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Inequitable Gains and Losses from Conservation in a Global Biodiversity Hotspot

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Abstract

A billion rural people live near tropical forests. Urban populations need them for water, energy and timber. Global society benefits from climate regulation and knowledge embodied in tropical biodiversity. Ecosystem service valuations can incentivise conservation, but determining costs and benefits across multiple stakeholders and interacting services is complex and rarely attempted. We report on a 10-year study, unprecedented in detail and scope, to determine the monetary value implications of conserving forests and woodlands in Tanzania's Eastern Arc Mountains. Across plausible ranges of carbon price, agricultural yield and discount rate, conservation delivers net global benefits (+US$8.2B present value, 20-year central estimate). Crucially, however, net outcomes diverge widely across stakeholder groups. International stakeholders gain most from conservation (+US$10.1B), while local-rural communities bear substantial net costs (-US$1.9B), with greater inequities for more biologically important forests. Other Tanzanian stakeholders experience conflicting incentives: tourism, drinking water and climate regulation encourage conservation (+US$72M); logging, fuelwood and management costs encourage depletion (-US$148M). Substantial global investment in disaggregating and mitigating local costs (e.g., through boosting smallholder yields) is essential to equitably balance conservation and development objectives.

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1 Introduction

Human activities threaten many thousands of species with extinction (Ceballos et al. 2020). On land, proximate threats include agricultural expansion, especially into tropical forest, and direct exploitation through harvesting and logging (IPBES 2019). Resulting greenhouse gas emissions accelerate climate change, exacerbating impacts on biodiversity. Nature's decline affects human wellbeing through altered flows of ecosystem services, but these flows are not distributed evenly across society (Brauman et al. 2020). Particularly where people depend on direct access to, and conversion of, natural resources, there will be trade-offs between nature conservation, immediate resource needs, and supporting future or remote beneficiaries (Ruijs et al. 2017).

Ecosystem service valuations can help incentivise conservation (Posner et al. 2016; Dasgupta 2021), but comprehensive assessments of the economic consequences of contrasting land-use options, which fully account for ecosystem services and costs, are scarce anywhere, and particularly in biodiversity hotspots in low-income countries (Fisher and Christopher 2007; Seppelt et al. 2011; Bennett 2017; Costanza et al. 2017; Lautenbach et al. 2019). Most region-wide valuations are limited by failure to consider: (1) complex interactions among multiple services; (2) direct and indirect costs of alternative management regimes; and (3) distributions of values across different stakeholders (which we believe are crucial for devising equitable interventions (Mastrángelo et al. 2019; Mandle et al. 2021; Termansen et al. 2023)). Here we report the findings of a decade-long programme of work to meet all of these challenges through detailed quantification of six groups of services and three cost types (management, damage and opportunity) in Tanzania's Eastern Arc Mountains, covering 5 million ha of the Eastern Afromontane Biodiversity Hotspot (Platts et al. 2011).

The Eastern Arc harbours exceptional levels of species endemism (Rovero et al. 2014). This, combined with large-scale loss (> 70% in the last century; Willcock et al. 2016) and continued degradation of closed-canopy forest (Ahrends et al. 2021), renders these habitats extremely vulnerable to future species extinctions. Tanzania has made progress in slowing forest clearance and declaring forest sites as protected areas, but reserve managers mostly report that funding is insufficient to meet their conservation objectives (Green et al. 2012); and miombo woodland, which is largely unprotected, continues to be lost rapidly (> 50% since 1975; Green et al. 2013), mainly for fuelwood and agriculture (Doggart et al. 2020). Over two million people live in the Eastern Arc (Platts et al. 2011); restricting their activities may incur locally-borne opportunity costs and exacerbate rural poverty (Fisher et al. 2011; Green et al. 2018). In a country where a third of the rural population lives below the national poverty line, with one in 10 in extreme poverty (World Bank 2019), and with a majority of rural people dependent on subsistence agriculture, it is crucial to understand whether and for whom safeguarding biodiversity and sustainable service provision represents a net economic gain. Similar tensions are played out in ecosystems and societies worldwide (Halpern et al. 2013; Ickowitz et al. 2017; Poudyal et al. 2018). Divergent local, national and international consequences of habitat conservation must be recognised and measured if interventions are to reconcile conflicting incentives across stakeholder groups.

In this paper, to determine economic gains and losses from conserving all remaining Eastern Arc forest and woodland, we compare two hypothetical pathways: unprotected and depleted (the "depletion pathway"), in which (as an extreme manifestation of ongoing habitat losses, even inside reserves) protected and conserved areas are degazetted at the start of the pathway (Golden Kroner et al. 2019), leading to unrestricted use and progressive

conversion of all forests and woodland to smallholder agriculture (Doggart et al. 2020); and protected and conserved (the "conservation pathway"), in which (as an extreme manifestation of effective conservation) management expenditure is increased to ensure sustainable use and conservation of all remaining forests and woodlands. We developed ecosystem service models over a 10-year period (2007–2017) built on socioeconomic surveys of thousands of Tanzanians (farmers and non-timber forest product (NTFP) producers, pitsawyers, carpenters, timber and charcoal dealers, hoteliers and protected area managers), combined with agricultural and household census data, land-cover data and > 2000 vegetation plots and disturbance transects. To address spatial and biophysical interactions among services, indirect costs and substitution behaviours, we simulated stocks, costs and interacting service flows through time at 1-ha resolution. Using a natural capital accounting approach (United Nations 2017; Turner et al. 2019; Hein et al. 2020.; Luisetti et al. 2020), we indicate monetary gains and losses through time under each pathway, given the suite of costs and (dis)services considered (and not withstanding important caveats covering monetary valuation of ecosystem services; Adams 2014; Dasgupta 2021). We then take the difference in outcomes between pathways as an indicator of the net benefits of continued retention of the Eastern Arc's remaining woody vegetation (Bradbury et al. 2021). We break these results down further by stakeholder group (local, national, international), and by mountain block for spatial comparison with biological importance. While our detailed results are obviously specific to the Eastern Arc, we believe the tradeoffs we uncover – particularly between the local-scale agricultural benefits and global-level emissions and extinction costs of continued habitat conversion – are likely to be typical of very many contexts globally, and thus suggest our findings are of broad relevance.

2 Methods

2.1 Study Region

The Tanzanian Eastern Arc spans a series of isolated mountain blocks stretching 650 km from the Pare Mountains in the north to the Udzungwa Mountains in the south (Platts et al. 2011) (Fig. 1). Eastern Arc forests are among the oldest on Earth, with origins of some taxa suggested to pre-date the breakup of Pangaea (Dinesen et al. 1994). Over 4800 plant species have been recorded in the Eastern Arc – 17% of the total plant richness of tropical Africa in 0.24% of the land area – of which 536 are endemic. At least 136 vertebrate species are endemic, with others awaiting description (Rovero et al. 2014). Given its biological importance and history of habitat loss and degradation, the Eastern Arc is considered a 'hyper hot' priority for conservation (Brooks et al. 2002). Local and national governments, concerned initially with preventing erosion, then timber management and, more recently, nature conservation, have established an extensive protected area network that encompasses 77% of forests and 20% of woodlands in the Eastern Arc. These reserves help to conserve global biodiversity and sustain flows of ecosystem services.

2.2 Valuation Pathways

We constructed temporally-explicit pathways (conservation versus depletion), comparing two possible extremes of management expenditure, and contrasted the subsequent flow and distribution of ecosystem (dis)services over time. This approach aims to overcome
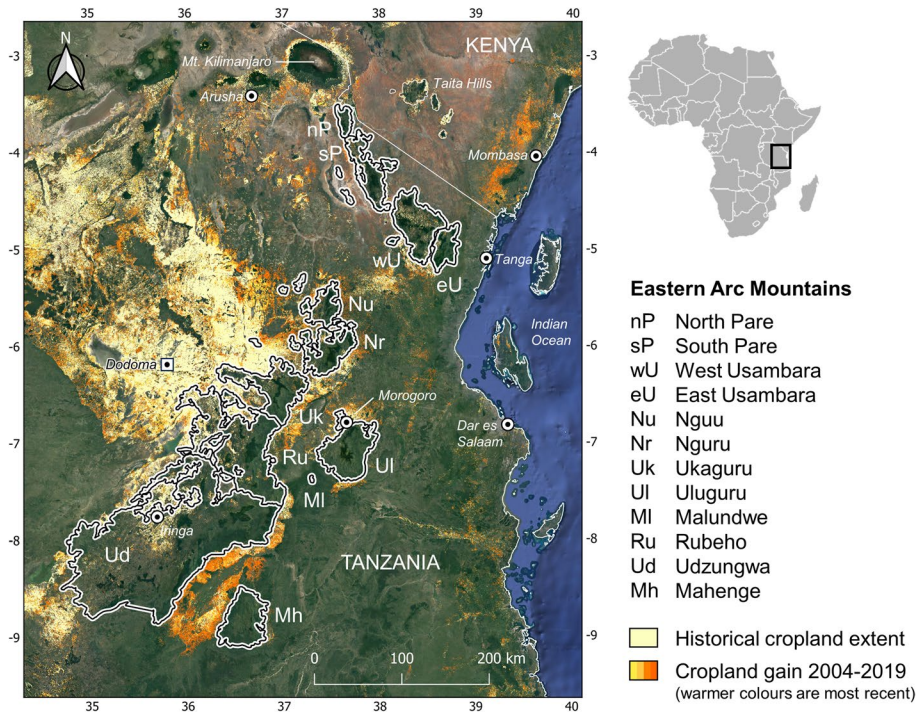
Fig. 1 Map of the Eastern Arc Mountains, showing the 12 mountain blocks in Tanzania. Cropland extent and gain are mapped according to recent global estimates from Potapov et al. (2022). Background satellite imagery is from https://earth.google.com/web/ (accessed 16 July 2023).

the limitations of simply comparing endpoints (forest versus agriculture), which would neglect service interactions and windfalls of gradual depletion, while a one-off assessment of windfalls would exaggerate their value (as supply would greatly exceed current levels of consumption).

Under the conservation pathway, management expediture is increased from a start date ($t = 0$, nominally 2010 in line with most of our data), to ensure sustainable use and conservation of all remaining forests and woodlands. This pathway assumes that no-take rules in IUCN Category I-II protected areas (currently termed National Parks and Nature Forest Reserves) are enforced and all other woody habitats in multi-resource use reserves are conserved, with offtake of woody vegetation capped at sustainable levels. At the other extreme, in the depletion pathway, funding for protected and conserved areas is withdrawn at the start of the pathway, leading to unrestricted use and progressive conversion to smallholder agriculture as the most likely alternative to forest conservation (Doggart et al. 2020). For the depletion pathway, we used observed rates and spatial correlates of forest and woodland clearance in Tanzania.

At the observed rate of forest and woodland loss in Tanzania (1.56% y^{-1}; Government of the United Republic of Tanzania 2017), applied as a fixed area loss rate relative to the initial forest and woodland area, it would take approximately 66 years for all Eastern Arc forests and woodlands – if unprotected – to be cleared. We therefore simulated our pathways over a 66-year period but focus mainly on the first 20 years, during which, under the

depletion pathway, a smaller area is cleared (30% of forests and woodlands) and changes to the supply of ecosystem services are largely linear (thick lines in Fig. 2). We include the full 66-year analysis as well (Supplementary Tables 2 and 3), to highlight the collapse in some service flows that could eventually ensue in the absence of protections (thin lines in Fig. 2) and to show changing sensitivities over the longer term (Fig. 4).

To generate spatial patterns of conversion under the depletion pathway, we used a 1-ha resolution analysis of land-use change for the region to rank pixels by their relative probabilities of conversion in the absence of protection (i.e., as a function of accessibility and potential for farming; Green et al. 2013). We applied this ranking to our land-cover map (Swetnam et al. 2011) at the deforestation rate of 1.56% y^{-1} relative to the initial forest and woodland area. Biomass windfalls from clearing the land for conversion (estimates from Willcock et al. 2012) were used for local and regional consumption of timber and NTFPs, with further consumption met from standing stock (applied spatially using the ecosystem service models described below).

In the conservation pathway, we capped offtake at sustainable levels, determined by standing volumes and tree growth rates. We queried the CABI Forestry Compendium (www.cabi.org/fc) and Plant Resources of Tropical Africa (www.prota4u.org) against the names and synonyms of Eastern Arc tree species, supplemented with a review of Google Scholar (*species name* AND ["growth rate" OR "increment"] AND ["Tanzania" OR "Africa" OR "tropical"]). Excluding outliers (eight records > 0.5 m^3 y^{-1}) we obtained 114 growth rates spanning 79 tree species. Growth rates were slower for woodland species than for forest species, and slower for species in high timber value classes (class I medians, 0.015 m^3 y^{-1} in woodland and 0.052 m^3 y^{-1} in forest; class II, 0.023 m^3 y^{-1} and 0.056 m^3 y^{-1}; classes III-V, 0.056 m^3 y^{-1} and 0.074 m^3 y^{-1}). At each time step, in both pathways, we applied these median rates to trees ≥ 10 cm diameter at breast height (dbh), converted to biomass units (Chave et al. 2009), and allocated growth in smaller stems (used for poles) and coarse woody debris (used for firewood and in charcoal kilns) proportional to tree growth and biomass ratios from (Willcock et al. 2012).

We estimated sustainable offtake to be the mean annual volumetric increment in the relevant stock, adjusted by a factor of 0.56 to allow for inefficiencies and disturbance during harvest (Armitage 1998). Throughout the conservation pathway, the annual allowable cut of timber (suitable species ≥ 30 cm dbh) was 0.73 m^3 ha^{-1} overall (mean across pixels for multi-resource use reserves), but much lower among high-value species due to scarcity and slower growth (class I, 0.0019 m^3 ha^{-1}; class II, 0.074 m^3 ha^{-1}). Among species suitable for charcoal (≥ 10 cm dbh, if not used for timber), the spatial mean for annual allowable cut was 2 m^3 ha^{-1}.

2.3 Natural Capital Accounting

We employed a natural capital accounting approach using two different methods: market prices (in the main text and figures) and resource rents (Remme et al. 2015; Sumarga et al. 2015) (Supplementary Table 3). Both approaches are internationally recognised and politically relevant under natural capital accounting rules (Obst et al. 2016; United Nations 2017; Turner et al. 2019; Hein et al. 2020; Luisetti et al. 2020). We acknowledge the limitations of accounting vis-à-vis dynamic analyses, including lack of inclusion of consumer surplus and the use of marginal values for potentially non-marginal changes. However, we did not have the data to estimate consumer and producer surplus for all services. More

importantly, the application of theoretical dynamic equilibrium models to largely informal economies such as Tanzania's, which operates far from equilibrium conditions, was not deemed appropriate as the model assumptions do not hold. Moreover, applying such models has rarely been considered feasible for any longitudinal, spatially-explicit ecosystem service assessment.

Under the market price method for accounting, we valued ecosystem services at total revenues (quantity×market price per unit). An exception is drinking water, where subsidies distort the market keeping tap water prices artificially low; we therefore used cost-based approaches (based on actual dam restoration project calculations). Under a 'residual value' resource rent (RR) method, we deducted costs from total revenues, including labour costs for provisioning (agriculture, timber, NTFPs) and cultural services (tourism). We used an estimate of the shadow price of labour in rural Tanzania, taken as the midpoint across estimates in the literature (Wiskerke et al. 2010; Mueller 2011; Nerman 2015; TZS 1500 day^{-1} in 2007–2008, applied as 2020 US\$1.51 day^{-1}).

We calculated present values of service and cost categories at discount rates ranging from 0 to 6% (Fig. 4), quoting in the text a lower rate of 1% (zero-discounting can be ethically incoherent (Dasgupta 2021)) and an upper rate of 5% (Bank of Tanzania rate in 2020), with a default of 3%. Extending the analysis beyond the 6% range does not change our broad conclusions. We express all price and cost data in 2020 US\$ using the mean exchange rate for the data-year (https://fxtop.com/en/historical-exchange-rates.php) and correcting for inflation using the US Consumer Price Index (www.usinflationcalculator.com).

2.4 Distributional Analysis

In order to dissect how costs and benefits of conservation vary across stakeholder groups, we defined three groups of people: local-rural (rural communities living within the Eastern Arc plus an 8-km buffer (Schaafsma et al. 2014b); Tanzanian other (city populations and other non-local Tanzanians); and international (everyone else). In our analysis, costs or benefits could flow to multiple stakeholder groups, and depended on the stakeholders' position along the value chain of a service and their exposure to costs through taxes and/or damages. We considered the distribution of total revenues across the three stakeholder groups using a Kaldor-Hicks Tableau (Krutilla 2005). For example, where local-rural labour forms an input to nationally sold products, the distributional analysis records actual wage payments as local-rural benefits and deducts these from other Tanzanians' benefits.

2.5 Ecosystem Services Benefits and Costs

Our valuation pathways and distributional analysis draw together diverse data types and methods from across disciplines. The following sections (*Management costs* through *Drinking water*) provide brief overviews of data and methods underlying each service or cost category, and refer to published sources where service-specific limitations and estimates of uncertainty are detailed.

2.5.1 Management Costs

We determined management costs in the conservation pathway using data on actual and estimated necessary expenditure from interviews with district forest officers, catchment managers and nature reserve conservators responsible for administering 482 (of around 500) protected areas in the Eastern Arc (Green et al. 2012). Expenditure included salaries, operating costs and capital expenditure. We predicted necessary expenditure for all forests and woodlands by regressing reported necessary expenditure (to meet all management objectives) against population pressure in a model that explained 40% of the variance (Green et al. 2012). We assumed that international stakeholders would pay additional management costs (necessary minus actual expenditure at t=0), as well as the portion (22%) of actual spend that is already funded by international donors (Green 2012). The costs to local-rural stakeholders and to other Tanzanians were 5% and 73% of actual expenditure, respectively (Green 2012). Management costs in the depletion pathway were zero.

2.5.2 Agriculture

In the conservation pathway, agricultural benefits accrue from 519,000 ha of pixels classified as woodland with scattered crops (Swetnam et al. 2011), of which we assumed half is under agriculture (Willcock et al. 2012). In the depletion pathway, farmers planted maize (which accounted for 63% of 135 sampled fields in the Eastern Arc (Green et al. 2018) on newly-converted land, with beans grown as a co-crop where the climate allows for two harvests per year. In both pathways, yields for both crops depended on climate, according to the surfaces described in (Thornton et al. 2009). We analyse the extent to which our conclusions are sensitive to yield increases ranging from 0.5 to five times higher yields based on studies from various locations in Sub-Saharan Africa (Rockström et al. 2009; Sanchez 2015). We estimated crop damage by wildlife at 7% of yields on all farmland within 200 m of Eastern Arc forest or woodland (Green et al. 2018), a distance that captures > 90% of crop damage at similar sites in East Africa (Naughton-Treves and Treves 2005). In the depletion pathway, we updated the damage zone and recalculated damage costs annually. We valued agricultural production at local market prices (a conservative estimate). For the RR approach, input costs were seed, fertiliser and labour. We used price and input data collected from surveys of 135 farmer households across 23 Eastern Arc villages (Green et al. 2018). We estimated labour costs at 55 person-days ha^{-1} y^{-1} for maize and 49 person-days ha^{-1} y^{-1} for beans, multiplied by the shadow price of labour in rural Tanzania ($1.51 day^{-1}). We attributed agricultural benefits and the costs of wildlife damage solely to local-rural stakeholders.

2.5.3 Nature-Based Tourism

Using visitor books from 48 hotels in the Eastern Arc, we recorded annual visitor numbers (by nationality), occupancy rates (bed-nights) and prices (Bayliss et al. 2014). Based on interviews with 28 hoteliers and visit rates to parks and reserves, we estimated that 29% of Tanzanians and 49% of international guests were motivated specifically by nature (Bayliss et al. 2014) (as opposed to reasons related to culture, climate, recreational activities or views). Reviewing travel guides, we identified a further 72 hotels within 30 km of the Eastern Arc, and estimated their nature-motivated bed-nights using

the data from the 48 surveyed hotels regressed against accommodation class (low or high budget), distance to forest, distance to paved roads and local population density (Bayliss et al. 2014). Separate models for Tanzanian and international visitors explained 21% and 52% of the variances respectively. We estimated annual revenues using the median price per bed-night from surveyed hotels, separately for low- and high-budget accommodation. In the depletion pathway, we updated visitation rates at mountain-block resolution annually, as a function of forest area remaining (using Table S3 from Balmford et al. 2015). For the RR approach, we deducted costs on the basis of an assumed 10% profit margin and a 20% fixed-cost margin of total revenue (Bayliss et al. 2014). For the distributional analysis, the value of tourism to local-rural stakeholders was estimated as the sum of revenues from low-budget hotels within 8 km of the Eastern Arc boundary, plus the variable costs from high-budget hotels within 8 km. We attributed the remainder of the valuation – all revenues from hotels > 8 km from the Eastern Arc, plus the fixed costs and profits of high-budget hotels within 8 km – to other Tanzanians.

2.5.4 Timber

To determine timber stocks, we matched each forest and woodland pixel to a subset of a total sample of 1726 vegetation plots (Ahrends 2010; Willcock et al. 2014; Shirima et al. 2015; WWF-Tanzania 2015) selected to be most similar in terms of forest type, location, elevational zone, logging history and governance. We defined three timber value classes (I, II and III-V) based on the Tanzania Forest Act (Government of the United Republic of Tanzania 2004) and refined these according to known occurrences and uses in the Eastern Arc (Ahrends 2011). Class-specific stock per pixel was drawn from Poisson (for stem counts) or log-normal (for dbh) distributions, using the mean observed stem counts or dbh values across matched plots, weighted linearly by plot area (because larger plots give more reliable per-ha estimates). For pixels classified as 'open woodland' and 'woodland with scattered crops' we used biomass ratios to infer stem densities of 45% and 39% relative to closed woodland (Willcock et al. 2012).

We determined rates of tree cutting using data from 500 disturbance transects (Ahrends et al. 2021). Along each transect, the proportion of stumps (among trees $\geq$ 10 cm dbh) was recorded. We regressed these stump proportions against distance to paved roads, distance to markets and population pressure in a boosted regression tree model that explained 42% of the variance. Most disturbance transects were in Forest Reserves, so for Nature Forest Reserves and National Parks we adjusted stump rates using ratios reported in (Green et al. 2012). For a subset of 367 transects, the proportion of recent stumps (< 1-year old) was determined in the field, based on absence of moss, lichens, fungi and evidence of weathering. We applied the mean proportion of recent stumps in each mountain block to the results of the stump rates model, multiplied by stocks, to obtain a cut rate (stems ha^{-1} y^{-1}) for each pixel. Based on surveys of 50 carpenters (Schaafsma et al. 2014a), we assumed that trees $\geq$ 30 cm dbh were cut for timber (taking precedence over charcoal; Schaafsma et al. 2012) and yielded four or more planks (imperial units of $1'' \times 10'' \times 12'$) according to: planks $= 4.75 \times (dbh/30.5)^{2.03}$.

To determine the flow of timber within each value class, we cross-calibrated these supply-side estimates against class-specific estimates of timber use (based on census and market data, and interviews with carpenters (Schaafsma et al. 2014a). We assumed that the supply of class III-V planks should equal (to the nearest 1000) domestic household use, while the ratio of class I to class II supply should match that observed in the

market (approximately 3:4). Imposing these constraints on modelled patterns of extraction, the supply of class I and II planks exceeded household use, because timber from the Eastern Arc also flows to commercial and foreign markets. We assumed that class I planks surplus to household use were for international markets (Milledge et al. 2007), while surplus class II planks went to commercial buyers in Dar es Salaam, Tanga, Arusha, Morogoro, Iringa and Dodoma (Schaafsma et al. 2014a).

In the conservation pathway, limits to sustainable offtake meant that initial use levels could not always be met from the locations indicated by the extraction model, especially for high-value, slower-growing timbers. In these cases, timber was harvested at sustainable rates from within 8 km. Extraction of class I-II planks could be further displaced within the same mountain block, and class I planks to the wider Eastern Arc as required, since market data suggest long travel routes for high-value timber (Schaafsma et al. 2014a). In each case we implemented offtake proportional to stocks, so that loggers displaced by conservation restrictions harvested proportionally more from stands with greater allowable offtake. Where initial use levels could still not be sustained, we allocated unmet use (as an opportunity cost) to would-be beneficiaries proportional to their initial consumption level. In the depletion pathway, windfalls of trees from conversion were available for timber before harvesting was imposed on the standing stock, using the heuristics described above. Throughout both pathways, wastage from sawing of planks was available for charcoal production or as firewood, given local use (Schaafsma et al. 2014b). Unused wastage was added to the coarse woody debris pool of the corresponding pixel.

We valued domestic planks using furniture and woodwork prices based on spatially-explicit market price maps derived from surveys of 50 carpenters, 20 timber dealers and four pitsawyers at 17 locations across the Eastern Arc (Schaafsma et al. 2014a). Timber planks form 50% of furniture prices, while other costs (including transport, materials and tools) add up to another 25%. We valued planks for export using the mean 2003–2015 FAO border price for non-coniferous tropical oundwood destined for China and India (www.fao.org/faostat/en/#data/FT), weighted by the total volume to each destination and assuming a sawnwood/oundwood efficiency of 1/3 for African mills (www.globaltimber.org.uk/rwevolume.htm). In the RR approach, we deducted input (timber and other) costs of furniture and woodwork.

For the distributional analysis, the value of timber to local-rural stakeholders consisted of furniture and woodwork revenues consumed in local-rural wards, plus the local costs (including labour of pitsawyers and carriers) of supplying planks to national and international markets (Schaafsma et al. 2014a). Other Tanzanian stakeholders benefited from national furniture revenues (minus local costs), plus the price of planks paid by commercial or international markets (minus local costs). The value to international stakeholders consisted of revenues from exported planks, minus the border price.

2.5.5 Non-Timber Forest Products (NTFPs)

We combined survey data from > 2000 households in 60 rural villages to construct household production functions relating the use and production of firewood, charcoal and thatch to household and environmental characteristics, such as available labour and capital, domestic use and market access (Schaafsma et al. 2014b). For poles, we estimated consumption based on the construction requirements of a typical rural house (wooden roof frame and pole walls; Schaafsma et al. 2014b). We then estimated household production of

NTFPs for unsurveyed households using census data and spatial covariates as described in (Schaafsma et al. 2014b). We estimated that a bundle of firewood weighed 17.5 kg, a pole weighed 5 kg, and a bag of charcoal weighed 30 kg but required 250 kg of biomass to produce (assuming kiln efficiency of 15% and wastage of 20%; Malimbwi et al. 2000; Neufeldt et al. 2015).

In the conservation pathway, NTFPs were harvested within 8 km (charcoal) or 4 km (firewood and poles) of production sites (Schaafsma et al. 2014b). As for timber, the amount taken from each pixel was proportional to available stock, and we allocated unfulfilled consumption to would-be beneficiaries as an opportunity cost. In the depletion pathway, windfalls of biomass were available to meet initial NTFP consumption levels within the same mountain block, before harvesting was imposed on standing stocks within 8 km or 4 km of production. In both pathways, we assumed that thatch was sustainable due to relatively low consumption, fast regrowth, and availability outside forests and woodlands (Schaafsma et al. 2014b). Poles were supplied from stems measuring 5–10 cm dbh (taken as 50% of stems < 10 cm dbh); thatch came from 'unmeasured' aboveground live biomass (as defined in Willcock et al. 2012); charcoal came from trees ≥ 10 cm dbh (competing with timber for trees ≥ 30 cm dbh) plus any wastage from timber production on the same site; and firewood came from coarse woody debris (including wastage from timber if not used for charcoal). Not all tree species are suitable for making charcoal: respectively 50%, 36% and 33% of species in timber classes I, II, III-V are suitable (Ahrends 2011), and so we allocated supply accordingly, given available stock.

We valued firewood, poles and thatch using local market price data (Schaafsma et al. 2014b). For charcoal, we collected price data along two main routes for transporting and selling it (Morogoro to Dar es Salaam, and Moshi to Tanga) and created a spatial price surface that explained 66% of the variance in price (Schaafsma et al. 2012). In our pathways, charcoal was transported to Dar es Salaam, Iringa, Morogoro and Tanga, proportional to consumption in these cities (assuming 75% of Dar es Salaam households and 54% of households in other urban areas use charcoal for cooking (National Bureau of Statistics Tanzania 2009), with annual per capita consumption of 168 kg (Van Beukering et al. 2007). In the RR approach, we deducted labour costs of $0.13 for each unit of firewood, thatch and poles (based on 45 min collection time; Schaafsma et al. 2014b) and $3.02 per charcoal bag (based on two days of labour input per bag; Luoga et al. 2000). For charcoal we furthermore deducted the difference between the city price and the price at the production site (per the price map; Schaafsma et al. 2012). This difference reflects the costs of transportation, taxes, bribes and licences.

In the distributional analysis, fewer than 5% of surveyed households said they sell these products, and so the value was split between local-rural stakeholders and other Tanzanians based on whether the producing household was in an urban (Morogoro and Iringa) or rural ward. Conversely, charcoal is nearly always sold on by producers to be transported for consumption in urban areas. We therefore took as the local-rural value of charcoal the price at the production site, and the value to other Tanzanians (the end-users) as the difference between this price and the city price.

2.5.6 Carbon Emissions and Sequestration

We tracked carbon per pixel in aboveground and belowground IPCC carbon pools, starting with values derived from a meta-analysis of literature and plot data (N = 2462 plots)

(Willcock et al. 2012), and updating these through time as land cover changed and biomass was extracted (assuming carbon to be 45.6% of dry biomass (Martin et al. 2018)). After t years since conversion to agriculture, the percentage decrease in soil organic carbon was given by $7.0791 \ln(t) + 23.127$ (Wei et al. 2014). Carbon was sequestered only in no-take reserves (conservation pathway), at rates derived from observed changes (1968–2007) in the carbon stored by live trees ≥ 10 cm dbh in intact African forests (Lewis et al. 2009; 0.63 tC ha^{-1} y^{-1}, from initial stocks of 202 tC ha^{-1}). We adjusted this rate based on the initial biomass and wood density of Eastern Arc forests, and extrapolated to unmeasured forest components (small trees and shrubs, live roots, litter and coarse woody debris) using biomass ratios from (Willcock et al. 2012).

For both the market price method and the RR approach, we valued emissions and sequestration at the EU ETS mean market price for 2020 ($28.55 tCO$_2$e^{-1}; https://uk.investing.com/commodities/carbon-emissions-historical-data), while noting this to be a conservative valuation given recent and anticipated future carbon prices (the Bank of England project > $100 tCO$_2$$^{-1}$ post-2030, and the EU ETS mean for 2022 was $92 tCO$_2$$^{-1}$), and compared with estimates of the damage costs associated with incremental increases in carbon emissions (Nordhaus 2017; Rennert et al. 2022; Tol 2023).

We distributed carbon values proportional to the population of each stakeholder group, so that the international group was assigned by far the highest proportion (99.36%), followed by Tanzanian other (0.58%), then local-rural (0.06%). Valuations for carbon were otherwise fixed across the stakeholder groups, because regional damages are poorly understood, and estimates vary widely. For example, the social cost of carbon emissions for Africa has been estimated at between 3 and 26% of the global total (Nordhaus 2017), which (scaling by population) equates to between 0.12% and 1.01% for Tanzania other, and between 0.01% and 0.10% for local-rural stakeholders. Thus, our estimates are near the middle of these ranges, and our broad conclusions remain robust across the range of estimates.

2.5.7 Drinking Water

We used the process-based Soil and Water Assessment Tool (SWAT) to calculate the role of forests and woodlands in regulating drinking water provision to Morogoro and Dar es Salaam. Agricultural expansion in the depletion pathway increased siltation rates in the Mindu reservoir, which supplies 85% of Morogoro's water. For both the market price method and the RR approach, we valued this impact using the replacement costs, i.e. the estimated cost of regaining reservoir capacity through remedial works (Ashagre et al. 2018). For Dar es Salaam, we based our valuation on the incidence of pump failure at the Upper Ruvu treatment works (supplying 30% of the city's water), which increased under the depletion pathway due to turbidity (Ashagre et al. 2018). We valued the cost of increased days (and consecutive days) without tap water using replacement costs, i.e. the market prices of substitution options, relative to residents' normal water costs (informed by literature and surveys of 36 kiosks, 22 pushcart vendors and six water trucks in Dar es Salaam).

These methods modify those previously reported (Ashagre et al. 2018) by: (1) restricting valuations to the contributions of forests and woodlands situated strictly within the Eastern Arc boundary(Platts et al. 2011) (rather than across the entire Ruvu river catchment); and (2) implementing agricultural expansion gradually, as per our conversion schedule. Due to the complexity of SWAT calibration we incremented depletion over five time-steps (*cf.*

annually for other services). The model itself, however, was run on a daily time-step, so we could assess the sediment levels that trigger pump shutdown. Costs of remedial works at the Mindu reservoir and of alternative sources of drinking water in Dar es Salaam were borne by city (i.e., Tanzanian other) stakeholders. Other city populations, as well as local-rural stakeholders, are also likely to benefit from water flow regulation provided by Eastern Arc habitats; however, the detailed longitudinal data necessary to calibrate reliably a process-based hydrological model were not available for other catchments.

2.6 Comparison with Biological Importance

We defined biological importance using mountain-block distributions of all plant and vertebrate species known to be endemic to the Eastern Arc (excluding nine plant and eight vertebrate species known only from Taita Hills in Kenya, and 48 plant and one vertebrate species not found in forest or woodland). We thus included 479 plant species (www.tropicos.org, accessed 13 March 2019) and 127 vertebrate species (Rovero et al. 2014) (20 birds, 11 mammals, 57 amphibians and 39 reptiles). We focused on endemics because of their importance for global biodiversity, range-wide vulnerability to Eastern Arc habitat loss, and because people in distant countries hold positive values for their conservation (Morse-Jones et al. 2012). We determined plant habitats using specimen labels and point localities; for vertebrates, we used habitats listed as suitable on the IUCN Red List (www.iucnredlist.org, accessed 6 March 2019). For 22 vertebrates with no habitat information, we assigned the majority habitat of the genus. Within each taxonomic group, we estimated its biological importance as its block-level richness for endemics divided by A^z, where A is the area of forest or woodland and $z = 0.25$ is taken as a representative value of the slope of the species-area curve. We then standardised these values (relative to the mean value across the Eastern Arc) and plotted them for each group separately (Fig. 5 insets) and for all groups combined (mean across groups, Fig. 5 main plot).

We then compared these biological values for each block with our estimate of the economic value of conserving them. The biological values of the blocks are largely attributable to the forests rather than woodlands (only 13 endemics are found only in woodland). Therefore, we refined our comparison by splitting the economic value of each block into that attributable to its forest and its woodland. We derived partial valuations for forests versus woodlands by simulating each pathway three times: first with benefits and costs flowing from both forest and woodland (b), then from forest only (f), and lastly from woodland only (w). The value of benefit or cost X attributed to forests was $X_b X_f (X_f + X_w)^{-1}$; the value attributed to woodlands was $X_b X_w (X_f + X_w)^{-1}$. This partialling out of contributions was necessary because some forest and woodland services substitute for one another or, in the case of drinking water, are modified by multiple land covers as they flow towards a beneficiary (and hence $X_b \neq X_f + X_w$).

2.7 Treatment of Uncertainty

Our analysis involves three assessments of uncertainty: (1) through the pathways (extreme bounds on what is plausible/possible in the system as a whole); (2) through sensitivity analysis of those parameters which dominated most of our conclusions: carbon price, agricultural production, discount rate and valuation period; and (3) through two different accounting approaches for monetary valuation (market prices and residual-value resource rents).

3 Results

Under the depletion pathway, summarised by the lines in Fig. 2, agricultural production increases with the area converted, moderated by its climatic suitability for crops. Crop damage by wild animals decreases as forest fragments are consumed by agriculture, while nature-based tourism declines as natural landscapes and charismatic forest species (e.g., rare monkeys, birds, chameleons) are lost from the vicinity of hotels. With the exception of thatch, flows of NTFPs (construction poles, firewood, charcoal) and timber (of different quality classes) are drawn from or indirectly affected by the same biomass pools, and thus fluctuate before eventually crashing as resources are depleted. After 20 years, a total of 478 Tg CO_2 is emitted, from aboveground carbon stocks and as fragile mountain soils are exposed and eroded. Sediment accumulates in Mindu Reservoir, affecting drinking water supply to Morogoro city, while high sediment loads in the Ruvu River increase the incidence of failure of the pumps supplying Tanzania's most populous city, Dar es Salaam.
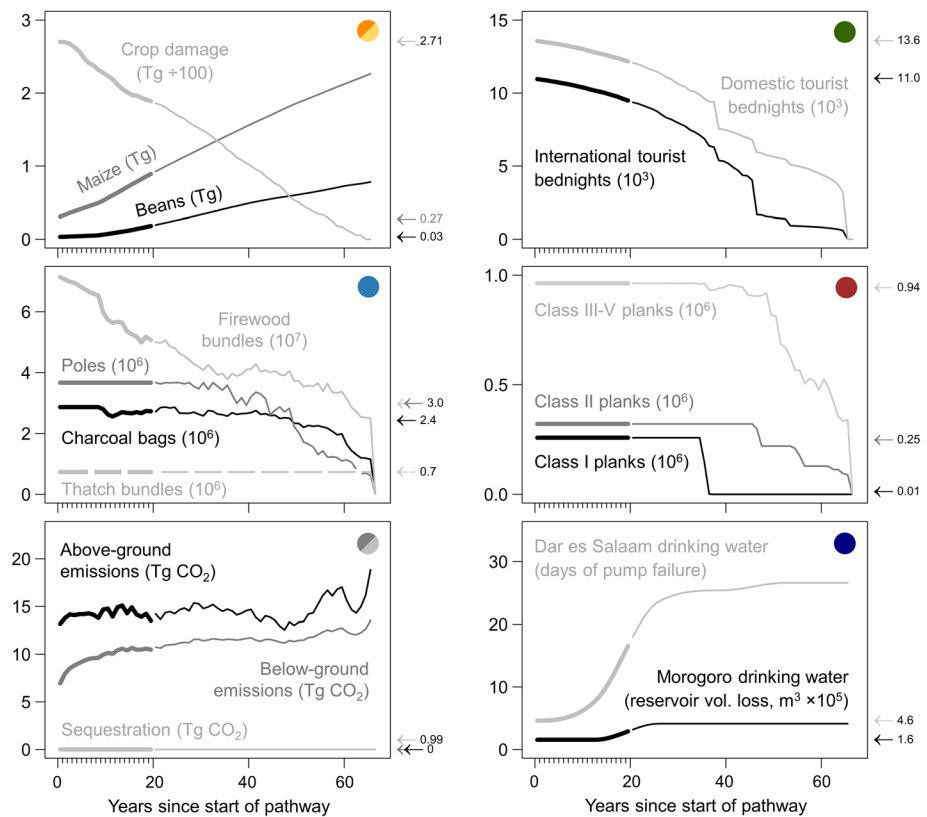
Fig. 2 Biophysical flows of services and disservices. Lines track the results of our depletion pathway, during which all remaining forests and woodlands in the Eastern Arc are unprotected and converted to agriculture over a 66-year period. Arrows mark the flow of services and disservices under a conservation pathway (constant over time) in which all forests and woodlands are protected and conserved. Thick lines span a 20-year valuation window, beyond which longer term market dynamics or responses to non-linear changes in supply may exceed the limits of marginal valuation. Coloured circles correspond to colours plotted in Fig. 3

By contrast, under the conservation pathway, increased management expediture ensures a steady flow of services (arrows in Fig. 2), while no-take reserves sequester 0.99 Tg CO_2 annually.

Tracking these flows to beneficiaries or cost-bearers within and beyond the Eastern Arc, we value the conservation pathway at \$161 M y^{-1} (millions of 2020 US\$; Fig. 3a) net of management costs (-\$21 M y^{-1}) and crop damage (-\$9 M y^{-1}). The depletion pathway begins with a loss of \$378 M y^{-1} but turns positive after 35 years, as the cost of carbon emissions (valued at the 2020 EU ETS mean market price, \$28.55 tCO_2^{-1}) is progressively offset by rising agricultural production (Fig. 3a). Discounted at $\delta = 3\%$ y^{-1} over 20 years, present values of agriculture, crop damage, NTFPs, timber and management are higher for depletion than for conservation, while the opposite holds true for tourism, carbon emissions, carbon sequestration and drinking water (Fig. 3b and Supplementary Table 1). Depletion also results in many hundreds (probably thousands) of species extinctions.

Combining all benefit and cost categories (Fig. 3c), conservation has a greater benefit to society as a whole than continued depletion: the net gain from conservation over a 20-year period (difference in net present value (NPV) of conservation and depletion pathways) is \$8.2B (ranging from [\$6.9B for $\delta = 5\%$ to \$9.8B for $\delta = 1\%$]) and is positive for all carbon prices $\geq$ \$6 tCO_2^{-1} (Fig. 4a).

However, disaggregating this global value across stakeholder groups reveals critical inequities (Fig. 3c and Fig. 4 subplots). For most carbon prices, discount rates and agricultural yields, local-rural stakeholders bear substantial net costs of conservation, while international stakeholders enjoy sizeable net benefits. Local losses are driven mainly by forgone benefits from agriculture ($-$\$1.6B [$-$\$1.2B, -\$2.1B for $\delta = 5\%$, 1% respectively]), and NTFPs and timber ($-$\$282 M [$-$\$241 M, -\$335 M]). International investments in protected area management (\$280 M [\$235 M, \$340 M]) would generate \$10.4B [\$8.7B, \$12.7B] in avoided CO_2 for international stakeholders, a return of \$37 per conservation dollar, net of \$38 M [\$32, \$46] in forgone timber exports. Outcomes for national-level stakeholders (city populations and other non-local Tanzanians) are more finely balanced ($-$\$75 M [-\$65 M, -\$88 M]), with high-value timber, charcoal and management costs (favouring depletion), and carbon emissions and drinking water (favouring conservation) holding most sway (Supplementary Table 1).

Breaking down our results spatially, we find there is a society-wide net gain of conservation for nearly all mountain blocks (Fig. 5). Moreover, there are strong correlations between our estimates of the per-unit-area net gains of conservation and each mountain block's biological importance. Previously reported relationships between biodiversity and ecosystem services have varied widely depending on the services included, biodiversity metric, comparison method and scale of analysis (Ricketts et al. 2016). Here we find that patterns also differ when net ecosystem service gains are disaggregated by stakeholder group: the relationship is positive overall, but negative for local-rural stakeholders (Fig. 5). This is because factors associated with greater endemism in the Eastern Arc, such as consistent rainfall and coastal aspect, support high vegetation biomass (and hence carbon benefits) but simultaneously favour human settlement through effects on agricultural suitability and access to coastal markets. This leads to higher local opportunity costs under conservation (and higher global costs under depletion) in the most biologically important places.
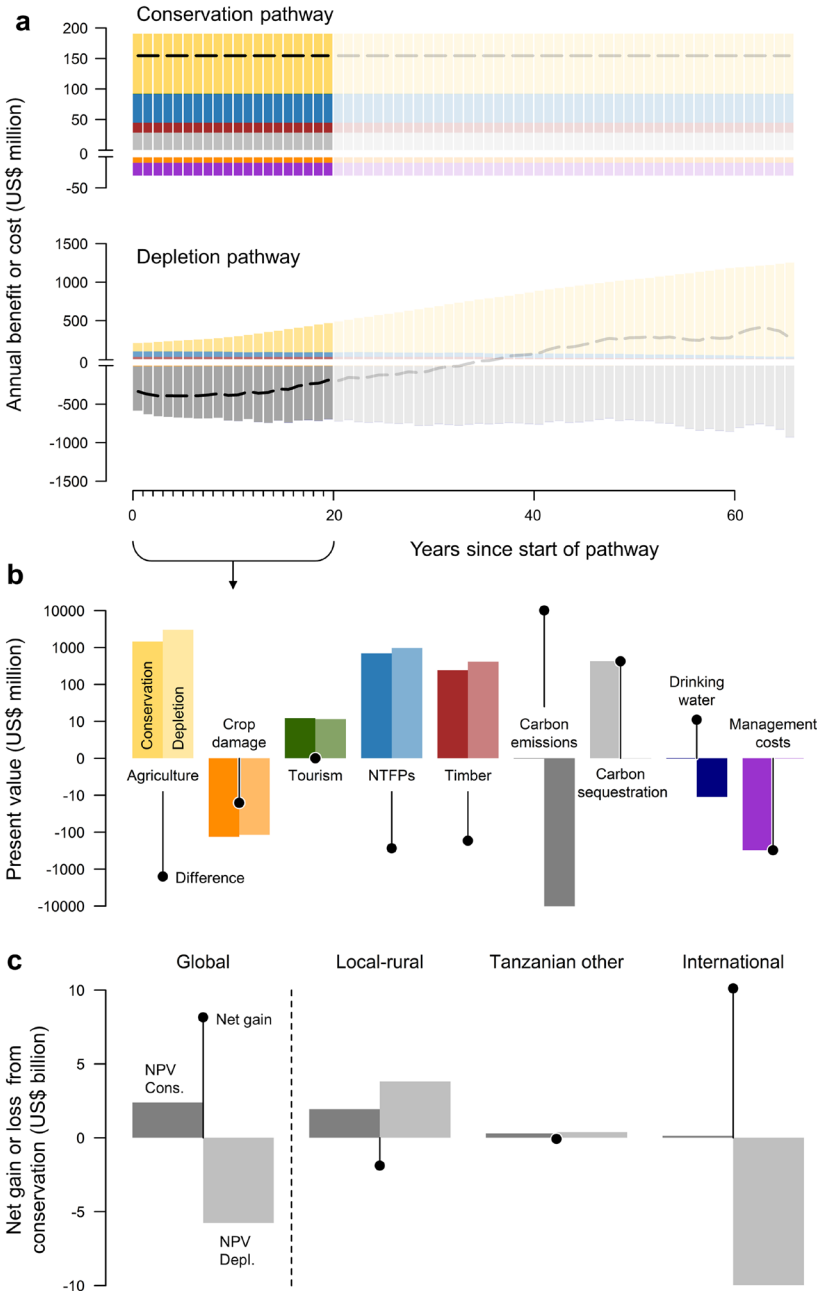
Fig. 3 Pathway valuations and hence net gains and losses from conservation in the Eastern Arc. a, Economic valuation of forest and woodland conservation versus depletion through time, by benefit or cost category (colour code in b). Dashed lines track annual benefits net of costs. b, Present values (PVs, 3% discount rate) for each benefit or cost category, under conservation versus depletion over a 20-year period (note log$_{10}$ scale on y-axis). Dots mark the difference between pathways (PV under conservation minus PV under depletion) for each category. In c, points mark net gains or losses from conservation (Cons., *cf.* depletion, Depl.) totalled across all categories over a 20-year period, plotted globally for all stakeholders combined and for different stakeholder groups. Values conservatively assume a carbon price of $28.55 tCO$_2^{-1}$
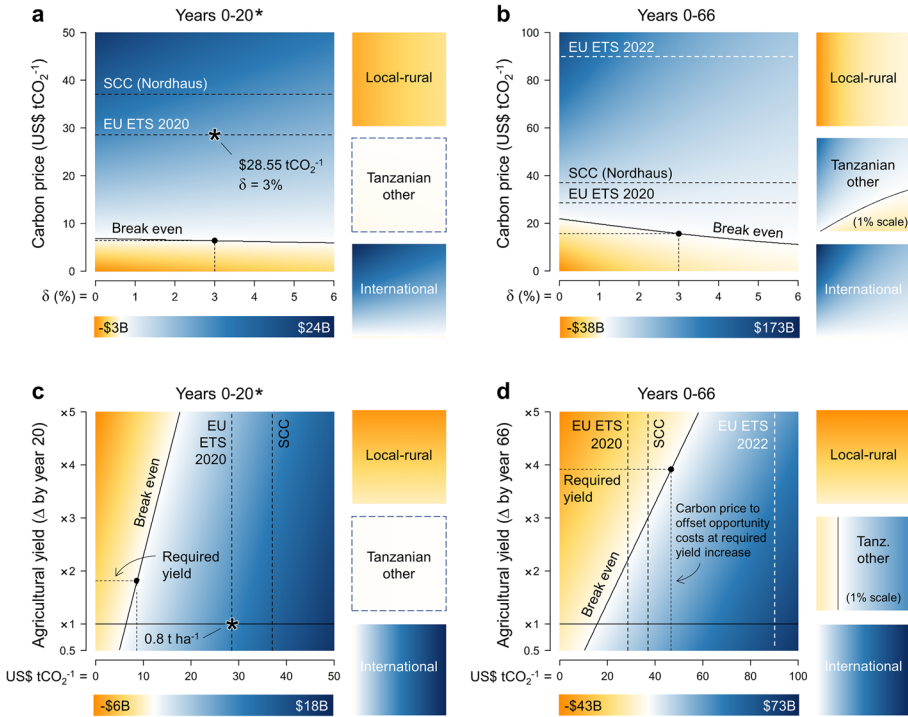
Fig. 4 Sensitivity of net gains or losses from conservation in the Eastern Arc to the valuation period, discount rate, carbon price and agricultural yield. Results shown for all stakeholders combined (four main plots) and for different stakeholder groups (12 subplots). For both valuation periods and all plausible discount rates, carbon prices and agricultural yields, international stakeholders gain a net benefit from conservation, while local-rural stakeholders bear a net cost. For other Tanzanians, benefits and costs are finely balanced. Dashed lines mark the EU Emissions Trading System (EU ETS) mean market prices for 2020 and 2022 and a conservative estimate of the Social Cost of Carbon (SCC) emissions (Nordhaus 2017). Asterisks mark the valuation period, discount rate, carbon price and agricultural yield (spatial median) used in Figs. 2 and 3. a-b, Globally, at a discount rate of $\delta = 3\%$, conservation has a net benefit for carbon prices $\geq \$6$ tCO_2^{-1} in the 20-year valuation, and for carbon prices $\geq \$16$ tCO_2^{-1} in the 66-year valuation (dotted lines). In the 66-year valuation, conservation has a net benefit for national stakeholders at carbon prices $\geq \$25$ tCO_2^{-1} (at $\delta = 3\%$, or $\geq \$8$ tCO_2^{-1} at $\delta = 1\%$). c-d, Sensitivity to changes in agricultural yield (assuming $\delta = 3\%$), which could be increased through improved inputs, or could decrease due to deteriorating soils, climate change or disease. Dotted lines mark yield increases (on existing Eastern Arc farmland) required to produce as much food as is forgone under conservation (compared with depletion), and the corresponding carbon prices needed to offset the resulting increases in opportunity cost ($\$9$ tCO_2^{-1} after 20 years, and $\$47$ tCO_2^{-1} after 66 years)

4 Discussion

Our findings highlight the urgent need to distribute the net costs of conservation fairly, considering both benefits received and ability to pay of different stakeholder groups (Kremen et al. 1979; Fisher and Christopher 2007; Armstrong 2019). Given the fine balance of national gains and losses from conservation (Fig. 3c and Fig. 4 subplots), addressing net local costs will – for the foreseeable future – require financial transfers from elsewhere.
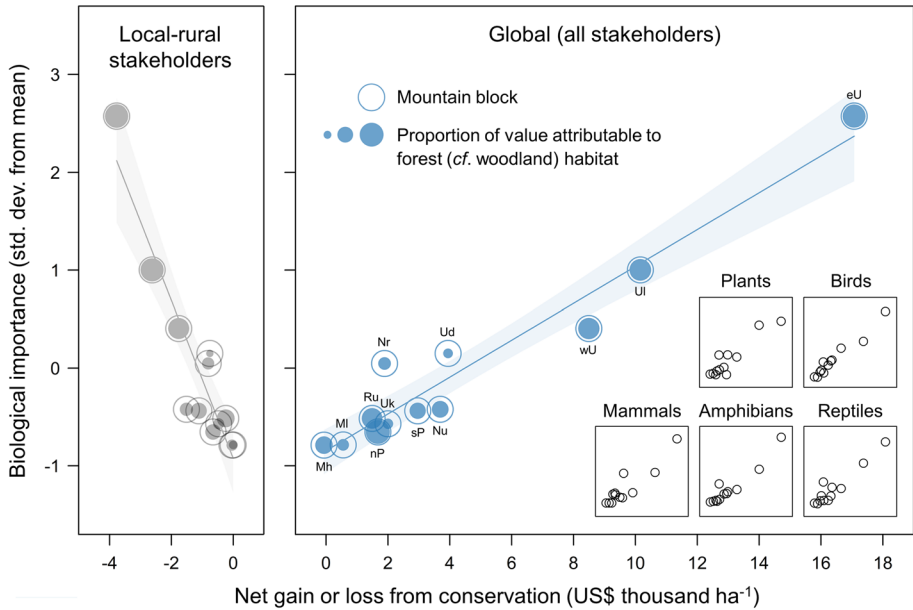
Fig. 5 Spatial congruence between the net gain or loss from conservation and the biological importance of Eastern Arc mountain blocks. Net gain or loss calculated according to benefits and costs attributable to forest and woodland conservation (*cf.* depletion) in each of 12 mountain blocks, from the point of view of all stakeholders combined (blue circles) and for local-rural stakeholders only (grey circles). Values discounted at 3% over 20 years, assuming a carbon price of $28.55 tCO_2^{-1}. Biological importance is the estimated per-ha richness of 479 plant species and 127 vertebrate species endemic to Eastern Arc forests and woodlands, balanced across taxonomic groups and plotted as standard deviations from the spatial mean (insets plot global relationships for each group separately). Variable dot sizes show the proportion of the total mountain block value attributable to forest habitats, which contain the majority of endemics (only 13 endemics restricted to woodland). Lines and shadings show linear regressions and 95% confidence intervals, for all stakeholders combined ($R^2 = 0.94$) and for local-rural stakeholders only ($R^2 = 0.87$). Mountain block abbreviations are detailed in Fig. 1

In the Eastern Arc, we estimate that conservation investments with an NPV of $2B (discount rate = 3%) would be required to mitigate local and national costs for a 20-year period, potentially via international payments for 20 Tg CO_2 sequestered plus 478 Tg CO_2 emissions avoided – equivalent to $6 tCO_2^{-1} (Fig. 4a). This is far below recent market prices (EU ETS 2022) and estimates of the social cost of carbon (Nordhaus 2017; Rennert et al. 2022; Tol 2023).

To qualify for payments through carbon markets or mechanisms such as REDD+, off-site effects must be factored in (Filewod & McCarney in press). Leakage from conservation in the Eastern Arc would probably displace some conversion to vacant land (albeit limited) in adjacent lowlands. However, natural vegetation in these areas supports fewer range-restricted species (Meng et al. 2016) and less carbon (Willcock et al. 2014) than in the Eastern Arc, and contributes less to hydrological regulation (Ashagre et al. 2018). Moreover, expanded lowland farming would partly offset the opportunity costs of forgone Eastern Arc agriculture. Nonetheless, in order to mitigate local costs while addressing the primary driver of habitat loss (and thus potential for leakage), we suggest international

finance should be invested in sustainable practices for improving yields on existing small-holder farms (Phalan et al. 2016; Jayne et al. 2019).

Agricultural intensification has not always delivered improved wellbeing, especially in the neotropics (Rasmussen et al. 2018), but given that > 90% of deforestation in Africa is driven by smallholder agriculture (Curtis et al. 2018; *cf.* 31% in Latin America and 9% in Southeast Asia), any effective solution there will need to involve yield improvements. We estimate that to track agricultural losses under conservation (versus depletion), yields on existing Eastern Arc farmland would need to increase progressively by 81% over 20 years, and ultimately by 292% (after 66 years). This is not implausible: similar increases have been rapidly achieved elsewhere in Africa using improved fertiliser and seed (Sanchez 2015), and can effectively reduce deforestation (Pelletier et al. 2020) especially where land rights are formalised (Wren-Lewis et al. 2020). Rising agricultural rent would increase the opportunity costs of conservation (Carrasco et al. 2014), but despite this (i.e., applying the above yield increases to both pathways) there remains a net global gain from conservation over 20 years (for carbon prices $\geq$ \$9 tCO_2^{-1}, Fig. 4c). In the longer term (66-year valuation, Fig. 4d), higher forgone yields across a larger area mean that carbon prices $\geq$ \$47 tCO_2^{-1} would be required to offset opportunity costs.

While unprecedented in detail, scope and setting, our analysis is of course not exhaustive. There were services we could not assess in monetary terms and/or at the required scale, including local water quality, hydropower, air pollution reduction, pollination, option and non-use values, and relational aspects (Díaz et al. 2015), as well as the collection of wild plants and hunting or capture of animals for food, medicine and trade. Inclusion of the former (regulating and cultural services) would accentuate the case for conservation across all three stakeholder groups, and especially locally, while accounting for omitted extractive uses could increase opportunity costs. We note also that our 20-year valuation window does not fully capture collapses in non-agricultural service flows in the absence of protection (lines in Fig. 2). Longer-term valuations are subject to demographic, cultural and climatic changes, technological developments, and unknowable market dynamics in response to non-linear changes in supply. These caveats notwithstanding, our conclusions of international gains and local losses from conservation hold in our full 66-year analysis (Fig. 4b, d and Supplementary Table 2), while the long-term balance for national stakeholders hinges on the carbon price and discount rate (gaining from conservation at $\geq$ \$25 tCO_2^{-1} for $\delta = 3\%$, or at $\geq$ \$8 tCO_2^{-1} for $\delta = 1\%$). The overall net gain from conservation also holds under an alternative valuation approach based on resource rents (Supplementary Table 3).

Our work shows that habitat conservation in a region of high endemism and significant human pressure provides overall net economic benefits, but with widely divergent outcomes across stakeholder groups. In contrast to international (and potentially national) gains from conservation, local stakeholders incur substantial net costs. This disparity corresponds roughly with the observed aggregate behaviour of these groups. Among local-rural stakeholders, ongoing forest degradation (Ahrends et al. 2021) and expansion of smallholder agriculture (Doggart et al. 2020) are understandable safeguarding responses to immediate livelihood risks. Although the international community has committed to reducing biodiversity loss and emissions from deforestation, in the Eastern Arc it currently pays a disproportionately small share of the costs of conservation. In the absence of substantially increased global funding to incentivise conservation by local stakeholders (Robinson et al. 2019), this economic freeriding risks continued diminution of the region's biodiversity and carbon stores. Moreover, we find that if conservation follows biodiversity priorities without addressing local costs, then

incentives for unsustainable resource-extraction and expansion of smallholder agriculture will continue to be highest in sites of greatest importance for biodiversity.

While the details of our findings are of course specific to our study region, other biodiversity hotspots in the Eastern Afromontane area (Mengist et al. 2022) and beyond (Weinzettel et al. 2018; Hugé et al. 2020) are facing similar anthropogenic threats and conservation challenges. Our study assessed most of the key ecosystem services that are produced by biodiversity hotspots across the world (Kermagoret and Dupras 2018; Rochette et al. 2021). We suggest that, as in the Eastern Arc, in very many of these regions the fundamental trade-off—between conservation and conversion to agriculture—is driven in large measure by non-marketed carbon and biodiversity values versus market revenues of agriculture (Ortiz et al. 2021; Williams et al. 2020). Indeed, the same tension is central to land-use policy decisions in temperate regions such as the UK (Dimbleby 2021).

We hope that our study demonstrates the value of linking extensive field data, robust ecosystem service models and contrasting, high-resolution land-use scenarios in order to assess the distribution of costs and benefits across user groups. Understanding the societal distribution of net gains and losses from conservation, across both time and space, is central to guiding equitable solutions and improving outcomes for people and biodiversity. Our primary recommendation is that investing in conservation is beneficial at societal level but can only be equitable on the condition of actual compensation payments (Poudyal et al. 2018, Kaczan et al. 2019). We believe this finding is likely to have broad relevance in very many biodiversity hotspots, and beyond.

Data availability The data used in this study come from a wide range of published sources as detailed and referenced in the relevant sections of the Methods, but restrictions apply to the availability of some of the data. For assistance with data permissions and collation, contact the corresponding author.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose

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