number of bird species seen increased. We assumed that the number of bird species likely to be seen was proportional to the number of species present (see ref. 12 for discussion). The resulting curves for the total opportunity cost and the total benefit of avian biodiversity at the Mabira Forest Reserve intersect at 114 species, at which point further increases in the number of bird species conserved can no longer be funded solely through redistribution of tourism receipts to local residents (Fig. 2, thick line). Because the forest is currently estimated to contain 143 forest bird species, this market-based model of avian biodiversity predicts a "surplus" of 29 bird species that cannot be conserved by market conditions alone. To conserve the full complement of forest bird species requires total revenue of $196,000.00, a 20-fold increase over the $9,500.00 in revenue that current market conditions provide. Although this cost–benefit analysis shows that a market-based conservation scheme would fail to conserve all bird species, such conservation would not result in a wholesale depletion of the reserve's avifauna. Rather this market-based scheme would provide enough compensation to offset conservation costs for a large portion of avian biodiversity. Note, however, that the analysis treats species as independent units and ignores the complex interactions of predation, competition, and other ecological mechanisms that may link individual species with one another. Incorporating these interactions could change the shape of the bird diversity supply curve.

Biophysical and economic conditions at the reserve are dynamic; therefore, we used our regression models to simulate additional scenarios of market-based conservation (Fig. 2). A "growth" scenario, using the current population growth rate (3.4%) and the location of current agricultural boundaries around the reserve, resulted in the total cost curve TC′. A scenario with entrance fees raised to revenue-maximizing levels resulted in total benefits curve TB′. Relative to the change in total benefits, the difference between total cost curves TC and

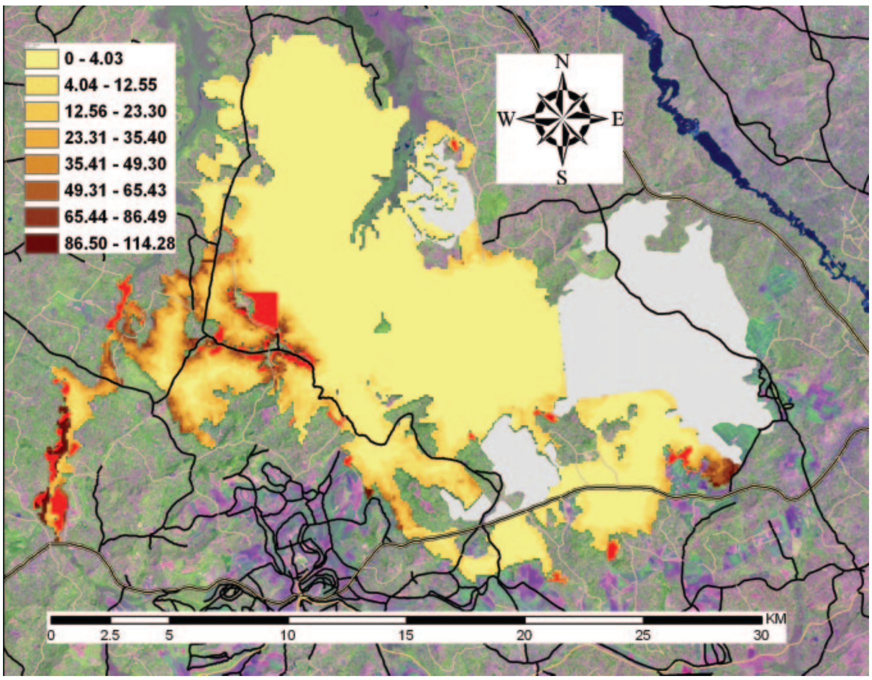


**Fig. 1.** Land rents for Mabira Forest Reserve in 2001. Rents have been converted to U.S. dollars. Darker areas indicate higher land rents, which are mostly in the western part of the reserve. Areas in red were deforested between 1986 and 2001. The local road network is also shown, as well as a 2001 Landsat image of the surrounding agricultural landscape. Areas in gray were deforested before 1986 and are now regenerating.

**Table 2. Logistic regression results for deforestation at the Mabira Forest Reserve from 1986 to 2001**

| Variable | Coefficient | SE | $\chi^2$ | *P* value | Standardized *B* |
|---|---|---|---|---|---|
| Intercept | 21.1 | 10.4 | 4.10 | 0.043 | |
| road_dist | −0.00062 | 0.00028 | 4.97 | 0.026 | −0.39 |
| hwy_dist | 0.00021 | 0.000095 | 4.78 | 0.029 | 0.40 |
| urban_dist | −0.0004 | 0.000099 | 16.4 | <0.0001 | −0.54 |
| jinja_dist | −0.00026 | 0.000094 | 7.41 | 0.0065 | −0.94 |
| lugazi_dist | −0.00007 | 0.00012 | 0.36 | 0.55 | −0.15 |
| river_dist | 0.0010 | 0.00064 | 2.39 | 0.12 | 0.17 |
| Slope | 0.040 | 0.0143 | 8.04 | 0.0046 | 0.25 |
| elev | −0.0049 | 0.0023 | 4.53 | 0.033 | −0.42 |
| bound_dist | −0.0038 | 0.00069 | 31.0 | <0.0001 | −1.46 |
| centroid_dist | 0.00030 | 0.00013 | 5.70 | 0.017 | 0.65 |
| ka | 0.73 | 0.38 | 3.73 | 0.053 | |
| kb | 1.09 | 0.52 | 4.31 | 0.038 | |
| popdens91 | 0.010 | 0.0038 | 7.59 | 0.0059 | 0.28 |

$n$ = 654; % deviance explained = 43%; −2 log likelihood = 262.9; likelihood ratio $\chi^2$ = 262.9, df = 13, $P <$ 0.00001. road_dist, distance to the nearest road; hwy_dist, distance to the nearest highway; urban_dist, distance to the nearest urban center; jinja_dist, distance to the town of Jinja; lugazi_dist, distance to the town of Lugazi; river_dist, distance to the nearest river; slope, slope in degrees; elev, elevation in feet; bound_dist, distance to nearest administrative boundary of Mabira Forest Reserve; centroid_dist, distance to the geographical center of the forest; ka, dummy variable for undifferentiated ferrisol; kb, dummy variable for crystalline basic ferrisol; popdens91, human population density in 1991.

TC′ was slight (note, however, that increases in human migration and demand for resources could increase the agricultural value of land, and hence the cost curve, more than this scenario predicts). In contrast, raising entrance fees to the revenue-maximizing level would result in the conservation of 131 forest bird species or ≈90% of the forest species found at the reserve. As a benchmark, the total cost curve M, which represents the total cost of conservation where each hectare of the reserve is valued equally at $114.00, is also shown. The intersection of current cost and benefit curves is at five species, a level that would represent a catastrophic loss of forest species. This latter result shows that agricultural homogenization has not only resulted in a landscape mostly devoid of forest birds (23) but also made ecological rehabilitation and conservation prohibitively expensive in this area.

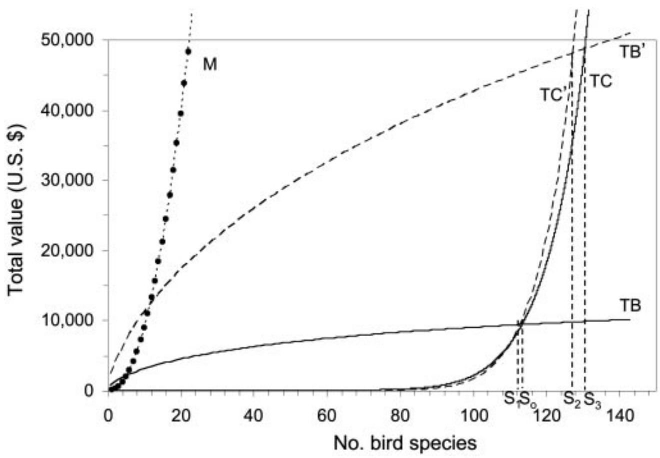


**Fig. 2.** Total cost–revenue curves under various scenarios for avian biodiversity conservation at the Mabira Forest Reserve. TC, the current total cost curve; TB, the current total revenue curve; TC′, the total cost curve under the growth scenario; TB′, the total revenue curve with optimal entrance fees; $S_0$, the current equilibrium supply of forest bird species; $S_1$, the equilibrium supply under the least favorable scenario; $S_2$, the equilibrium supply with changes in the total cost and total revenue curves; $S_3$, the equilibrium supply under the most optimistic scenario; M, the total cost curve with land values held constant ($114.00 per hectare).

## Discussion

Although conventional wisdom suggests that biodiversity conservation is often a noncompetitive form of land use and, therefore, requires subsidizing, our results suggest that the economic benefits derived from avian biodiversity could protect 80–90% of a tropical forest reserve's bird species. Although the cost of conserving the remaining 10–20% is very high, preservation of up to 90% of the forest's avifauna through redistribution of ecotourism revenue would be a remarkable achievement, given the high pressure on forest resources in sub-Saharan Africa and the poverty level of local residents. We make a number of simplifying assumptions on both the ecological (e.g., species independence and the species–forest area relationship) and economic (e.g., preferences are accurately measured by the choice experiment approach) fronts to arrive at these conclusions; the conditions under which these assumptions are valid should be examined in future work.

The tangible economic demand of tourists for increasing levels of biodiversity is strong evidence that consumers may actually prefer higher numbers of species to lower numbers and, more critically, be willing to pay for it. This result has important implications for ecotourism and protected areas because areas rich in biodiversity may be able to charge more for visitation rights than less diverse areas and, hence, may provide a mechanism for funding conservation of highly speciose ecosystems. More research on other taxonomic groups is necessary to determine how general these preferences are.

Our results also indicate that if land values across the reserve were uniform at the current level of agricultural rents ($114.00 per hectare), market-based conservation would fail badly, with the forest habitat for almost the entire complement of forest species being converted to agriculture. Put another way, purchasing land to reforest agricultural areas to support forest bird communities would be economically infeasible. This difficulty suggests that a "window of opportunity" for *in situ* conservation exists in the Mabira Forest area and that preserving existing forest now will be far cheaper (and probably more ecologically

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meaningful) than attempting to rehabilitate degraded ecosystems in the future.

Finally, our estimates of the economic benefits of species diversity are similar in magnitude to those found for related ecosystem goods and services at local levels (24, 25) and much lower than estimates of global values such as carbon sequestration/storage and existence values for unique areas (26). More importantly, the ability to transfer benefits that accrue globally to residents of developing countries, where much of the world's biodiversity lies, has proven difficult, as problems in implementing international environmental agreements such as the Convention on Biological Diversity and Kyoto Protocol have illustrated. Therefore, the policy implications of global-scale values will probably remain limited until international benefit-transfer agreements are reliably implemented. In the interim, we suggest that "biodiversity markets" involving international tourists and local residents may offer a promising complement to existing conservation approaches in at least some areas of the tropics.

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