Originally published as:


DOI: https://doi.org/10.1038/s41586-022-04629-w
Projected environmental benefits of replacing beef with microbial protein

Florian Humpenöder\textsuperscript{1*}, Benjamin Leon Bodirsky\textsuperscript{1,4}, Isabelle Weindl\textsuperscript{1}, Hermann Lotze-Campen\textsuperscript{1,2}, Tomas Linder\textsuperscript{3}, Alexander Popp\textsuperscript{1}

\textsuperscript{1}Potsdam Institute for Climate Impact Research, Potsdam, Germany.
\textsuperscript{2}Humboldt University of Berlin, Berlin, Germany.
\textsuperscript{3}Swedish University of Agricultural Sciences, Uppsala, Sweden.
\textsuperscript{4}World Vegetable Center, Shanhua, Tainan, Taiwan.

*Corresponding author
humpenoeder@pik-potsdam.de
Summary paragraph

Ruminant meat provides valuable protein to humans, but livestock production has many negative environmental impacts, especially in terms of deforestation, greenhouse gas (GHG) emissions, water use and eutrophication\(^1\). Besides a dietary shift towards plant-based diets\(^2\), imitation products including plant-based meat, cultured meat, and fermentation-derived microbial protein (MP) have been proposed as means to reduce the externalities of livestock production\(^3\text{-}^7\). Life cycle assessment (LCA) studies have estimated substantial environmental benefits of MP, produced in bioreactors using sugar as feedstock, especially compared to ruminant meat\(^3\text{-}^7\). Here, we present an analysis of MP as substitute for ruminant meat in forward-looking global land-use scenarios towards 2050. Our study complements LCA studies by estimating the environmental benefits of MP within a future socio-economic pathway. Our model projections show that substituting 20% of per-capita ruminant meat consumption with MP globally by 2050 (on protein basis) offsets future increases of global pasture area, cutting annual deforestation and related CO\(_2\) emissions roughly in half, next to lower methane emissions. However, further upscaling of MP, under the assumption of given consumer acceptance, results in a non-linear saturation effect on reduced deforestation and related CO\(_2\) emissions - an effect which cannot be captured with the method of static LCA.

Main

Global total livestock production has strongly increased in the last decades, in particular the production of ruminant meat has more than doubled since 1961\(^8\). Current livestock production systems, especially ruminant-based farming system, have substantial environmental consequences in terms of greenhouse gas (GHG) emissions, land use, terrestrial acidification, eutrophication and freshwater withdrawals\(^3\). The global food system is responsible for one-third of global anthropogenic GHG emissions, with livestock production being a major contributor in particular due to CH\(_4\) emissions from the digestive processes (enteric fermentation) of ruminants\(^9\text{-}^{10}\). Land use for livestock production is particularly high, accounting for 80% of global agricultural land if pasture land for grazing and cropland for animal feed production are considered\(^11\text{-}^{12}\). Moreover, it is estimated that the production of livestock feed accounts for 41% of total agricultural water use, with ruminant
meat production being the single largest water consumer. Further increases of livestock production are projected for the coming decades, specifically in present middle-income countries, driven by population growth and dietary shifts towards animal-based products due to increasing average individual incomes.

A gradual shift towards diets with less animal-farmed protein, in particular ruminant meat, in favor of plant-based protein sources, as suggested by the flexitarian diet of the EAT-Lancet Commission, would be healthier for people and more sustainable for the planet.

Adoption of the EAT–Lancet planetary health diet in high-income nations alone could yield a substantial double climate dividend due to GHG emission reduction and carbon sequestration. However, the question is how such a fundamental behavioral transformation could be achieved at globally relevant scales, considering that key barriers for the substitution of meat with plant-based protein sources include the sensory experience of eating meat, the taste as well as subjective concerns about the risk of protein deficiency.

Alternative protein sources

An alternative to largely plant-based diets is to substitute meat by analogs that mimic taste and texture of animal-farmed products. Meat analogs can be broadly categorized into three groups: plant-based meat substitutes (e.g. soybean burger patties), cultured meat (animal cells cultured in growth medium), and fermentation-derived MP (microbial biomass produced in bioreactors, also known as single-cell protein). Plant-based meat analogs primarily rely on agricultural crops (e.g. soybean) grown on cropland (roughly comparable to plant-based diets). In contrast, commercially available MP for human consumption (mycoprotein), is derived from fungal mycelium cultivated in heated bioreactors using sugar as feedstock. The fermentation process largely decouples the production of edible MP from local biophysical conditions, which might become especially relevant under climate change. However, cropland is still needed for growing sugar crops. Edible MP produced by methanotrophic or hydrogen-oxidizing chemosynthetic bacteria, which rely on methane or hydrogen and CO₂ instead of sugar as energy source, is currently under development and not yet commercially feasible. In a similar fashion, the cultivation of animal cells in a growth medium to produce cultured meat could be largely decoupled from traditional agriculture. However, cultured meat is still in an early development stage with many unknowns, particularly with respect to composition and costs of the growth medium. Here, we focus on
sugar-based MP produced via biological fermentation, which is available commercially today in grocery stores in multiple countries. Biological fermentation has been applied at industrial scale for the production of mycoprotein since the 1980s\(^4,24\). Mycoprotein is microbial biomass with meat-like texture and high protein content\(^4,6\). The protein quality of mycoprotein, measured by essential amino acid content and digestibility, is equivalent to ruminant meat\(^6,24\). Moreover, mycoprotein has been Generally Recognized As Safe (GRAS) by the Food and Drug Administration (FDA) in the USA since 2002\(^4,25\).

The environmental benefits and trade-offs of mycoprotein have been analyzed in life cycle assessment (LCA) studies, suggesting substantially lower GHG emissions (~80%), water use (> 90%), and land use (>90%) for each unit of ruminant meat substituted with mycoprotein\(^3,7\). But LCA studies also indicate that the replacement of other livestock products such as pork and chicken with mycoprotein would not result in substantial environmental benefits\(^7,25,26\). However, many effects of large-scale substitution of animal-farmed products are likely to be non-linear and cannot be scaled up based on static LCA footprints of current production systems. The substitution of livestock products with fermentation-derived analogs has not been studied so far in a dynamic system model accounting for future population growth, food demand, land-use dynamics, agricultural intensification or international trade. Only a single study estimated the total global land savings of alternative protein sources based on population and food production systems of the year 2011, without quantifying the associated GHG emissions and environmental impacts\(^27\).

**Future scenarios of sugar-based MP**

Here, we analyze the environmental effects of partially substituting ruminant meat with sugar-based MP in global forward-looking scenarios between 2020 and 2050. In line with previous studies, we assume that biological fermentation for single-cell protein production requires sugar cane grown on cropland as feedstock (see methods for details)\(^28,29\). We limit the substitution of livestock products to ruminant meat, for which previous LCA studies estimated the largest environmental benefits (in contrast to pork and chicken)\(^7\). To this end, we use the global multi-regional MAgPIE 4 open-source land-use modelling framework\(^30,31\). The MAgPIE framework has been used earlier to study the impacts of replacing animal feed with MP. We build on this previous research and use the middle-of-the-road SSP2 (shared socio-economic pathways) scenario, which features increasing population, income and
livestock demand (Extended Data Figure 1, Supplementary Figure 2), as our reference scenario (SSP2-Ref-MP0)\textsuperscript{15,28}. In three alternative scenarios we assume that 20% (MP20), 50% (MP50) and 80% (MP80) of the per-capita protein consumption from ruminant meat is replaced with sugar-based MP in each model region by 2050 (Figure 1a, Extended Data Figure 2). To mimic the typical adoption of new technologies and products by consumers, the fade-in of MP follows an S-shaped curve from 2020 onwards, reaching the target in 2050. The scenario-specific per-capita consumption of ruminant meat and MP is multiplied with the corresponding population to obtain total demand, which is used as driver in the model (Figure 1b). In summary, all scenarios are driven by the same overall demand for food crops, feed, livestock products and bioenergy, but differ in the substitution targets of ruminant meat with MP (Extended Data Figure 3, Supplementary Figure 2, Supplementary Figure 4, Supplementary Figure 3).

Figure 1: Future scenarios of ruminant meat and Microbial Protein (MP) as protein sources in human diets. a) global per-capita protein consumption of ruminant meat and MP between 2020 and 2050 for the reference scenario (MP0) and three MP scenarios, in which 20%, 50% and 80% of the per-capita protein consumption from ruminant meat is substituted with sugar-based MP by 2050. The substitution is phased-in in each model region from 2020 onwards following an S-shaped adoption curve (see Extended Data Figure 2 for regional numbers). b) Total ruminant meat and MP demand, used as driver for the MAgPIE simulations, obtained by multiplication of scenario-specific per-capita consumption with corresponding population (Extended Data Figure 1). Food losses along the supply chain between demand and consumption are accounted for. Historical data from FAOSTAT\textsuperscript{c}. c) Overall feed and feedstock demand for livestock production and MP fermentation. Pasture-based feed demand includes grass for feeding livestock. Cropland-based feed/feedstock demand includes crops for feeding livestock and sugar cane for MP fermentation.
Land use dynamics

Land-use change, as projected by the MAgPIE model, differs substantially between the reference and MP scenarios. In the reference scenario (MP0), cropland and pasture both increase at the cost of forest and non-forest vegetation between 2020 and 2050 at the global level (Figure 2). The increase of cropland (175 Mha) and pasture (96 Mha) by 2050 is driven by SSP2-based demand for food crops, feed and livestock products (Supplementary Figure 2, Supplementary Figure 4). The global loss of forest (178 Mha) and non-forest vegetation (92 Mha) by 2050 is largely driven by demand from Sub-Saharan Africa and Latin America (Extended Data Figure 7). In the MP20 scenario, global loss of forest between 2020 and 2050 is much lower (78 Mha), largely because pasture area, in contrast to the reference scenario, does not expand. At the same time, the increase in global cropland by 2050 is similar in both scenarios. The reason for the pasture dynamic is that the 20% per-capita substitution of ruminant meat with MP by 2050 results in rather static total global ruminant meat demand from 2025 onwards (Figure 1b), which (notably) is sufficient to largely offset future increases of overall pasture feed demand at global level (Figure 1c). For cropland, mainly two counteracting processes cancel out each other in MP20: Crop-based feed demand for ruminant meat production is reduced, while sugar cane demand as feedstock for MP fermentation is increased (Figure 1c, Extended Data Figure 5).

Higher substitution targets of ruminant meat with MP in the MP50 and MP80 scenario enhance the land-savings effects observed for the MP20 scenario. Further reductions of pasture-based feed demand (Figure 1c) result in declining global pasture area between 2020 and 2050 (Figure 2). In consequence, cropland increasingly expands into those freed up pasture areas, thus saving forest and non-forest vegetation from conversion. In the MP80 scenario, there is almost no loss of forest and non-forest vegetation between 2020 and 2050 at global level (Figure 2). In comparison to the reference scenario, deforestation and loss of non-forest vegetation is especially reduced in the Congo Basin, Central America and the Amazon Basin (Supplementary Figure 5).
Figure 2: Global land-use change between 2020 and 2050 for major land types. In the reference scenario, cropland and pasture expand at the costs of forest and non-forest vegetation (part of other land). In the MP scenarios, comparable cropland expansion causes much less deforestation and conversion of non-forest vegetation due to increasing pasture-to-cropland conversion, which is facilitated by lower feed demand from pastures (Extended Data Figure 5). See Extended Data Figure 6 and Extended Data Figure 7 for regional results and validation data.

Non-linear substitution effects

The substitution of ruminant meat with MP reduces several food-related environmental pressures, which can be mapped to the Sustainable Development Goals (SDGs). The SDGs are aspirational goals with global coverage towards 2030. Here, we use the following set of environmental indicators, partly adapted from a recent study on SDGs where MAgPIE was contributing in a multi-model framework approach: deforestation (SDG15: Life on Land), CO₂, CH₄ and N₂O emissions from agriculture and land-use change (SDG13: Climate Action), agricultural water use (SDG06: Clean Water and Sanitation) and nitrogen fixation (SDG15). For consistency and for the analysis of relative effects, all environmental indicators reflect annual values. Since the scope of MAagPIE is limited to agriculture and land use, we do not account for energy requirements and energy-related GHG emissions of MP production in this study (see discussion for implications).

In the reference scenario, global annual deforestation increases from 3.7 Mha yr⁻¹ in 2020 to 4.8 Mha yr⁻¹ in 2030 and 8.4 Mha yr⁻¹ in 2050 (Figure 3a), mainly driven by forest-to-pasture conversion for animal grazing in Sub-Saharan Africa (Supplementary Figure 4, Extended Data Figure 7). In the MP20 scenario, these global annual deforestation rates are about halved, resulting in 3.7 Mha yr⁻¹ in 2050. A further increase of ruminant meat substitution to 50% by 2050 (MP50) again roughly halves global annual deforestation, resulting in 1.5 Mha yr⁻¹ in 2050. The same trend continues in the MP80 scenario, resulting in
0.6 Mha yr⁻¹ in 2050. Hence, the substitution of ruminant meat with MP supports the achievement of SDG target 15.2 of halting deforestation.

Our results show a non-linear relationship between different levels of ruminant meat substitution and annual deforestation (Figure 3g). The reason for the non-linear relationship is that land-use change typically does not depend on the level of production, but on structural change in agricultural production. In the absence of land degradation, changes in land management or any other disturbing effects, no additional cropland or pasture is needed to maintain agricultural production at the same level. However, to increase the production more land and/or higher yields are needed. Likewise, a reduction of land-based production could decrease managed land and/or reduce the land-use intensity. In our scenarios, the substitution of ruminant meat with MP strongly reduces the demand for animal feed from pastures. In the MP20 scenario, global feed demand from pasture is rather constant from 2020 onwards, in contrast to an increasing trend in the reference scenario (Figure 1c). Therefore, no increase of global pasture area is needed in MP20 by 2050, which explains the strong reduction of deforestation relative to the reference scenario (56%). However, the forest-saving effect saturates with higher substitution targets in MP50 (82%) and MP80 (93%), in which the global pasture feed demand decreases compared to the reference scenario (Figure 1c).

CO₂ emissions from land-use change are strongly driven by changes in forest cover, and hence follow the same non-linear pattern as observed for annual deforestation (Figure 3b). The CO₂ emissions reported here reflect net CO₂ emissions as they account for carbon losses through deforestation and conversion of non-forest vegetation as well as for carbon gains from afforestation and regrowth of vegetation on abandoned agricultural land. In the reference scenario, global net CO₂ emissions from land-use change decrease from 3957 Mt CO₂ yr⁻¹ in 2020 to 3048 Mt CO₂ yr⁻¹ in 2030, followed by an increase to 5496 Mt CO₂ yr⁻¹ in 2050. The global increase of net CO₂ emissions is largely driven by two counteracting regional dynamics. From 2020 onwards, CO₂ emissions in Latin America decline but strongly increase in Sub-Saharan Africa, both driven by differing socio-economic developments in terms of population and food demand (especially for ruminant meat; see SI for regional details). In the MP20 scenario, net CO₂ emissions amount to 2392 Mt CO₂ yr⁻¹ in 2050, which correspond to a relative reduction of 56% compared to the reference scenario (Figure 3g). In line with the
non-linear relationship for deforestation, the reduction of net CO$_2$ emissions from land-use change shrinks with higher substitution targets. In MP50 and MP80, net CO$_2$ emissions amount to 951 and 734 Mt CO$_2$ yr$^{-1}$ in 2050, respectively. These levels correspond to relative reductions of 83% and 87% for MP50 and MP80, respectively. Hence, the substitution of ruminant meat with MP could strongly reduce net CO$_2$ emissions from land-use change. Such emissions reductions can be considered to support the targets of SDG13, although there are no quantitative targets for sectoral emission reductions.

**Linear substitution effects**

The substitution of ruminant meat with MP also reduces CH$_4$ and N$_2$O emissions from agriculture (SDG13), agricultural water use (SDG06) and nitrogen fixation (SDG15) (Figure 3c-f). In contrast to land-use change and associated net CO$_2$ emissions, these indicators largely depend on the level of production. Hence, each unit of ruminant meat replaced with MP yields about the same reduction of environmental pressures, indicating a rather linear relationship (Figure 3g).

Agricultural CH$_4$ emissions, which are largely caused by enteric fermentation in the rumen of cattle (belching), increase in the reference scenario from 208 to 282 Mt CH$_4$ yr$^{-1}$ between 2020 and 2050 at global scale. The reduced number of cattle in the MP scenarios results in lower CH$_4$ emissions, which amount to 250, 210 and 172 Mt CH$_4$ yr$^{-1}$ in 2050 for MP20, MP50 and MP80, respectively. In relative terms, these numbers reflect reductions of 11%, 26% and 39% by 2050 compared to the reference scenario. Similarly, N$_2$O emissions from agricultural soils (fertilizer application) and animal waste management, increase in the reference scenario from 9.5 to 13.4 Mt N$_2$O yr$^{-1}$ between 2020 and 2050. The reduced number of cattle in the MP scenarios lowers the increase of global N$_2$O emissions to 10.1-12.4 Mt N$_2$O yr$^{-1}$ by 2050, which corresponds to relative reductions of 7-25%. Hence, the substitution of ruminant meat with MP has distinct effects on CH$_4$ and N$_2$O emissions from agriculture. At the regional level, Sub-Saharan Africa, Latin America and Asia show the strongest reductions of CH$_4$ and N$_2$O emissions, which is largely driven by the scale of total ruminant meat substituted with MP (Extended Data Figure 3, Extended Data Figure 9).

The effects of ruminant meat substitution on agricultural water use (SDG06) and nitrogen fixation (SDG15) are rather small. Global agricultural water use for food and feed crops increases in the reference scenario from 3057 to 4200 km$^3$ yr$^{-1}$ between 2020 and 2050.
Reduced demand for animal feed crops in the MP scenarios limits the increase of agricultural water use to 3868-4137 km³ yr⁻¹ by 2050, which correspond to relative reductions of 1-8%. However, this will likely not be sufficient to achieve SDG target 6.4 (“sustainable withdrawals and supply of freshwater”), as already today water withdrawals in many parts of the world tap into environmental flow requirements. Similarly, nitrogen fixation, a proxy for nitrogen losses to the environment and hence ecosystem degradation, increases from 172 to 234 Mt N yr⁻¹ between 2020 and 2050 in the reference scenario. Reduced demand for animal feed crops in the MP scenarios limits the increase of nitrogen fixation to 212-227 Mt N yr⁻¹ by 2050, which correspond to relative reductions of 3-9%. However, these levels are substantially above a target value of 90 Mt N yr⁻¹ for SDG 15.5².
SSP2, a middle-of-the-road scenario for future population, income and food demand. We use the spatially explicit land use model MAgPIE. Our scenarios are based on regional results and sources of validation data. g) Relative difference of environmental indicators, compared to the reference scenario, in 2050 as function of scenarios with increasing ruminant meat substitution. Most indicators, including methane emissions, show a linear relationship. However, both deforestation and related net CO2 emissions are reduced by 56%, already at 20% per-capita substitution of ruminant meat with MP, followed by a saturation effect at higher substitution rates. The reason for this non-linear effect is that deforestation, and hence net CO2 emissions, depend on structural change in agricultural production. In contrast, the indicators with linear relationships largely depend on the level of production.

Discussion

Here, we present the first analysis of substituting ruminant meat with sugar-based MP in forward-looking land-use scenarios. For our model-based projections with global coverage until 2050 we use the spatially explicit land use model MAgPIE. Our scenarios are based on SSP2.
quantify the environmental benefits of substituting 20%, 50% and 80% of per-capita ruminant meat consumption with MP by 2050 in each model region. Notably, the reduced animal feed demand in the 20% case (MP20) is sufficient to offset future increases of global pasture area, which translates into 56% less deforestation and 56% less net CO₂ emissions from land-use change by 2050, both compared to the reference scenario. In the 50% and 80% case, deforestation is further reduced, resulting in relative reductions of 82% and 93% by 2050, respectively. Similarly, net CO₂ emissions from land-use change are reduced by 83% and 87% in the 50% and 80% case, respectively. The reason for this non-linear substitution effect is that land-use change, and hence net CO₂ emissions, depend on structural change in agricultural production, as opposed to the level of production. The substitution of ruminant meat with MP also reduces non-CO₂ emissions from agriculture, agricultural water use and nitrogen fixation. However, these environmental indicators largely depend on the level of production, and hence decrease rather linearly with increasing substitution targets. In particular, global agricultural CH₄ emissions are reduced by 11%, 26% and 39% at per-capita substitution targets of 20%, 50% and 80% by 2050, respectively.

Previous LCA studies have estimated substantial environmental benefits of MP derived from fungal mycelium (mycoprotein) over ruminant meat at the product level. Here, we assess the consequences of large-scale substitution of ruminant meat with sugar-based MP in global forward-looking scenarios on a set of environmental indicators. Due to the methodological differences, our results cannot be compared directly to existing LCA outcomes. However, our results complement existing LCA studies on the substitution of ruminant meat with MP. First, our study provides an estimate of the absolute and relative reductions of food-related environmental pressures for different substitution targets until 2050, globally and for 12 geopolitical regions. Second, our study shows that the large-scale upscaling of MP as substitute for ruminant meat results in a non-linear saturation effect on land-use change and associated net CO₂ emissions - an effect which cannot be captured with the method of static LCA. Similarly, environmental pressures are context-dependent and are not reduced equally around the globe, dependent on the development of socio-economic factors such as population dynamics, diet patterns and international trade. This underpins the importance of using a dynamic system model rather than static LCA for estimating the environmental benefits of MP as substitute for ruminant meat.
At the same time, the use of forward-looking modeling tools for analyzing the substitution of ruminant meat with MP implies that the quantified environmental benefits depend on scenario assumptions. Here, we analyze the substitution of ruminant meat with MP in the context of a SSP2-based scenario, which is broadly characterized by the continuation of current demographic, environmental, technological, and societal trends into the future. However, our results would likely differ under a more sustainable setting such as SSP1 (Sustainable Development), which is characterized by slower population growth, increased environmental awareness and reduced consumption of livestock products. Under this setting some environmental benefits of replacing ruminant meat with MP are likely smaller because of a) overall lower pressure on land (lower population and dietary change) and b) improved regulation of externalities such as deforestation. This could especially affect the two indicators for which we identify non-linear substitution effects: deforestation and associated net CO₂ emissions, both of which depend on structural change in agricultural production. For instance, global forest cover is estimated to be rather constant throughout the 21st century under a SSP1 setting (SSP1-NDC), in contrast to declining forest cover under a comparable SSP2 setting (SSP2-NDC). Hence, the relative reduction of deforestation and net CO₂ emissions attributable to the substitution of ruminant meat with MP is likely smaller under SSP1 compared to SSP2. On the contrary, environmental benefits of substituting ruminant meat with MP might be stronger under a more pessimistic background setting such as SSP3 (Regional Rivalry), which is characterized by high population growth in low-income countries, low priority for addressing environmental problems and resource-intensive diets. However, the use biotechnology for solving environmental problems seems inconsistent with the overall SSP3 narrative.

Further factors influencing the scenario setup and thus the outcome include assumptions about land-based climate change mitigation measures (e.g. bioenergy, forest protection and afforestation) and climate change impacts on land (e.g. crop yields and carbon stocks in ecosystems). In this study, which is the first of its kind, we deliberately focus on analyzing the basic effects of substituting ruminant meat with MP under a SSP2 reference scenario without further assumptions on land-based mitigation and climate change impacts. We do, however, account for existing national polices on forest protection, afforestation and bioenergy (Supplementary Figure 3). In addition to climate protection measures, future...
national policies in support of the transition towards a bioeconomy might increase the 
demand for biomass grown on agricultural land. In our results, the substitution of ruminant 
meat with MP reduces deforestation through increased pasture-to-cropland conversion. 
Alternatively, the pasture areas no longer needed for livestock grazing could be partly 
repurposed to biomass cultivation. However, depending on the scale, the production of 
additional biomass might offset the environmental benefits of MP, especially with respect to 
deforestation and associated net CO₂ emissions. To avoid such trade-offs, policies promoting 
biomass cultivation should be complemented by forest protection policies.

Our study is limited to the replacement of ruminant meat with sugar-based MP that is 
currently commercially available for human consumption (mycoprotein). Edible MP 
produced by methanotrophic or hydrogen-oxidizing chemosynthetic bacteria (power-to- 
food) is an emerging technology that, in contrast to mycoprotein, does not rely on biomass 
as energy source. Therefore, the land-use requirement of power-to-food is considerably 
smaller compared to mycoprotein, unless the hydrogen or methane itself is being produced 
using biomass. The climate impacts of MP produced via power-to-food are estimated to be 
lower compared to mycoprotein, but strongly depend on the use of low-emission energy 
sources. Cultured meat is another future technology that might play an important role in 
replacing animal-sourced protein in the future. LCA studies indicate that cultured meat 
production might require smaller quantities of agricultural inputs and land than ruminant 
meat production. However, those benefits could come at the cost of higher energy 
requirements, which might undermine the GHG emission savings of cultured meat 
production, depending on the availability of decarbonized energy generation. 

Precision fermentation is a further future technology relevant to the alternative protein space, which 
could be utilized to produce milk protein (as ingredient for dairy analogs) or egg white. At 
the time of writing, however, no public data for inclusion in our modelling framework on land- 
based feedstock requirements of cultured meat and precision fermentation is available. 
Nevertheless, our results for the substitution of ruminant meat with MP can be interpreted 
as a proxy for the large-scale substitution of ruminant meat or dairy products with other 
biotechnology-enabled alternatives such as cultured meat or fermentation-based milk 
analogs.
Our study covers several environmental indicators, including deforestation, GHG emissions from agriculture and land-use change, agricultural water use and nitrogen losses. However, we do not account for the environmental consequences of sugar-based MP production beyond the land-use sector. Especially, our modelling framework is not capable of tracking the energy requirements and energy-related GHG emissions of MP production, which is of key importance for assessing the sustainability of MP production. Based on LCA studies, it has been estimated that mycoprotein production has about the same energy requirements as conventional ruminant meat production. However, this proxy should be interpreted with care because the energy requirements for mycoprotein and ruminant meat production have been calculated with different methods. Moreover, the type of energy needed for MP and ruminant meat production differs. For ruminant meat, animal feed production is a major energy consumer (e.g. diesel for tractors and natural gas for synthetic nitrogen fertilizer production). In contrast, in cell-cultured food production the whole idea is that bioreactors replace animals. Instead of feeding animals, the feedstock is processed in bioreactors, which use electricity for regulating the temperature and other functions of the bioreactor. Therefore, the land-related GHG emission savings of sugar-based MP shown in our study need to be contrasted with energy-related GHG emissions for assessing the net effect. To avoid that GHG emission savings in the land-use sector are offset or even exceeded by GHG emissions from the energy sector, a large-scale transformation towards cell-cultured food, as assumed in our scenarios, would need to be complemented by a large-scale decarbonisation of electricity generation. It is anticipated that recent technological advancements and cost reductions in solar photovoltaics, wind and battery storage could make renewable energy cost-competitive compared to carbon-based fuels in the near future and that considerably higher electrification shares across different sectors are possible.

Moreover, if MP would replace ruminant meat at large-scale, as assumed in our scenarios, this transformation would likely reduce the provision of non-food animal by-products such as hides and skins for leather products, organs for pet food, fat for chemicals, bones and blood for fertilizers as well as non-food services from animal husbandry such as traction and insurance, the latter being especially relevant in low-income countries. These non-food by-products, which are often by-products of meat production, would need to be replaced by alternatives such as synthetic leather, synthetic fertilizer or plant-based fats,
causing additional GHG emissions and other environmental impacts which are not considered in our assessment. Partly, non-food by-products could be replaced in the future by fermentation-enabled alternatives such as fungi-based leather. However, in analogy to MP this could result in higher energy-related GHG emissions, depending on the sustainability of energy production.

Future research could address some of the identified gaps by studying the impacts of meat and dairy analogs in an integrated assessment model, which accounts for energy demand and production including GHG emissions, and economy-wide impacts, next to a detailed representation of land-use dynamics. In addition, this would allow to analyze the role of meat and dairy analogs as part of a portfolio of climate change mitigation options.

Methods

Land-use model MAgPIE

The Model of Agricultural Production and its Impact on the Environment (MAgPIE) is developed and used to assess the competition for land and water, and the associated consequences for sustainable development under future scenarios of rising food, energy and material demand. The model version we use here is MAgPIE 4.3.4 (see data availability statement at the end of the article for details). MAgPIE combines economic and biophysical approaches to simulate spatially explicit global scenarios of land use within the 21st century and the respective interactions with the environment (Supplementary Figure 1). The MAgPIE framework has been used to simulate mitigation pathways for different Shared Socioeconomic Pathways (SSPs) and contributed to several IPCC reports.

MAgPIE is a global multi-regional partial equilibrium model of the land-use sector. The model integrates regional economic conditions such as demand for agricultural commodities, technological development and production costs as well as spatially explicit data on biophysical constraints into an economic decision-making process, based on the concept of recursive dynamic cost optimization. Geographically explicit data on biophysical conditions are provided by the Lund-Potsdam-Jena managed land model (LPJmL) on a 0.5 degree resolution and include e.g. carbon densities of different vegetation types, agricultural productivity such as crop yields and water availability for irrigation. Due to computational constraints, all model inputs in 0.5 degree resolution are aggregated to simulation units for
the optimization process based on a clustering algorithm. Available land types in MAgPIE are cropland, pasture, forest, other land (including non-forest vegetation, abandoned agricultural land and deserts) and settlements. Cropland (rainfed and irrigated), pasture, forest and other land are endogenously determined, while settlement areas are assumed to be constant over time. The cropland covers cultivation of different crop types (e.g. temperate and tropical cereals, maize, rice, oilseeds, roots), both rainfed and irrigated systems, and two second generation bioenergy crop types (grassy and woody). International trade is based on historical trade patterns and economic competitiveness. Food demand is derived based on population growth and dietary transitions, accounting for changes in intake and food waste, the shift in the share of animal calories, processed products, fruits and vegetables as well as staples.

Here, we derive the following environmental indicators from MAgPIE (see Extended Data Table 1 for structured overview), of which most have been used in previous studies. Annual deforestation (Mha yr\(^{-1}\)) is calculated based on differences in forest area between time steps. Since the calculation is based on changes of forest area, annual deforestation may vary substantially between time steps (stock-flow problem). To avoid that our results are biased by the values of single years, we calculate in a post-processing step an average value of annual deforestation by applying a function (low-pass filter) that distributes values of annual deforestation over time, while making sure that the time integral over the modeled period remains the same. Similarly, annual net CO\(_2\) emissions (Mt CO\(_2\) yr\(^{-1}\)) from land-use change are calculated based on changes in carbon stocks of vegetation, and therefore may vary substantially between time steps (stock-flow problem). To avoid biased results, we therefore apply the low-pass filter function also on annual net CO\(_2\) emissions from land-use change. Carbon stocks changes in vegetation are subject to land-use change dynamics such as conversion of forest into agricultural land. In case of afforestation or when agricultural land is set aside from production, regrowth of natural vegetation absorbs carbon from the atmosphere (removals). N\(_2\)O emissions (Mt N\(_2\)O yr\(^{-1}\)) from agricultural soils (fertilizer application) and animal waste management are estimated based on nitrogen budgets for croplands, pastures and the livestock sector. CH\(_4\) emissions (Mt CH\(_4\) yr\(^{-1}\)) from agriculture include emissions from enteric fermentation, animal waste management and rice cultivation, which are estimated based on feed demand, manure, and rice cultivation area,
Nitrogen fixation (Mt N yr\(^{-1}\)) is a proxy for nitrogen losses to the environment and hence ecosystem degradation. Nitrogen inputs on cropland via industrial (e.g. production of inorganic fertilizers) and intentional biological fixation are calculated based on a nitrogen budget approach\(^{2,51}\). Agricultural water use (km\(^3\) yr\(^{-1}\)) depends on the water requirements of crops, the available water for irrigation, the irrigation efficiency and the irrigation infrastructure, which can be extended endogenously based on cost-effectiveness\(^{52}\). For more information on the MAgPIE modelling framework we refer to the model source code and the documentation (see data availability statement).

**Microbial protein in MAgPIE**

Fermentation-based MP production has been implemented in an earlier version of MAgPIE to study the impacts of replacing animal feed with microbial protein\(^{26}\). Building on this previous research, we included a refined implementation of MP production into MAgPIE version 4.3.4\(^{31}\) to study the impacts of replacing ruminant meat with MP in human diets. In line with the literature on MP for human consumption, we assume a DM protein content of 45% in microbial biomass (based on mycoprotein)\(^{4,6}\). For the production of MP, we assume that sugar cane, grown on cropland, is needed as feedstock. Based on Pikaar et al 2018\(^{28}\), we assume that 4.3 ton of sugar cane are needed to produce 1 ton of microbial biomass, all on dry matter (DM) basis. This implies that ~0.2326 ton DM microbial biomass can be produced from 1 ton DM sugar cane. Assuming that 1 ton DM sugar cane yields 0.3363 ton DM sugar, we get 0.69 ton DM microbial biomass from 1 ton DM sugar, which is well within the range of 0.42-0.87 ton DM microbial biomass per ton DM sugar published in Lapeña et al 2020, Table 1\(^{29}\). Sugar cane cultivation is largely limited to tropical and subtropical regions. Therefore, in our modelling framework, temperate and boreal regions partly rely on imports of feedstock for MP production. For ruminant meat, we assume a food protein content of 33% in DM (own calculations based on FAOSTAT\(^{8}\) using a DM content of 41%). The DM food protein content of 33% reflects an average value across different ruminant meat products including beef, ground beef and processed meat. The corresponding fresh matter food protein content of 13.5% is comparable to other estimates for the average food protein content of beef products\(^{53,54}\). We use the DM protein content for the per-capita substitution of ruminant meat with MP. Together, with the DM protein content of 45% in microbial biomass, this implies that 1 ton DM ruminant meat is replaced by 0.73 ton DM MP. With respect to costs, we assume that
each ton DM MP costs 789 USD, based on Table S9 in Pikaar et al 2018. The costs account
for energy, oxygen, nitrogen and phosphorus requirements. Feedstock costs are excluded to
avoid double accounting, since MAgPIE has its own feedstock costs. We do not account for
environmental consequences of MP production beyond the land-use sector. In particular, we
do not account for energy requirements and energy-related GHG emissions of MP production.

Scenario assumptions

The reference scenario (SSP2-Ref-MP0) is based on SSP2 with respect to population,
income, diets, land-use regulation and trade. The MP scenarios (SSP2-Ref-MP20, SSP2-Ref-
MP50 and SSP2-Ref-MP80) differ from the reference scenario only with respect to the per-
capita substitution of ruminant meat with MP in human diets. The consumption of per-capita
protein summed over ruminant meat and MP remains the same (Figure 1a). In the MP
scenarios, we assume that 20%, 50% and 80% of the per-capita ruminant meat consumption
is substituted with MP by 2050 in each model region. The fade-in of MP follows an S-shaped
curve to mimic the typical adoption of new technologies and products by consumers. In our
modelling framework, livestock commodities (ruminant meat, whole-milk, pork, poultry meat
and eggs) are produced in five animal food systems (beef cattle, dairy cattle, pigs, broilers and
laying hens). The production of ruminant meat is allocated to beef cattle and dairy cattle
systems according to historical shares. However, the substitution of ruminant meat with MP
in our scenarios only aims at only reducing ruminant meat from beef cattle. Dairy production
remains largely unchanged, even at high MP substitution rates (Extended Data Figure 4). Our
scenario setup with relative substitution rates (20%, 50% and 80%) by 2050 in each model
region is designed to allow for straightforward comparison of environmental indicators
between scenarios and regions. However, this implies that low-income countries would cut
ruminant meat consumption with the same level of ambition as high-income countries,
neither accounting for the overall share of livestock products in diets and the likelihood of
adopting novel diets nor addressing the economic and cultural context in which a substitution
of ruminant meat with MP would take place.
Code availability

The source code for MAgPIE 4.3.4 is openly available at https://github.com/magpiemodel and http://doi.org/10.5281/zenodo.4730378. The model documentation can be found at https://rse.pik-potsdam.de/doc/magpie/4.3.4/.

Data availability

The numerical scenario results, including instructions for reproduction, and analysis scripts supporting the findings of this study are available at https://doi.org/10.5281/zenodo.5794460 under a CC-BY-4.0 license.

References


43. Rogelj, J. et al. Mitigation pathways compatible with 1.5°C in the context of sustainable development. in *Special Report on the impacts of global warming of 1.5 °C* (Intergovernmental Panel on Climate Change, 2018).

44. Smith, P. et al. Interlinkages between desertification, land degradation, food security and greenhouse gas fluxes: Synergies, trade-offs and integrated response options. in *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems* (Intergovernmental Panel on Climate Change, 2019).


Acknowledgments

This work received funding from the European Union’s Horizon 2020 research and innovation program under grant nos. 821124 (NAVIGATE) and 821471 (ENGAGE). Further support is provided by the Global Commons Stewardship (GCS) project funded by the University of Tokyo (grant no 94104), the GreenPlantFood project funded by the Research Council of Norway (grant no 319049), and the Food System Economics Commission (FSEC) funded by Wellcome Trust (grant agreement no. 221362/Z/20/Z), Rockefeller Foundation (2020 FOD 008) and IKEA Foundation (G-2009-01682).

Author contributions

F.H. and A.P. designed the overall study and analyzed the results. F.H. extended the MAgPIE model code with contributions from B.L.B. and I.W. F.H. performed the MAgPIE scenario modelling and created all figures and tables. F.H. wrote the main manuscript text with important contributions from A.P., H.L.C., B.L.B., I.W and T.L. All authors commented on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at LINK
Supplementary information The online version contains supplementary material available at LINK
Correspondence and requests for materials should be addressed to F.H.
Peer review information The authors and Nature thank three anonymous referees for their thorough and constructive review.
Reprints and permissions information is available at www.nature.com/reprints.
### Extended Data Tables and Figures

<table>
<thead>
<tr>
<th>SDG</th>
<th>Indicator and Unit</th>
<th>Definition</th>
<th>SDG target for 2030/2050</th>
<th>Source / Comment</th>
</tr>
</thead>
<tbody>
<tr>
<td>SDG 6</td>
<td>Agricultural water use (km³ yr⁻¹)</td>
<td>Water use for irrigation and other agricultural purposes</td>
<td>-</td>
<td>Bonsch et al⁵²</td>
</tr>
<tr>
<td>SDG 13</td>
<td>CO₂ emissions from land-use change (Mt CO₂ yr⁻¹)</td>
<td>Annual net CO₂ emissions accounting for carbon losses through deforestation and conversion of non-forest vegetation as well as for carbon gains from afforestation and regrowth of vegetation on abandoned agricultural land. The calculation of annual net CO₂ emissions is based on carbon stock changes between time steps.</td>
<td>-</td>
<td>Humpenöder et al⁴⁸ To avoid that our results are biased by the values of single years (stock-flow problem), we calculate in a post-processing step an average value by applying a low-pass filter function that distributes values over time, while making sure that the time integral remains the same.</td>
</tr>
<tr>
<td>SDG 13</td>
<td>CH₄ emissions from agriculture (Mt CH₄ yr⁻¹)</td>
<td>CH₄ emissions from enteric fermentation, animal waste management and rice cultivation, estimated based on feed demand, manure, and rice cultivation area, respectively.</td>
<td>-</td>
<td>Popp et al⁵⁰      Stevanović et al⁴⁹</td>
</tr>
<tr>
<td>SDG 13</td>
<td>N₂O emissions from agriculture (Mt N₂O yr⁻¹)</td>
<td>N₂O emissions from agricultural soils (fertilizer application) and animal waste management, estimated based on nitrogen budgets for croplands, pastures and the livestock sector.</td>
<td>-</td>
<td>Bodirsky et al⁵¹  Stevanović et al⁴⁹</td>
</tr>
<tr>
<td>SDG 15</td>
<td>Annual deforestation (Mha yr⁻¹)</td>
<td>Annual loss of primary and secondary forest due to conversion to agricultural land. The calculation of annual deforestation is based on changes in forest area between time steps.</td>
<td>Halting deforestation</td>
<td>To avoid that our results are biased by the values of single years, we calculate an average value by applying a low-pass filter function (same as for CO₂ emissions).</td>
</tr>
<tr>
<td>SDG 15</td>
<td>Nitrogen fixation (Mt Nr yr⁻¹)</td>
<td>Nitrogen fixation is a proxy for nitrogen losses to the environment and hence ecosystem degradation. Nitrogen inputs on cropland via industrial (e.g. production of inorganic fertilizers) and intentional biological fixation are calculated based on a nitrogen budget approach.</td>
<td>90 Mt Nr yr⁻¹</td>
<td>Soergel et al²     Bodirsky et al⁵¹</td>
</tr>
</tbody>
</table>

*Extended Data Table 1: Environmental indicators from MAgPIE used in this study, and their mapping to SDGs.*
Extended Data Figure 1: Regional projections of a) population and b) income for SSP2 assumed in MAger in comparison to historical data (validation). The projections of population and income are based on KC and Lutz55 and Dellink et al56. Historical data from World Bank World Development Indicators (WDI)57 and James et al58. The historical data has been processed using the pik-piam/mrvalidation R package59.

Extended Data Figure 2: Per-capita consumption of a) ruminant meat and b) microbial protein at regional level in MAger projections compared to historical data (validation). Units are in kcal/capita/day (left axis) and g protein/capita/day (right axis). Historical data from Bodirsky et al69. The historical data has been processed using the pik-piam/mrvalidation R package59.
Extended Data Figure 3: Total demand for a) ruminant meat and b) microbial protein, accounting for population and per-capita consumption, at regional level in MAgPIE projections compared to historical data (validation). Historical data from FAO\textsuperscript{56}. The historical data has been processed using the pik-piam/mrvalidation R package\textsuperscript{55}.

Extended Data Figure 4: Ruminant meat and dairy production at global level in MAgPIE projections compared to historical data (validation). Historical data from FAO\textsuperscript{56}. The historical data has been processed using the pik-piam/mrvalidation R package\textsuperscript{55}. 
Extended Data Figure 5: Comparison of a) feed needed for ruminant meat production and b) feedstock needed for microbial protein production under different scenarios at global level. c) shows the corresponding system-wide land-use change for cropland and pasture.
Extended Data Figure 6: Land cover (a–d) at regional level in MAgPIE projections compared to historical data (validation). Historical data from FAO. The historical data has been processed using the pik-piam/rvalidation R package.
Extended Data Figure 7: Regional land-use change between 2020 and 2050.

Extended Data Figure 8: Environmental indicators in MAgPIE projections compared to historical data (validation): a) deforestation (regional) and b) agricultural water use (global; no regional historical data available). Historical data from FAO\(^9\), Foley et al\(^3,1\), Wada et al\(^3,2\) and Wisser et al\(^3,3\). The historical data has been processed using the pik-piam/mrvalidation R package\(^3,4\).
Extended Data Figure 9: Environmental indicators at regional level in MAgPIE projections compared to historical data (validation): a–c) GHG emissions from agriculture and land-use change, and d) nitrogen fixation. For the conversion of N₂O and CH₄ emissions into CO₂ equivalents (right axis) we used GWP100 factors of 265 and 28, respectively. Historical data from Gasser et al., the EDGAR emissions database version 4.2⁶ and Bodirsky et al.¹. The historical data has been processed using the pik-piam/mrvalidation R package⁵⁰.
Projected environmental benefits of replacing beef with microbial protein

Supplementary Information (SI)

Florian Humpenöder1*, Benjamin Leon Bodirsky1,4, Isabelle Weindl1, Hermann Lotze-Campen1,2, Tomas Linder3, Alexander Popp1

1Potsdam Institute for Climate Impact Research, Potsdam, Germany.
2Humboldt University of Berlin, Berlin, Germany.
3Swedish University of Agricultural Sciences, Uppsala, Sweden.
4World Vegetable Center, Shanhua, Tainan, Taiwan.

*Corresponding author: humpenoeder@pik-potsdam.de

Regional ruminant meat consumption in the reference scenario (SSP2-Ref-MP0)

In the reference scenario (MP0), global per-capita protein consumption from ruminant meat remains rather constant at about 6-7 g protein cap\(^{-1}\) day\(^{-1}\) (Figure 1). These global developments are driven by heterogeneous regional patterns. For instance, ruminant meat plays a minor role in India due to cultural and religious particularities (Extended Data Figure 2). Overall, regions in the Global North (e.g. USA, EU, Australia) show slightly declining per-capita ruminant meat consumption (from about 12 to 10 g protein cap\(^{-1}\) day\(^{-1}\) between 2020 and 2050 in USA and EU), while Latin America shows rather constant ruminant meat consumption (~12 g protein cap\(^{-1}\) day\(^{-1}\)). In contrast, regions in the Global South (e.g. Sub-Saharan Africa, India, Middle East and North Africa) are characterized by much lower protein consumption from ruminant meat in 2020, followed by a rapid increase towards 2050. For instance, per-capita ruminant meat consumption in Sub-Saharan Africa increases from about 5 to 9 g protein cap\(^{-1}\) day\(^{-1}\) between 2020 and 2050 (Extended Data Figure 2). In combination with a rising population (Extended Data Figure 1), this results in a considerable increase of total demand for ruminant meat in regions of the Global South (Extended Data Figure 3). The combined effect of rising population and increasing per-capita consumption is particularly strong in Sub-Saharan Africa (doubling of total ruminant meat demand between 2020 and 2050).
Supplementary Figure 1: Top: MAgPIE 4 framework simplified modular structure and module interactions; Bottom: Map of MAgPIE regions. Regional definitions: CAZ (Canada, Australia and New Zealand); CHA (China); EUR (European Union); IND (India); JPN (Japan); LAM (Latin America); MEA (Middle East and north Africa); NEU (non-EU member states); OAS (other Asia); REF (reforming countries); SSA (Sub-Saharan Africa); USA (United States). Both figures are reproduced from Dietrich et al 2019 (https://doi.org/10.5194/gmd-12-1299-2019), CC-BY-4.0.
Supplementary Figure 2: Total demand for a) food crops and b) livestock products at regional level in MAgPIE projections compared to historical data (validation). Historical data from FAO (https://www.fao.org/faostat). The historical data has been processed using the pik-piam/mrvalidation R package (https://doi.org/10.5281/zenodo.4317826).
Supplementary Figure 3: Assumptions for bioenergy and afforestation in MAgPIE for SSP2-Ref (same for all scenarios), based on existing national policies and other projections. a-b) show global and regional demand for first generation bioenergy (sugar, starch and oil crops). c-d) show global and regional demand for second generation bioenergy (dedicated lignocellulosic bioenergy crops). e-f) show global and regional afforestation patterns.
Supplementary Figure 4: Total global and regional livestock feed demand in MApIE projections. a-b) Feed demand from cropland (including crops, residues and forage). c-d) Feed demand from pasture (livestock grazing).
Supplementary Figure 5: Map showing the difference of forest and non-forest vegetation land cover in 2050 between the MP50 and the MP0 scenario. Green color indicates a higher share of forest and non-forest vegetation in a grid-cell in MP50.