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Land use intensification causes the spatial contraction of woody-plant based ecosystem services in southwestern Ethiopia

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Integrating biodiversity conservation and food production is vital, particularly in the tropics where many landscapes are highly biodiverse, and where people directly depend on local ecosystems services that are linked to woody vegetation. Thus, it is important to understand how woody vegetation and the benefits associated with it could change under different land-use scenarios. Using a comprehensive, interdisciplinary study in southwestern Ethiopia, we modeled current and future availability of woody plant-based ecosystem services under four scenarios of landscape change. Land-use scenarios with intensified food or cash crop cultivation would lead to the contraction of woody-plant based ecosystem services from farmland to forest patches, increasing pressure on remaining forest patches. This raises questions about the viability of conventional intensification combined with land sparing—where conservation and production are separated—as a viable strategy for conservation in tropical landscapes where woody-plant based ecosystem services are vital to the lives of local communities.

Integrating food production and biodiversity conservation is a pressing challenge across the world[1,2]. Because land-use strategies are central in addressing this challenge[3], one widely used conceptual model to achieve such integration is the 'land sparing' versus 'land sharing' model, e.g., refs. 4–6. In land sparing, some areas are strictly protected, while the remaining lands are used for intensive agricultural production, e.g., refs. 5,7. For a given level of agricultural yield, this approach is particularly useful for protecting species of conservation concern, such as those specialized on largely undisturbed areas of natural vegetation, e.g., refs. 5,8. Indeed, the importance of near-natural areas for sensitive species has been known for many decades[9,10].

In contrast, land sharing denotes a situation where the equivalent agricultural yield is generated across larger areas. This extensification of agriculture is possibly (but not necessarily) at the expense of strictly protected land[4,11]. Agro-ecological cropping methods including agroforestry, intercropping, conservation agriculture, and mixed crop-livestock systems are examples of land sharing[6,12,13]. Low-intensity agricultural land-use is often very heterogeneous, and this can benefit a wide range of species that are tolerant of medium levels of human disturbance. It can also help to connect forest patches and reduce pressure from the surrounding forest. Highly sensitive species, however, may be absent from such agricultural land because they depend on yet more undisturbed areas, e.g., refs. 5,8.

The challenge of integrating biodiversity conservation and food production is particularly pertinent in the tropics[14,15]—where many landscapes are highly biodiverse, but where local people also strongly depend on local ecosystems and use agrobiodiversity to support their livelihoods[16–18]. In such landscapes, food production levels are clearly important for food security; but beyond that, many other factors also influence the well-being of local people.

One vital factor influencing human well-being is the access local people have to a variety of ecosystem services (ES). Local people's access to ES is limited by spatial characteristics of the services[19,20], the method applied to obtain ES, access to land, technology, capital, and knowledge[21,22], power asymmetries[23,24], and prevailing development policies[25]. In many

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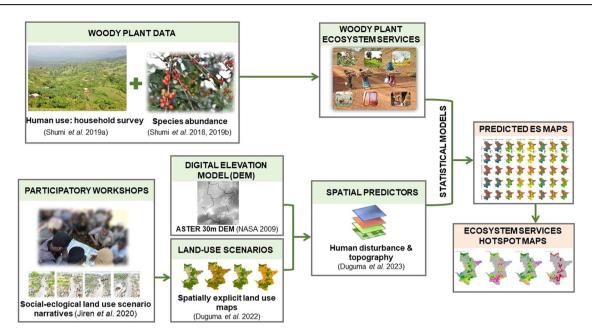
Fig. 1 | Overview of our interdisciplinary methodological approach, showing input data (both social and ecological) and methods (photographs taken by Girma Shumi). The arrows in the figure show the methodological flows starting from input data (woody plant ecosystem services from species and household surveys, and spatial predictors from scenario maps and digital elevation model), which were combined using statistical modeling to predict ecosystem services and ecosystem service hotspots. Details are available in the "Methods" section.

smallholder-dominated landscapes in the tropics, many ES are directly used and valued by local people, e.g., refs. 26,27. Of these services, most are linked to woody vegetation within the landscape[28–30]. Trees and shrubs are used, among other things, as a source of fuelwood, fodder, construction wood or medicine; to make ploughing tools or household utensils; they can support the production of commodities such as honey or coffee; and some help to maintain soil fertility [29–31].

At times when calls are increasing to protect more land for biodiversity conservation—for example through the 30 × 30 initiative[32]—it is vital to not lose sight of how local livelihoods in the tropics are intimately dependent on the direct appropriation of ES, especially those generated by trees and shrubs within farming landscapes. To that end, spatially explicit maps of tree-based ES under different scenarios of land use change that are based on integrated social-ecological field data could be very useful, but to the best of our knowledge have not been generated to date.

In this paper, we build on a unique, comprehensive dataset from southwestern Ethiopia, which draws on (i) scenarios of landscape change generated together with over 30 local stakeholder groups; (ii) distribution data of over 33,000 individual stems of trees and shrubs of over 100 species, collected through field surveys, and (iii) detailed information based on household surveys on how local species of trees and shrubs are used directly and as sources of ES by local people. In addition to these datasets, we used a high-resolution land use-land cover map generated from Sentinel satellite imagery.

Combining these datasets, two specific objectives of this paper were (i) to predict the current availability of woody-plant based ES in the landscape, and (ii) to quantify potential changes thereof under alternative scenarios of landscape change. Following Duguma et al.[33], we modeled ES in farmland and forest separately and merged the results. From predicted ES maps, we calculated the richness of ES hotspots—that is, overlaps of (combined) priority areas for different ES—because such areas are especially important for the ongoing provision of services (Fig. 1). We hypothesized that land sparing and land sharing scenarios would cause different changes to ES, such that ES hotspots would differ in extent and location between different scenarios.

Our work shows that conventional agricultural intensification based on land sparing scenarios would cause a displacement of woody-plant based ES from agricultural land to forested areas. Agricultural land-use intensification would thus very likely cause increased exploitation of the remaining forests as a source of vital ES, as well as loss of local access to ES. Such unintended side-effects of agricultural intensification are likely important in many tropical landscapes, and must be considered carefully when making policy recommendations about the integration of food production and biodiversity conservation.

Results
The scenarios
Our study focused on the Jimma coffee forest landscape in southwestern Ethiopia, Jimma zone. The participatory scenario planning process—described in detail in the "Methods" section—resulted in four qualitative narrative scenarios. The resulting scenarios were entitled 'Gain over grain', 'Mining green gold', 'Coffee and conservation', and 'Food first'. Brief summaries of the storylines of these scenarios are presented in Table 1 (for details see refs. 34,35). The scenarios considered a wide range of plausible environmental, social, and economic changes. Two scenarios—namely 'Gain over grain' and 'Coffee and conservation'—outline smallholder-based development pathways. Both integrate trees and shrubs within the farmland, and do not prioritize large-scale or industrial agricultural practices. In contrast, the scenarios 'Mining green gold' and 'Food first' imply large-scale and industrialized production of coffee and cereal crops, respectively. As in many other intensively used conventional agricultural landscapes around the world, these scenarios imply a homogenization of land covers, a loss of tree and shrub diversity within farmland areas, and a conversion of small forest patches to intensive farming. Large patches of forest are retained (i.e., "spared") in both scenarios (Fig. S1). The narrative scenarios were translated into spatially explicit land-use maps based on a current high-resolution land-use map derived from Sentinel satellite imagery, as well as rules grounded in the scenario logic. Translation from text to maps considered key features of the scenarios in relation to topography (elevation, slope), farmland heterogeneity as well as proximity to forest edge and roads[35]; details of the translation process are presented in the methods as well as in Tables S4–S7.

Woody-plant species and their ecosystem services
In surveys of 72 plots in farmland and 108 plots in forest, we identified 128 species of woody plants. The most abundant species (>1000 individuals)

Table 1 | Brief summaries of social-ecological scenarios envisioned for southwestern Ethiopia for the year 2040, for details see ref. 34

Scenario	Main storyline
Gain over grain: Local cash crops	This scenario prioritizes smallholder farmers' specialization and commercialization to boost development focused on cash crops such as coffee, the stimulant drug khat (*Catha edulis*), and fast-growing trees on available farmland and without expanding into the forest. The production of food crops is limited: little space remains for cultivating cereal crops, and few farmers maintain small cereal fields in the most fertile land. Incomes increase for some households, but inequality also increases, and traditional institutions collapse.
Mining green gold: Coffee investors	This scenario is characterized by the intensification and specialization of coffee production through large investors who use modernized production approaches with high external inputs. Smallholder land, communal land, and forests conducive for coffee investment have been transferred to capital investors for the creation and expansion of coffee plantations. Local farmers are left to farm marginalized areas unsuitable for large-scale coffee plantations. Social injustice increases and local and traditional knowledge is being lost.
Coffee and conservation: Biosphere reserve	This scenario is based on a more balanced land-use approach and best-practice sustainable resource management that combines sustainable agriculture, environmentally friendly coffee production, and tourism. The landscape is a diversified mosaic of forest and farmland; livestock production and communal grazing take place much like at present, and people grow fruit, vegetables, and grains. Aggregate profits generated are modest, but social capital and cultural integrity are high.
Food first: Intensive farming and forest protection	This scenario is driven by climate change making coffee production less viable, and by food production failing elsewhere in the country. Large amounts of food are now produced in the region through intensive, large-scale agriculture, which involves land consolidation, the clearing of woody vegetation, and the expansion of cropland into flat areas and wetlands. Remaining patches of natural forest are strictly protected. Social injustice increases and local and traditional knowledge are eroded.

included *Coffea arabica* L., *Vernonia auriculifera* Hiern., *Maytenus arbutifolia* (A. Rich.) Wilczek, *Justicia schimperiana* (Hochst. ex Nees) T. Anders., *Chionanthus mildbraedii* (Gilg & Schellenb.) Stearn, and *Dracaena afromontana* Mildbr (see refs. [36,37] for details). Drawing on surveys of 180 households, we identified 52 species used for house construction purposes, 38 species for farm implements, 38 species for fuelwood, and 21 species for medicine. Other widespread uses of woody species included the provision of bee forage (20 species), soil fertility (17 species), animal fodder (17 species), and poles and timber (9 species). In each case, specific diameter thresholds were applied, such that, for example, only individual trees with a diameter (DBH) > 10 cm could be used for poles and timber (for details, see ref. [26]).

We modeled each of these ES (i.e., the number of stems providing a given service in a given vegetation plot) in response to land use, topographic and human disturbance variables, separately in farmland and forest. In farmland, land cover diversity and slope were the most frequently selected predictor variables (seven out of eight models), and elevation was the second most frequently selected variable (four of eight models) (Table 2). In forest, elevation was the most frequently selected variable (six out of eight ES models), and current distance from the forest edge was the second most frequently selected variable (four out of eight models) (Table 3).

Change in woody-plant based ecosystem services under alternative scenarios
Predicted maps of individual woody-plant based ES revealed a strong effect of land-use scenarios on ES generation (Fig. S2). Hotspots were identified for each ES (detailed in the "Methods" section). The overlay of all ES hotspots produced ES hotspot richness (Fig. 2).

In the current landscape, woody-plant based ES hotspots spatially coincided most notably in forest, but numerous ES hotspots also occurred within farmland. The extent of forest (53%) and farmland (47%) in the baseline landscape was approximately balanced[33], Fig. 3B.

Under the 'Gain over grain' scenario, ES distributions remained similar to the current landscape. The 'Coffee and conservation' scenario showed an even more dispersed distribution of woody-plant-based ES across the entire landscape compared to the current landscape and the 'Gain over Grain' scenario, with numerous ES hotspots occurring in farmland. The maximum hotspot richness for the current landscape as well as for the 'Gain over grain' and 'Coffee and conservation' scenarios was six. Patterns in ES hotspot richness did not drastically change between the current landscape and the 'Gain over grain' and 'Coffee and conservation' scenarios (Fig. 2, Table S1). In all three landscapes, the highest hotspot richness was found in disturbed forests, in forest edges, and in small forest patches.

Contrary to this, the predicted maps for the 'Mining green gold' and 'Food first' scenarios showed a strongly simplified landscape with distinct and contracted areas in which ES generation was concentrated. Under these two scenarios, hotspot richness increased to up to eight ES hotspots coinciding spatially. At the same time, areas in the landscape that generated not a single ES hotspot also increased (Table S1), and farmland areas generally supported fewer ES hotspots than in the baseline or the other two scenarios.

Discussion
Our findings show that, for southwestern Ethiopia, intensive agricultural practices—for either cash crops or food crops—would lead to a contraction of woody-plant-based ES, from a mixture of farmland and forested areas to remnant forest patches. Assuming local people need access to these ES, these results imply both a decrease in local accessibility of ES and increased pressure on remaining forest patches in scenarios of agricultural intensification. The effectiveness of sparing such patches from human influence, in this context, is questionable from a practical perspective, and could have negative implications for local livelihoods. We showed this using an analysis of ecosystem service hotspot richness for the present landscape in comparison with four future socio-economic land-use scenarios. Below we discuss our findings in detail, first in the context of the current landscape, then for the land-use scenarios, and against the backdrop of land sharing and land sparing approaches.

Current landscape context
In the current landscape, the highest hotspot richness was found mostly at the edges of forest, in small patches of forests and in disturbed or fragmented forests (Fig. 2). This coincides with locations that the local community can easily access. At present, the landscape is characterized by a forest and farmland mosaic dominated by smallholder farmers, whose main economic activities are dependent on subsistence agriculture, livestock rearing, and coffee production[27,30]. Even though the forest is formally owned by the state, local people have access rights to many ES generated from the forest through different mechanisms such as customary mechanisms and inheritance[29,38] as well as historically developed social standards and norms, e.g., ref. [38].

Compared to the past, present access to ES generated from woody plants is more constrained due to a decrease in forest extent[27,33,39]. Additional factors that can constrain current access for different community members to ES are distance to forest, rules and regulations on forest governance such as an increased protection status of the forest, forest ownership, and property rights and tenure insecurity, e.g., refs. [26,27,40]. Such factors that modify access are also found elsewhere. For instance, in the Solomon

Table 2 | Modeling results in farmland for woody-plant associated ES

ES	Terms	Coefficients	Std. Error	Pr(>|z|)	R²
House construction	(Intercept)	5.476	0.114	<2e−16	0.283
	Elevation	0.267	0.143	0.062	
	Farmland type	0.229	0.119	0.054	
	Land cover diversity	0.518	0.133	9.70E−05	
	Slope	0.417	0.130	0.001	
Farm implements	(Intercept)	2.349	0.302	7.84E−15	0.206
	Farmland type	0.328	0.201	0.102	
	Land cover diversity	0.678	0.215	0.002	
	Slope	0.399	0.224	0.074	
Fuel wood	(Intercept)	5.999	0.103	<2e−16	0.229
	Percent woody vegetation in 2 km	0.244	0.120	0.042	
	Slope	0.106	0.119	0.372	
Medicine	(Intercept)	5.550	0.116	<2e−16	0.198
	Elevation	0.290	0.132	0.028	
	Farmland type	0.142	0.121	0.240	
	Land cover diversity	0.234	0.124	0.060	
	Slope	0.304	0.133	0.022	
Poles and timber (Conditional model)	(Intercept)	1.324	0.156	<2e−16	0.109
	Elevation	0.402	0.186	0.031	
	Historical farmland distance	−0.323	0.152	0.034	
	Farmland type	0.415	0.145	0.004	
	Land cover diversity	0.417	0.162	0.010	
	Slope	−0.488	0.165	0.00314	
Poles and timber (Zero-inflation model)	(Intercept)	−3.790	1038.997	0.997	
	Elevation	1.475	0.749	0.049	
	Farmland type	6.280	2936.430	0.998	
	Percent woody vegetation in 200 m	−0.932	0.613	0.129	
	Slope	−1.177	1.511	0.436	
Soil fertility	(Intercept)	5.442	0.206	<2e−16	0.163
	Elevation	0.356	0.205	0.083	
	Land cover diversity	0.212	0.123	0.084	
	Slope	0.229	0.124	0.065	
Bee forage	(Intercept)	4.964	0.132	<2e−16	0.215
	Farmland type	0.236	0.133	0.076	
	Land cover diversity	0.251	0.131	0.055	
Animal fodder	(Intercept)	3.873	0.138	<2e−16	0.185
	Land cover diversity	0.347	0.133	0.009	
	Slope	0.268	0.152	0.077	

For each ES, the table shows the terms included in the selected model, their coefficients, standard errors, *p*-values and R². All models were negative binomial (model: glmmTMB (truncated >0, negative binomial distribution, link = log, except Poles and Timber, which was modeled with zero-inflated negative binomial and negative binomial).

Table 3 | Modeling results in forest for woody-plant associated ES

ES	Terms	Coefficients	Std. Error	Pr(>|z|)	R²
House construction	(Intercept)	5.178	0.063	<2e−16	0.237
	Elevation	−0.337	0.063	7.31E−08	
	Forest distance	−0.043	0.060	0.473	
	Heat load index	0.122	0.066	0.063	
Farm implements	(Intercept)	2.872	0.059	<2e−16	0.334
	Elevation	−0.519	0.070	1.03E−13	
	Slope	0.127	0.064	0.045	
Fuel wood	(Intercept)	4.776	0.191	<2e−16	0.298
	Elevation	−0.625	0.129	1.17E−06	
	Forest distance	−0.235	0.077	0.002	
Medicine	(Intercept)	3.736	0.095	<2e−16	0.227
	Forest distance	−0.419	0.108	0.0001	
	Forest type	−0.174	0.113	0.123	
	Heat load index	0.361	0.094	0.0001	
	Topographic wetness index	0.216	0.098	0.027	
Poles and timber	(Intercept)	0.799	0.132	1.54E−09	0.301
	Elevation	0.599	0.120	6.31E−07	
	Forest distance	0.302	0.107	0.005	
Soil fertility	(Intercept)	3.222	0.276	<2e−16	0.236
	Forest type	−0.542	0.148	0.0003	
	Heat load index	0.063	0.087	0.465	
Bee forage	(Intercept)	4.068	0.336	<2e−16	0.309
	Elevation	−0.953	0.194	9.32E−07	
	Percent woody vegetation in 500 m	−0.374	0.119	0.002	
	Topographic wetness index	−0.130	0.110	0.235	
Animal fodder (Conditional model)	(Intercept)	3.538	0.185	<2e−16	0.175
	Elevation	0.187	0.154	0.225	
	Forest distance	0.196	0.101	0.052	
	Forest type	0.237	0.129	0.067	
	Heat load index	−0.151	0.083	0.068	
Animal fodder (Zero-infl. model)	(Intercept)	−17.358	3179.662	0.996	
	Forest type	−7.651	1531.706	0.996	

For each ES, the table shows the terms included in the selected model, their coefficients, standard errors, *p*-values and R². All models were negative binomial (model: glmmTMB (truncated >0, negative binomial distribution, link = log, except Poles and Timber, which was modeled with zero-inflated negative binomial and negative binomial).

Islands, physical availability (e.g., quantity, quality, and location/distance) and rights regarding appropriation and management are some of the main factors limiting access to ES[20], while in Nepal, restricted collection period/time (i.e., Dec–Jan, and May–Jun) of forest products from community forestry is one of the limiting factors identified for access to ES[23]. In addition, local communities' access to ES can be limited by power relationships, information, technology, tools and markets[21,24]. With these factors that shape access in mind, we discuss below how land-use scenarios affect woody-plant based ES distribution, and how this in turn is likely to influence local access to ES.

Land sharing scenarios: gain over grain and Coffee and conservation
The 'Gain over grain' scenario showed a similar distribution of ES hotspots to the current landscape. This similarity exists because the extent of
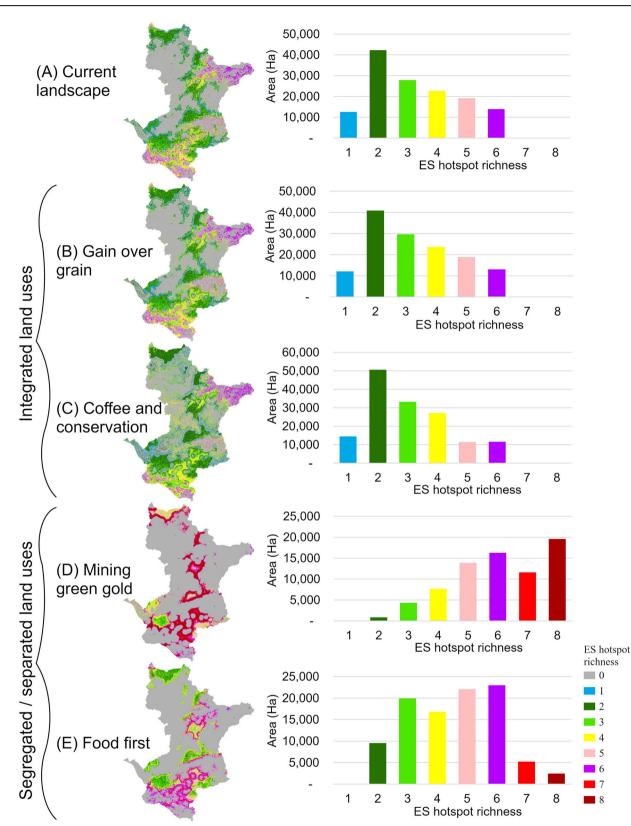
Fig. 2 | Richness of ecosystem services hotspots throughout the landscape. Panel **A** shows the current landscape, while panels **B–E** show four scenarios of plausible future changes. In the legend, for all the panels, zero (0) shows the complete absence of even a single ecosystem service hotspot, while eight (8) shows the overlap of all eight ecosystem services considered in this study. Ecosystem services hotspot richness of 0 (gray in maps) accounted for approximately 51% both in the current landscape and the 'Gain over grain' scenario, 47% in 'Coffee and conservation', 74% in the 'Mining green gold' scenario, and 65% in 'Food first' scenario (see Table S1 for details).
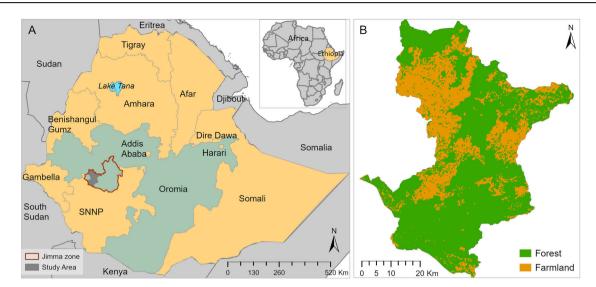
Fig. 3 | Location map of the study area in Jimma Zone, Oromia, Ethiopia. In panel **A**, SNNP stands for Southern Nations Nationalities and People's Region[74]. Panel **B** shows the present day land cover map that illustrates the distribution of forest (in green color) and farmland (in brown) (from Duguma et al.[33]).

farmland woody vegetation and forest area remained unchanged relative to the status quo in this scenario, while specialization in commercial cash crops took place on farmland[34]. These cash crops—namely coffee, khat, and eucalyptus—could potentially increase the income of smallholder farmers, e.g., refs. 34,41,42.

Despite this possible advantage, evidence suggests that eucalyptus plantations, for instance, which were established to substitute for woody-plant-based ecosystem service losses in the past due to deforestation, could not adequately substitute the full suite of ES generated from native forest trees[43]. Indeed, specialization on cash crops in the farmland could have negative effects in the long term because agrochemical use is common for such crops in Ethiopia, e.g., refs. 41,44. Furthermore, cash crops such as khat have a potential to cause social disorder (such as conflict, crime, and mistrust) that affect local traditions[34,44]. In addition, as more farmland is occupied by cash crops, local community may face food insecurity and low dietary diversity because of a lack of food crops. Finally, under this scenario local community could encounter similar access issues to woody-plant-based ES as in the current landscape, relating to the physical distribution of the forest, rules and regulations on forest governance, property rights, and tenure insecurity (see previous section).

The 'Coffee and conservation' scenario also showed a degree of similarity with the current landscape in ES hotspot distribution. Under this scenario, the area in the landscape that generated no woody-plant-based ES decreased. ES hotspots in this scenario were more widely distributed in the landscape due to restoration and regeneration of degraded farmland in this scenario[34,35]. At the same time, the area that generated high levels of many ES simultaneously (i.e., five or six ES) was also reduced, indicating that forests in this scenario may be under less intense human pressure than presently.

Farmland heterogeneity is widely acknowledged to be key for restoring and sustaining farmland biodiversity[45], and as we show here, also underpins the availability of many woody-plant based ES. In addition to absorbing pressure from the forest, based on physical availability and distribution of forest and woody plants, this scenario would likely increase access to ES for the local community.

One possible limitation of this scenario is that farming on degraded steep slopes was replaced by regeneration and restoration of woody plants, which could, in the short term, reduce food availability. Similar trade-offs have been acknowledged in different parts of the world as a challenge for integrating farming and conservation, e.g., refs. 1,6. In the long run, however, biodiversity-friendly farming as implied in this scenario may be most suitable to ensure social-ecological resilience.

Land sparing scenarios: mining green gold and Food first

'Mining green gold' and 'Food first' were based on land-use intensification involving large-scale land consolidation and mechanized farming for coffee plantation and food crops, respectively[34]. In both scenarios, no integration occurred of food production and biodiversity conservation, and remaining forest patches were to be "spared" through strict regulations limiting access for local communities.

Compared to the current landscape, these scenarios revealed strong changes in ES hotspot richness; richness increased in the smaller available area and contracted to the center. This effect occurred because of a decrease in the total amount of woody vegetation, including its widespread loss in farmland, as well as a contraction of near-natural forest patches. The contraction of woody-species based ES hotspots could increase the distance and time for many local community members to access woody-plant based ES; as well as putting potentially high levels of pressure on the remaining forest patches.

Similar findings elsewhere, for instance in Argentine Chaco, showed widespread and major losses in multiple ES as a result of agricultural expansion into forests[46]. Moreover, "land sparing" caused negative impact on human well-being in Para, Brazil[47], and has already been shown to reduce access to important provisioning ES in southwest Ethiopia[29,43]. While both physical and legal factors could limit access to ES by the local community, such strict protection of remaining forest is vital for the conservation of native species in the context of a "land sparing" strategy[5,8,48].

Further, the production method used in these two scenarios—industrialized production including agrochemical inputs and large-scale investment—in itself is likely to cause problems for farmland biodiversity and many smallholder farmers. Previous studies on large-scale agricultural intensification, for instance, on socio-economic outcomes in Southeast Asia[49], deforestation patterns in Cambodia[50], or impacts on indigenous communities in tropical Africa such as Ethiopia[29,43,51], Rwanda[52,53], and Tanzania[54] have consistently shown that many local stakeholders were excluded from the potential benefits of increased production. The two scenarios do, however, have potential benefits for the Ethiopian economy at large, for example through generating incomes from exports[34].

Finally, several studies elsewhere in the world, for example, in Southeast Asia, revealed that yield increases caused by agricultural intensification stimulated further agricultural encroachment, e.g., refs. 55,56 rather than supporting the strict protection of remnant forest. Conversely, if strict protection of remaining forest patches was indeed successful, this very likely would exacerbate existing inequalities in access to ecosystem services, as

evidence from some tropical African countries such as Ethiopia[27], Rwanda[52,53], and Tanzania[54] has shown. The two intensification-based scenarios considered therefore may not lead to the effective "sparing" of remaining forests, or if sparing is successful, community well-being may be seriously impaired due to reduced access to woody-species based ES.

Limitations and future research

Although the general results and conclusions of our work are very likely robust—and probably applicable to other parts of the world—we appreciate that some limitations are unavoidable in multi-facetted empirical work such as what we presented. All findings draw on the quantitative and qualitative data generated from the woody plant survey, household survey, different stakeholder discussions, and land-use scenario maps. By definition, none of these data sources are necessarily perfect—their accuracy may be influenced by sampling errors, subjectivity of stakeholders, or the accuracy in image classification. We are confident, however, that the striking general patterns derived are robust.

Future research may need to explore which areas of the landscape experience positive or negative changes in woody plant-based ES provisioning under each scenario. More broadly, future research could examine similar scenarios in other landscapes, to assess if there are indeed general implications of landscape commodification or land-use intensification on local livelihoods that extend beyond our study area.

General implications

Our work represents a systematic evaluation of future land-use strategies on long-term ecosystem service provisioning that could guide land-use management policies for integrated biodiversity conservation and sustainable development in smallholder farming landscapes. In a heterogeneous world, land-use choices must take into account circumstances depending on spatial characteristics, actors' rationalities, local contexts and socio-economic dynamics[56]. We may need both land sharing and land sparing in different contexts and to different extents—because both have individual and complementary benefits but also shortcomings[4,6]. As land sparing literature has shown, forest matters for biodiversity, especially for the conservation of rare or otherwise sensitive species. But agricultural land has important complementary values for biodiversity, and can be critical, as we showed here, for the generation of ES that are vital for local people. Considering the dependence of local people on woody-plant based ES is vital in many landscapes of the Global South in particular. If local needs for woody-plant based ES are not considered in conservation planning, conservation measures will most likely not be successful, because people are likely to go into the forest and then illegally extract these ES from the forest out of necessity.

Methods

Our methodological approach was interdisciplinary. Briefly, it involved the integration of different disciplinary data—participatory scenario narratives developed with local stakeholders, spatially explicit land-use and land cover maps based on the narrative scenarios, data on woody-plant use collected via a household survey, data on woody species distribution collected using ecological field surveys in different land-uses, as well as topographic variables and human disturbance variables generated from land-use and land cover maps (Fig. 1). We used ArcGIS Pro[57] and R[58] to integrate and analyze the data. We statistically modeled individual ES, predicted the selected models spatially, extracted individual ES hotspots and aggregated ES hotspots to produce ES hotspot richness map. The specific methods are explained step by step below.

Study area

Our study focused on the Jimma coffee forest landscape in southwestern Ethiopia, Jimma zone (Fig. 3). The area is characterized by a forest and farmland mosaic dominated by smallholder farmers, whose main economic activities are cereal crop production, livestock rearing, and coffee production. The study area is undulating, and falls within altitudes of approximately 1200 to 3000 m above sea level. The study region receives annual rainfall in the range of 1500 to 2000 mm[59], with the main rainy seasons between June and September, although occasional rainfall occurs throughout the year. The mean annual temperature is approximately 20 degrees Celsius[60], with mean daily minimum and maximum temperatures of 12 and 28 degrees Celsius, respectively[61]. We used the classification of farmland and forest[33] to separately model ES in farmland and forest, because different drivers operate in these two very different environments. Modeling results were finally merged for the whole landscape.

Scenarios

Scenario development process. The scenario development process for this specific landscape was documented in detail by Jiren et al.[62] and Jiren et al.[34]. Briefly, participatory scenario planning was conducted to envision landscape change up to 2040. First, Jiren et al.[62] identified thirty-five broadly representative stakeholders concerned with issues around food security and biodiversity conservation in the study area, based on an in-depth stakeholder analysis. These stakeholders included local people and community-level organizations (community leaders, religious leaders, community cooperatives, health professionals, and elementary school teachers), governmental organizations from multiple sectors, non-governmental organizations, and civil society organizations. Following the identification of stakeholders, participatory scenario planning workshops were conducted at different levels of government and in different rounds of workshops, including a validation workshop[34]. This scenario development process resulted in four qualitative narrative scenarios ('Gain over grain', 'Mining green gold', 'Coffee and conservation', and 'Food first') that are briefly summarized in Table 1. In addition to the initial validation by stakeholders[34], Duguma et al.[35] discussed in detail the plausibility of each scenario based on current government policies and independent research, and confirmed that all scenarios are plausible for the study region.

Translation of scenarios. We briefly summarize the translation steps here—details were presented by Duguma et al.[35]. To translate the narrative scenarios developed by participatory scenario planning[34], the following steps were followed. First, a baseline map of current LULC was created from Sentinel-2 satellite imagery. Second, translation rules were created for each scenario detailing how specific LULC types should be converted under each scenario. The rules were established using a combination of land cover classes, biophysical elements (such as slope, heterogeneity, and altitude), and distance from forest edge—for example, where narrative text indicated that new coffee plantations were established, we specified logical rules where such coffee plantations would likely occur (e.g., at the right altitude, on flat agricultural land (see Tables S4–S7 for a list of all rules). Third, to then produce spatially explicit scenario maps based on these rules, the proximity-based scenario generator of the Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) software[63] was used.

Data

Datasets used for our study are indicated in Fig. 1. Briefly, two datasets were used to model potential ES provided by woody-plants: field data on woody-plant use and woody-plant species (the outcome variable) and spatial predictor variables (indicators of human disturbance and topographic variables)[64].

Ecosystem services by woody-plants. We surveyed woody plants in 72 individual 1 ha plots in farmland and in 108 individual 20 m by 20 m plots in forest[26,37], which were stratified across major landscape gradients. Use of woody-plant based ES was assessed from 180 randomly selected households[26]. For this study, of eleven major uses delivered by over 100 woody plant species, we focused on eight ES which we considered the most important ones in the daily lives of local community[29–31]. These were house construction, farm implements, fuel wood, bee forage, medicine, poles and timber, soil fertilization, and animal fodder. Detailed

descriptions and definitions of these response variables are available in supplementary material Table S2[30]. We used woody-plant species abundance to quantify and map the potential ES provided by woody plants (individuals of tree and shrub species with a height of at least 1.5 m[26,37], with diameter thresholds varying for each ES (Table S2)). Abundance was estimated within 20 m by 20 m plots in forest, and 1 ha plots in farmland. Farmland results were downscaled to 20 m by 20 m before merging forest and farmland results across the entire landscape. Thus, results were expressed as the number of individual trees potentially providing a particular ES within each 20 m by 20 m pixel across the entire landscape.

Candidate predictors. Fifteen candidate social-ecological predictors were identified based on our knowledge of the landscape, the ES considered, and literature on drivers of ES, e.g., refs. 65,66, as well as data availability for the baseline and future scenarios. These included both topographic variables and indicators of human disturbance. Details of predictor variables were presented in Duguma et al.[33] and are summarized in Table S3. Predictor variables were examined for their approximate normality using histograms, transformed where required, and center-scaled. After problematic variables were removed (i.e., those highly redundant with other variables or strongly zero-inflated), we used VARIMAX rotated PCA to identify five dominant, uncorrelated dimensions of the predictor variables.

For farmland, this process selected elevation, slope, percent woody vegetation (in a 200 m radius), landscape diversity (at 1 ha), and the historical (1985) distance to the forest edge. Elevation was found to correlate positively with current distance to forest edge, and negatively with landscape diversity (at 1 ha) and percent woody vegetation (in both a 500 m and 2 km radius). Slope was correlated positively with heat load index, topographic roughness, and negatively with topographic wetness index. We also included the binary variable of farmland age (extent prior to 1985).

For forests, this process selected current distance to the forest edge, slope, elevation, heat load index, and topographic wetness index. Current distance from the forest edge was positively correlated with percent woody vegetation (at 500 m and 2 km radius), slope was positively correlated with roughness, and elevation was positively correlated with historic (1985) distance to the forest edge. We also included the binary variable of forest age (extent prior to 1985).

Statistical modeling and spatial prediction
We used generalized linear models due to their direct interpretability, which facilitates model assessment. We selected separate models for each ecosystem service in each major land cover (i.e., farmland versus forest) by first assessing the full model (i.e., a linear additive combination of the selected predictors) with Poisson and negative binomial distributions, both without and with zero inflation (with the zero inflation echoing the core full model) using the R package *glmmTMB*[67].

Where these full models had convergence issues, we iteratively removed parameters (starting with those with the largest absolute coefficients) until there were no further issues. We assessed these models for zero-inflation, dispersion, and AIC. For the selected models, we then reduced the number of variables in each model by comparing all combinations of sub-models based on AICc using the R package *MuMIn*[68]. The top 5 models were then compared using repeated cross-validation (10 fold, with 3 repeats) and metrics of root mean squared error, explained deviance (R squared), and mean average error using the R package *yardstick*[69]. We then performed checks of model residuals using the R package *DHARMa*[70]. Where this process did not produce satisfactory models, we also assessed models that used alternative predictors, removed extreme outliers, and/or included quadratic terms on elevation. We conducted modeling in R version 4.1.2[58], including the packages mentioned above. Spatial prediction was done using the 'terra::predict' command in the R package *terra*[71]. We mapped each ES for farmland and forest separately and merged the results to the landscape scale.

Ecosystem services hotspot richness
We used a hotspot analysis approach following Qiu et al.[72] and Mitchell et al.[73] to identify areas important for ES. We defined hotspots as pixels in the upper 20th percentile of values of areas in the landscape for each potential ES. To arrive on the 20th percentile we used a quantile classification approach for individual ES at a cut threshold of 80% in R software. The upper 20th percentile was extracted to represent the hotspot of each ES in ArcGIS Pro2.9. This approach is an effective and simple way to identify areas with a high priority for long-term ecosystem service maintenance[73] and is useful to communicate findings to stakeholders. Finally, we overlaid hotspots of individual ES to map the richness of ES hotspots. Based on this, we evaluated changes in ES hotspot richness under the four scenarios relative to the current landscape.

Data availability

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Author contributions

D.W.D., J.S., D.J.A., and J.F. conceived the ideas and designed methodology; G.S. designed vegetation data collection method, collected the data, and identified the plant species; D.W.D. and E.L. analyzed the data. The first draft of the manuscript was written by D.W.D. All authors contributed critically to the draft, read and approved the final manuscript for publication.

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