Current Biology

Carbon Storage and Land-Use Strategies in Agricultural Landscapes across Three Continents

Highlights

- Above-ground carbon stocks decline rapidly with increasing agricultural yields

- Land sparing could potentially lower carbon losses compared to other strategies

- Reducing agricultural demand is key, as all strategies result in carbon stock losses

- Results are consistent for contrasting farming systems across three continents

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In Brief

Williams et al. evaluate the potential effects of land-use strategies on above-ground carbon stocks in contrasting farming systems across three continents and find that land sparing (high-yield agriculture combined with habitat conservation) consistently has a higher potential to sustain regional above-ground carbon stocks than any other strategy.

CellPress

Report

Carbon Storage and Land-Use Strategies in Agricultural Landscapes across Three Continents

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SUMMARY

The loss of carbon stocks through agricultural land-use change is a key driver of greenhouse gas emissions [1–4], and the methods used to manage agricultural land will have major impacts on the global climate in the 21st century [4–9]. It remains unresolved whether carbon losses would be minimized by increasing farm yields and limiting the conversion of natural habitats ("land sparing"), or maximizing on-farm carbon stocks, even at the cost of reduced yields and therefore greater habitat clearance ("land sharing"). In this paper, we use field surveys of over 11,000 trees, in-depth interviews with farmers, and existing agricultural data, to evaluate the potential impacts of these contrasting approaches, and plausible intermediate strategies, on above-ground carbon stocks across a diverse range of agricultural and natural systems. Our analyses include agroforestry and oil palm plantations in the humid tropics of Ghana; cattle ranching in dry tropical forest in Mexico; and arable cropping in temperate wetlands and forests in Poland. Strikingly, despite the range of systems investigated, land sparing consistently had a higher potential to sustain regional above-ground carbon stocks than any other strategy. This was the case in all three regions and at all plausible levels of food production, including falls in demand. However, if agricultural production increases to meet likely future demand levels, we project large decreases in above-ground carbon stocks, regardless of land-use strategy. Our results strongly suggest that maintaining above-ground carbon stocks will depend on both limiting future food demand and minimizing agricultural expansion through linking high-yield farming with conserving or restoring natural habitats.

RESULTS

Carbon Stocks Declined Rapidly with Conversion from Natural Habitats

To model the relationship between above-ground carbon stocks and agricultural yields, we measured tree biomass at sample points in 25 or 26 1-km^2 sites in each region, across a range of agricultural yields, from zero-yielding natural habitats to high-yield agriculture. In Ghana, sites ranged from moist evergreen and moist semi-deciduous tropical forest through mosaics of agroforestry, remnant vegetation, and mixed agriculture, to oil palm plantations. In Mexico, we investigated tropical dry and semi-deciduous forests and cattle ranching systems, from low intensity grazing on pastures and natural vegetation through to intensively managed improved pastures and supporting maize production. Finally, in Poland, we sampled fen mires and flood plains on organic soils and temperate mixed deciduous forests on mineral soils as natural habitats, and a gradient from mixed agriculture to intensive arable farms. See STAR Methods for details on yield and carbon stock estimation and modeling approach.

For each region, we fitted flexible non-linear functions to the data and found that relationships were similar across regions, with consistent, rapid declines in above-ground carbon stocks between natural habitats and agricultural sites (Figure 1). There were two minor exceptions: in Ghana, calorific yields were highest in oil palm plantations, which also contained higher carbon stocks than most intermediate- and low-yielding sites consisting of small-holder mixed cropping systems. Stocks in oil palm, however, remained well below those in zero-yielding forests. In Poland, above-ground stocks in sites on organic soils were highest at very low yields but remained well below stocks in forest sites.

Land Sparing Offered a Greater Potential to Conserve Regional Carbon Stocks than All Other Strategies Assessed

To assess the potential impacts of different land-use strategies on regional carbon stocks, we calculated a range of plausible future agricultural demand levels, from close to zero to probable 2050 demand levels. We estimated the agricultural land required to meet each demand level, at all plausible yields, from the lowest yields that could meet demand to 125% of current maximum observed yield in each region, assigning remaining land to natural habitats (Figure 2). Finally, we used the relationships between yield and above-ground carbon stock density (Figure 1) to estimate carbon stocks in both the agricultural and non-agricultural land, summing the two to obtain a regional estimate, and dividing by the area of the region to obtain a mean above-ground carbon stock across the region (see STAR Methods for details).

Across all regions, projected above-ground carbon stocks decreased under all land-use strategies as production levels
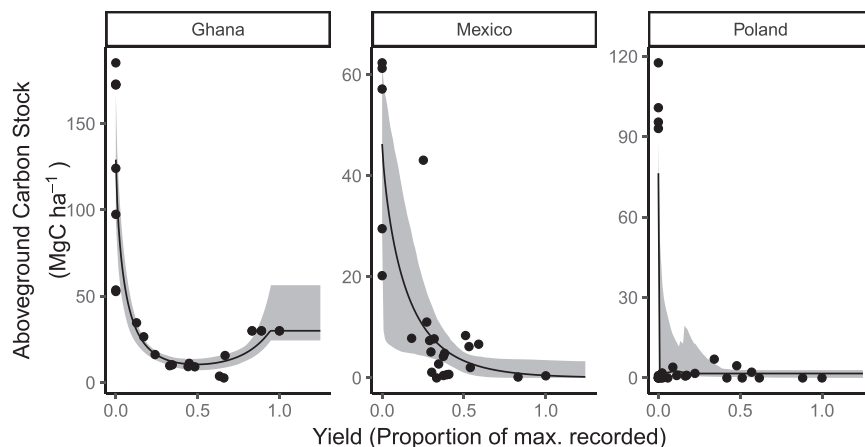
Figure 1. Relationships between Above-Ground Carbon Stock Density and Agricultural Yield in Three Farming Systems

Relationships between above-ground carbon stock density and agricultural yield in three farming systems. Shaded areas show the bootstrapped 95% confidence intervals around estimates. See STAR Methods for details on yield and carbon stock estimation and modeling approach. See Figure S1 for separate curves fitted to different soil types in Poland and Figure S2 for the uncapped curve for Ghana.

See also Table S1.

increased, but land sparing consistently resulted in greater regional stocks than any other strategy (Figure 3, Figure S3). Land sharing consistently resulted in lower stocks than any of the 148 intermediate strategies we examined, although the relative difference varied between regions, being greater in Poland, which had very low above-ground stocks on any agricultural land, than in Ghana or Mexico, where low-yield sites maintained slightly higher stocks (Figure 1). As yields in intermediate strategies increased, so did projected regional carbon stocks because strategies became more similar to land sparing, and greater areas of baseline habitats were projected to survive (Figure S4).

DISCUSSION

Despite the wide range of ecosystems and farming systems we investigated, patterns in above-ground carbon stocks were remarkably consistent: in each system, stocks were far lower on agricultural sites of any yield than in natural habitats, and differences between agricultural sites of different yields were relatively small. The rare exceptions—in organic soil sites in Poland, and high-yield sites in Ghana—did not alter this overall pattern. We also projected consistent declines in regional stocks as agricultural production increased. These results strongly suggest that minimizing agricultural expansion will conserve regional above-ground carbon stocks to a greater extent than attempting to conserve stocks on agricultural land. For any given level of agricultural production, this will require maximizing agricultural yields and linking yield increases to natural habitat conservation: a land sparing approach [10].

Importantly, land-sparing scenarios resulted in lower stock losses, relative to a landscape consisting entirely of natural habitat, than all other strategies and at all realistic production targets, including reductions in production. The land sparing-land sharing continuum has been characterized as a dichotomy [11, 12] or based on the assumption that food production must increase [11]; our results show that, for our diverse study systems and for above-ground carbon stocks, neither characterization is justified. Rather, land sparing has the potential to outperform all other agricultural strategies we modeled, and to do so at all plausible production targets. Indeed, land-sparing scenarios had the greatest advantage over land-sharing strategies at lower production targets.

Our analyses strongly imply that minimizing agricultural expansion through limiting growth in demand, and combining high-yield agriculture with natural habitat protection has the greatest potential for conserving carbon stocks. This supports previous work investigating the potential impacts of land-use strategies on carbon stocks [13–15], which found that stocks declined as production targets increased and that land sparing has the potential to minimize the trade-off between regional food production and carbon stocks. Our analyses expand this work by exploring a wide range of agricultural yields and comparing all feasible land-use strategies, as well as using a consistent analytical framework across a diversity of regions. Our results using this framework also support a previous analysis of the Mexican study system based on a more complex scenario-building approach [15]—suggesting our main conclusion may be robust to the exact analytical method used. Given the breadth of our study systems in terms of climate, natural habitats, and agricultural systems, it also seems likely that these results hold for other naturally forested systems, or habitat types with considerable above-ground carbon stocks, though may not necessarily apply in systems such as grasslands, where most biomass is below ground [16, 17].

We were not able to include data on below-ground carbon stocks or carbon fluxes but have several reasons to believe that their inclusion would not change our overall findings. Carbon stocks in below-ground biomass are typically closely correlated with above-ground biomass [18] and so likely show similar responses to agricultural yields. Soil organic carbon also shows large declines with conversion from natural habitats to most agricultural lands [19, 20], and while yield increases may result in additional losses, it seems likely that these initial declines are greater than subsequent changes—again meaning that land sparing would have the greatest potential for carbon retention. The climate-change impacts of land-use strategies will depend on both carbon stocks and net greenhouse gas emissions [21], which can increase with yields [6]. If this increase were sufficiently large, then it could counter the benefits of greater landscape-wide retention of carbon stocks that land sparing permits. However, differences in fluxes from high-yield, compared to low-yield, systems are small relative to changes in carbon stocks from conversion to agriculture, meaning that land sparing is still likely to minimize carbon emissions [5, 22].

Using low-yield, relatively high-carbon farming has been suggested as a strategy to reduce edge effects and increase
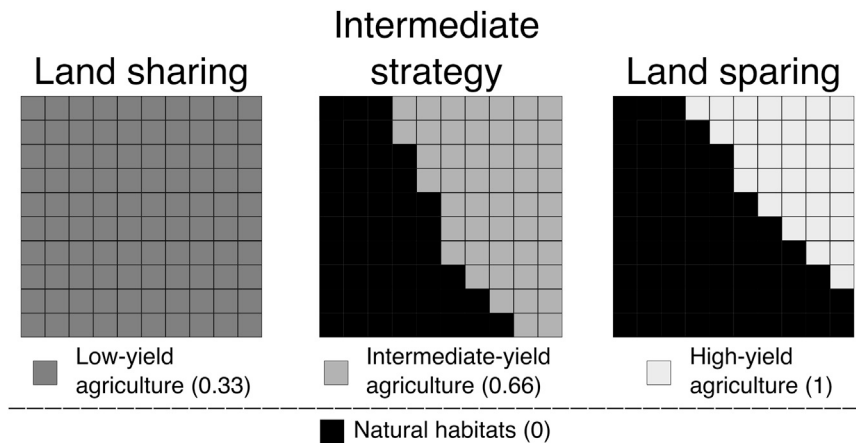
Figure 2. Schematic of Three Different Land-Use Strategies: Land Sharing Uses All Available Land at the Lowest Possible Yields

Schematic of three different land-use strategies: land sharing uses all available land at the lowest possible yields; land sparing maximizes yields and conserves natural habitats; intermediate strategies use yields between these two extremes. All landscapes produce the same amount of food, with numbers representing the relative yields of different agricultural lands. We show a representative intermediate strategy but tested hundreds of strategies between land sharing and land sparing.

connectivity between spared patches [23]. However, such a strategy will necessarily reduce the area of land spared and will only outperform land sparing if edge effects greatly reduce carbon stocks in natural habitats but are largely eliminated when natural habitats abut low-yield farming. The small differences in carbon stocks between agricultural sites of different yields, and the large declines compared to natural habitats, do not suggest that these conditions are present in our study systems. Similarly, while previous analyses [24, 25] suggest that edge effects could reduce regional carbon stocks under land-sparing and intermediate strategies, the very low stocks under land sharing mean any such changes are unlikely to alter our conclusions.

Our results provide insights for the UN's Reducing Emissions from Deforestation and Forest Degradation program (REDD) [1], highlighting the value of focusing on coupled efforts to boost farm yields and slow habitat conversion [6, 26]. However, our findings suggest that efforts to increase on-farm above-ground carbon stocks—for example, through the planting of shade trees [27] —are unlikely to maintain regional stocks if interventions involve a yield penalty, as they do in the systems we studied. Interventions that increase carbon stocks without reducing agricultural yields could be effective. For example, intensive silvopastoral systems involving banks of protein-rich woody legumes may increase both yields and on-farm carbon [28]. However, our results strongly suggest such approaches should be used as part of a land-sparing strategy and explicitly linked to habitat conservation rather than being used to compensate for the loss of natural habitats.

Despite its advantages, land sparing is unlikely to occur passively; rebound effects mean that increasing yields may not reduce local land clearance if it increases the profitability of farming, particularly for goods with highly elastic demand such as palm oil or meat [29–31], while protecting habitats may not benefit regional carbon stocks if there is leakage of habitat clearance to other areas [32, 33]. The far lower stocks on agricultural land, compared to natural habitats, mean that any degree of land sparing is likely to reduce the loss of regional carbon stocks [34], but rebound and leakage will reduce these benefits. Instead, "active land sparing" will be needed: the coupling of yield increases with habitat protection through land-use zoning; economic instruments such as taxes or subsidies; strategic invest-

ment to alter the relative profitability of agriculture near and far from agricultural frontiers; or environmental standards and certifications [26, 35].

Our results complement multiple analyses that have found similar and consistent results for trade-offs between biodiversity and food production across the world [13, 15, 36–39]; for each region and taxon, land sparing was projected to conserve larger populations of more species than any other strategy. Relationships between agricultural land-use strategies and the provision of other ecosystem services is less clear [40]. If on-farm ecosystem services to agriculture—such as pollination or pest control—increase yields, after allowing for any land taken out of production in order to maintain them, then conserving them can be part of a land-sparing strategy, so there need be no conflict between their retention and conserving carbon stocks or biodiversity. If, however, there is a trade-off between food production and service provision—as may be likely for water quality maintenance [41, 42] or cultural services [43]—then the least damaging land-use strategy will be determined by the exact nature of this relationship, and there remains the possibility of trade-offs between services. Finally, how land-use strategies interact with and affect the livelihoods and welfare of local people—both farmers and those dependent on natural habitats—is likely to depend on local and national context. Each strategy is likely to result in winners and losers, and ensuring that land-use plans are fair and equitable is a major challenge for researchers and policy makers [21].

These caveats notwithstanding, given rising global food demand [6], the urgent need to reduce greenhouse gas emissions [44], and widespread declines in biodiversity [45], our results form an important step for policy makers to plan sustainable landscapes. Using data from thousands of trees, in study sites from three diverse regions of the world, we found that above-ground carbon stocks decline rapidly along a yield gradient. Land-sparing scenarios were therefore projected to result in lower losses of carbon stocks than all other strategies examined, including land sharing. This result greatly expands previous analyses [13–15] by testing a far wider range of strategies across a wider range of agricultural and natural systems and by providing a clear and repeatable framework for evaluating how land-use strategies affect carbon stocks. Given the strength of our results and the breadth of our study systems, we suggest
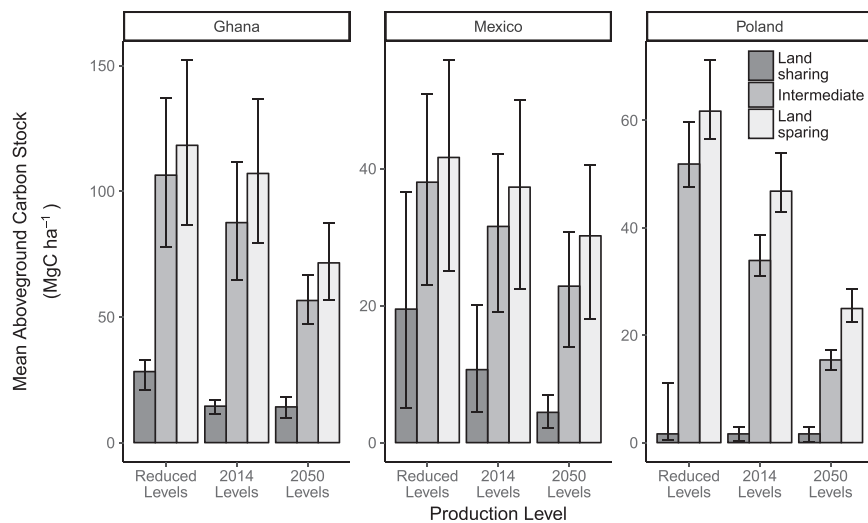
Figure 3. Projected Mean Above-Ground Carbon Stocks Averaged across Entire Study Regions under Different Land Use Strategies at Different Production Levels

Projected mean above-ground carbon stocks averaged across entire study regions under different land use strategies at different production levels. Dark colors show projected stocks under projected 2050 production levels; intermediate colors show stocks under 2014 production levels; light colors show stocks with production at 50% of 2014 levels. We tested 148 possible intermediate strategies but show the results for when yields are halfway between those under land sharing and land sparing. Error bars show the bootstrapped 95% confidence intervals around estimates—see Quantification and Statistical Analysis in STAR Methods for details and Figures S3 and S4 for explanation as to why, despite the overlap of confidence intervals, we conclude that land sparing outperforms all other strategies.

that these patterns are likely to be repeated across forested biomes. This provides crucial insights for programs such as REDD+ and emphasizes the need to think about the whole landscape when assessing agricultural strategies: coupling yield increases with habitat protection will be vital if we are to both provide food for a rapidly growing population and maintain global carbon stocks in the 21st century.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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  - Estimating future production targets
  - Regional carbon stocks under different future land-use scenarios
- DATA AND SOFTWARE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and one table and can be found with this article online at https://doi.org/10.1016/j.cub.2018.05.087.

AUTHOR CONTRIBUTIONS

Conceptualization: D.R.W., A.B., R.E.G.; Methodology: D.R.W., A.B., R.E.G., C.F., B.P.; Formal Analysis: D.R.W., C.F.; Investigation: D.R.W., C.F., B.P.; Resources: D.R.W., C.F., B.P.; Data curation: D.R.W.; Writing – Original Draft: D.R.W., A.B., R.E.G., B.P.; Writing – Review & Editing: D.R.W., A.B., R.E.G., B.P.; Visualization: D.R.W., A.B., R.E.G., B.P.; Supervision: A.B., R.E.G., B.P.

DECLARATIONS OF INTEREST

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Above-ground carbon stocks in sites	This paper	Deposited in the University of Cambridge's Apollo repository (https://www.repository.cam.ac.uk/) and at Mendeley Data https://doi.org/10.17632/n5fb8k259n.1
Agricultural yield data	This paper	Deposited in the University of Cambridge's Apollo repository (https://www.repository.cam.ac.uk/) and at Mendeley Data https://doi.org/10.17632/n5fb8k259n.1
Environmental stressor for tropical allometric equations	[46]	Location-specific environmental stressor E retrieved from: http://chave.ups-tlse.fr/pantropical_allometry/readlayers.r
Estimates of carbon stocks in oil palm plantations	[47]	Time-integrated above-ground carbon stocks of oil palm plantations
Wood density estimates	[48], [49]	https://datadryad.org//resource/doi:10.5061/dryad.63q27/2
Polish soil types	[50]	https://esdac.jrc.ec.europa.eu/, European Soil Database v2.0
Current food demand – Ghana	[36]	Original data from various sources, described in Supporting Online Material for [36]
Current food demand – Mexico	[15]	Original data from various sources, described in [15] and Electronic Supplementary Material
Current food demand – Poland	[51]	Original data from various sources, described in [51]
Food demand projections for 2050 – Ghana and Mexico	This paper, based on [52]	Business-as-usual projections from [52], adjusted for 2050
Agricultural demand projections – Poland	[51]	Original data from various sources, described in [51]
Experimental Models: Organisms/Strains		
Multiple species of trees	NA	NA
Software and Algorithms		
R version 3.x	[53]	http://www.r-project.org, RRID:SCR_001905
R package alabama	[54]	https://cran.r-project.org/web/packages/alabama/
R package raster	[55]	https://cran.r-project.org/web/packages/raster/
Allometric equations for tropical tree biomass	[46]	N/A
Allometric equations for temperate tree biomass	[56]	N/A
Equations for palm biomass	[57]	N/A
Code for fitting density-yield functions	This paper	Deposited in the University of Cambridge's Apollo repository (https://www.repository.cam.ac.uk/) and at Mendeley Data https://doi.org/10.17632/n5fb8k259n.1

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, David R. Williams (davidwilliams@ucsb.edu)

METHOD DETAILS

Study regions
We investigated the impacts of different land-use strategies on three continents with contrasting natural vegetation and agricultural systems. In each region, we investigated a range of land-use types along yield gradients, from zero-yielding natural habitats to the highest sustainable yields in the region. In southwest Ghana, this gradient ranged from moist evergreen and moist semi-deciduous to mosaics of agroforestry, remnant vegetation, and mixed agriculture, and finally to oil palm plantations [36]. In Yucatán state, Mexico, the gradient was from tropical dry, semi-deciduous and evergreen forests to low yield cattle ranches with few inputs and grazed semi-natural habitats, through to intensively managed ranches with improved pastures and supporting maize production [15]. In

the Lubelskie voivodeship in Poland, we surveyed fen mires, flood plains and temperate mixed deciduous forests as natural habitats, with along with mixed agriculture with remnant natural vegetation, and high-yield arable farms [51]. Note that we were unable to include data from northern India analyzed in Phalan et al., 2011 [36] because this did not include information on the size of the trees surveyed.

We conducted fieldwork in 2006-2007 (Ghana) and 2012-2014 (Mexico and Poland). In each region, we ensured our study sites were in regions of uniform topography and climate, and selected sites across the full range of agricultural yields present. In Ghana and Mexico, all baseline sites consisted of the same habitats and we ensured sites were evenly distributed across available soil types. In Poland, survey sites were selected across a gradient of farm yields separately for organic soils and mineral soils. Baseline sites were fen mires and flood plains on organic soils, and mixed deciduous forests on mineral soils. We classified each site as either "organic" or "mineral" dependent on their soils [50]. In total we collected data at 76 sites: 25 in Ghana and Mexico, and 26 in Poland. Site characteristics are described in detail in [15, 36, 51].

Details of study site selection
Ghana: our study region consisted of seven districts (Wassa West, Ahanta West, Mpohor Wassa East, Shama Ahanta East, Birim North and Kwaebibirem) containing the four large oil palm plantations present in Ghana during the fieldwork period. We scored each forest reserve larger than 20 km^2 and within 20 km of the plantation for similarity to the plantation in terms of soil type, annual precipitation, annual potential evapotranspiration and ecological zone and selected the highest scoring reserve. The area of farm mosaic between the plantation and the selected forest reserve that matched both in terms of elevation, soil, and precipitation, was then used for sampling other agricultural sites. Within each landscape and land-use type (plantation, forest reserve, farm mosaic) we then randomly selected two 1 km^2 sites to sample, adding an additional square to capture a wider range of yields. **Mexico:** we used Google Earth to classify areas within the study region (the Oriente region of Yucatán state) into forest; mosaics of forest, grazed secondary vegetation and pasture; and open pastures, and randomly selected five 1 km^2 sites in forest, four in mosaics, and three in open pastures. In addition, we used key informant interviews to identify ranches focused on fodder production, high-yield cattle production with irrigated or improved pastures, and intensively managed silvopastoral systems; selecting four of each, with an additional ranch combining fodder production with improved pastures, and centring sites on each ranch. This semi-randomized approach was necessary due to the rarity of these high-yielding land uses, and the fact that management could vary considerably from one land-holding to the next. **Poland:** within our study region (15 countries in the east of the Lubelskie region) we used CORINE land cover data [58] to classify each 1 km^2 cell in the region as one of: three types of natural habitat (mixed/deciduous forests, fen mires, flood plains); hay meadows and pastures (> 95% pasture); mixed farm mosaics (> 50% heterogenous agriculture/pasture, > 95% agricultural land); or arable farmland (> 75% arable land, > 95% agricultural land); also classifying them by soil type (mineral, with a baseline habitat of forest, or organic, with a baseline of fen mires or flood plains). We then randomly selected nine cells in natural habitats (four forest, three fen mire, two floodplain); four in meadows/pastures; eight in mixed farm mosaics; and five in arable farms. In addition to matching by soil type, we ensured that sites were matched for altitude, topography and local climate. The selected agricultural sites covered a wide range of yields and coverage of natural vegetation in each region, with 0%–70%, 0%–99%, and 1%–52% uncultivated land in Ghana, Mexico, and Poland, respectively (see Table S1).

Estimating agricultural yields
We mapped each site using a combination of Google Earth imagery and site visits [15, 36, 51], classifying land-uses as agricultural land, remnant natural vegetation or other uses. We then used farmer interviews (Ghana and Mexico) or a combination of interviews and government data (Poland) to estimate the annual food production for each site [15, 36, 51]. We converted yield (total production divided by the total area of a site, including non-crop habitat) into standardized metrics of energy (in GJ) for Ghana and Poland, and protein (in kg) for Mexico [15, 36, 51] (see Table S1). We used these metrics because agriculture in Ghana and Poland is driven largely by demand for food energy, whereas in Mexico it is driven by demand for animal protein specifically.

Collecting reliable yield data from farmers can be difficult, particularly for subsistence farmers and smallholders who keep few written records [59, 60]. To minimize systematic biases all interviews in a region were carried out by the same people who were familiar with the agricultural systems being investigated [61]: BP in Ghana, DRW in Mexico, and two Polish graduate students – Grzegorz Siwek and Jarosław Szuwarski – in Poland. We spoke with the individuals most likely to provide accurate data: usually the owner or tenant farmer, but sometimes the manager or administrator. We made it clear that we were not affiliated with any governmental or non-governmental organization, reducing the risk that farmers would alter their responses in the hope of obtaining additional assistance [61]. In each system we used standardized questionnaires: in Ghana and Poland, we collected data on the harvest of each crop in the past year (including the number of harvests) and the area devoted to it, adjusting for any land kept as fallow; in Mexico we collected data on the number and weight of animals bought and sold each year, the areas of different pasture types, and the fodder and supplements used, as well as on yields of any fodder crops grown. Respondents sometimes used non-standard units such as 'ropes' and 'baskets' in Ghana or 'mercates' in Mexico; in each case, we clarified exactly what the measurement was and converted to SI units. Where possible, we checked yields against other data sources: in Ghana, interviews were often conducted in small groups, reducing the risk that farmers would systematically over- or under-report their yields, while monthly oil palm yields were provided by plantations; in Mexico, several ranches allowed DRW access to their records, providing exact data on livestock bought and sold; in Poland, county-level yield data were available [62] and closely matched the estimates obtained from farmers [51]. It is worth noting that the large differences in above-ground carbon stocks between non-agricultural and agricultural sites, and the relatively

small differences between different agricultural sites, means that the relationships between carbon stocks and yields are almost certainly concave in each region, meaning that a land-sparing strategy will be the least damaging irrespective of realistic uncertainty in yield measurements [10].

Yucatecan cattle ranching requires three interdependent farming types: breeding ranches, which produce calves; finishing ranches which raise animals to slaughter weight; and fodder ranches that produce fodder for both breeding and finishing ranches [15]. To estimate overall yields of ranches, we therefore converted all production into a common currency: kilograms of edible cow protein. Detailed methods for the conversions are described in [15].

QUANTIFICATION AND STATISTICAL ANALYSIS

Estimating above-ground carbon stocks

For every site in Mexico and Poland, we surveyed trees with a diameter-at-breast-height (dbh) $\geq$ 10 cm using square 25 × 25 m plots in Poland, and a modified Gentry plot consisting of six 2 × 50 m belt transects in Mexico [15, 63]. In addition, we surveyed all trees with a dbh $\geq$ 5 cm in a subplot (one 2 × 50 m transect in Mexico, one 5 × 5 m subplot in Poland) due to the smaller size structure of vegetation in these regions. We established 10 (Mexico) or 12 (Poland) plots in each forest site, but doubled this number in non-forest sites due to far lower tree densities. We recorded dbh, height when possible, and species for each living tree within the plot, only counting trees where the center of the trunk at ground level was within the plot. We translated local names to scientific names where necessary and checked them against a standardized taxonomy [64]. In Ghana, we followed a similar protocol, with 12 25 × 25 m plots in each forest site, and 24 such plots in all agricultural sites except oil palm plantations – which did not hold any non-oil palm trees – but we did not record dbh measurements for all non-native trees and instead estimated missing values from recorded values. Carbon stocks in oil palm plantations will vary considerably as palms mature, meaning that a survey at a single time period will not provide a reliable, lifetime estimate, of stocks [47]. We therefore used published estimates of above-ground stocks in oil palm, adjusted for differences due to palm age [47].

In Ghana and Mexico, we estimated live above-ground biomass of all trees except palms using Model (4) from [46], when height data were recorded, or Model (7) when height was not recoded, and using wood density data from [48] (taking the mean of all values for unidentified species). Palm biomass is not well described by allometric equations designed for dicotyledonous species and so we used Equations 1 and 2 from [57] to estimate their biomass (with the exception of oil palm plantations in Ghana). In Poland, we used previously published, species-specific allometric equations to estimate above-ground biomass [56]. In all regions, we excluded dead trees, while for partially dead individuals we scaled above-ground biomass estimates by the proportion of the tree estimated to be living. Finally, we estimated live above-ground carbon density by summing the biomass for each tree in a site, assuming a carbon fraction of 50% [65] and dividing by the area surveyed, adjusting for the different areas surveyed for small (5 $\leq$ dbh $\leq$ 10 cm) and large (dbh $\geq$ 10 cm) trees (see Table S1 for site level above-ground carbon stocks).

Fitting carbon density-yield functions

To model the effects of agricultural yield on above-ground carbon stocks, we followed [36] and used maximum-likelihood optimization to fit two possible density-yield functions:

$$(1): \; d = e^{(b_0 + b_1 x^\alpha)} \qquad \text{(Equation 1)}$$

$$(2): \; d = e^{(b_0 + b_1 x^\alpha + b_2 x^{2\alpha})} \qquad \text{(Equation 2)}$$

where:

d = estimated live above-ground carbon density for the site (MgC ha^{-1})

x = the yield of the site in food energy (Ghana, Poland) or meat protein equivalents (Mexico) (GJ ha^{-1} or kg ha^{-1})

b_0, b_1, b_2, and α are constants estimated from the data. α is constrained to be positive and not to exceed 4.6 as the likelihood of the data and the shape of the model curves varied little above this value, making precise maximum-likelihood modeling impossible (see [36]).

We fitted models using the constrained optimization function ConstrOptim in R [53], modifying a previously developed script [39]. ConstrOptim is sensitive to starting parameters, so we first fitted ordinary least-squares regressions for the two models, varying α from 0.1 to 4.58 and selecting the version of each model with the smallest residual sum of squares. We then used the values for b_0, b_1, b_2, and α from these models as starting values in ConstrOptim. We considered predicted carbon stock values more than 150% of the highest recorded as unrealistic and used the function ConstrOptim.nl from the package alabama [54] to fit models if such values were predicted. We calculated each model's residual deviance ($-2 *$ log-likelihood) and selected Model (1) for reasons of parsimony unless Model (2) had a residual deviance more than 3.84 lower (the critical chi-square value at p = 0.05 for one degree of freedom). Due to the very different characteristics of wetland and forest sites on organic and mineral soils, respectively, in Poland, we fitted separate models for each site type and weighted regional carbon stocks based using a 3:1 ratio of mineral to organic soils, based on the relative coverage of each soil type in the region (Figure S1). In addition, in Ghana, the best fitting model predicted high carbon stocks for very high yielding farmland (Figure S2). However, we did not anticipate any high-yielding system having greater

above-ground carbon stocks than high-yielding oil palm plantations, so we capped stocks in high-yield agricultural sites at the values recorded in plantations.

To obtain a measure of uncertainty around estimates, we performed a bootstrapping analysis. We took random samples of sites, with replacement, from the survey sites available in each country, splitting organic and mineral soil sites in Poland. We drew sites at random until the number of sites in the bootstrap sample was equal to the number of sites in the region. We then fitted density-yield curves to this sample and repeated the process 1,000 times. For Ghana and Polish organic soil sites, we fitted all curves using the ConstrOptim.nl function to avoid unrealistically high estimates (see above). Due to the extreme sensitivity of ConstrOptim.nl to starting values, some iterations failed to converge. We discarded these, and repeated the sampling procedure until we had 1,000 iterations of successful model fits for each country / soil combination. We used each fitted model to estimate carbon stocks at different yields and calculated the 2.5th and 97.5th percentile of these estimates to obtain 95% confidence intervals around our estimates.

Estimating future production targets

To assess how future changes in production may affect above-ground carbon stocks, we modeled future demand for food energy (Ghana and Poland) and meat protein (Mexico) to 2050. We estimated 2014 production for each country based on government data [15, 36, 62]. In Ghana and Mexico, agriculture is largely driven by national food demand and we used previously developed food demand scenarios [52] to forecast food demand to 2050. In Poland, by contrast, increasing domestic demand and international exports, and a growing demand for biofuels means that production is likely to increase despite a projected fall in the regional population. We therefore used governmental data [62] to model annual changes in production over the period 2005-2014, and projected this relationship forward to 2050.

Regional carbon stocks under different future land-use scenarios

We estimated mean above-ground carbon stock densities for each region under a range of production levels and land-use strategies. Due to the uncertainty in future demand projections, we investigated production levels from close to zero to considerably higher than estimated 2050 levels, allowing us to model carbon stock levels under both increasing and decreasing production. We then assessed the consequences for carbon stock of meeting these production levels via an array of land-use strategies: land sharing, where the whole region is farmed at the minimum permissible yield (i.e., the lowest yield that can meet the production target); land sparing, where yields are set to the highest achievable yields and all remaining land is assigned to natural habitat; and 148 intermediate strategies spread evenly across the range of all other permissible yields. To allow for future agricultural improvements, we assumed that maximum achievable yields in 2050 would be 125% of the highest yields we recorded in the field.

At each production level, we estimated the area under different land uses for each strategy, and then used the carbon density-yield functions to estimate the above-ground carbon density of land under agriculture and in natural habitats. We then took the mean of these densities, weighted by the areas of each land use. In Poland, we obtained separate estimates for forest (mineral soil) and wetland (organic soil) sites and obtained a mean estimate across the two soil types, weighted by their relative coverage in the region. We repeated this analysis for each iteration of the bootstrapping analysis and calculated, for a given production target, the number of iterations for which each strategy resulted in the highest projected above-ground carbon stocks. In Ghana and Poland, land sparing was projected to result in the highest above-ground carbon stocks for > 99% of iterations at all production targets. In Mexico, land sparing outperformed all other strategies for at least 71% of iterations, with this number rapidly rising to > 90% at all but the very lowest production target. (Figure S3). In all countries, intermediate strategies never outperformed a land sparing strategy based on the same bootstrapping iteration (Figure S4), although some did outperform the best-fit curve – resulting in the 95% confidence intervals in Figure 3.

DATA AND SOFTWARE AVAILABILITY

All data and R code for fitting density-yield functions are available online at the University of Cambridge Apollo Repository: https://www.repository.cam.ac.uk/ and at Mendeley Data: https://doi.org/10.17632/n5fb8k259n.1

Supplemental Information

Carbon Storage and Land-Use Strategies

in Agricultural Landscapes across Three Continents

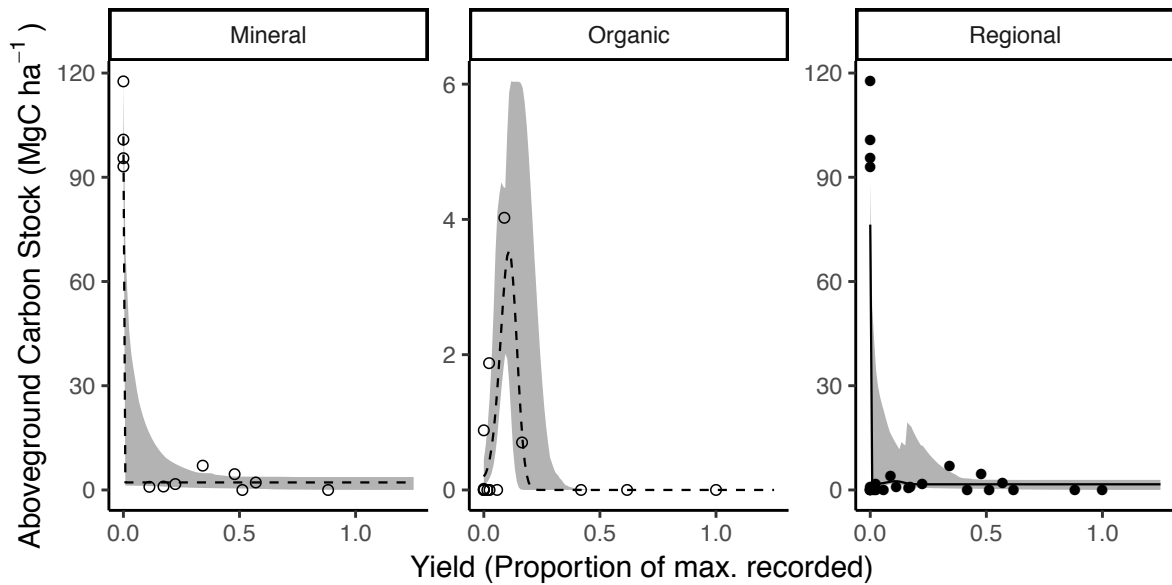David R. Williams, Ben Phalan, Claire Feniuk, Rhys E. Green, and Andrew Balmford

Figure S1. Density yield curves for above-ground carbon stocks on mineral and organic soils in Poland, and the regional relationship. Related to Figure 1 and "Quantification and statistical analysis" in STAR Methods.
Density yield curves for above-ground carbon stocks on mineral and organic soils in Poland, and the regional relationship, based on a 3:1 ratio of soil types across the study region. Note the different scales for y-axes, with maximum above-ground stocks on wetland soils being <5% of those in mineral soils. Shaded areas show the bootstrapped 95% confidence intervals around estimates – see "Quantification and statistical analysis" in STAR Methods for details.
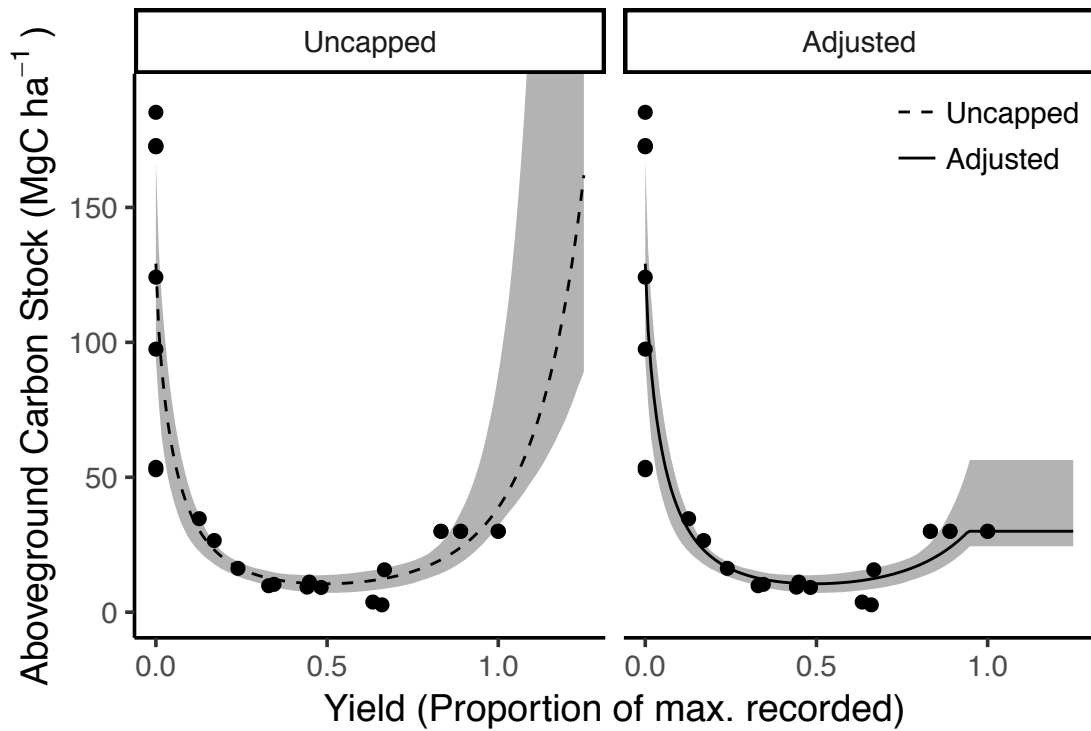
Figure S2. Density yield curves for above-ground carbon stocks in Ghana. Related to Figure 1 and "Quantification and statistical analysis" in STAR Methods.
Density yield curves for above-ground carbon stocks in Ghana. The dashed line shows the uncapped predictions from the best fit relationship; the solid line shows the same relationship, but adjusted so that very high yield sites were not predicted to have unrealistically high above-ground carbon stocks. Shaded areas show the bootstrapped 95% confidence intervals around estimates – see "Quantification and statistical analysis" in STAR Methods for details.
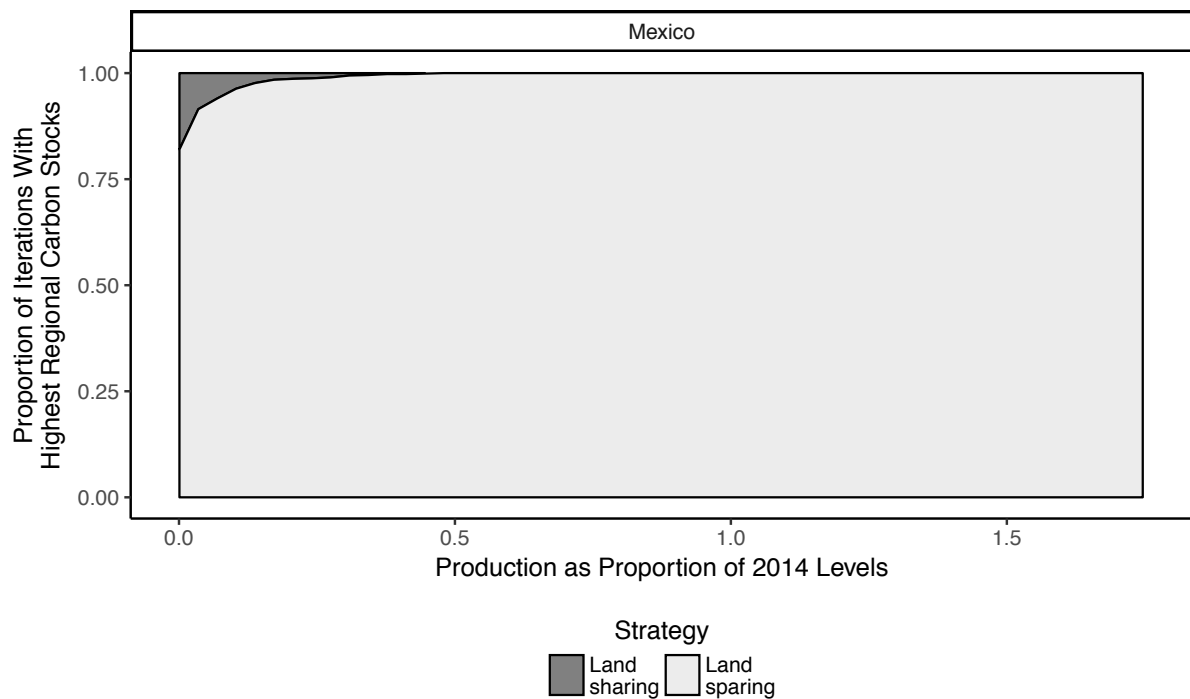
Figure S3. Variation in the land-use strategy with the greatest projected aboveground carbon stocks in Mexico, across all production targets investigated. Related to Figure 3 and "Quantification and statistical analysis" in STAR Methods.
Variation in the land-use strategy with the greatest projected aboveground carbon stocks in Mexico, across all production targets investigated. For clarity, the figure excludes the highest and lowest 2.5% of iterations and so corresponds to the confidence intervals in Figure 3. In Ghana and Poland, land sparing was projected to result in the highest aboveground carbon stocks for >99% of iterations at all production targets.
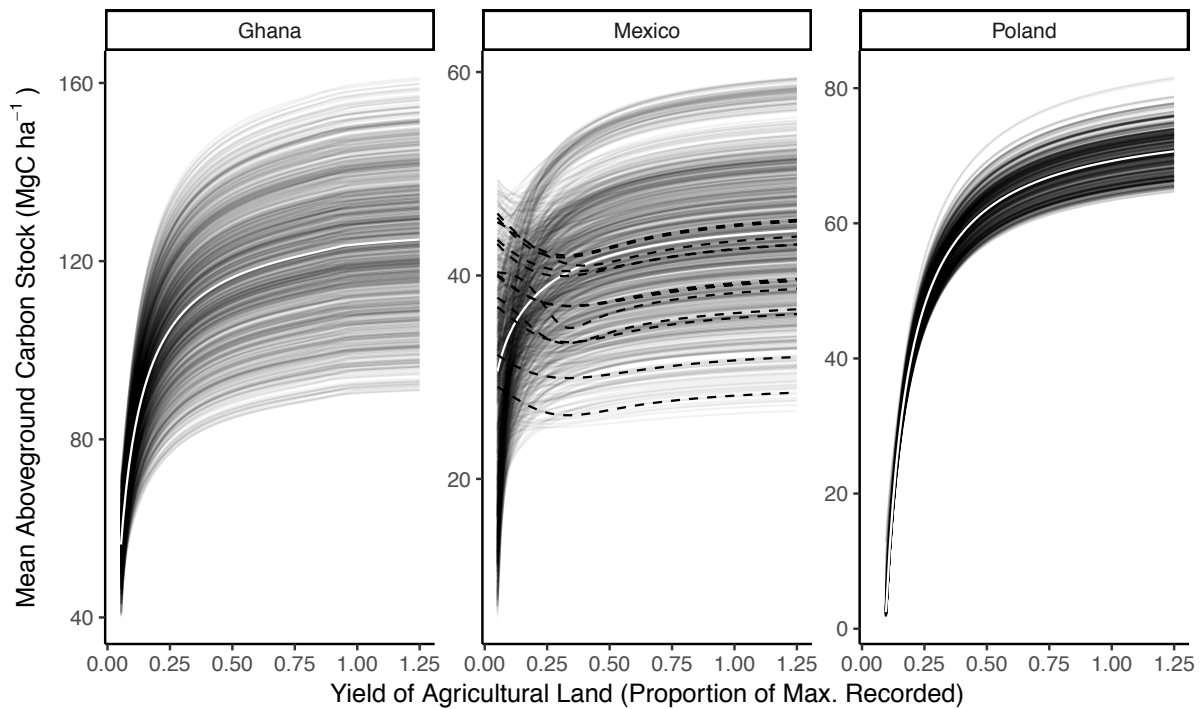
Figure S4. Projected mean above-ground carbon stocks averaged across entire study regions under different land use strategies at a single production target. Related to Figure 3 and "Quantification and statistical analysis" in STAR Methods.
Projected mean above-ground carbon stocks averaged across entire study regions under different land use strategies at a single production target. The lowest yields shown represent land sharing and the highest land sparing; and others are intermediate strategies. Each line represents one of the 1000 bootstrapped iterations; dashed lines highlight the very few iterations where land sharing outperformed land sparing; the white line in the middle of the distribution shows the best-fit line. For clarity, the figure excludes the highest and lowest 2.5% of iterations and so corresponds to the confidence intervals in Figure 3. Note that the production target shown is extremely low (20% of 2014 production), in order to illustrate iterations where land sharing outperformed land sparing: at higher targets, land sparing outperformed all other strategies across >99% of iterations. Also note that yields under land sharing differ between regions due to differences in production targets (see "Regional carbon stocks under different future land-use scenarios" in the "Quantification and statistical analysis" section of the STAR Methods for details).