Predictable waves of sequential forest degradation and biodiversity loss spreading from an African city

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Tropical forest degradation emits carbon at a rate of ~0.5 Pg·y^{-1}, reduces biodiversity, and facilitates forest clearance. Understanding degradation drivers and patterns is therefore crucial to managing forests to mitigate climate change and reduce biodiversity loss. Putative patterns of degradation affecting forest stocks, carbon, and biodiversity have variously been described previously, but these have not been quantitatively assessed together or tested systematically. Economic theory predicts a systematic allocation of land to its highest use value in response to distance from centers of demand. We tested this theory to see if forest exploitation would expand through time and space as concentric waves, with each wave targeting lower value products. We used forest data along a transect from 10 to 220 km from Dar es Salaam (DES), Tanzania, collected at two points in time (1991 and 2005). Our predictions were confirmed: high-value logging expanded 9 km·y^{-1}, and an inner wave of lower value charcoal production 2 km·y^{-1}. This resource utilization is shown to reduce the public goods of carbon storage and species richness, which significantly increased with each kilometer from DES [carbon, 0.2 Mg·ha^{-1}; 0.1 species per sample area (0.4 ha)]. Our study suggests that tropical forest degradation can be modeled and predicted, with its attendant loss of some public goods. In sub-Saharan Africa, an area experiencing the highest rate of urban migration worldwide, coupled with a high dependence on forest-based resources, predicting the spatiotemporal patterns of degradation can inform policies designed to extract resources without unsustainably reducing carbon storage and biodiversity.

biodiversity conservation | carbon emissions | reducing emissions from deforestation and forest degradation | sustainability | tropical forest degradation

Approximately one-third of remaining tropical forest has been degraded through selective logging (1), a practice that adds carbon at a rate of ~0.5 Pg·y^{-1} to the atmosphere (2). Forest degradation is broadly defined as the long-term reduction of the overall potential supply of goods and services, including carbon storage, wood production, and biodiversity conservation. The impacts of individual forms of tropical forest degradation are understood in outline; for example, industrial logging reduces carbon stocks (3–5) and changes biodiversity, often reducing it (5–8). Deforestation and degradation patterns have been related to road access, road density, topography, and biophysical characteristics such as soil fertility (9–12). Yet, forest degradation dynamics driven by the sequential exploitation of a series of goods of various qualities, with attendant losses in public goods, have not been tested systematically. This knowledge is critical if optimal policies are to be implemented to manage forests to enhance delivery of public goods such as climate regulation and biodiversity retention. In particular, the policy instrument entitled "Reducing Emissions from Deforestation and forest Degradation" (REDD), which is currently being negotiated within the United Nations Framework Convention on Climate Change (2, 13), focuses overwhelmingly on deforestation. Forest degradation is receiving less attention because of difficulties in monitoring degradation as well as understanding its drivers, leading to uncertainty in formulating possible policy interventions (14–16).

Economic theory (von Thünen model) (17) provides a general model to predict patterns of forest degradation. This asserts that land is allocated to the activity that provides the maximum net value ("rent" in economic terms), which, in turn, is the largest gain from the land minus the costs incurred to obtain that gain (17–19). This translates to a prediction that waves of forest degradation will emanate from major demand centers and expand into nearby forested areas, targeting resources in sequence, starting from those of highest value (19). Such a sequence of demand, linked to resource utilization, has been demonstrated for unmanaged fisheries, where it is termed "fishing down the food web" (20–22), but has not been shown for the exploitation of differently valued tropical forest products, nor has it been linked to impacts of forest degradation on public good provision. Here, we test economic resource use theory predictions against ground observations of forest degradation along a 210-km transect running south from the demand center Dar es Salaam (DES), Tanzania, over a period of 14 years (1991–2005).

Results

Changes Between 1991 and 2005. We found three distinct degradation waves emanating from DES in accordance with the von Thünen model (Fig. 1 and Tables S1 and S2). In 1991, the innermost degradation wave, which comprised the extraction of low-value wood for charcoal production, extended up to 50 km from DES and was dominant within a 20-km distance from the city. This largely provided cooking fuel for DES residents. A second degradation wave extracted low- and medium-value timber for local and DES consumption in construction and for export. This middle wave extended 20–100 km from DES and was dominant at distances of 20–50 km from DES. Beyond 50 km, an

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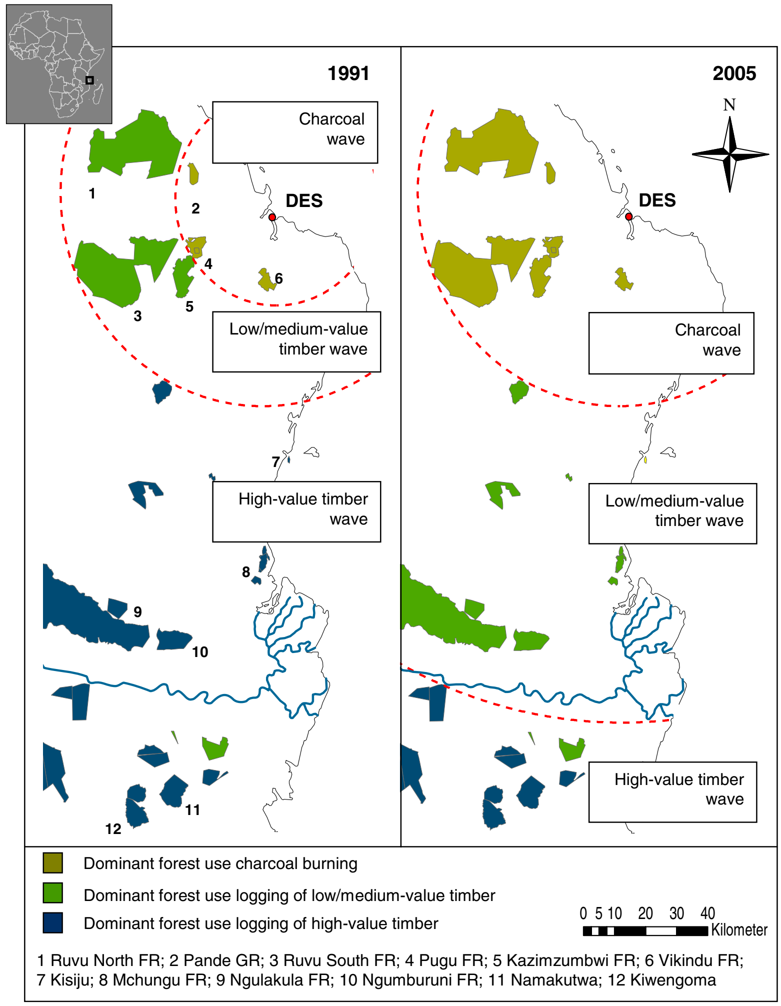

Fig. 1. Map of the degradation waves of dominant forest use in the study area in 1991 and 2005. The numbered forests were those used in the study (with the exception of no. 9 because of dangerous field conditions). Charcoal burning has moved a road distance of 30 km from DES in this time period, and medium-value timber logging has moved 160 km. The outer boundary of high-value timber logging was already outside the study area in 1991. Muhoro and Nyamwagne, the two forests south of the Rufiji River (green), do not follow the general degradation pattern because they are plantation forests.

outermost wave extracted high-value timber for DES consumption in construction and for export.

The order of concentric degradation waves remained the same in 2005 (Fig. 1 and Tables S1 and S2), but each had expanded significantly. Charcoal production had become the dominant use up to 50 km from DES but extended to 170 km from DES, with the outer boundary of this wave having moved 120 km since 1991, and the outer boundary of the area where charcoal production is the dominant use having moved 30 km (2 km·y^{-1}). Charcoal production sites (pits or earth mound kilns, mean size 8 × 8 m) covered ~8% of the forest area within a 20-km distance of DES. At a distance of 170 km, they covered 0.3%, and beyond 210 km, no charcoal production was found (Fig. 2*A*). The sharp drop in charcoal production sites at an increasing distance from DES is likely to have been driven by the cost of transporting the charcoal to DES, making the marginal gain from production small to negative at greater distances from the city. However, as nearby forests are exhausted, charcoal prices increase and charcoal production further from DES becomes more attractive, as shown by DES charcoal prices, which increased from US $0.18 kg^{-1} in 1997 to US $0.27 kg^{-1} in 2007 (23, 24) (US $ 2009, calculated using a gross domestic product deflator).

In 2005, medium-value timber logging [round wood export value up to US $250 per cubic meter at the time (25)] dominated at 50–170 km from DES, and the outer bound of this second wave had moved 110 km, reaching the forests south of the Rufiji River (Fig. 1). High-value timber logging [round wood export value ~US $330 per cubic meter at the time (25)] started at 170 km (the inner boundary of high-value timber logging wave having moved ~9 km·y^{-1}), was dominant starting from 210 km and continued to at least 220 km (the maximum extent of our sampling from DES) (Fig. 1). Timber logging removed tree species in sequence. Two high-value timber species [*Milicia excelsa* (Welw.) C. C. Berg and *Brachylaena huillensis* O. Hoffm.] have been entirely depleted, and stocks of two others [*Pterocarpus angolensis* D.C. and *Khaya anthotheca* (Welw.) C.D.C.] have almost been exhausted (Table S2). Mean timber value per tree stump increased US $0.1 per kilometer from DES (US $ in the year 2005) (Fig. 2*B*). Furthermore, the proportion of trees logged below their legal minimum harvestable diameter dropped from 100% at ≤20 km from DES to 50% at distances ≥200 km. The observed increase in both mean harvested tree size and mean timber value with increasing distance from DES and the high proportion of undersized harvested trees far from DES are likely to be indicative of unsustainable harvesting.

Thus, in line with resource use theory, forest degradation waves are expanding rapidly from DES; the charcoal burning and medium-value timber "wave fronts" have expanded by 120 and 110

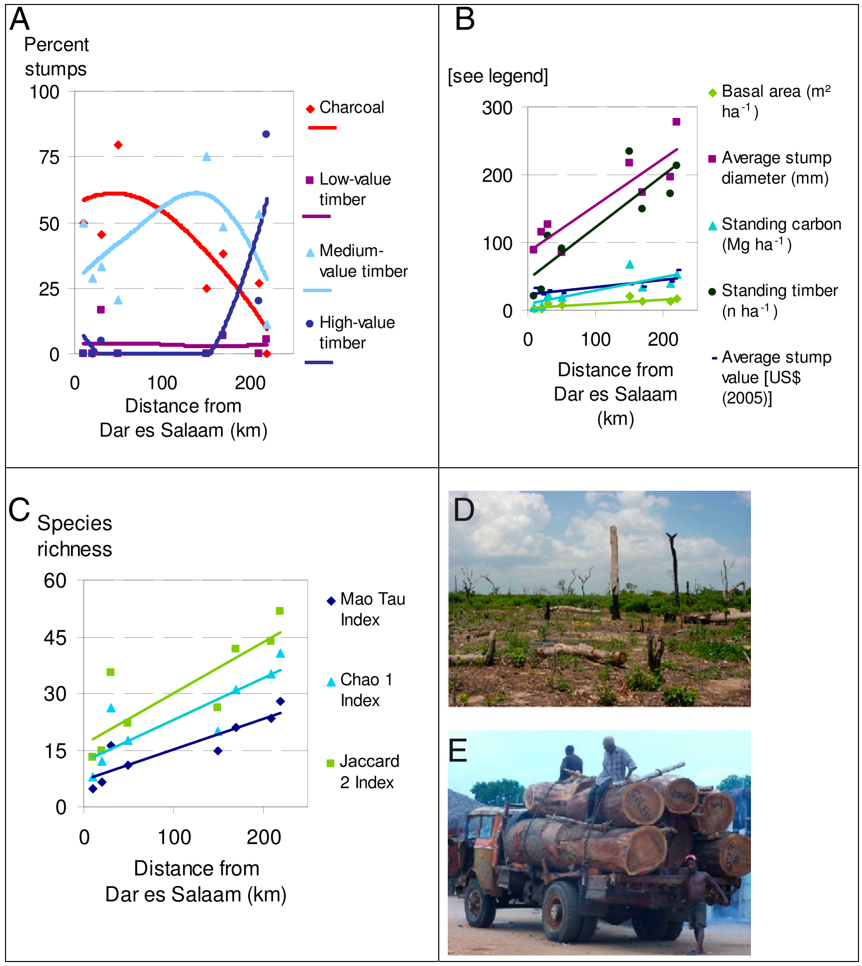

Fig. 2. Patterns in forest use and condition at increasing distance from DES. (*A*) Forest use at increasing distance from DES, quantified as the numbers of stumps of trees used for charcoal burning ($R^2 = 0.73$) or as low-, medium-, or high-value timber ($R^2 = 0.01$, 0.41, and 0.74, respectively), presented as interpolated lines using a Loess function (span = 2). (*B*) Forest condition with distance from DES measured using forest structure (basal area, average stump diameter, standing timber, and above-ground live tree or standing carbon) and economic (average stump value) variables. (*C*) Estimated tree species richness at differing distances from DES using observed species richness (Mao Tau Index) and total species richness (Chao 1 and Jaccard 2 Indices) estimators, each randomized 50 times over eight transect sections (total sample area = 0.4 ha). (*D*) Kisiju forest at a distance of 90 km from DES has almost been destroyed since 1991, and all woody resources have been converted to charcoal. (*E*) Illegally logged high-value timber harvested at a distance of 200 km from DES. For the production of *A*, *B*, and *C*, $n = 8$ independent data points (forests), respectively.

km, respectively, between 1991 and 2005. The inner boundary of the high-value timber logging wave expanded 120 km, close to the edge of the study area. Multiple regression models showed that of the seven (eight in the case of species diversity) tested factors that may predict levels of degradation in the 10 forests studied in 2005 (Table S3), distance from DES, with one exception, was the sole significant predictor and explained between 60 and 80% of variation (Table S4). Only the average stump value was better explained by the accessibility of the forests to lorries, which may indicate that accessibility is a stronger factor in high-value timber logging than distance; however, the two variables were also strongly inversely correlated (Pearson correlation = −0.72; Table S3). Importantly, we found no relationship between the level of degradation within a forest and management policies or institutions governing that forest (Table S4).

Consequences of Forest Degradation. Moving beyond a simple von Thünen model, we couple the extraction results with the loss of public goods (carbon storage and biodiversity), an inherent trade-off. The systematic depletion of forest resources resulted in declines in carbon storage and biodiversity (Fig. 2 *B*–*D*). In 2005, within a 20-km radius of DES, forests had 25 trees per hectare (bootstrapped SE = ±3.46), compared with 99 trees per hectare (bootstrapped SE = ±6.35) within a radius of >20 and ≤50 km and 193 trees per hectare (bootstrapped SE = ±15.11) at a radius ≥200 km (Fig. 2*B*). Thus, at ≤50 km from DES, forest canopies were no longer closed, and at ≤20 km, the forests were practically removed. Generally, between 1991 and 2005, there were major declines in tree density (trees per hectare), above-ground carbon ($Mg \cdot ha^{-1}$), and mean tree diameter in a given forest, further illustrating how forest conditions have deteriorated (Figs. S1 and S2).

Estimates of total species richness increased from 8–13 tree species (depending on the index used: Chao 1 Index or Jaccard 2 Index) per sample area (0.4 ha) in the forest closest to DES to 41–52 tree species in the forest furthest from DES (Fig. 2*C*). On average, forests had 0.1 more species per sample area with each kilometer from DES. Similarly, above-ground carbon storage in live trees increased from 4 $Mg \cdot ha^{-1}$ (bootstrapped SE = ±2.84) in the forest nearest to DES to 52 $Mg \cdot ha^{-1}$ (bootstrapped SE = ±4.99) in the forest furthest from DES (Fig. 2*B*), increasing, on average, by 0.2 $Mg \cdot ha^{-1}$ with each kilometer from DES. A first-order estimate of the above-ground carbon lost from the forests in the study area (258,000 ha) between 1991 and 2005 is ~0.2 $Tg \cdot y^{-1}$, equivalent to over a quarter of the annual emissions of carbon from fossil fuel use in Tanzania over the same period (26).

Discussion

The progressive decline in the value of harvested woody resources at a given distance from DES over the past decade and increasing distance of transport for equivalent-value products over time suggest a likely unsustainable "logging down the profit margin" scenario akin to the sequential "fishing down the food web" resource utilization patterns seen in unmanaged marine habitats (21). At current levels of demand and continued outward expansion of the exploitation waves, we predict that there will be no high-value timber species remaining in Tanzanian coastal forests up to 220 km from DES in 2010 (Fig. 2*E*) and up to the southern Tanzanian border within 37 y.* A recently opened bridge across the Ruvuma River at the southern Tanzanian border is likely to facilitate encroachment of the degradation wave into Mozambique. Charcoal burning is predicted to continue to expand in line with urban demand and a lack of affordable alternatives, and the inner wave of charcoal extraction is very likely to continue traveling outward (27). It is probable that these trends will be accompanied by further reductions in public goods such as carbon storage, biodiversity retention, and supply of water. With raw material exports to generate foreign currency revenue for sub-Saharan governments, alongside 73% of the urban population across sub-Saharan Africa [currently experiencing the world's fastest rate of urbanization (28)] reliant on biomass fuels, mainly charcoal (29), the implications derived from our analysis extend beyond Tanzania. An ability to predict the future spatiotemporal dynamics of forest degradation across sub-Saharan Africa may provide a vital tool for targeted policy interventions for biodiversity preservation, climate change mitigation, and human development, particularly within the context of REDD.

To date, modest capacity in the forestry sector, typical of the vast majority of African countries (30), and high demand for natural resources have meant that governance in the forest reserves analyzed in this study has been weak (25). This is despite a strict forest resource extraction licensing system clearly stated in Tanzania's Forest Act (no. 14 of 2002) and a ban on roundwood exports (Forest Regulations of 2004, Government Notice no. 153). For example, in 2005, records from China show it imported 10 times more timber from Tanzania than Tanzania's total declared exports, with the Tanzanian government losing estimated revenue of US $58 million (25). Consequently, degradation patterns from 1991 to 2005 followed the predictions of economic resource use theory, irrespective of the forests' management or protected area type. However, the only forest in 1991 in our study area that did not have legal reserve status, Kisiju, had been cleared entirely by 2005, a typical fate of nongazetted forests in Tanzania (31), showing that although government restrictions do not currently prevent degradation, they can successfully prevent complete deforestation. It is also important to note that the ratio of management types to the number of forests in this study was high. It is therefore possible that we have underestimated the effects of particular management types on reducing degradation. For example, another study focusing mostly on less accessible mountain areas of Tanzania suggests that participatory forest management (PFM) has a positive effect on forest condition (32). Furthermore, as is common across sub-Saharan Africa, all the forests in this study were government owned, whereas private or collective ownership or stronger governance could alter the balance of economic incentives, and therefore lead to different dynamic patterns of degradation (19).

Our Tanzania study provides three insights of importance to the debate on using payments to ensure that the decisions of economic actors affecting a given piece of land favor carbon storage and high biodiversity rather than leading to net carbon release to the atmosphere and reduced biodiversity. First, deforestation and degradation waves should be represented in state-of-the-art models of the "opportunity costs" of avoiding deforestation and degradation (i.e., the foregone economic benefits from alternative land uses) if these models are to depict the complex real-world spatiotemporal patterns of carbon or biodiversity losses from forests. This may allow discrimination between models that predict 3-fold differences in the costs of reducing deforestation by 10% by 2030 (33) and would help to reduce the uncertainty associated with the costs of post-Kyoto REDD schemes proposed as an important mechanism within the United Nations Framework Convention on Climate Change to mitigate carbon dioxide emissions through conserving tropical forests (13). Second, carbon fluxes from degradation are significant, suggesting that mitigating degradation, rather than merely avoiding deforestation, should feature more strongly in ecosystem service payment schemes such as those proposed in REDD. Third, models of degradation dynamics may enable the identification of areas that are differentially vulnerable to carbon loss, enabling spatially targeted REDD policies and incentives to be applied to prevent the relevant type of degradation activity (e.g., extraction of charcoal vs. low-value timber vs. high-value timber). Addressing these issues is made even more urgent because achieving carbon dioxide emission reductions in this way is time-limited and economically irreversible: once degradation has occurred, it cannot be avoided in the future.

Materials and Methods

Study Area. DES is a rapidly expanding city of some 3–4 million people on the Indian Ocean coast of East Africa. Forest product demand is increasing sharply to meet expanding markets overseas (particularly China) as well as a rising domestic demand for building materials and cooking fuel (34, 35). This pattern of increasing consumption, combined with weak resource management practices, is typical of other tropical regions (36–38), making the forests around DES a potentially valuable model system for testing forest degradation theory. The East African coastal forests, thought to have once formed a belt along the East African coast from southern Somalia to northern Mozambique, now remain as a series of highly fragmented forest patches covering less than 10% of their climatically suitable habitat (31). Because of their exceptionally high levels of palaeo-endemism, multiple conservation priority schemes have identified them as one of the most important areas for biodiversity conservation worldwide (39–41).

Field Data Collection. In 1990–1994 (median of January 1, 1991), 11 forests were sampled in coastal Tanzania, noting the type of extractive activities that were occurring in each forest (42). In each of the forests, one to three plots of different size ranging from 0.025 to 0.25 ha were located at random in areas stratified according to the type of forest vegetation (n = 45 plots, total area sampled = 4 ha), with all trees with a diameter ≥100 mm at reference height [1.3 m along the stem or above buttresses (drh)] measured and identified to species. In 2004–2005 (median of January 7, 2005), eight of these forests were resampled and two additional forests were surveyed. The forests were chosen to span a distance range of 10–220 km from DES and to have similar climate, topography, soils, and socioeconomic conditions (Fig. S3 and Table S5). Within each forest, we randomly located transects (10 × 500–1,500 m in length) to sample 0.1% of the area of each of the 10 forests. Within each transect, all trees and stumps ≥50 mm drh were recorded as alive, naturally dead, or cut and were measured and identified to species (when possible) (n = 12,018). Again, we noted the types of extractive activities occurring, including quantifying the number of charcoal production pits. All survey data are provided for the purpose of replicating and building on this work: dataset I for for the 2005 survey and dataset II for the 1991 surveys are presented in Datasets S1 and S2.

Calculation of Variables for the Analysis (2005 Data Only). *Timber value.* Trees qualifying as timber were defined as all trees with straight stems at least 3 m in length and ≥150 mm drh. We categorized each stem as "high-value,"

*The inner wave boundary was at 170 km in 2005 and moves 9 km·y^{-1}. The road distance between DES and the southern Tanzanian border is ~500 km.

"medium-value," or "low-value" timber or as "suitable only for charcoal production" based on published use data (43, 44) and calculated the density of suitable timber trees and the average drh and basal area sum of all trees. ***Value of extracted timber.*** For each forest, we calculated the average stump diameter and the average "stump value" based on the mean royalties that the Tanzanian Government collects for felling the respective species (US $ in the year 2005).

Carbon stocks. Above-ground carbon stocks were computed using the Dry Forest allometric equation of Chave et al. (45). This computes the carbon stored in individual trees using drh and the wood specific gravity of each stem. Wood specific gravity was taken from a global database (46). When wood specific gravity data were not available for a species, genus-level values were used (47).

Species diversity. Three area-standardized species richness estimates were calculated (Mao Tau Index, Chao 1 Index, and Jaccard 2 Index) for all trees ≥150 mm drh, each computed over a subsample of eight plots (corresponding to a total of 0.4 ha) with 50 iterations, using EstimateS (48). Species richness standardized by area is sometimes referred to as "species density" (49) as opposed to species richness standardized by number of individuals.

Forest Use Changes Between 1991 and 2005. The estimate of total carbon loss in the DES and Pwani regions in Tanzania was calculated as follows. The dominant extractive activity (charcoal burning, medium-value timber logging, and high-value timber logging) was established for all forests ($n = 33$) in 1991 and 2005 (degradation stages; see dataset I in Table S1). For forests for which no data were available, we estimated the degradation stage based on the degradation wave predictions established in this study verified against expert opinion. The loss of carbon associated with the transition from one degradation stage to another (e.g., from medium-value timber logging to charcoal burning) was calculated as the average difference in carbon stored among forests in these different degradation stages in 2005. The rationale for basing the rates of carbon loss on spatial data in 2005, instead of on temporal changes since 1991, is the greater data availability for 2005. Total carbon stored in the area in 1991 and 2005 was computed as the sum of the products of each forest's size (hectares) and the average amount of carbon stored per hectare in a forest of that particular degradation stage. Given that forests may have remained in the same degradation stage but still have lost considerable amounts of carbon, our estimate is likely to be conservative.

Modeling Spatial Degradation Patterns in 2005. We fitted linear regression models for each of eight dependent variables [average stump value (US $ 2005); average stump diameter (millimeters); standing timber ($n \cdot ha^{-1}$); average basal area ($m^2 \cdot ha^{-1}$); standing carbon ($Mg \cdot ha^{-1}$); and Mao Tau, Chao 1, and Jaccard 2 Indices] with seven predictor variables representative of economic rent: distance from DES (kilometers) and distance from the main DES road (kilometers) (Fig. S3), forest truck accessibility, population (population density in wards within a distance of 2 km from the focal forest reserve), management authority (Table S5), protected area type (Table S5), and presence or absence of PFM initiatives (32). For species diversity only, we also included the forest altitude range as an additional candidate predictor, because the range of available habitats is likely to influence the capacity for species co-occurrence. Distance from DES and distance from the main DES road were measured using a car odometer, and therefore represent road distances. Forest truck accessibility was measured as the sum of scores for three attributes: (*i*) main road to forest graded, (*ii*) roads within forest graded, and (*iii*) terrain easily accessible (i.e., no steep hills). If an attribute was fulfilled, a score of 1 was assigned; otherwise, a score of 0 was assigned. Figures for average population density by ward were based on Tanzania's National Bureau of Statistics estimates (50). Forest altitude range was derived from a high-resolution digital elevation model (Shuttle Radar Topography Mission version 4).

To establish significant predictors for the level of the forest degradation, we used a linear regression approach. Two predictor pairs, forest truck accessibility and distance from DES and forest truck accessibility and altitude range, were strongly collinear (Table S3), a situation that may lead to inflated SEs (51) and alter the significance levels of predictors and interaction terms (52). We therefore reduced the predictor set for each dependent variable to the strongest uncorrelated set according to the predictive power of variables in univariate tests (53). This elimination procedure left us with six (seven in the case of species diversity) candidate predictors (Table S3). Because this set was still impractically large, we used hierarchical partitioning (54) in each case to identify a smaller subset of the predictors most likely to play a critical role in determining the value of the dependent variable. In recognition of the fact that the parsimony approach may lead to the exclusion of driving variables (9), we also present all predictors and their levels of correlation in Table S3. Using the reduced set of predictors (Table S3), we then fitted linear regression models and, where the hierarchical partitioning indicated potentially high conjoint contributions, their interactions. Model validation procedures followed (55) and indicated no heterogeneity of variance and the presence of normality in the residuals. To find the minimal adequate model, we applied a backward stepwise selection using the partial *F* statistic. Model validation on the final model was then carried out once more. It is noted that the number of data points available for the analysis was small. However, the dataset contributing to each of these points was extensive. This, in conjunction with the strongly emerging pattern and its consistency across all tested variables, increases our confidence in the reliability of the analysis. All statistical analyses were performed using "R" statistical and programming environment version 2.9.2 (56) as well as its libraries "boot" (57) and "hierpart" (58). SEs are based on 1,000 nonparametric bootstrap replicates.

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