# Greenhouse-gas payback times for crop-based biofuels

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A global increase in the demand for crop-based biofuels may be met by cropland expansion, and could require the sacrifice of natural vegetation. Such land transformation alters the carbon and nitrogen cycles of the original system, and causes significant greenhouse-gas emissions, which should be considered when assessing the global warming performance of crop-based biofuels. As an indicator of this performance we propose the use of greenhouse-gas payback time (GPBT), that is, the number of years it takes before the greenhouse-gas savings due to displacing fossil fuels with biofuels equal the initial losses of carbon and nitrogen stocks from the original ecosystem. Spatially explicit global GPBTs were derived for biofuel production systems using five different feedstocks (corn, rapeseed, soybean, sugarcane and winter wheat), cultivated under no-input and high-input farm management. Overall, GPBTs were found to range between 1 and 162 years (95% range, median: 19 years) with the longest GPBTs occurring in the tropics. Replacing no-input with high-input farming typically shortened the GPBTs by 45 to 79%. Location of crop cultivation was identified as the primary factor driving variation in GPBTs. This study underscores the importance of using spatially explicit impact assessments to guide biofuel policy.

ver the past few decades, many countries have adopted bioenergy directives that aim to increase the share of renewable energy and to reduce greenhouse-gas (GHG) emissions from the use of fossil fuel<sup>1</sup>. The production of liquid biofuels for the transportation sector in particular has experienced substantial growth since 1990<sup>2</sup>. Despite rapid developments in the field of second- and third-generation biofuels (produced from lignocellulosic biomass and microalgae, respectively), only firstgeneration biofuel production from energy crops, such as corn, soybean, rapeseed and sugarcane, is commercial at present<sup>3,4</sup>. A growing demand for energy crops in the future may be met either by increasing the amount of agricultural land or by increasing crop production on existing agricultural land. Expansion of agricultural land requires the sacrifice of other land cover, such as abandoned lands, pastures or natural systems. The last of these can be especially problematic from a climatic point of view, given that natural forests and grasslands store large amounts of carbon that may be released to the atmosphere on their conversion to agricultural use, thereby disturbing the global carbon balance<sup>5,6</sup>. Most of the carbon in natural terrestrial systems is stored in biomass and soil<sup>7</sup>. Removal of natural biomass may result in large releases of carbon through post-harvest combustion and decomposition. Crops also store carbon in their biomass during growth, but the regular harvest of many crops impedes long-term carbon storage. In addition, agricultural land use may alter the balance between inflows and outflows of the soil carbon pool through changes in vegetation, increasing erosion and soil disturbance through farming activities such as tillage and irrigation<sup>8,9</sup>. Conversion of native forest to croplands may result in a large loss of soil

carbon stocks, releasing more than 40% of the original stock to the atmosphere<sup>7</sup>.

Changes in the global carbon balance due to land conversion are especially relevant in the case of biofuel production given that carbon and nitrogen emissions from deforestation and land-use intensification may nullify the environmental benefits of displacing fossil fuels<sup>10,11</sup>. The impact of biofuel production on the global carbon balance can be quantified by calculating carbon payback times<sup>12-16</sup>, also known as carbon debt repayment times<sup>10</sup>, carbon break-even points<sup>17</sup> or carbon compensation points<sup>18</sup>. The carbon payback time is defined as the period over which the total GHG savings due to displacement of fossil fuels by biofuels equals the initial losses in ecosystem carbon stocks caused by land conversion. These measures are analogous to the more widely known energy payback times that are used in impact assessments of, for example, photovoltaic systems. Here, we propose the term greenhouse-gas payback time (GPBT) in assessing the impact of crop-based biofuel production on the balance of multiple GHGs. These GPBTs depend on the following: the amount of biogenic carbon dioxide  $(CO_2)$  emitted to the atmosphere due to the removal and burning or decay of the original carbon-storing biomass; the amount of biogenic CO<sub>2</sub> and dinitrogen oxide (N<sub>2</sub>O) emitted to the atmosphere due to soil mineralization and (de)nitrification processes following land conversion, that is, the net difference between the original soil stocks and those of the bioenergy system; the annual amount of N<sub>2</sub>O emitted to the atmosphere due to fertilizer application during crop cultivation; the amount of fossil GHGs emitted per unit of produced bioenergy (including emissions from machinery use and transportation) relative to the

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amount of fossil GHGs emitted per unit of fossil energy that is produced and combusted; the amount of bioenergy gained through biofuel production, which depends on the feedstock yield, feedstock-to-biofuel conversion efficiency, and energy content of the biofuel.

The GHG emissions associated with the production of cropbased biofuels (including related land-use change) have been assessed extensively before<sup>19-22</sup>. Previous assessments have shown that emissions vary with the type of crop that is cultivated, the location of cultivation, and the intensity of farm management practices. However, most previous work has consisted of case studies that focused on specific countries or regions, and researchers have thus failed to identify the implications of growing various crops worldwide. Development of standardized, globally applicable metrics, such as GPBTs, is a precondition for progress towards a sustainable biofuel trade. Therefore, the first aim of our study was to derive spatially explicit, high-resolution GPBTs for potential cropbased biofuel production on a global scale, taking into account the conversion of natural vegetation to feedstock cropland. These GPBTs were calculated for the production of bioethanol from corn grain, sugarcane sucrose and winter wheat grain, which could replace fossil gasoline, and for production of biodiesel from rapeseed and soybean oil, which could replace fossil diesel. The cultivation of the biofuel crops was simulated spatially explicitly. using the global crop model EPIC (see Supplementary Information). Second, we assessed the reduction in GPBTs when high-input croplands replace no-input croplands of the same crop (that is, farm intensification). Finally, we analysed how geographic location, management regime and crop type affect the GPBTs. To our knowledge, the present study is the first to calculate GPBTs at a global scale, and the first to quantitatively assess the the relative importance of the three primary drivers of GPBT variation.

#### **By-products**

The crop-based biofuel production processes studied here produce significant quantities of by-products to which part of the GHG emissions should be allocated. Examples are corn stover, rapeseed meal and soybean meal, and dried distiller grains with solubles from corn and wheat, which are used as animal feed, and sugarcane bagasse, which can be used in electricity production. Three commonly used methods to allocate emissions between the biofuel and its by-products are those based on energy content, mass and market value<sup>23</sup>. The outcomes of the GPBT calculations vary with these different approaches. When allocation is included on an energy basis, GPBTs are on average 61% shorter than when applying no allocation. For mass-based and market value-based allocation, this is 67% and 30%, respectively. The results given below are those using energy-based allocation. The outcomes of mass-based and market value-based allocation can be found in the Supplementary Information.

## Cropland replacing natural vegetation

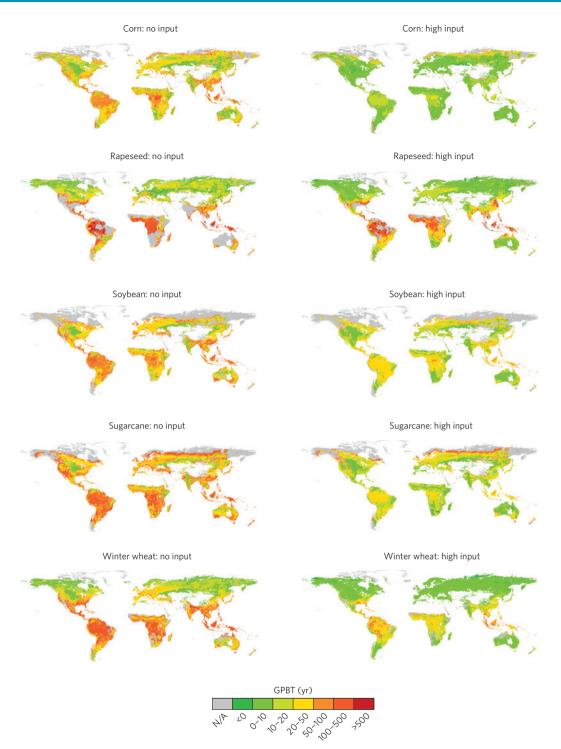
When taking the replacement of natural vegetation by croplands as a starting point for biofuel production, the GPBTs for our biofuel production systems varied from 1 to 162 years (95% range; median of 19 years) depending on the crop, management intensity and location. The spatial distribution of global GPBTs for each cropmanagement combination is shown in Fig. 1. The longest GPBTs were found in the tropical regions of South America, Africa and Southeast Asia, where we calculated a median GPBT of 51 years (95% range of 7 to 313 years) when converting tropical moist forest to cropland for biofuels and 27 years (95% range of 3 to 164 years) when replacing tropical grasslands. Shorter GPBTs were found in the temperate and boreal regions, where the median GPBT was 20 years (95% range of 3 to 103 years) when converting temperate broadleaf forest to biofuel cropland, 19 years (95% range of 1 to 155 years) when replacing temperate coniferous forests, 10 years (95% range of 0 to 87 years) when replacing boreal forests and taiga, and 6 years (95% range of 0 to 54 years) when replacing temperate grasslands. In <1 to 3% of the grids, particularly in the temperate and boreal regions, we found negative GPBTs, which resulted from cropland soil organic carbon (SOC) stocks that exceeded the total carbon stock in the soil and biomass of the reference vegetation.

Under no-input farming, rapeseed-based biodiesel production yielded the shortest GPBTs, that is, a global median of 21 years (95% range of 1 to 404 years). Bioethanol production from sugarcane under no-input farming yielded the longest GPBTs, with a global median of 60 years (95% range of 8 to 209 years). In the tropical regions all crops had longer GPBTs, with soybean and sugarcane performing best: median GPBTs of 77 years (95% range of 13 to 141 years) and 90 years (95% range of 13 to 190 years), respectively. Under high-input farming, the median GPBTs for all crops were 45 to 79% shorter compared with no-input farming. Corn and winter wheat performed best in this case: median GPBTs of 6 years (95% range of 0 to 29 years) and 8 years (95% range of 0 to 57 years), respectively.

We compared our GPBTs with those obtained in a few studies in which payback times were obtained for specific crop-based biofuels<sup>10,13,15,16</sup>. In general, we found wider GPBT ranges than those of previous studies. Given that the biomass carbon losses due to land conversion are similar (ref. 13 also used IPCC data; ref. 10 used average data from the literature), the differences can be attributed to the highly variable SOC and crop yields. For example, we found short (or, in some cases, negative) GPBTs when the SOC content in cropland was higher or only slightly lower than the total carbon in the natural system. These circumstances were not observed in the previous studies, which used relatively high estimates of SOC in the natural system and applied a default decrease in the amount of SOC following conversion to cropland, based on scientific literature<sup>10,13</sup>. However, we obtained long GPBTs in grids where the SOC in the cropland was lower than the total carbon in the natural system and where the crop yield was low. The previous studies typically focused on crop cultivation in regions where the crops are grown at present or where the climatic conditions allow for their cultivation in the near future. In the present study, however, we simulated potential crop cultivation worldwide, which implies that more regions with relatively low yields were included (for example, sugarcane cultivation in temperate regions and rapeseed cultivation in tropical regions). This inclusion explains why more variability was observed in the present study than in previous studies.

## No input versus high input

Large differences in GPBTs were associated with the use of two types of farm management. We observed that replacing no-input farming with high-input farming tends to shorten the GPBTs, often by more than 100 years (Fig. 2). High-input farming generally resulted in greater SOC losses to the atmosphere and higher GHG emissions from fertilizer and machinery compared with farm management without the input of fertilizer and irrigation. Nevertheless, cultivating biofuel crops under high input resulted in shorter GPBTs in 95 to 99% of the global grids due to higher crop yields, which offset the higher GHG emissions. Although lower rates of fertilizer application evidently lead to lower GHG emissions, we conclude that a reduction in fertilizer application will be counterproductive if it results in large decreases in yields. However, it should be noted that the two farm management scenarios analysed in the present study differed only in the application of nitrogen fertilizer and irrigation. Other farm management practices that affect GHG emissions, such as tillage, potassium and phosphorus fertilizer application, stover removal and crop rotation, were not addressed.



**Figure 1** | **Global maps of GPBTs for the five bioenergy crops under no-input and high-input farm management.** White areas (for example, deserts and ice cover) were deemed unsuitable for agricultural land use a priori. Grey areas were excluded because their modelled crop yields were below the yield threshold (see Supplementary Information). These maps were constructed at a 5-arcmin resolution.

#### **Explained variance**

We identified the effects of crop type, management system and location on the variance in grid-specific GPBTs. Overall, 90.7% of the variance in GPBTs was attributable to differences in location (Supplementary Table 5). The other factors were of less importance: farm management and the type of crop accounted for 6.5% and 2.5% of the variance in the GPBTs, respectively, and the remaining 0.3% was due to crop-management interactions. These findings stress the importance of accounting for spatial differences

when assessing the influence of crop-based biofuel production on GPBTs.

Although significant differences in GPBTs were found between different crops, the effect of crop type on the global GPBTs was small compared with the influence of location. However, most crops included in the present study were annual crops, which have no long-term storage of carbon owing to frequent harvest. Perennial grasses and permanent crops (for example, oil palm) generally produce higher yields and have the potential

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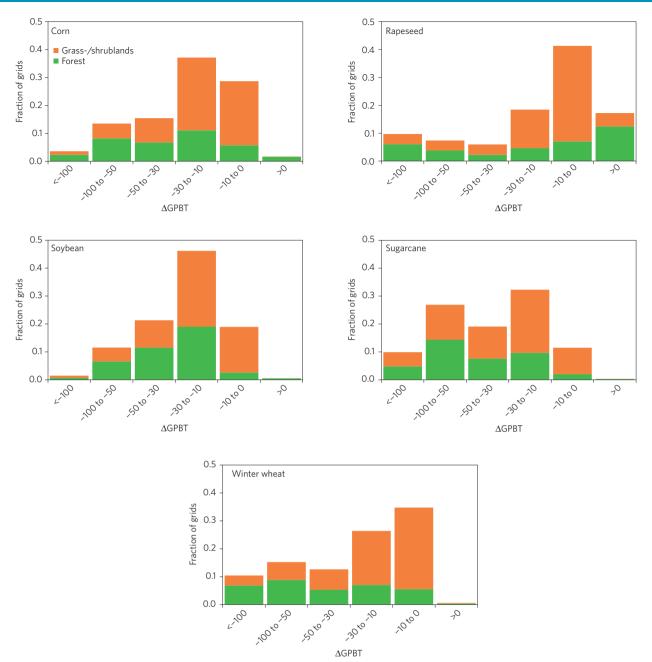


Figure 2 | Histograms of  $\triangle$  GPBT showing the change in payback times when converting no-input farming to high-input farming of the same feedstock crop. The colours denote the two primary classes of natural vegetation that were replaced by agricultural land, that is, forests and rangelands, based on the classification in ref. 33.

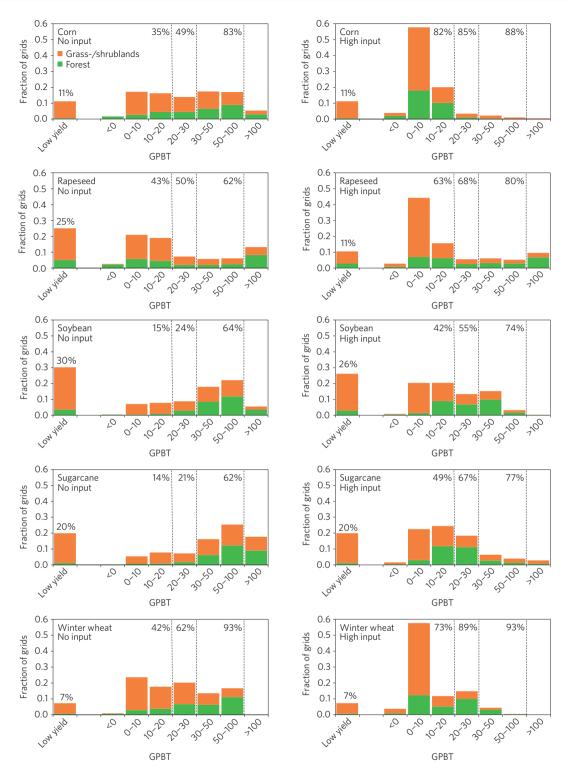
to sequester more carbon in soil and biomass<sup>8,24</sup>. Sugarcane, the only perennial crop in our study, was indeed found to have higher average yields (7 to 25 times) and slightly higher SOC stocks (3 to 7%) than the other crops, which were partly negated by a more inefficient crop-to-fuel conversion. Earlier studies on the effects of biofuel produced from permanent crops were inconclusive. For example, ref. 13 reported shorter carbon payback times for oil palm biodiesel compared with several annual crop-based biofuels, whereas ref. 10 reported that palm biodiesel yielded the longest carbon payback times. Lignocellulosic biomass, such as switchgrass, miscanthus, and grassland mixtures, is frequently considered to be a suitable replacement for degraded croplands<sup>10,25</sup>, but the effect of replacing natural vegetation with these crops has not been extensively studied. However, under favourable conditions, lignocellulosic crops can maintain higher

SOC contents than mature forests and native grasslands<sup>26,27</sup>, and therefore biofuel production from lignocellulosic biomass is worth further investigation.

## Implications

Whether biofuel production in a specific location may be favourable or unfavourable for mitigating climate change depends on the total production period of the cropland during which it is used for biofuel feedstock cultivation in that location<sup>15</sup>. For example, the Intergovernmental Panel on Climate Change (IPCC) proposes an average of 20 years as the typical cultivation period before cropland is converted to a different land use<sup>28</sup>. In this case, therefore, the GPBT in a specific location should be shorter than 20 years for the biofuel production to be beneficial versus the use of fossil fuels in terms of total GHG emissions. Additional locations would

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**Figure 3** | **Histograms of the GPBTs for the five energy crops under no-input and high-input farm management.** The colours denote the two primary classes of natural vegetation that were replaced by agricultural land, that is, forests and rangelands, based on the classification in ref. 33. The dashed lines denote various cropland production periods that may be assumed, which affect the number of grids (expressed as percentages) where biofuel production is beneficial versus the use of fossil fuels in terms of total GHG emissions. The low yield bar denotes the percentage of grids for which no GPBTs were calculated because the modelled yield was less than the threshold value.

qualify as beneficial when assuming a cropland production period of 30 or possibly 100 years<sup>15</sup>. Frequency distributions of the GPBTs indicating the effects of assuming various cropland production periods are shown in Fig. 3. Under no-input farming, the GPBT was shorter than 20 years in only 14 to 43% of the grids. When assuming a 100-year cropland production period<sup>15</sup>, this areal extent increases to 62 to 93% of the grids. A similar trend was evident in high-input farming: there, the GPBT was shorter than 20 years in 42 to 82% of the grids, and shorter than 100 years in 74 to 93% of the grids (Fig. 3).

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#### Limitations and uncertainties

The data used in our GPBT calculations come with uncertainties and limitations that should be considered when interpreting the results. First, the crop model simulations with EPIC include only a limited number of natural land cover types (that is, deciduous forest, coniferous forest, rangelands), which are used to simulate the global natural soil carbon content. Therefore, the crop model simulations do not fully encompass the complexity of certain natural systems such as peatlands and mangroves, which are particularly relevant in that they store large amounts of carbon and nitrogen in their organic soils<sup>29,30</sup>. Previous studies indicated that replacing tropical peatlands with oil palm plantations results in the release of up to  $35 \text{ MgCO}_2 \text{ e} \text{ ha}^{-1} \text{ yr}^{-1}$  from the soil alone during the first 25 years of cultivation<sup>31,32</sup>, thereby leading to a payback time of 75 to nearly 700 years<sup>18</sup>. Ref. 13 calculated payback times ranging between 750 (sugarcane) and 12,000 (soybean) years when agriculture replaces peat forests.

Second, the IPCC maps<sup>33</sup> used to derive the biomass carbon stocks in natural ecosystems do not fully address local differences in carbon densities. The maps show generic carbon stocks for a variety of natural land cover types, and thus any variation within each land cover type is not accounted for. Such variation may be expected, for example, in the case of temperate forests, where land-use history varies greatly among forest sites<sup>34</sup>. Nevertheless, we conclude that the IPCC maps adequately address the most important spatial differences in global biomass carbon stocks for the purposes of the present study.

Third, the fossil GHGs emitted during cultivation and refining of biofuel crops are based on data from a limited number of countries. The global average GHG emission data used in the present study were based on studies from Switzerland, France, Germany, Spain, the US and Brazil<sup>35</sup>. A comparison of the available country-specific fossil GHG emissions indicated that the greatest international variations, that is, 32% and 11%, were associated with the cultivation of rapeseed and refining of rapeseed, respectively, which demonstrates that the variation between these countries is moderate to low. However, other than in the few countries mentioned above, no attention has been paid to international differences in farming techniques, transportation or refining technology, and, consequently, on fossil GHG emissions in the biofuel production chain. Projecting emissions based on this selection of countries to all countries across the globe will probably underestimate the emissions (and GPBTs) from developing countries that lack optimal techniques and infrastructure for the cultivation and refining of feedstock crops. However, the available data are too limited to improve the coverage of this assessment.

Fourth, we did not account for the potential effects of a changing climate and higher atmospheric  $CO_2$  concentrations on future carbon and nitrogen cycles. Although higher  $CO_2$  concentrations may enhance crop yields<sup>36,37</sup>, a temperature increase will probably decrease yields, particularly at low latitudes<sup>38</sup>. The amount of carbon stored in vegetation biomass is expected to increase with increasing temperatures<sup>39</sup>, whereas decomposition rates are expected to increase with increasing atmospheric  $CO_2$  concentrations, thereby limiting soil carbon storage<sup>40</sup>. The net outcome of these contrasting changes remains largely unclear<sup>38</sup>; therefore, these are not accounted for in our GPBT calculations.

Fifth, we did not address the relation between biofuel demand and agricultural production in our study. Other studies have modelled the link between biofuel demand and agricultural production thoroughly, which requires an understanding of the implications of policymaking and economics, including the complex relationship between fuel and food prices<sup>14,41,42</sup>.

Finally, previous studies have shown that biofuels are generally disadvantageous compared with fossil fuels with respect to environmental impact categories such as acidification, eutrophication, ozone depletion and human toxicity<sup>43–45</sup>, and replacing natural vegetation with croplands may affect local biodiversity<sup>18</sup>. Therefore, the biofuel feedstocks that performed well in the present study may not be the best options when considering the total environmental impact.

#### Conclusions

We developed spatially explicit GPBTs for crop-based biofuels on a global scale, which allows for a more-detailed spatial assessment of the global warming concerns and benefits of biofuel production than was possible earlier. Under no-input cultivation, rapeseedbased biodiesel vielded the shortest GPBTs, whereas sugarcane yielded the longest GPBTs. High-input farming strongly reduced the climatic impact of biofuels. Specifically, fertilization and irrigation resulted in higher crop yields, which offset the negative effects of decreases in soil carbon and higher GHG emissions from farming activities, particularly emissions of dinitrogen oxide from fertilizer application. Geographic location was found to be the most important factor controlling the environmental performance of the biofuel production systems included in the present study: the location affects the replaced natural carbon stocks and the carbon stocks and crop yields in the bioenergy system. For example, crop cultivation in tropical forest regions typically resulted in long GPBTs (medians of 17 to 51 years), whereas cultivation in temperate regions yielded substantially shorter GPBTs (medians of 6 to 20 years). Careful selection of growing locations is thus a prerequisite for the contribution of biofuel crops to the mitigation of climate change.

#### Methods

Methods and any associated references are available in the online version of the paper.

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## Author contributions

P.M.F.E., R.v.Z., M.v.d.V., M.O. and M.A.J.H. developed the methodological framework; E.S. performed the EPIC model simulations; M.v.d.V., J.B. and R.S. performed the post-processing of the simulation results; P.M.F.E. performed the GPBT calculations and statistical analyses; and all contributed to the writing of the paper.

#### **Additional information**

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to P.M.F.E.

## **Competing financial interests**

The authors declare no competing financial interests.

#### Methods

The GPBTs for the biofuel production systems of crop x cultivated under management strategy j in location i were calculated using the following equation

$$GPBT_{x,i,j} = \frac{\Delta GHG_{soil,x,i,j} + \Delta GHG_{biomas,x,i,j}}{(M_{fossil} - M_{bio}) \times Y_{x,i,j} \times BF_x \times E_x}$$

where  $\Delta$ GHG<sub>soil</sub> is the difference between stocks of SOC and nitrogen in natural and agricultural soil (MgCO<sub>2</sub>e ha<sup>-1</sup>);  $\Delta$ GHG<sub>biomass</sub> is the difference between carbon stored in natural and crop biomass (MgCO<sub>2</sub>e ha<sup>-1</sup>);  $M_{\text{fossil}}$  is the life-cycle fossil fuel GHG emissions during production and combustion of gasoline or diesel (MgCO<sub>2</sub>e MJ<sup>-1</sup>);  $M_{\text{bio}}$  is the life-cycle fossil fuel GHG emissions during biofuel production, including crop fertilizer application (MgCO<sub>2</sub>e MJ<sup>-1</sup>); Y is the crop yield (kg ha<sup>-1</sup> yr<sup>-1</sup>); BF is the biofuel conversion efficiency, that is, the amount of biofuel that can be generated per amount of crop x; and E is the energy content of the crop x biofuel (MJ kg<sup>-1</sup>). The carbon stored in dead material was not included as the contribution of dead material to the total carbon pool is typically low: <3% in forests<sup>46</sup> and <1% in grasslands<sup>47</sup>.

The two farm management strategies under investigation were no-input and high-input cultivation. A scenario where no-input cultivation is converted to high-input cultivation to improve crop production was studied as an alternative to the expansion of agricultural lands at the expense of natural vegetation. GPBTs for this land-use scenario were calculated using the equation

#### $\Delta GPBT_{x,i} = GPBT_{x,i,high input} - GPBT_{x,i,no input}$

The SOC content of the agricultural systems and natural systems was simulated using the environment policy integrated climate (EPIC) model<sup>48</sup>. For each combination of crop type and management strategy, the EPIC model simulates the SOC content as the amount of organic carbon in the soil to a depth of 30 cm (Mg C ha<sup>-1</sup>), thereby accounting for the carbon content of crop residues, carbon respiration from the soil, leaching of carbon from the soil profile to lower layers, and carbon lost in runoff and eroded sediment. Regarding SOC in natural systems, the EPIC model distinguishes between forest and rangeland (that is, grass- and shrubland) vegetation. Emissions of dinitrogen oxide (N<sub>2</sub>O) resulting from soil mineralization were assumed to be directly proportional to the loss of soil carbon, following ref. 24. The EPIC model was also used to simulate spatially explicit dry-matter yields of grain (corn and winter wheat), seed (rapeseed) and beans (soybeans), and the entire plant in the case of sugarcane.

The amounts of carbon stocked in natural biomass were based on the IPCC Tier-1 Global Biomass Carbon Map for the Year 2000 of ref. 33, which provides default carbon densities for both above- and below-ground biomass of various natural vegetation types at a  $1 \times 1$ -km spatial resolution. The amount of carbon stored in crop biomass was set to zero because annual harvesting of crops hinders the long-term storage of carbon.

Life-cycle GHG emissions related to the production and use of biofuels and fossil fuels were obtained from the ecoinvent v3 database<sup>35</sup>. For fossil fuels, we used

the global average of GHGs associated with the production of 1 MJ of fossil fuel energy. For the biofuels, we included only GHGs emitted during the production (for example, use of farming machinery, refining) of 1 MJ of bioenergy. Carbon emissions during combustion of biofuels were not included owing to the short rotation time of crops, implying a negligible global warming potential<sup>49</sup>.

Direct N<sub>2</sub>O emissions from fertilizer application during high-input crop cultivation were based on the nonlinear response between nitrogen fertilizer application and soil N<sub>2</sub>O emissions reported in ref. 50. Indirect emissions through nitrogen volatilization (through NH<sub>3</sub> and NO<sub>x</sub>) and from the leaching and runoff of nitrogen from fertilizer applications were calculated using IPCC default emission factors<sup>51</sup>.

For fossil fuel, as well as for biogenic GHG emissions,  $CO_2$ ,  $N_2O$  and methane were summed on the basis of their global warming potentials over a 100-year period, that is, 1, 265 and 30  $CO_2$ -equivalents ( $CO_2e$ ), respectively<sup>52</sup>.

To address by-products of biofuel production systems, GHG emissions were allocated based on energy content, mass and market value. In the main text, we present the results of energy content-based allocation. Results of mass-based and market value-based allocation are presented in Supplementary Figs 1–4.

We determined the variance between grid-specific GPBTs that was attributable to type of crop used for biofuel production, management regime during crop cultivation, and cultivation location. This variance was calculated using an ANOVA as the sums of squares for crop type and management regime factors, and the residual representing the spatial variability. The sum of squares of each factor and the residual were divided by the total sum of squares to provide a measure of the explained variance. The analyses were conducted using the R statistical software, v3.0.2, in RStudio.

A detailed account of the methods is available in the Supplementary Information.

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