



The opportunity cost of animal based diets exceeds all food losses

Alon Shepon^a, Gidon Eshel^b, Elad Noor^c, and Ron Milo^{a,1}

^aDepartment of Plant and Environmental Sciences, Weizmann Institute of Science, 7610001 Rehovot, Israel; ^bPhysics Department, Bard College, Annandale-on-Hudson, NY 12504-5000; and ^cInstitute of Molecular Systems Biology, Eidgenössische Technische Hochschule Zürich, CH-8093 Zürich, Switzerland

Edited by Molly M. Jahn, University of Wisconsin–Madison, Madison, WI, and accepted by Editorial Board Member Ruth S. DeFries February 16, 2018 (received for review August 7, 2017)

Food loss is widely recognized as undermining food security and environmental sustainability. However, consumption of resource-intensive food items instead of more efficient, equally nutritious alternatives can also be considered as an effective food loss. Here we define and quantify these opportunity food losses as the food loss associated with consuming resource-intensive animal-based items instead of plant-based alternatives which are nutritionally comparable, e.g., in terms of protein content. We consider replacements that minimize cropland use for each of the main US animal-based food categories. We find that although the characteristic conventional retail-to-consumer food losses are $\approx 30\%$ for plant and animal products, the opportunity food losses of beef, pork, dairy, poultry, and eggs are 96%, 90%, 75%, 50%, and 40%, respectively. This arises because plant-based replacement diets can produce 20-fold and twofold more nutritionally similar food per cropland than beef and eggs, the most and least resource-intensive animal categories, respectively. Although conventional and opportunity food losses are both targets for improvement, the high opportunity food losses highlight the large potential savings beyond conventionally defined food losses. Concurrently replacing all animal-based items in the US diet with plant-based alternatives will add enough food to feed, in full, 350 million additional people, well above the expected benefits of eliminating all supply chain food waste. These results highlight the importance of dietary shifts to improving food availability and security.

livestock | food systems | animal-based diet | plant-based diet | opportunity food loss

The environmental costs of the current food system and the disproportionate contribution of animal-based food items to these costs are by now firmly established (1–5). To meet the food demand of predicted population increases on resource-intensive diets (such as those characterizing most developed nations), future food supply will need to roughly double in the coming decades (6). Proposed strategies for enhancing food production while alleviating environmental burdens include reducing food loss (7), increasing agricultural productivity (8–10), producing animal-based foods on marginal lands and byproducts (11–13), and shifting toward plant-based diets (1, 2, 8, 14–18).

Conventional food loss refers to available food that is lost before consumption, notably due to spoilage and leaky supply chains. Reducing such losses is recognized as a vital strategy for combating food insecurity (8, 16), yielding more actually eaten food per unit of resource input or pollution output. Globally, approximately a third of all production is lost to conventional food loss (7), representing large resource and economic waste (19). In the United States, total food loss from retail to consumption is estimated at about one third of supply (19, 20), with loss of fresh vegetables and meat being about 30% and 40% on a mass basis, respectively (19). These values rise further due to extra losses from production to retail which are estimated to be $\approx 10\%$ (21). Food waste, a subset of food loss, is due to human activities and choices independent of losses due to such natural phenomena as pest outbreaks or climate variability.

Although the postproduction loss across the supply chain is similar for plant- and animal-based items, the production of a gram protein (or calorie) from animal sources requires about an order of magnitude more resources and emissions than producing a gram of protein from plant sources (1–3, 18, 22, 23). Consequently, shifting to plant-based diets confers substantial environmental savings, comparable to or even surpassing projected improvements in agricultural productivity (1, 2, 24, 25). In other words, due to the disparate resource requirements of plant- and animal-based food items, replacing animal-based items with more resource-efficient plant alternatives will increase food availability by permitting reallocation of production resources from feed to human food (8, 14–17, 22, 26, 27). Favoring resource-intensive food items like beef and pork over plant alternatives thus carries a substantial opportunity cost. Here we analyze the loss associated with such dietary choices as an effective food waste we term “opportunity food loss.” Because opportunity food losses reflect consumer choices, dietary preferences play a key role in determining their magnitude and mitigation. Unlike conventional food loss, opportunity food loss is hidden food that can be recovered via changes in diets. A schematic demonstration of conventional and opportunity food losses is presented in Fig. 1. Starting from a land parcel (left-hand side), the protein yields propagate through the field-to-consumer conversion pipeline (left to right), including feed-to-food losses for animal-based items. The edible food availability differences between the animal and plant food production pathways at the farm gate and the consumer level are the opportunity food losses at production and consumption levels, respectively.

Garnett (28) introduced qualitatively the concept of opportunity costs in the context of livestock consumption, but a rigorous definition and quantitative implementation putting it on

Significance

With a third of all food production lost via leaky supply chains or spoilage, food loss is a key contributor to global food insecurity. Demand for resource-intensive animal-based food further limits food availability. In this paper, we show that plant-based replacements for each of the major animal categories in the United States (beef, pork, dairy, poultry, and eggs) can produce twofold to 20-fold more nutritionally similar food per unit cropland. Replacing all animal-based items with plant-based replacement diets can add enough food to feed 350 million additional people, more than the expected benefits of eliminating all supply chain food loss.

Author contributions: A.S., E.N., and R.M. designed research; A.S. and G.E. performed research; A.S., G.E., E.N., and R.M. analyzed data; and A.S., G.E., and R.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. M.M.J. is a guest editor invited by the Editorial Board.

This open access article is distributed under [Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 \(CC BY-NC-ND\)](https://creativecommons.org/licenses/by-nc-nd/4.0/).

¹To whom correspondence should be addressed. Email: ron.milo@weizmann.ac.il.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1713820115/-DCSupplemental.

Published online March 26, 2018.

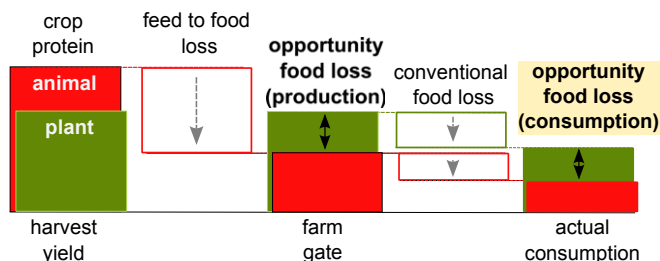


Fig. 1. Conventional and opportunity food loss for plant- and animal-based food. As an example we show poultry versus its plant-based replacement diet. Although feed crops (red bar at the left-hand side, equal to $\approx 4 \times 10^5$ g protein/ac annually) have a higher protein yield per acre than plant food crops, inefficient feed-to-food conversion results in much less animal protein available at the consumption level. Conventional food loss (pertinent to both the plant- and animal-based food) is the loss throughout the supply chain (from field to consumer). Favoring the more inefficient animal-based items carries an opportunity cost due to producing and consuming fewer food protein, which we define as opportunity food loss. The opportunity food loss at the consumer level (right-hand side) is a function of both the opportunity food loss at production (farm gate) and the conventional food loss. The opportunity food losses of the other animal categories are shown in Fig. 3. Fig. S1 presents the same analysis per food calorie.

equal footing to the widely discussed conventional food loss was not done according to our knowledge. Here we compare the land use of each individual animal-based food item in the US food system with that of a nutritionally comparable plant-based alternative diet. Because plant alternatives need less land per unit protein or energy, replacing animal-based items with plant alternatives frees up agricultural land that can then be repurposed for growing additional food. Comparing this added food potential for the key animal categories—beef, pork, poultry, dairy, and eggs—quantifies the opportunity food losses their consumption represents and the food availability opportunities their replacement by plant-based alternatives offers (Fig. 1).

Expanding earlier work on poultry or plant replacement of beef (17, 22), we examine transitions from each of the major five animal categories into a nutritionally comparable plant-based diet. We expand the exclusive focus on calories and proteins to other important micronutrients to reveal the full nutritional changes entailed in the proposed dietary shifts. Last, we advance a quantitative interpretation that renders dietary shifts directly comparable to conventional food losses, thus unifying these two highly significant and potentially synergistic food security improvement measures.

Results

We use linear programming to devise land-minimizing alternative plant-based diets that are nutritionally comparable (in the key macronutrients and micronutrients) to each of the five major animal food items in the mean American diet [see *Materials and Methods* and supporting information in Eshel et al. (22) for further details]. Fig. 2 presents the differences in nutrient delivery by the protein- and calorie-conserving plant replacement diets and the animal items they replace. Full detailed compositions are given in Dataset S1. Compared with the replaced animal food items, plant-based diets deliver more of most micronutrients but less of a few (e.g., vitamin B₁₂). Highlighting the differences across a wide range of nutrients enables us to compare each item in the animal portion of the mean American diet to its alternative plant-based diet and quantify the resource use efficiency and food waste effects of dietary shifts. Fig. 3 presents the feed-to-food protein cascade of the five major animal-based food items (on the left-hand side), their respective plant-based alternative diets (right-hand side, on the same rows), and the opportunity food loss (percentage at the middle) associated with replacing each given a fixed land area. Because all plant diets conserve the caloric and protein delivery of the animal items they replace, the opportunity food loss values at consumption reflect differences in

consumer-level available calories and protein that a given land area can deliver. We find that the opportunity food losses at the consumer level range from 40% for eggs to 96% for beef (the most and least efficient animal food categories). Put differently, nutritionally comparable plant-based diets optimized to nutritionally replace eggs and beef produce twofold and 20-fold more protein per acre than the eggs and beef they replace. Although eggs and beef bracket this range, poultry and eggs are comparable to each other, as are pork and beef, and dairy is between those extremes.

To clarify the values presented in Fig. 3, consider the example of beef. Its consumer level opportunity loss of 96% means that the land area that would deliver 100 g (after all processing and delivery losses) of human-edible protein when used for the production of the plant replacement diet can produce only 4 g of edible beef, resulting in an opportunity food loss of 96 g protein. Using conventional food loss values of beef and plants of $\approx 45\%$ and $\approx 35\%$ (red and green downward pointing arrows in Fig. 3) translates to beef and its plant substitutes delivering at the farm gate (production) $4/(1 - 0.45) \approx 7$ g and $100/(1 - 0.35) \approx 155$ g protein, respectively. At the farm level, the difference between beef and its plant substitute diet is 148 g protein or $(155 - 7)/155 = 95\%$, which is what we refer to as the opportunity food loss at production. Eliminating conventional food loss along the beef supply chain can save at most about $7 - 4 = 3$ g protein, whereas favoring a nutritionally equivalent plant diet over beef (thus eliminating the opportunity food loss) can deliver an additional 96 g protein at the consumer level. For the above calculation, the relation between the opportunity food loss (denoted $FL_{opp-prod}$ at production and $FL_{opp-cons}$ at the consumer level) and conventional food loss (denoted FL_{st} for standard loss) can also be derived using Eq. 4 detailed in *Materials and Methods*. We next scale up the above results nationally. We use the dietary shift potential (17)—the number of additional people that can be fully fed as a result of land repurposing associated with a dietary shift—to calculate the food availability gains expected from dietary shifts away from each of the livestock categories (assuming full use of the national cropland but excluding pastureland; see *Materials and Methods* and Dataset S2 for calculations).

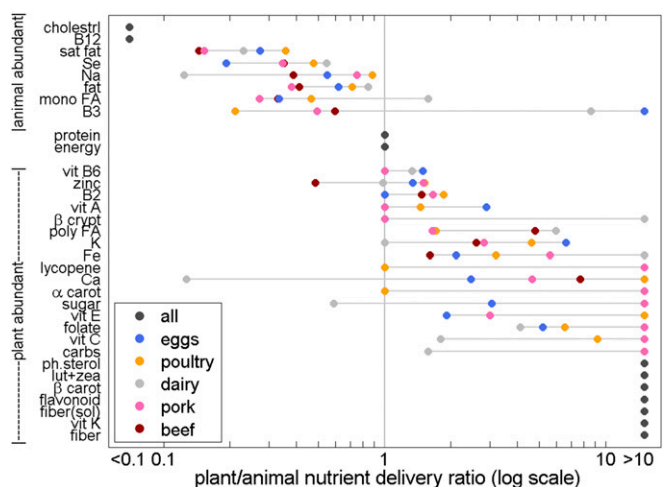


Fig. 2. Nutrient delivery comparison of animal-based food items to their plant-based replacement diets. Presented nutrients are indicated along the left vertical axis. The horizontal axis shows the plant/animal ratio of nutrient delivery. Note the \log_{10} scale, bound by 0.1 and 10. Values that exceed this range are indicated as <0.1 or >10 . Nutrients that exist only in animals (e.g., B₁₂) or plants (e.g., fiber) are also indicated as <0.1 and >10 , respectively. Values to the right/left of the equality (ratio = 1) vertical line are more/less abundant in the plants alternative diets compared with their animal food counterparts. As the two black symbols in the energy and protein lines indicate, the plant-based replacement diets minimize land requirements while conserving protein and calories (denoted “energy” above).

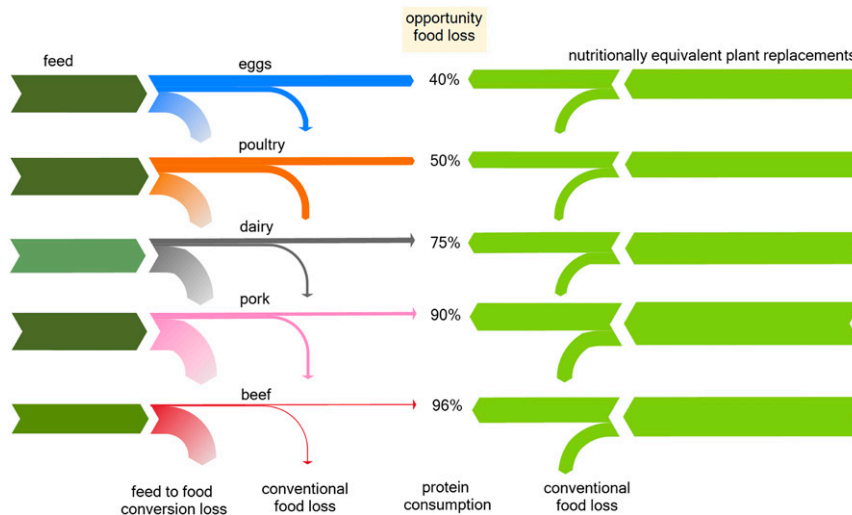


Fig. 3. The protein opportunity food loss from production to final consumption for the five major animal categories and their plant-based replacement diets. Each row represents the cascade of protein from field to fork for each of the major animal categories and their plant-based replacement diet. Arrow thicknesses are proportional to the absolute value. Shades of green denote differing composition in feed due to inclusion of processed roughage. Protein feed-to-food conversion efficiencies are calculated in ref. 17. Nutritionally equivalent plant-based diets differ in the items they comprise for each of the five plant replacement diets, thus presenting different protein yields (breadths of arrows) for the same land area used for all starting arrows. Opportunity food loss values at consumption are given as percentages in the middle, representing the difference in protein content between potential ready to eat plant replacement diets (right) and the respective animal category (left), all for an identical land resource investment. For instance, if reallocated to the production of plant-based replacement diet, the arbitrary land area needed to produce the feed for 4 g of beef protein will yield 100 g of protein of human-destined nutritionally equivalent plant diet, which is an opportunity food loss at the consumer level of 96%. Fig. S2 is a presentation of this figure using food calories instead of protein.

Population-level replacement of beef, pork, dairy, poultry, and eggs individually with nutritionally comparable plant diets produces enough additional food to meet the full dietary needs of 163, 19, 25, 12, and 1 million additional people, respectively (Eq. 5). Put differently, every two typical Americans who choose to substitute beef in their diet with a nutritionally equivalent combination of plant items will save enough resources to fully feed an additional third. The savings from most other animal categories are about an order of magnitude smaller. Concurrently replacing all animal-based products in the mean American diet using all feed croplands with nutritionally comparable or superior plant alternatives (Eq. 6) can sustain ≈ 350 million additional people or $\approx 120\%$ of the US population for years 2000–2010. In comparison, production-to-consumer conventional food loss is ≈ 30 – 40% of total production (19–21), and thus, the effect of recovering the opportunity food loss collectively is larger than completely eliminating all conventional food losses in the United States.

Our dietary shift potential calculations can be refined to analyze the contribution of each age group in the US population and suggest relevant age- or sex-specific policies (*Materials and Methods and Dataset S3*). If we assume that each age group consumes a diet equal in composition to the mean American diet but proportional to its average caloric intake, we can calculate the contribution of each age group to the total dietary shift from demographic data on the distribution of ages and sexes in the US population. For example, if Americans under 5 y of age do not change their eating habits at all (e.g., due to consumer choice or dietary concerns), the dietary shift potential due to the remainder of the population switching to plant-based foods would drop by 20 million people to ≈ 330 million people. The adult population in the age group of 20–60 y has the dominant dietary shift potential of 200 million people. Fig. S6 summarizes the land requirements of the animal portion of the mean American diet and its plant-based replacement segmented by age and sex and translates the land use differences to dietary shift potential values.

The dietary shifts we consider here will also entail economic shifts. The full economic implications of replacing production of feed plus livestock with production of plant-based food are difficult to estimate given the complexity of the economic system and the difficulty in predicting changes in human consumption

patterns and behavior. We can therefore only explore some of the economic implications of a national-level dietary transition from animal-based foods to plants.

The contribution of the entire food sector to the US economy is estimated at 5% of total national GDP (29). Agricultural added value (averaging ≈ 100 billion dollars over 2000–2010) (30) contributes 0.8% to the total GDP (29). Because we consider only domestic dietary shifts, we analyze only livestock and edible crops for domestic production, which amounts to 65% of total agricultural production value (30). Combining the above, livestock and edible crops for domestic consumption account for $\approx 65\% \times 0.8\% = 0.5\%$ of total GDP. Because about 70% of this domestic production is due to livestock (including feed crops) (30), the overall economic contribution of the domestic livestock sector (excluding export) is $\approx 70\% \times 0.5\% = 0.35\%$ of total GDP. Plants for domestic consumption are responsible for the complementary added value, 0.15% of total GDP.

Although animal-based foods contribute more to agricultural GDP than plant-based ones, both categories contribute roughly equal amounts of protein to the mean American diet (3, 31). Therefore, the economic effect of replacing the animal portion with a plant-based substitute along the entire supply chain will likely result in an economic loss. That amount is challenging to predict but might be partially offset by growth in new sectors such as production of meat replacements.

There is an economic benefit due to the additional food that will be produced as a result of the dietary shift. The additional food whose production is made possible by the considered dietary shift implemented can feed 350 million additional plant-based diets. The value of this surplus export will offset some of the loss from the decrease in livestock production. Its value on international markets and the resulting creation of emerging market sectors requires a more thorough analysis.

Shifting to plant diets and the large associated plant food surpluses can also potentially reduce import of nonanimal products [accounting for 80% of the 2000–2010 value of agricultural imports (30)], further enhancing agricultural trade surplus. Because our calculation is based on reconfiguring production to account for domestic dietary shifts (excluding export but including import),

eliminating the consumption of the animal portion in the mean American diet does not affect any export of feed and animal-based foods.

We also note the economic benefits from rearing cattle on marginal pasturelands and via feeding industrial byproducts, which can be redirected to export once the dietary shift to plants is fully deployed. Our recent analysis (13) suggests that these two resources can deliver about 45% of current US beef consumption. This reconfigured beef production would further increase the fraction of current livestock sector jobs that can be maintained under the new diet.

We now examine the health and social costs implications of the proposed dietary transition, which would augment plant-based food consumption that currently lags behind national dietary recommendations. Such effects were recently evaluated in a study that analyzed the economic implications of global dietary shifts to plants (2). We use the values of avoided deaths in the United States that are expected from reductions in red meat consumption and an increased consumption of nutritionally similar plant items. The monetary values of avoided disease burden and greenhouse gas (GHG) emissions eliminated are estimated to be roughly 63 and 18 billion dollars, respectively. The combined 80 billion dollars saved are about 0.6% of US GDP (for years 2000–2010), similar to the contribution of agricultural production to total GDP.

Discussion

In this paper, we highlight a key path to food availability gains in the US food system and the potential gains associated with alternative allocation of the national cropland resources. Compared with an optimized plant-based diet, consuming US animal-based products entails a large effective food waste, which we term opportunity food loss. Conventional food loss refers to actual food lost (which may be recoverable), whereas the opportunity food loss highlights effective food losses that follow dietary choices. Consistent with earlier findings, eggs and poultry are the most efficient animal-based food items, and their opportunity costs are thus the lowest. Conversely, relatively inefficient beef, pork, and dairy have much higher opportunity costs.

Peters et al. (27) calculated the carrying capacity assuming various diets in the US including the current mean American diet, alternatives adhering to health guidelines, and vegetarian diets and found that the different diets vary in the number of people they can support between 400 and 800 million. According to their analysis, 735 million Americans could be sustained on a healthy vegan diet using the currently utilized croplands, in close proximity to the ≈ 650 million American carrying capacity calculated here following the full dietary transition to plant-based foods (350 million people fed surplus food plus 300 million of the current population). Land requirement per capita per year in the vegan diet (27) is very similar to the per capita land requirement calculated here of the full mean American diet following the national level dietary transition (≈ 0.3 acre/cap; Dataset S2), despite the former consisting of $\approx 2,150$ kcal per capita daily, whereas the current analysis maintains the current mean American diet daily caloric intake of $\approx 2,500$ kcal. This similarity in land requirement despite different caloric intake probably stems from two reasons. First, our carrying capacity calculation uses land optimization for the portion of the plant foods replacing the animal portion. Second, a substantial portion of the mean American diet which our calculus does not change is based on processed foods—mostly sugar and high-fructose corn syrup—which have a low land footprint compared with the healthier diets proposed by Peters et al. (27).

Although our analysis concentrated on opportunity costs in terms of food gains or losses, the ramifications of consuming animals vs. plants include other considerations worth noting. For example, replacing milk and beef in the United States with plant-based alternatives liberates almost 700 million pastureland acres for wilderness preservation and reverses overgrazing induced ecosystem degradation (3, 23).

Our results represent the food waste associated with a modern food system developed to produce large amounts of animal food. In other countries, with different livestock production systems and consumption patterns, results may differ, consistent with the conclusion of Garnett (28). In developing countries, where diets are based on grains and tubers with little meat and where alternatives are few and limited, livestock are at times crucial for food security. There the opportunity costs are effectively zero. In pasture-based systems, where cattle graze on unproductive pastureland alone and deliver some additional food, the opportunity cost in terms of food gain or loss may reverse in favor of animal products.

The total economic benefits or costs due to shifting diets at the domestic level and producing surplus food (mostly to export) depend on many assumptions and analyses that are beyond the scope of this research. The considered shifts to plant-based diets will lead to broad economy-wide changes whose overall effects are difficult to predict. However, we find economic benefits due to GHG emissions savings and improved health. Future research will need to evaluate if these benefits augment direct national economic benefits or offset, at least to some extent, national economic losses. A detailed analysis (e.g., using computable general equilibrium models) is essential for a realistic economic assessment that takes adequate note of sectorial interrelatedness and full national economy complexity but is beyond the scope of this paper.

The main contribution of this work lies in extending the notion of food loss beyond the conventional definition to include the effective costs of dietary choices. Beyond minimizing food waste at various inefficiency hot spots along the supply chain, the current findings identify food items—especially beef, pork, and dairy—that are associated with disproportionately large hidden loss and are thus optimal targets for policy changes aimed at increasing food security and availability. Although conventional and opportunity food losses are independent, comparing the two is helpful for guiding future food policy. The calculations presented here show that favoring plant-based diets over less efficient animal-based ones can potentially feed more humans than complete elimination of conventional food losses. Surprisingly, this holds even for the most efficient livestock categories, eggs and poultry. Nonetheless, the two food waste reduction strategies are independent and should be pursued in tandem. Together, waste reduction and dietary shifts offer substantial food availability gains.

Materials and Methods

Our calculations are based on earlier quantification of the environmental performance of the US food system (3, 17, 23). Key numerical building blocks include the composition of the mean American diet (17), the land resources required for producing each of the food items in that diet (3, 17, 23), and feed-to-food conversion efficiencies (17). We use these data to devise optimal plant-based diets using plant items common in the current mean American diet. Here optimal is defined as diets minimizing crop land requirement.

The optimization uses linear programming to find masses of about 60 plant items (17, 22) in the replacement diet. The masses of these plant items together form an energy- and protein-conserving plant-based diet (among other constraints given below) to which we refer as “nutritionally equivalent” to a given animal item. The constraints imposed for being nutritionally equivalent are that the calories and protein delivered will be equal; that the content of total fat and cholesterol will not be higher than in the animal food item; and that the content of total fiber, vitamin B6, vitamin A, vitamin C, vitamin E, total folate, total K, vitamin B2, polyunsaturated fatty acids, soluble fiber, total flavonoid, iron, α and β carotene, lycopene, lutein, zeaxanthin, β -cryptoxanthin, potassium, and phytosterols will not be lower than in the animal food item. We also constrain the total mass of the replacement diet to be at most double the mass of the replaced animal item. The mass of each plant item was not allowed to exceed 50 g (or 3 g for garlic). Although the numerical values of these upper bounds are somewhat arbitrary, the bounds qualitatively help ensure a diverse and palatable diet that crudely mimics the variety of real food choices.

We define the standard conventional food loss ($FL_{i,c}$) across the entire (production-to-consumption) supply chain for a specific food item i as

$$FL_{st}(i) = \frac{c_{prod} - c_{cons}}{c_{prod}}, \quad [1]$$

where c_{prod} and c_{cons} denote the content of protein for item i at the production (*prod*) and consumption (*cons*) levels. Our conventional food loss calculation includes production to consumer losses by combining US Department of Agriculture's available data on food loss for each food commodity from retail to consumption (19) with estimated loss from production to retail (21).

Next, we define the opportunity food loss between an animal-based item or diet and its plant-based replacement at consumption (*cons*). By comparing the land (l) needed to consume a certain animal item and its nutritionally comparable alternative plant diet, we can quantify the amount of additional food the same land resources can yield upon replacing the animal product with more efficient plant alternatives, i.e., the opportunity food loss associated with choosing the inefficient animal option over the more efficient plant diet. The definition of the opportunity food loss addresses a pair of food items or diets, each with a unique land requirement. The definition can be used for any specific item being replaced or for a set of items (e.g., all animal items, denoted a) with a defined set of items in a replacement diet (in our case the plant-based items, denoted p).

For a given land resource, the opportunity food loss (at consumption), $FL_{opp-cons}$, of replacing item/s a with a nutritionally comparable set from p is

$$FL_{opp-cons}(a, p) = \frac{c_p/l_p - c_a/l_a}{c_p/l_p}, \quad [2]$$

where c_a/l_a and c_p/l_p are the consumed yield (e.g., consumed protein per unit of land area) for the animal item and its nutritionally comparable plant alternative, respectively. For animals, the average consumed protein yield refers to the amount of animal-based human food protein that will be delivered from a plot of agricultural land producing feed (and not to the feed protein itself). Because by definition we choose the plant replacement diet to have the same amount of protein as its replaced animal item ($c_a = c_p$), Eq. 2 reduces to

$$FL_{opp-cons}(a, p) = \frac{\frac{1}{l_p} - \frac{1}{l_a}}{\frac{1}{l_p}} = \frac{l_a - l_p}{l_a}, \quad [3]$$

where l_a and l_p denote the crop land area of the animal item and its plant diet alternative that produces the same consumed protein, respectively. Implicitly, Eq. 3 highlights the fact that the opportunity food loss depends on the agrotechnological yields per acre, the biologically governed feed-to-food conversion of livestock, and the conventional food losses across supply chains (Fig. 1).

Opportunity food loss at the production level represents only the agrobiological differences, filtering out the conventional food losses across supply chains (Fig. 1). It can be deduced from the opportunity food loss at the consumption level as presented in Eq. 4. For this purpose we define the reciprocal of loss (i.e., unlost, consumed food fraction) as efficiency. The opportunity food efficiency at the production level, denoted as $1 - FL_{opp-prod}$, is a function of both the opportunity food efficiency at consumption, $1 - FL_{opp-cons}$, and the conventional food efficiencies of both animal- and plant-based items and is expressed as

$$(1 - FL_{opp-prod}(a, p)) = (1 - FL_{opp-cons}(a, p)) \times \frac{(1 - FL_{st}(p))}{(1 - FL_{st}(a))}, \quad [4]$$

where $1 - FL_{st}(a)$ and $1 - FL_{st}(p)$ are the conventional food efficiencies of the animal food item and its plant-based substitute diet, respectively. The opportunity food loss at production is then easily isolated from Eq. 4 by subtracting the right hand side of the equation from [1].

Dietary Shift Potential. The US dietary shift potential (in units of number of people) for a shift from diet a to diet p is defined as

$$DSP(a, p) = \frac{P(l_a - l_p)}{l_{MAD} - l_a + l_p}, \quad [5]$$

where P is the total population size in the United States and l_{MAD} is the mean American diet land area per capita calculated as 0.75 acre per capita (17). For a combination of items being replaced, e.g., for evaluating the concurrent replacement of all animal categories, the equation can be explicitly written using the sum of the per capita land requirements of each item l_i as

$$DSP(a, p) = \frac{P(\sum_i l_{a_i} - \sum_i l_{p_i})}{l_{MAD} - \sum_i l_{a_i} + \sum_i l_{p_i}}. \quad [6]$$

We expand the above definition to include a calculation of the contribution of each age group j to the overall dietary shift based on the contribution of each age group j in the overall population (Dataset S3). Eq. 7 summarizes this derivation as a function of the total dietary shift potential (Eq. 5):

$$DSP_j(a, p) = DSP \frac{P_j e_j}{\sum_j P_j e_j}, \quad [7]$$

where P_j is number of individuals in age group j and e_j is the per capita daily caloric intake of group j . Fig. S6 and Dataset S3 present the contribution of each age group to the overall dietary shift potential.

Sensitivity Analysis. We perform a sensitivity analysis to examine the robustness of our results. First, we examine the shadow prices of the optimized results for each of the five replaced animal food items (Dataset S4). The shadow prices reflect the relative incremental change in the cost function (land area of the replacement plant diet) for a change in an individual nutrient constraint imposed by the replaced animal diet. The results show that protein of poultry and eggs and energy of poultry have the highest values. The sensitivity of the model to the protein and energy values of poultry's plant replacement diet is also apparent in the changes in the minimized land area when increasing and decreasing each nutrient by 10% at a time (with the rest held constant) (Fig. S3). The plant replacement diet of poultry has no solutions in the cases of increasing protein or decreasing calories (energy) by 10% when the other nutrients are held constant. These results imply that the high protein-to-calorie ratio of poultry and eggs (Fig. S4) is what underlies this sensitivity. Because in our model we impose isocaloric and isoprotein plant replacement diets, the algorithm seeks plant items that can deliver such ratios, resulting in diets that are ubiquitous in soy, which has similar characteristics but is limited by an upper bound of 50 g. Last, the sensitivity of the results to these attributes is also apparent when we perform 10^4 Monte Carlo runs (using uniform distribution) for each of the animal categories when the nutritional constraints imposed by the replaced animal diet are changed randomly by $\pm 10\%$ (Fig. S5). When we reperform these Monte Carlo runs for poultry's and eggs' replacement diets and relax the protein/energy constraints by imposing no energy constraint while requiring similar protein amounts, poultry's and eggs' replacement diets show greater stability (more clustered with less outliers) with total increase of 10 kcal and 60 kcal for eggs' and poultry's replacement diets compared with their animal food counterparts, respectively. Because the mean American diet does not suffer from lack of calories or proteins, relaxing our imposed isocaloric and isoprotein constraints without compromising health (nutrient deficiency) is evidently feasible.

Bioavailability. Although absorption of nutrients is never whole, what is essential for the comparison is not absolute bioavailability but rather the bioavailability difference between the animal source and its plant-based substitute. Such differences are most often reported (32–34) for iron, zinc, calcium, B12, protein, and fatty acids. Because bioavailability differences between plant and animal diets are possible, the 1:1 nutritional comparison we employ in our model and Fig. 2 may be objectionable to some, but we are limited in making a compensation for this issue for the following reasons. Although vegetarians were traditionally advised to increase consumption of some minerals so as to allow for reduced absorption, new evidence has called this view into question (32–34). Although plant mineral sources and absorption vary widely [e.g., iron (35) and calcium (36)], increased absorption efficiency and compensatory adaptation in vegetarians ingesting fewer nutrients are likely (32, 34, 37), but absorption modulation by other factors complicates authoritative resolution of this issue [e.g., plant abundant vitamin C (38)]. In general, bioavailability varies greatly among specific diets, rendering mean animal to plant absorption ratios (i.e., amount of animal in the diets) questionable in predicting bioavailability (39). For example, in a recent comparison of animal and plant diets (31) the authors ignored bioavailability variation. In our model (Fig. 2), plant-based replacement diets usually deliver 2–10, 3–10, and 1–2 times as much iron, calcium, and zinc as the animal items they replace, respectively (with the exception of zinc for beef and calcium for milk). These overwhelming additions offset any putative bioavailability differences. Moreover, traditional food preparation practices (e.g., fermentation and soaking) tend to increase bioavailability of some nutrients (38, 40, 41). In our calculations, we use nutritional values of raw vegetable items, but these might increase through cooking. In western diets with abundant supplies of micronutrients it is not clear if reduced bioavailability has any bearing on health. For example, despite lower iron stores, vegetarians do

not appear to have greater incidence of iron deficiency anemia (33). Because excess iron is also a risk factor for such noncommunicable diseases as type 2 diabetes (42) or metabolic syndrome (43), lower iron ingestion among vegetarians may in fact prove protective (44). Melina et al. (32) argue that protein from a variety of plant sources successfully meets essential amino acid requirements when caloric requirements are met and that legumes and soy are reliable protein sources that also provide other essential nutrients. Our plant-based replacement diets include various sources of plants, and all include soy, which has a complete protein. Consequently, the plant replacements in this paper generally match or exceed the protein quantity and quality of the replaced items.

- Tilman D, Clark M (2014) Global diets link environmental sustainability and human health. *Nature* 515:518–522.
- Springmann M, Godfray HCJ, Rayner M, Scarborough P (2016) Analysis and valuation of the health and climate change cobenefits of dietary change. *Proc Natl Acad Sci USA* 113:4146–4151.
- Eshel G, Shepon A, Makov T, Milo R (2014) Land, irrigation water, greenhouse gas, and reactive nitrogen burdens of meat, eggs, and dairy production in the United States. *Proc Natl Acad Sci USA* 111:11996–12001.
- Nijdam D, Rood T, Westhoek H (2012) The price of protein: Review of land use and carbon footprints from life cycle assessments of animal food products and their substitutes. *Food Policy* 37:760–770.
- Aleksandrowicz L, Green R, Joy EJM, Smith P, Haines A (2016) The impacts of dietary change on greenhouse gas emissions, land use, water use, and health: A systematic review. *PLoS One* 11:e0165797.
- Alexandratos N, Bruinsma J (2012) World agriculture towards 2030/2050: The 2012 revision. ESA Working Paper 12-03 (Food Agric Organ UN, Rome).
- Gustavsson J, Cederberg C, Sonesson U (2011) *Global Food Losses and Food Waste—Extent, Causes and Prevention* (Food Agric Organ UN, Rome).
- Foley JA, et al. (2011) Solutions for a cultivated planet. *Nature* 478:337–342.
- Tilman D, Balzer C, Hill J, Befort BL (2011) Global food demand and the sustainable intensification of agriculture. *Proc Natl Acad Sci USA* 108:20260–20264.
- Roos E, et al. (2017) Greedy or needy? Land use and climate impacts of food in 2050 under different livestock futures. *Glob Environ Change* 47:1–12.
- van Zanten HHE, Mollenhorst H, Klootwijk CW, van Middelaar CE, de Boer IJM (2016) Global food supply: Land use efficiency of livestock systems. *Int J Life Cycle Assess* 21: 747–758.
- Roos E, Patel M, Spangberg J, Carlsson G, Rydhmer L (2016) Limiting livestock production to pasture and by-products in a search for sustainable diets. *Food Policy* 58: 1–13.
- Eshel G, et al. (2018) A model for 'sustainable' US beef production. *Nat Ecol Evol* 2: 81–85.
- Cassidy ES, West PC, Gerber JS, Foley JA (2013) Redefining agricultural yields: From tonnes to people nourished per hectare. *Environ Res Lett* 8:034015.
- West PC, et al. (2014) Leverage points for improving global food security and the environment. *Science* 345:325–328.
- Godfray HCJ, et al. (2010) Food security: The challenge of feeding 9 billion people. *Science* 327:812–818.
- Shepon A, Eshel G, Noor E, Milo R (2016) Energy and protein feed-to-food conversion efficiencies in the US and potential food security gains from dietary changes. *Environ Res Lett* 11:105002.
- Ranganathan J, et al. (2016) *Shifting Diets for a Sustainable Food Future* (World Resources Institute, Washington, DC).
- Buzby JC, Hyman J (2012) Total and per capita value of food loss in the United States. *Food Policy* 37:561–570.
- Hall KD, Guo J, Dore M, Chow CC (2009) The progressive increase of food waste in America and its environmental impact. *PLoS One* 4:e7940.
- Kader A (2005) Increasing food availability by reducing postharvest losses of fresh produce. *Acta Hort* 682:2169–2176.
- Eshel G, Shepon A, Noor E, Milo R (2016) Environmentally optimal, nutritionally aware beef replacement plant-based diets. *Environ Sci Technol* 50:8164–8168.
- Eshel G, Shepon A, Makov T, Milo R (2015) Partitioning United States' feed consumption among livestock categories for improved environmental cost assessments. *J Agric Sci* 153:432–445.
- Popp A, Lotze-Campen H, Bodirsky B (2010) Food consumption, diet shifts and associated non-CO2 greenhouse gases from agricultural production. *Glob Environ Change* 20:451–462.
- Hedenus F, Wirsenius S, Johansson DJA (2014) The importance of reduced meat and dairy consumption for meeting stringent climate change targets. *Clim Change* 124: 79–91.
- Pradhan P, Lüdeke MKB, Reusser DE, Kropp JP (2013) Embodied crop calories in animal products. *Environ Res Lett* 8:044044.
- Peters CJ, et al. (2016) Carrying capacity of U.S. agricultural land: Ten diet scenarios. *Elem Sci Anthr* 4:000116.
- Garnett T (2009) Livestock-related greenhouse gas emissions: Impacts and options for policy makers. *Environ Sci Policy* 12:491–503.
- US Bureau of Economic Analysis (2017) Gross domestic product by industry data. Available at https://www.bea.gov/industry/gdpbyind_data.htm. Accessed November 21, 2017.
- US Census Bureau (2012) Statistical abstract of the United States, section 17: Agriculture. Available at <https://www.census.gov/library/publications/2011/compendia/statab/131ed/agriculture.html>. Accessed November 21, 2017.
- White RR, Hall MB (2017) Nutritional and greenhouse gas impacts of removing animals from US agriculture. *Proc Natl Acad Sci USA* 114:E10301–E10308.
- Melina V, Craig W, Levin S (2016) Position of the academy of nutrition and dietetics: Vegetarian diets. *J Acad Nutr Diet* 116:1970–1980.
- Hunt JR (2003) Bioavailability of iron, zinc, and other trace minerals from vegetarian diets. *Am J Clin Nutr* 78(3 Suppl):633S–639S.
- Hunt JR, Roughead ZK (1999) Nonheme-iron absorption, fecal ferritin excretion, and blood indexes of iron status in women consuming controlled lactoovo vegetarian diets for 8 wk. *Am J Clin Nutr* 69:944–952.
- Collings R, et al. (2013) The absorption of iron from whole diets: A systematic review. *Am J Clin Nutr* 98:65–81.
- Titchenal CA, Dobbs J (2007) A system to assess the quality of food sources of calcium. *J Food Compos Anal* 20:717–724.
- Hunt JR, Roughead ZK (2000) Adaptation of iron absorption in men consuming diets with high or low iron bioavailability. *Am J Clin Nutr* 71:94–102.
- Gibson RS, Heath ALM, Szymlek-Gay EA (2014) Is iron and zinc nutrition a concern for vegetarian infants and young children in industrialized countries? *Am J Clin Nutr* 100(Suppl 1):459S–468S.
- Perignon M, Barré T, Gazan R, Amiot MJ, Darmon N (2018) The bioavailability of iron, zinc, protein and vitamin A is highly variable in French individual diets: Impact on nutrient inadequacy assessment and relation with the animal-to-plant ratio of diets. *Food Chem* 238:73–81.
- Hotz C, Gibson RS (2007) Traditional food-processing and preparation practices to enhance the bioavailability of micronutrients in plant-based diets. *J Nutr* 137: 1097–1100.
- Raes K, Knockaert D, Struijs K, Van Camp J (2014) Role of processing on bio-accessibility of minerals: Influence of localization of minerals and anti-nutritional factors in the plant. *Trends Food Sci Technol* 37:32–41.
- Zhao Z, et al. (2012) Body iron stores and heme-iron intake in relation to risk of type 2 diabetes: A systematic review and meta-analysis. *PLoS One* 7:e41641.
- Abril-Ulloa V, Flores-Mateo G, Solà-Alberich R, Manuel-y-Keenoy B, Arija V (2014) Ferritin levels and risk of metabolic syndrome: Meta-analysis of observational studies. *BMC Public Health* 14:483.
- Haider LM, Schwingshackl L, Hoffmann G, Ekmeckioglu C (2016) The effect of vegetarian diets on iron status in adults: A systematic review and meta-analysis. *Crit Rev Food Sci Nutr* 1–16.

ACKNOWLEDGMENTS. We thank the following individuals for their important help with this paper: Kerem Avital, Ziv Barshira, Inge van den Bijgaart, Moran Blueshtein, Taga Budniatzy, Brett Cotler, Carolyn Dimitri, Avi Flamholz, Tal Haiken, Tamar Makov, Noam Prywes, Marco Springmann, and Tong Wu. This research was supported by the European Research Council (Project NOVCARBFIX 646827), the Israel Science Foundation (Grant 740/16), Beck Canadian Center for Alternative Energy Research, Dana and Yossie Hollander, Ullmann Family Foundation, Helmsley Charitable Foundation, The Larson Charitable Foundation, Wolfson Family Charitable Trust, Charles Rothschild, and Selmo Nussenbaum. R.M. is the Charles and Louise Gartner professional chair.