Comparative terrestrial feed and land use of an aquaculture-dominant world

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Reducing food production pressures on the environment while feeding an ever-growing human population is one of the grand challenges facing humanity. The magnitude of environmental impacts from food production, largely around land use, has motivated evaluation of the environmental and health benefits of shifting diets, typically away from meat toward other sources, including seafood. However, total global catch of wild seafood has remained relatively unchanged for the last two decades, suggesting increased demand for seafood will mostly have to rely on aquaculture (i.e., aquatic farming). Increasingly, cultivated aquatic species depend on feed inputs from agricultural sources, raising concerns around further straining crops and land use for feed. However, the relative impact and potential of aquaculture remains unclear. Here we simulate how different forms of aquaculture contribute and compare with feed and land use of terrestrial meat production and how spatial patterns might change by midcentury if diets move toward more cultured seafood and less meat. Using country-level aquatic and terrestrial data, we show that aquaculture requires less feed crops and land, even if over one-third of protein production comes from aquaculture by 2050. However, feed and land-sparing benefits are spatially heterogeneous, driven by differing patterns of production, trade, and feed composition. Ultimately, our study highlights the future potential and uncertainties of considering aquaculture in the portfolio of sustainability solutions around one of the largest anthropogenic impacts on the planet.

aquatic farming | livestock | animal feed | land use | human diets

What we eat and how we produce food has tremendous impact on the planet, especially with an expected population of nearly 10 billion people by 2050 (1, 2). Approximately 40% of terrestrial land is already cultivated or grazed (3), which has contributed to rapid loss of species diversity and habitats (4), unsustainable freshwater use (4, 5), substantial pollution in terrestrial and aquatic ecosystems (6), and large greenhouse gas emissions (7) over the past century. The extent and degree of impacts driven by our food systems has led to multiple environmental and health studies quantifying the benefits of shifting diets away from meat to typically more seafood and plant-based consumption (7, 8). However, the rising growth in seafood consumption and the increasing importance of aquaculture (i.e., aquatic farming) to meet that demand (9)—even if global reform of fisheries comes to fruition (10)—raises new questions and concerns for future sustainable food production if diets continue to shift to more seafood.

Aquaculture is the fastest-growing food industry in the world and already produces more biomass than either wild seafood or beef (3, 9), making it a fundamental part of future food production. Fed aquaculture (finfish and crustaceans requiring direct feed input) currently comprises over 70% of cultured seafood production (excluding seaweed), and is rapidly growing, mostly from freshwater finfish, like carp (11). The remaining biomass comes almost entirely from molluscs, filter-feeding taxa (e.g., mussels and oysters) that extract resources from the surrounding environment, thus requiring no added feed (i.e., unfed) (9). Considerable attention has focused on fish-based inputs of aquaculture feeds (12), but due to limits of such aquatic sources, fed species now largely and increasingly depend on terrestrial feed crops (11, 13). Thus, aquaculture now competes for crop resources with livestock, the energy industry, and direct human consumption—raising concerns of aquatic farming's impact on global food resiliency (14). However, country-level patterns of land use arising from crop-based feeds from aquaculture are not well understood, in large part because most models only consider livestock and trade can confound the exact area of land attributed to animal feed within a given country (15). Aquatic and terrestrial farmed animals differ in feed requirements and energy efficiency (feed conversion to biomass) and increasing use and inclusion of certain crop types (e.g., maize) that support the continued rise in animal production could have significant consequences for feed and land use if diets shift to more cultured seafood and less terrestrial protein.

Animal production is expected to significantly increase by 2050 to meet per-capita human consumption demands (mean production increase ± SD = 52 ± 12%; *Materials and Methods* and Fig. 1) (7, 16). However, there is considerable scope for shifts in the type and amount of protein consumed, as demonstrated by the rapid growth of poultry production overtaking and rivaling other meat products worldwide (17). Using scenario-based simulations, we explore how shifts in global diets toward cultured seafood and away from meat, and associated increases in aquaculture production levels, in turn change the comparative pressure on feed-crop requirements, and how that might translate to changes in area and location of land use for crops and grazing. We compare three scenarios in 2050 that

Significance

Studies are revealing the potential benefits of shifting human diets away from meat and toward other protein sources, including seafood. The majority of seafood is now, and for the foreseeable future, farmed (i.e., aquaculture). As the fastest-growing food sector, fed aquaculture species increasingly rely on terrestrial-sourced feed crops, but the comparative impact of aquaculture versus livestock on associated feed and land use is unclear—especially if human diets shift. Based on global production data, feed use trends, and human consumption patterns, we simulate how feed-crop and land use may increase by midcentury, but demonstrate that millions of tonnes of crops and hectares could be spared for most, but not all, countries worldwide in an aquaculture-dominant future.

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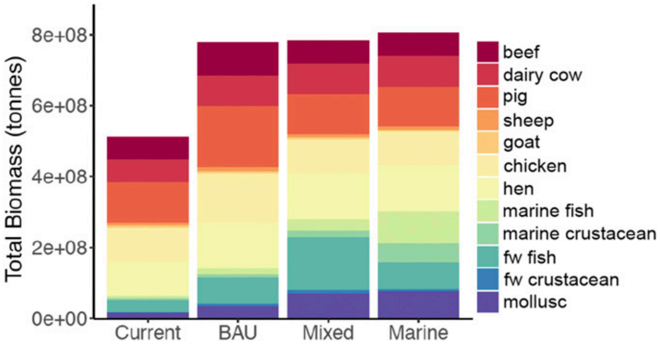

Fig. 1. Current and average projected 2050 live-weight biomass of each taxonomic group and animal production scenario. Scenarios are based on a mean 52% (SD ± 12%) increase in total, live-weight business-as-usual (BAU) animal production necessary to meet projected global edible protein demand in 2050. fw, freshwater.

differ in the sources of animal protein: (*i*) business-as-usual consumptive trends and production needs (i.e., more terrestrial than aquatic protein); (*ii*) the additional 2050 meat demand is instead met entirely by aquaculture with current ratios of freshwater and marine production (mixed scenario); (*iii*) the additional 2050 meat demand is replaced by predominantly marine aquaculture (marine scenario). The alternative "seafood" scenarios bound realistic paths for different aquaculture sources due to uncertainties around future consumer tastes (18) and geographic distinctions of marine versus freshwater production (9). To simulate feed and land-use consequences of each scenario, we account for the heterogeneity in animal feed compositions, increased use and homogenization of crop-based feed, increases in future production efficiencies of animals and crops, and global trade patterns (7, 16). In all cases, we simulate the major protein sources: beef, dairy cow, pig, goat, sheep, broiler chicken, laying hen, freshwater and marine finfish, crustacea, and mollusc (*Materials and Methods*).

Results and Discussion

Future aquaculture production (mixed and marine scenarios) would need to increase more than four times current levels to replace an expected (average) 46% increase in meat and provide the equivalent edible protein (Fig. 1). Several studies—on which we base our scenarios—project the aquaculture business-as-usual scenario approximately doubling by 2050 (7, 19, 20). Our seafood scenarios essentially double baseline projections, requiring production levels just over what would be required for more prescribed global pescetarian diet trends (assuming constant wild catch) (7). Increasing predominantly fed marine aquaculture (marine scenario) appears less feasible, requiring an almost 13-fold increase, assuming molluscs continue contributing 25% of production as they do presently and freshwater production still increases business as usual (average 120%). This is primarily a consequence of fewer countries currently producing marine aquaculture, marine production consisting of mostly molluscs with lower edible biomass (*SI Appendix*, Table S1), and overall less production (approximately one-third of all aquaculture). However, future marine production is expected to continue to grow quickly (9) and expand into offshore waters (21), which may result in differing local to global impacts of marine versus freshwater aquaculture.

Assessing seven of the most dominant crops increasingly used in farmed animal diets (Fig. 2*A*), we find that even when aquaculture provides over one-third of simulated biomass produced under both seafood scenarios, over 90% of feed crops still go to produce terrestrial animals. This highlights the comparative magnitude of pressure that land-based species place on the terrestrial food system, and the relative efficiency of aquatic organisms (Fig. 2*B*). Shifting toward cultured seafood-dominant diets reduces annual feed-crop requirements by 598.7 (SD ± 172.5; mixed) to 564.7 (±168.1; marine) million tonnes compared with business as usual. Notably, the variability (SD) around the mean feed-crop estimates demonstrates the potential hundreds of millions of tonnes of savings that could come from global improvements in future animal efficiencies (livestock, poultry, and aquaculture). However, while total crop requirements are reduced under the 2050 seafood scenarios, total use of the seven feed crops assessed in this study still rises to two times current levels due to an expanding population, increased per-capita consumption of animal protein, dairy cows and laying hens allowed to increase, and a greater proportion of these crops included into future animal diets (*Materials and Methods* and *SI Appendix*).

The future area of cropland needed for feed increases under all future scenarios, but we find that millions of hectares are spared with human diets based on a larger proportion of cultured aquatic protein (mixed: total spared land ± SD = 75.9 ± 13.5 million hectares; marine: 69.9 ± 13.3 million hectares) (Fig. 3 *A*–*C*). Again, the variability (SD) illustrates the potential tens of millions of hectares that could be spared with ubiquitous increases in animal efficiencies (Fig. 3*C*). However, savings are not uniform. While most countries spare cropland (mean ± SD = 180 ± 5 regions; 413.7 ± 73.7 1,000 hectares), substantial increases in land use for feed occur in nearly a dozen countries (Fig. 3*D*). Several regions risk requiring 30% or more cropland for feed than under the business-as-usual scenario (Fig. 3*B*), including Chile, Egypt, and Norway, which are all significant producers of fed marine aquaculture and assumed to domestically supply a portion of feed if the associated crop is produced in country (*Materials and Methods*). It is important to note this does not necessarily mean an expansion of total cropland, but rather an increased use of cropland (existing or new) for feed. Notably, compared with business as usual, the aquaculture scenarios reduce cropland burden for feed in biodiverse regions of conservation concern, such as Brazil (25% spared, equal to 11.6 ± 2.1 million hectares).

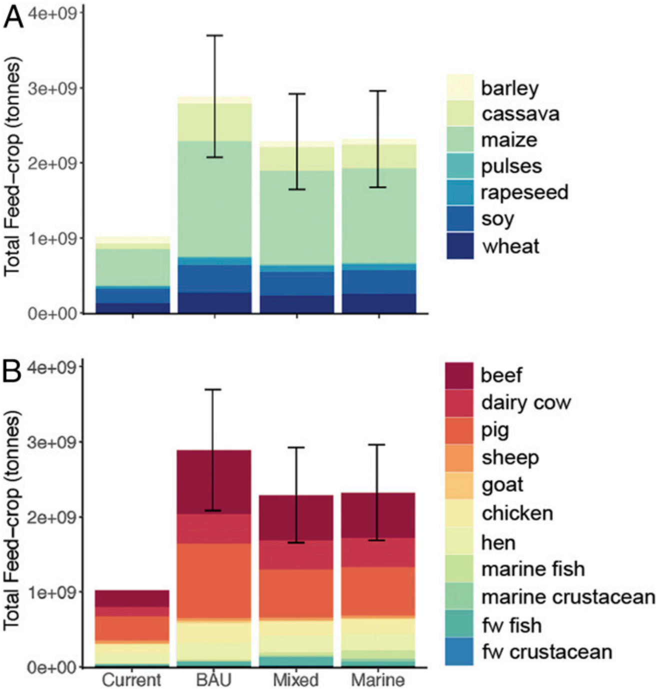

Fig. 2. Mean feed-crop requirements for each animal protein production scenario. Total average (±SD) global feed-crop equivalence (tonnes) for each (*A*) crop type and (*B*) animal group for the four scenarios: current (baseline), business-as-usual (BAU) 2050, proportional substitution of 2050 meat production with mixed (freshwater and marine) aquaculture, and meat substitution from primarily marine sources. fw, freshwater.

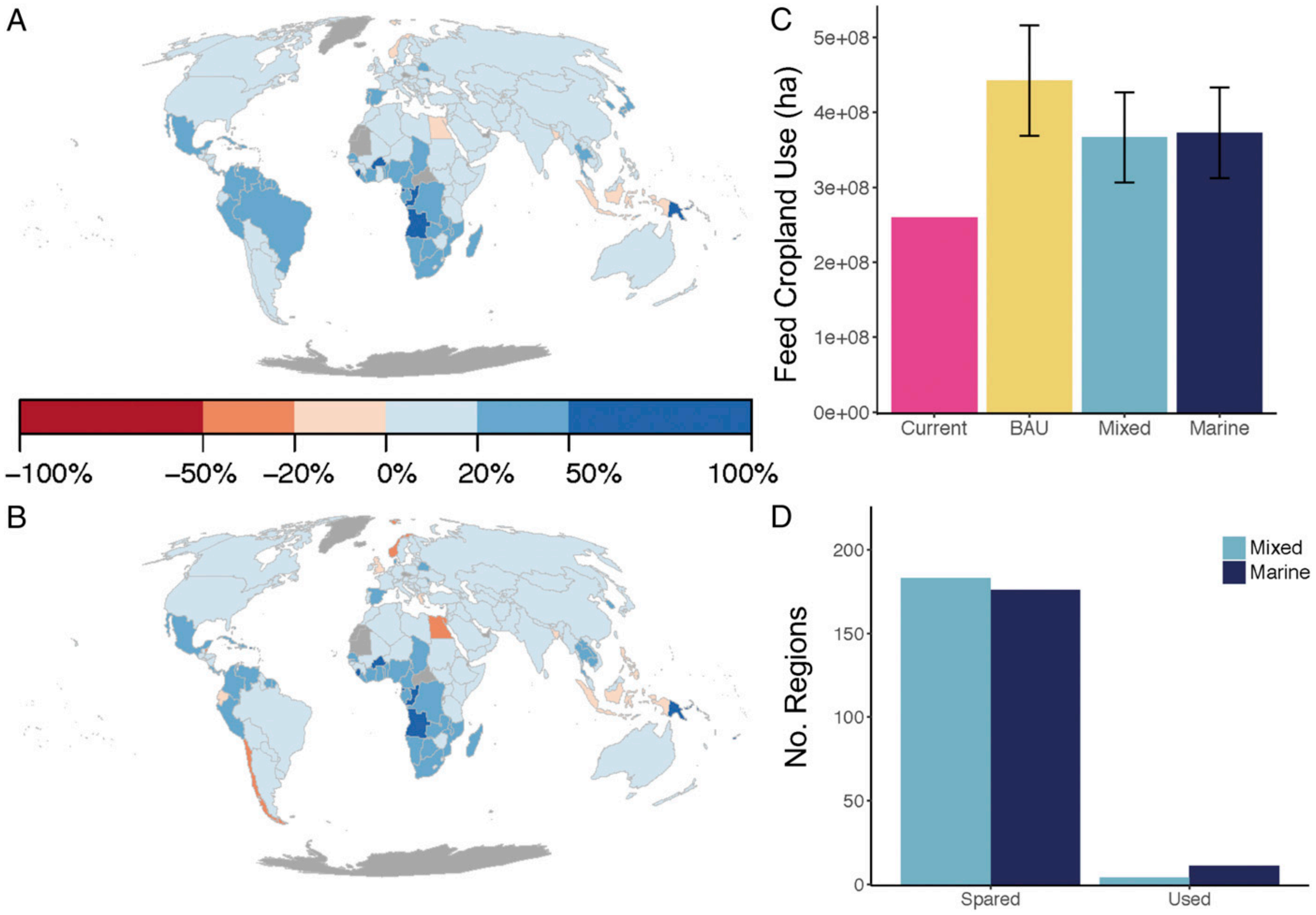

Fig. 3. Amount and location of changes in cropland for feed under different protein future scenarios. Percent of feed-based cropland spared (blues) or used (reds) to meet crop demands based on a comparison of business-as-usual (BAU) 2050 meat-based diet to seafood diet scenarios, from (*A*) mixed (freshwater and marine) aquaculture or (*B*) predominantly marine aquaculture. *C* depicts the total average land use (±SD) from crops for feed under each scenario and (*D*) displays the distribution of FAO regions that would spare more and use more in land use. Countries in gray do not change or are not applicable.

Land-use savings from shifting toward aquaculture-based diets are even greater when we account for land used for grazing. Roughly three-quarters of all agricultural land is currently used for grazing ruminants (cows, sheep, and goats) (4). We used published estimates of global animal grazing feed ratios to reflect the amount of regional livestock biomass produced from pasture (versus crop feed) to calculate the extent of land required per unit of ruminant biomass (*Materials and Methods*) (5). After accounting for grazed and cultivated land, switching future growth in meat consumption to seafood spares an extent twice the size of India (747–729 million hectares mixed and marine scenarios, respectively; Fig. 4). Savings are, again, not evenly distributed (country-level mean ± SD = 3.21 ± 11.2 million hectares; range = 0–141 million hectares). Under both aquaculture scenarios, nearly all countries reduce their total feed production footprint with more cultured seafood than meat (Fig. 4*A*). For instance, Brazil could spare an average 12 times more land under both seafood scenarios if grazed land is considered—the most savings of any country from reduced reliance on grazed livestock (see *SI Appendix* for full list).

Increases of molluscs (unfed cultivated species) in future diets can result in an obvious reduction in required feed, and thus land use. Our future simulations assume consumption of molluscs remains proportionally constant across all scenarios (25% of aquaculture production). A diet shift toward more bivalves could thus provide protein and greater spared land, as well as possible ecosystem services, including improved local water quality, coastal protection, and even habitat for wild species (22). Due to a lower edible percentage, a comparatively greater volume of molluscs would have to be cultured, which could negatively affect aquatic systems (e.g., divert energy flow) (23). Molluscs may also be more sensitive to environmental stressors (e.g., ocean acidification) (24), and require relatively consistent and abundant primary production (i.e., phytoplankton) to grow effectively (25). These factors, combined with global preferences for finfish, may limit dietary shifts to farmed molluscs. Ultimately, increases in aquaculture production may not be as limited by biophysical or space constraints as terrestrial production, but instead by economic, cultural, and political factors (21).

Shifting diets to more cultured seafood has comparatively lower impact on feed and land use, but does not eliminate such pressures and could result in other environmental and dietary shortcomings. Current aquaculture technology and best practices can help reduce some negative effects, including pollution and disease (26), but do not negate stresses that can arise from improper planning and weak oversight, such as escapes and habitat degradation (27). With globalized markets, local aquaculture-based impacts could be minimized by more even distribution of aquatic farms (i.e., "spread the wealth" and impact) in the most suitable areas (e.g., offshore) (21). However, the high crop-input levels simulated here would likely compromise the micronutrient benefits of fish, emphasizing the importance of other alternative-feed sources (e.g., omega-3 eicosapentaenoic acid and docosahexaenoic acid) from an environmental and human health perspective (28).

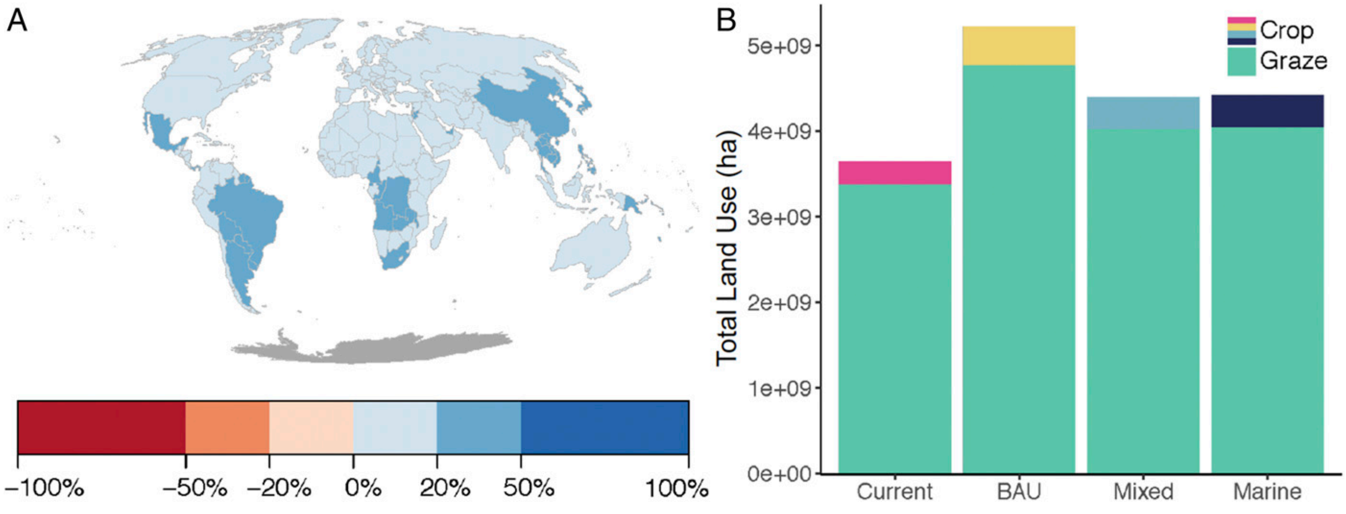

Fig. 4. Amount and location of changes in total land use under different 2050 animal production scenarios. (*A*) Percent of land spared (blues) or used (reds) accounting for grazing and crop demands based on a comparison of business-as-usual (BAU) 2050 meat-based diet to seafood diet scenarios, sourced from mixed (freshwater and marine) aquaculture. Marine results are equivalent to the mixed scenario outputs and thus not depicted. (*B*) Total average land use from crops (rainbow colors) and grazing (green color) for feed of each scenario. SDs of cropland use were too small at the grazing scale and thus not presented (see Fig. 3 for SD). Countries in gray do not change or are not applicable.

Our future scenarios assume crop use increases to support continued growth in animal production, given other feed-based resources are limited, namely forage fish (e.g., anchovies, herrings, sardines, etc.) used for fishmeal and oil (11, 29, 30). Capture fisheries landings, including forage fish, have remained relatively unchanged for several decades (9), meaning additional growth of farmed animal production—particularly aquaculture, which now uses most (~73%; pigs and poultry 25%) of the fishmeal and oil (29)—will increasingly rely on alternative feedstuffs, such as crops. In the future, it is likely the decades-long tradition of feeding forage fish to farmed animals will continue, but in continually smaller proportions and/or to select, higher-value species (e.g., salmonids) (11, 29). Whether greater inclusion of crops and other alternative feeds (e.g., omega-3 algae) (31) will reduce fishing pressure on forage fish or other unreported aquatic species fed to farmed animals (32) depends on supply (scalability and cost) of nutritionally equivalent feeds (29) and other emergent demands (e.g., greater human consumption of forage fish) (33). Nonetheless, it appears the future potential to ease exploitation and use forage fish in other ways exists, especially if incentives and management move toward sustainable feed practices.

Minimizing future impacts of the human diet on terrestrial and aquatic environments will rely on trade-offs between domestic and imported supplies of the type of animal protein and feed from efficient and sustainable producers (15). Aquaculture is a food system and thus will have an impact on the environment. If greater adoption of cultured seafood into human diets did occur, similar to the rise of poultry (17), policy interventions that protect biodiversity from cropland expansion, like the Forest Code for Brazil (34), would remain important, and greater understanding the effects of aquaculture on wild aquatic systems at an ecosystem level would be critical (35). What this study demonstrates is the relative potential, but not sole solution, for reducing one of the largest pressures on the planet (agricultural land use) compared with current food system trends. Incentives and policies considering aquaculture as part of the portfolio of food sustainability solutions at a local to global scale—from supporting access and adoption of new or improved feed ingredients and species efficiencies, to strategic farm siting and seafood distribution—could provide substantial benefits for humans and the environment into the future (36).

Materials and Methods

We simulated meat production and associated crop and grazing land requirements for livestock, poultry, and fed aquaculture species for 230 Food and Agriculture Organization of the United Nations (FAO) regions (196 countries) under three future scenarios. "Regions" account for countries and territories according to International Organization for Standardization country coding. Estimates for future animal feed and associated land use were calculated using a combination of current country-level estimates of primary animal production around the globe, reported future protein demands and trends for 2050, country animal feed composition from data repositories and literature, and country crop production of major feed types and associated projected efficiencies of those crops. Below we describe each component and assumption of the model in detail. Current values were used to parameterize the "baseline model" and test operating model outputs against other feed and land-use estimates to ensure realistic results were produced (*SI Appendix*). All analyses were performed in R, Version 3.4.1 (37).

Animal Production. To set baseline ("current") conditions, we first compiled country-level estimates of the most globally important protein sources by volume (tonnes) for livestock and poultry (which includes beef, pork, sheep, goat, dairy cow for milk, broiler chicken, laying hen for eggs) and aquaculture [which includes fed freshwater finfish and crustaceans, marine and brackish (referred to as marine henceforth) finfish and crustacean, and unfed molluscs] (3, 9, 38). Unfed silver and bighead carp were excluded from the analysis (9). We extrapolated average biomass of hens and dairy cows, as only head-count FAO data were available. We did this by estimating the conversion factor (1 head = *X* tonnes) of broiler chickens and beef cows based on reported total global number (head count) and FAO-estimated biomass of these animals (conversion factors for hen = 0.0014 tonnes; dairy cow = 0.23 tonnes).

A large proportion of livestock (beef, dairy cows, sheep, and goats) are fed via grazing (38), so we distinguished between animal biomass produced from crop-based feed (Eq. **1**) versus grazing (Eq. **2**). Presently, the majority of agricultural land use is pasture for grazing, and land-use implications for conservation are very different for crop versus grazing areas (4). However, data on the ratio of feed to grazing over a ruminant animal's lifetime for each country are unavailable. To capture a level of per-country differences, we assigned regional proportions of grazing (versus feed) derived from Mekonnen and Hoekstra (5) to all ruminants and associated countries (*SI Appendix*, Table S2). All nonruminant animals (excluding unfed molluscs) were assumed to be 100% fed. The biomass values were calculated as

$$b_{a,j} = B_{a,j} P_j, \qquad [1]$$

where $b_{a,j}$ is the estimated feed-based biomass (tonnes) of animal a in country j, $B_{a,j}$ is the total biomass of animal a of country j, and P_j is the proportion of animal biomass of country j that is produced by feed (non-grazing). Biomass of grazed livestock ($G_{r,j}$) of ruminant (r) (i.e., cattle, goats, and sheep) was calculated as

$$G_{r,j} = B_{r,j}\left(1 - P_j\right), \qquad [2]$$

where $B_{r,j}$ is the total biomass (tonnes) of ruminant livestock r of country j and $(1 - P_j)$ is the proportion of (ruminant only) biomass of country j that is produced from grazing.

Future (year 2050) business-as-usual biomass production values were calculated based on average projected change in wealth-driven protein consumption from previous studies, disproportionate production increase expected to occur in developing regions, and ratios of average live-weight total biomass of an animal to consumable protein (*SI Appendix*, Table S1). To capture a level of uncertainty in modeling human consumptive futures, we randomly sampled (n = 500) across a maximum (+20%) and minimum (–20%) range of percent animal productions originally derived from Tilman and Clark, and informed by Alexandratos and Bruinsma (16) who reported ~20% difference in predicted future meat-production requirements [see Hunter et al. (39) for details] (*SI Appendix*, Table S3). To account for the majority of production growth anticipated to occur within developing nations, we also added or subtracted a constant of 10% to the projected percent production increase for developing and developed countries, respectively, based on FAO reports (9, 38) (*SI Appendix*, Table S3). We used the resulting averages in projected live-weight animal production for the crop-feed and land-use calculations (Fig. 1). Under all future scenarios, animal production growth occurs where it already exists, proportional to current levels, and wild catches are assumed constant.

We chose seafood scenarios (includes freshwater and marine species) that allowed us to explore and clearly compare some of the consequences and plausibility of substantial global diet shifts toward more cultured seafood and less meat. One major assumption of our study is that countries have the socioeconomic ability to switch to seafood. This may be difficult for certain countries, particularly in more developing, arid climates (e.g., some African nations). Investment and growth in aquaculture is growing considerably in such regions (9), but the actual ability for aquaculture to substitute for cattle (the largest agricultural feed and land user) is beyond the scope of this study. In addition, production is driven by demand, and it is unknown if future populations could or should value (socially, culturally, and economically) seafood more than land-based meat production. Ultimately, the scenario approach allows us to highlight the possible implications of a more aquaculture-dominant world.

Crop-Feedstock Calculations. Although a variety of products can enter the diet of a farmed animal, we focused on the most abundant and commonly reported inputs across animal and crops types, specifically wheat, maize, soy, rapeseed, pulses, barley, and cassava products (3, 7, 14). Together these inputs currently contribute to 74% of terrestrial feed and have been consistently and increasingly present in global crop-based feeds over the last 50 y (*SI Appendix*, Fig. S1) (3). If the significant linear trend (linear model: $P < 0.001$, $R_{\text{adj}}^2 = 0.85$) toward homogenization of crop-based feedstocks persists to 2050, these seven crops would contribute an average of 88% (SE ± 0.6%) to animal feed.

We account for country-level variability of crop-based feed at the animal level:

$$C_{i,a,j} = b_{a,j} A_{i,a} F_a c_{i,j}, \qquad [3]$$

where $C_{i,a,j}$ is the estimated crop-equivalent tonnage of total i crop needed to feed animal a in country j, $b_{a,j}$ is the total biomass of animal a of country j on feed (Eq. **1**), $A_{i,a}$ is the average proportion of feed from crop i for animal a (from feed composition), F_a is the feed conversion ratio of animal a, and $c_{i,j}$ is the harmonizing constant of crop i, country j (derived from reported FAO commodity balance sheets) (3).

For the current-based model, we derived information on proportion of each crop type in animal feed stocks (average composition, $A_{i,a}$, Eq. **3**) of livestock, poultry, and fed aquaculture (finfish and crustaceans) from existing sources (3, 7). Initial average animal feed-crop compositions were derived from Tilman and Clark (7). We assigned the regional feed proportions for aquaculture to their associated countries. However, these feed-crop proportions were not originally differentiated for freshwater and marine species. More specifically, estimated feed composition in Tilman and Clark did not account for aquatic-based inputs—which can be substantial for fed aquaculture (e.g., protein and oil contributions from forage fish) (11, 13). Most freshwater species (e.g., carp) tend to have smaller proportions of aquatic inputs compared with marine species (e.g., salmon). To address this, we decreased the Tilman and Clark pulse proportional estimates (a large protein-based input) in aquaculture feeds to better reflect the larger use of aquatic-based sources (4% less for freshwater species and no pulse inputs for marine species) (11, 13). Regions without distinct aquaculture feed composition estimates (n = 30) were assigned the average (other), which included East Europe and Commonwealth of Independent States and Small Island countries and territories.

For future scenarios, we account for increasing trends of crop inclusion and feed homogenization into the diets of farmed animals (*SI Appendix*, Fig. S1) by adjusting the relative proportional contribution of crops in feed of all groups based on the respective linear trends of global FAO feed values (*SI Appendix*, Fig. S2). We increased the average animal crop-feed proportion ($A_{i,a}$) of wheat (2%; $R_{\text{adj}}^2 = 0.30$, F-stat = 23.4, df = 51, $P < 0.001$), maize (11%; $R_{\text{adj}}^2 = 0.86$, F-stat = 323.2, df = 51, $P < 0.001$), soy (1%; $R_{\text{adj}}^2 = 0.57$, F-stat = 70.7, df = 51, $P < 0.001$), and cassava (2%; $R_{\text{adj}}^2 = 0.71$, F-stat = 129.7, df = 51, $P < 0.001$), decreased barley (–4%; $R_{\text{adj}}^2 = 0.43$, F-stat = 38.1, df = 51, $P < 0.001$), and left rapeseed ($R_{\text{adj}}^2 = 0.06$, F-stat = 3, df = 51, $P = 0.09$) and pulse ($R_{\text{adj}}^2 = -0.01$, F-stat = 0.76, df = 51, $P = 0.37$) proportions unchanged. On average, the increase resulted in 8% (SD ± 5%) greater crop inclusion across regional animal diets in 2050. In the event changing the average animal-feed composition exceeded 100% of the diet, we decreased maize contribution until diets balanced (*SI Appendix*, Table S4). These increases in crop contribution into the diets of farmed animals represent feed homogenization that can be driven by limits of other source feeds, including fish-based inputs that have remained constant while animal production (livestock and aquaculture) continues to increase (11, 29, 40). We tested the sensitivity of the model to animal-feed composition by comparing all future scenarios with compositions held constant versus the above increases (*SI Appendix*, Fig. S3). Greater inclusion and homogenization of feed, coupled with increased production, translates to a 27% (±2%) greater use of these crops in our simulations, predominantly from maize and cassava. Thus, the relative differences in feed crops and land use of the seafood scenarios to business as usual are more meaningful than the absolute differences to current levels that do not account for other terrestrial inputs. We also recognize we simulate a more extreme case of future crop diet inclusion, which could be reduced with non–crop-based alternative sources if they become available and economically competitive to crops feed stuffs.

To account for uncertainty and possible average improvements in animal feed efficiencies (F_a), the baseline current model and all future scenarios were calculated 500× from randomly sampled values pulled from uniform distributions of feed-conversion ratios. Parameter F_a is a unitless metric that describes the efficiency of an animal to convert feed to biomass (tonne input per tonne gained), and thus can be used to calculate feed requirements based on biomass of an organism. Currently, there is no dataset of country-level efficiencies (5). Instead, we looked across primary and gray literature for realistic ranges for all animal groups (*SI Appendix*, Table S5), specifically analyzing the aquaculture regional efficiencies and temporal trends reported by Tacon and Metian (11, 40) and regional efficiencies reported by Mekonnen and Hoekstra (5) to bound F_a ranges. For aquaculture, a linear trend in improved efficiencies results in an average 2050 F_a equal to 1.1 (SE ± 0.04) (F-stat = 25.6, df = 174, $R^2_{\text{adj}} = 0.12$, $P < 0.001$), which we set as our minimum for the aquaculture groups, creating comparable distributional trends (*SI Appendix*, Figs. S4 and S5). In fact, the salmon industry already reports achieving feed efficiencies of 1.1 (41). For livestock and poultry, the majority of efficiencies across taxa and regions for the feed-based categories ("industrial" and "mixed") tend to be less than 20 (*SI Appendix*, Fig. S5; median = 5.40, Q_1 = 3.30, Q_3 = 12.8) (5). We set our ranges based on the global, taxonomic estimates, which resulted in comparable patterns [*SI Appendix*, Fig. S5 and Table S5; livestock and poultry F_a ($n_{\text{simulations}}$ = 500) median = 6.10, Q_1 = 3.30, Q_3 = 9.13].

Once we estimated the required amount of each dry-matter crop feed (tonnes) from the proportions of animal biomass that comes from feed (versus grazing; b_j), average animal-feed composition ($A_{i,a}$), and feed-conversion ratios of each animal (F_a), we then harmonized our baseline model outputs to FAO country-level feed-crop equivalence values (Eq. **3**). More specifically, for each country a harmonizing constant ($c_{i,j}$) was derived from the FAO commodity-balance estimates so our average feed-crop outputs approximately reflected the absolute FAO values for each crop type in accordance with other studies (3, 42). Harmonizing provides a realistic and consistent baseline of feed crops, while allowing additional disaggregation by other factors (42); in our case, animal production type. In addition, use of the commodity FAO outputs provides the crop equivalence relevant for calculating land use.

Trade of crops varies among countries, but is not sufficiently reported to determine the exact area of land attributed to animal feed (versus production for direct human consumption or biofuels) within a country. To capture this heterogeneity, we employed a balanced-trade approach (i.e., trade is assumed to balance crop deficits of regional production, with no trade barriers) (15), which measures total tonnage ($¢_{i,j}$) of each feed crop i in country j from the summation of domestic production ($D_{i,j}$) and export ($E_{i,j}$):

$$¢_{i,j} = D_{i,j} + E_{i,j}, \qquad [4]$$

$$D_{i,j} = C_{i,a,j} d_{i,j}, \qquad [5]$$

$$E_{i,j} = \left(C_{i,a,j} - D_{i,j}\right) e_{i,j}, \qquad [6]$$

where $C_{i,a,j}$ is the estimated tonnage of i crop needed to feed animal a in country j (from Eq. **3**), $d_{i,j}$ is the proportion of domestically produced crop i in country *j*, and $e_{i,j}$ is the global proportional contribution of exports of crop *i* from country *j*. These formulations assume that the amount of each crop used for feed within a country matches the proportions of each domestic crop produced ($d_{i,j}$, calculated from total, current domestic supply of production and imports; Eq. **5**) (3) and that countries that export crops continue to do so to match their current proportional contribution to global trade of the specified crop ($e_{i,j}$; Eq. **6**) (3). Thus, we assume current net-exporting countries meet any domestic feed deficits not achieved by the proportion of domestic production, and that both proportions ($d_{i,j}$ and $e_{i,j}$) remain constant across all future scenarios. While future global production patterns will be driven by economic conditions and marginal efficiencies of increased production across space, predicting new and/or divergent expansion from current patterns is outside the scope of this study. Our goal was to highlight potential consequences of uneven production and trade given realistic (i.e., current) patterns.

Land-Use Calculations. Total cropland and grazing land were separately calculated based on our estimates of total crop-feed requirements of each country ($\text{¢}_{i,j}$; Eq. **4**) and animal biomass of ruminants from grazing ($G_{r,j}$; Eq. **2**). Total hectares of cropland ($U_{i,j}$) used to produce feed-crop *i* in country *j* across all protein sources was calculated as

$$U_{i,j} = \text{¢}_{i,j} h_{i,j}, \qquad [7]$$

where $\text{¢}_{i,j}$ is the total tonnage of *i* feed crop in country *j* (from Eq. **4**) and $h_{i,j}$ is the area-yield ratio of *i* crop (ha t^{-1}) in country *j*. We then translated $G_{r,j}$ into area of land (hectares) needed to graze livestock ($g_{r,j}$) as

$$g_{r,j} = G_{r,j} \beta, \qquad [8]$$

where β is the area-biomass constant (72.4 ha tonne^{-1}) for ruminant livestock to scale our estimates to the current global pasture estimate (4), since the specific country-level ratio of intensive versus extensive farming biomass is unknown. Our values thus provide a simplified baseline for relative comparison of future alternative production scenarios and do not account for possible intensification feedbacks between crops and grazing that could reduce future pasture needs.

Total area-yield ratios ($h_{i,j}$; Eq. **7**) now and in the future were based on FAO yield estimates (3). Where estimates were not available for a given country, we used the regional average for the associated FAO region. Future values were calculated based on FAO 2050 global projections of increases in production efficiencies for each crop (wheat = 27%; corn = 22%; soy = 28%; rapeseed = 43%; pulses = 50%; barley = 17%) (16). Only cereal percentages were differentiated between global and developing nations (developing: wheat = 31%; corn = 31%). No estimates were given for cassava or any other root vegetable, so country averages (32–33%) were assigned and appear consistent with plausible future improvements (43). We followed FAO's assignment of "developed" and "developing" nations for each country.

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