



OPEN

Food system by-products upcycled in livestock and aquaculture feeds can increase global food supply

Vilma Sandström¹✉, Anna Chrysafi¹, Marjukka Lamminen², Max Troell^{3,4}, Mika Jalava¹, Johannes Piipponen¹, Stefan Siebert⁵, Ollie van Hal^{6,7}, Vili Virkki¹ and Matti Kummu¹✉

Many livestock and aquaculture feeds compete for resources with food production. Increasing the use of food system by-products and residues as feed could reduce this competition. We gathered data on global food system material flows for crop, livestock and aquaculture production, focusing on feed use and the availability of by-products and residues. We then analysed the potential of replacing food-competing feedstuff—here cereals, whole fish, vegetable oils and pulses that account for 15% of total feed use—with food system by-products and residues. Considering the nutritional requirements of food-producing animals, including farmed aquatic species, this replacement could increase the current global food supply by up to 13% (10–16%) in terms of kcal and 15% (12–19%) in terms of protein content. Increasing the use of food system by-products as feed has considerable potential, particularly when combined with other measures, in the much-needed transition towards circular food systems.

The current structure of the global food system results in sub-optimal food availability, as a large proportion of the resources used in livestock and aquaculture feeds could be consumed by humans. Up to 40% of all arable land and more than 30% of cereal crop production is used for animal feeds^{1,2}, and approximately 23% of all captured fish are destined for non-food uses, mainly for fish and livestock feeds³. This food–feed competition reduces the efficiency of the existing food system, as environmental and resource costs are higher when arable land is used for animal feed production instead of directly contributing to human consumption^{4–6}.

Increasing the feed use of food system by-products—that is, the secondary products created alongside the primary, human-consumable products—has been proposed as a solution to increase resource use efficiency^{7–10}, to reduce food–feed competition¹¹ and to increase food system circularity^{10,12,13}. In addition, using food system by-products as feeds can reduce the environmental pressure on arable land and freshwater ecosystems, as well as reduce greenhouse gas emissions and fertilizer application^{8,10,13–16}. Increasing the use of by-products and crop residues as feed can also be cost-effective since many of them are widely available, low-cost materials¹⁷. However, some non-food-competing feedstuffs are less suitable for feed use; for example, crop residues are fibrous and of low digestibility and poor protein quality, and others, such as some crop processing by-products, are protein dense but low on energy¹⁰. Yet, some non-food-competing feedstuffs can be improved through processing or additives¹⁸. Despite the challenges, part of the food-competing feed use could be replaced with non-food-competing feedstuffs without negatively impacting productivity^{19,20} (Supplementary Tables 7 and 8).

In this study, we assess the potential of improving circularity in the global food system by increasing the use of food system by-products and residues in animal feeds. This approach provides

a much-needed systemic view of the highly interlinked global food system and advances the research field on three main fronts. First, global datasets including both feed material flows and the availability of food system by-products and residues at this level of detail do not exist. While different models and reports provide data on livestock^{21–23} or aquaculture feed use^{24,25}, these data are not harmonized throughout the global food system. Furthermore, while some studies have estimated feed use in both agriculture and aquaculture systems, they do not account for country-level differences in feed use²⁶ or have only regional focus²⁷. Here we combined and harmonized data from various sources including crop, livestock and aquaculture production, as well as wild fisheries, and quantified the dynamics of global feed flows in remarkable detail (Fig. 1 and Methods).

Second, material flows related to food system by-products have been estimated and reported only sporadically^{10,15,17,22,28}, thus, a comprehensive understanding of those flows is lacking. We overcame this by analysing the availability of different by-products and residues followed by quantifying their current feed use and the potential availability to further increase their feed use. Third, existing studies have assessed the feed use potential of individual by-products within specific production systems (Supplementary Tables 7 and 8) and have analysed scenarios of livestock production that could be sustained by restricting their feed use to non-food-competing feedstuffs^{8–11,29}. On the basis of our quantification of global food system material flows, we extend this knowledge by assessing the replacement potential of food-competing feedstuff with by-products and residues while simultaneously considering their regional availability and nutritional constraints in both the aquaculture and livestock production sectors (Methods). The nutritional constraints that dictate the replacement potential are based on an extensive literature review of feed experiment studies (Supplementary Tables 7 and 8). Combining the three advances, we are able to show that increased

¹Water & Development Research Group, Aalto University, Espoo, Finland. ²Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland.

³Beijing Institute of Ecological Economics, Royal Swedish Academy of Sciences, Stockholm, Sweden. ⁴Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden. ⁵Department of Crop Sciences, University of Göttingen, Göttingen, Germany. ⁶Louis Bolk Institute, Bunnik, the Netherlands. ⁷Animal Production Systems group, Wageningen University, Wageningen, the Netherlands. ✉e-mail: vilma.sandstrom@aalto.fi; matti.kummu@aalto.fi

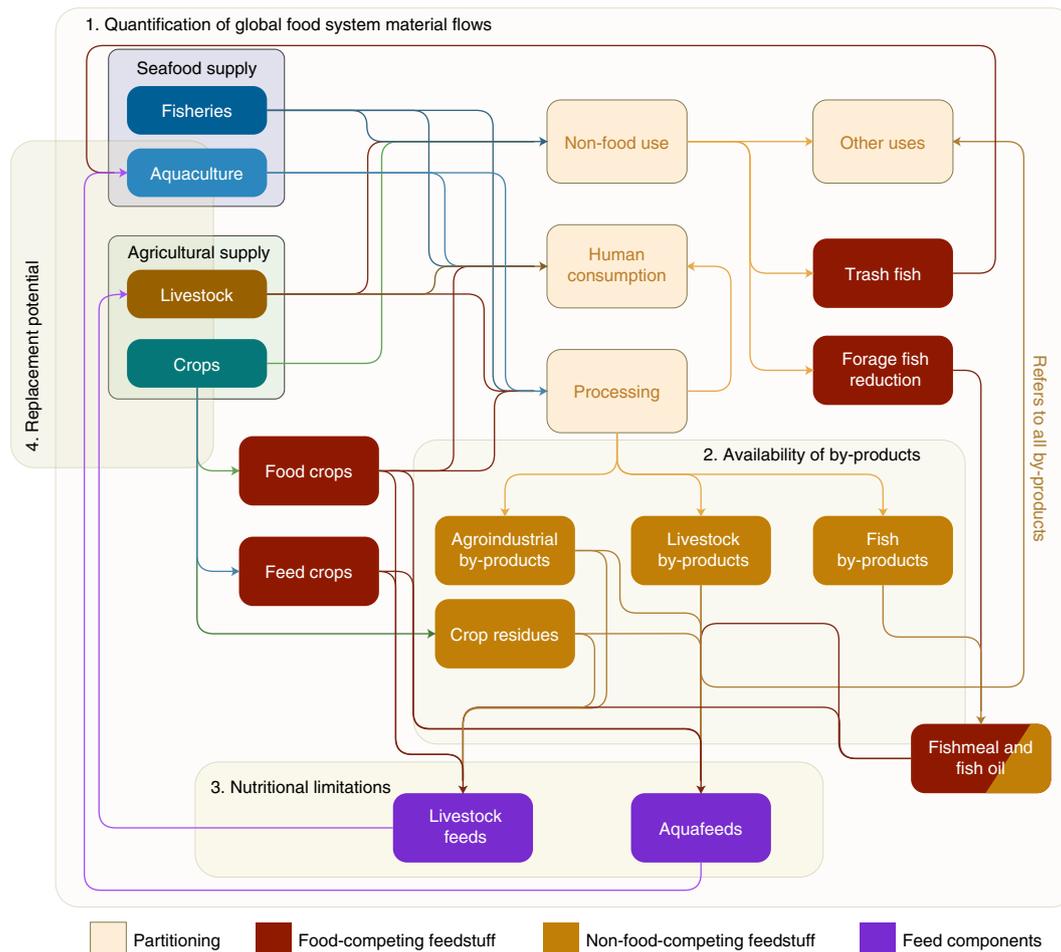


Fig. 1 | Global food system material flows considered in this study. Four main phases were considered in the analysis: (1) quantification of global food system material flows—we quantified global food system material flows including the potential production of by-products and the feed use in both terrestrial and aquatic food systems; (2) availability of by-products—we analysed the availability of the by-products by subtracting their current feed use from potential production, assuming that all non-used by-products would be available for feed; (3) nutritional limitations—using existing literature, we considered to what extent by-products can replace food-competing feedstuff in animal feeds, accounting for impacts on productivity; and (4) replacement potential—we estimated the amount of food-competing feedstuff that could be replaced with non-food-competing feedstuff. See Methods for the quantitative interpretation of the flows as well as the data used for each phase.

utilization of food system by-products and residues in animal feeds could theoretically lead to a considerable upsurge in the global food supply.

Results

Food-competing feedstuff use. We first combined data from various sources, using production data for primary products for 2016–2018 (refs. ^{2,30}) and feed composition data for livestock and aquaculture for 2010 (refs. ^{21,31}) to analyse the current feed flows (Fig. 1 and Methods). We focused on the feed use of food-competing feedstuff including cereals, oilseed oils, pulses and whole fish used in fishmeal and fish oil production (Supplementary Table 3; see Methods for assumptions).

Approximately 15% (940 million tons in dry matter) of the total feedstuffs (6,100 million tons) used in livestock and aquaculture production consisted of food-competing feedstuff that could be directly used as human food (Fig. 2). This is in line with existing estimates^{1,23} (Supplementary Information). However, animal production systems differ substantially in their food-competing feedstuff use^{21,31,32}. At the global level, up to 49% of feed use in aquaculture (total feed use, 67 million tons), 68% in poultry

(total 421 million tons) and 38% in pork meat production (total 1,200 million tons) consisted of food-competing feedstuff, while for cattle meat (total 5,200 million tons) and dairy (total 1,920 million tons), the share was only 3–4% (in quantities of feed in dry matter). The low share of food-competing feedstuff in cattle feed is mainly due to the large share of global cattle production being extensive grazing systems, which have high feed conversion ratios (kg feed per kg output), consuming high amounts of feed consisting mainly of roughages such as grass and hay. Diets in industrial feedlot cattle systems often include a higher share of food-competing feedstuff. For example, in some North American and European industrial beef cattle systems, the diets in the finishing phase can consist of more than 70% (ref. ²¹) food-competing feedstuff. However, these systems are highly optimized, having lower feed conversion ratios³³ and consequently lower total feed consumption. Furthermore, we found that regional variation in food-competing feedstuff use is notable, the minimum being less than 4% in Africa and values ranging through 7% in Oceania, 8% in Latin America, 15% in Europe and 16% in Asia to a maximum of almost 20% in North America. These differences reflect regional variations both in animal species farmed (that is, the relative

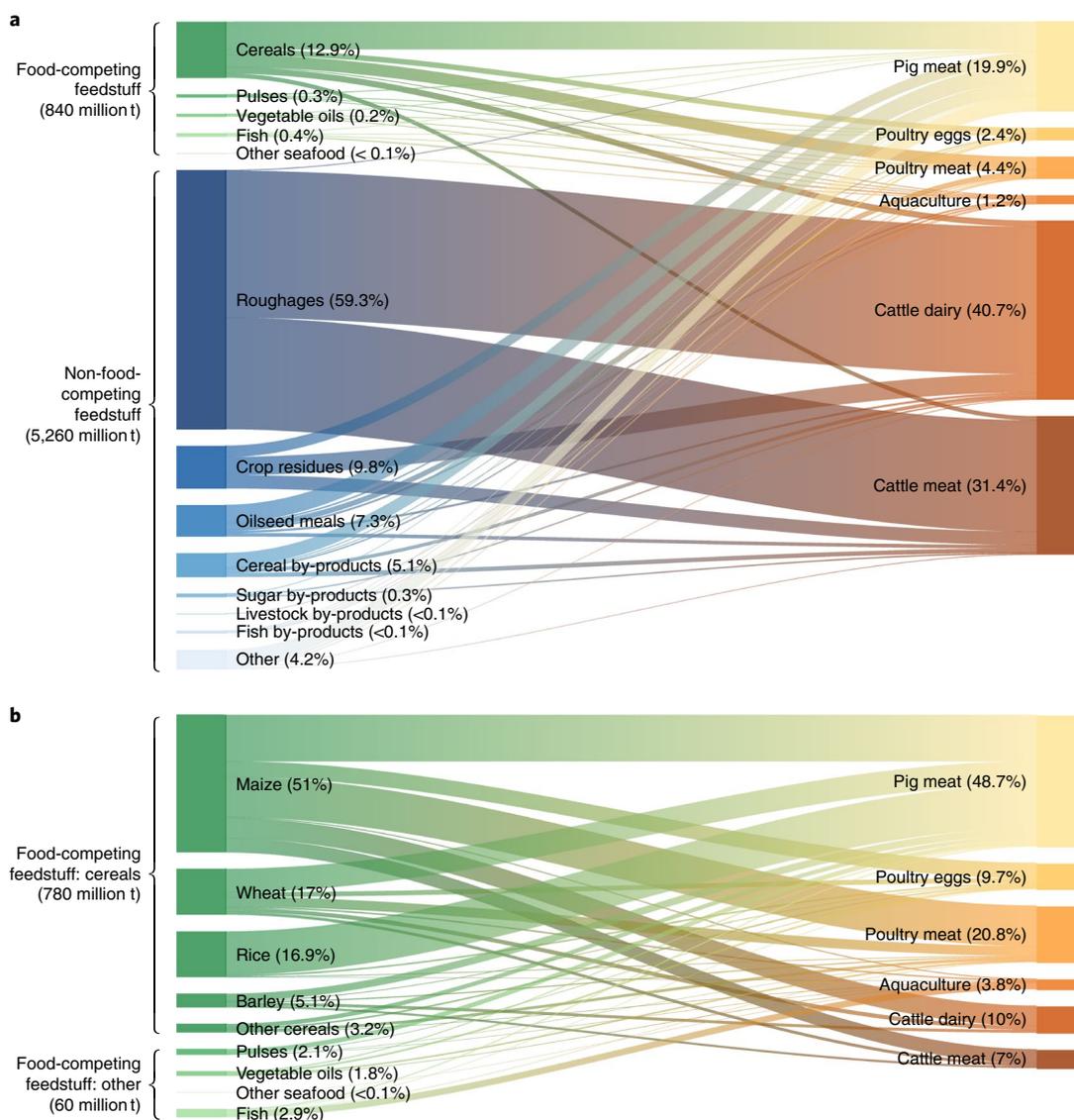


Fig. 2 | Feed use material flows in the global food system (dry matter weight). **a**, All feed flows. **b**, Flows for only food-competing feedstuff. The percentages refer to the shares of the feed use categories (on the left) and the shares of the feed use in specific animal production groups (on the right) of the total global feed use. The feedstuffs included in each category are described in Supplementary Tables 3 and 4. The data sources used are given in Methods. Material flows in terms of protein content are shown in Extended Data Fig. 1.

proportions of different animals) and in production mode (that is, intensive versus extensive systems).

At the global level, however, most of the feed use consists of materials not suitable for human consumption, mainly roughages such as grass foraged by cattle (Fig. 2a). Cereals form by far the largest group of food-competing feedstuff use, in which maize is the most important feed cereal, followed by wheat, rice and barley (Figs. 2b and 3a,d). Notably, fish products (fishmeal and fish oil) are important sources of protein (Fig. 3b and Extended Data Fig. 1) and fat (Fig. 3c) when examining the global feed protein and fat flows. They can also be important for the supply of healthy fatty acids (EPA and DHA). Similarly, the importance of oilseed oils increases when looking at the fat content (Fig. 3c).

Availability of food system by-products. In this study, we identified four main categories of food system by-products: (1) crop residues (that is, the plant material remaining after harvesting, including parts such as straw, leaves, stalks, roots and stover);

(2) crop processing by-products, including cereal bran and distiller's grains (including distiller's grains from biofuel and brewer's grains from barley beer industries), sugar by-products (including sugarcane and sugar beet molasses and sugar beet pulp), oilseed meals (including rapeseed, soybean, sunflower seed, palm kernel, sesame seed, cottonseed, groundnut and other oilseed meals) and citrus pulp; (3) livestock by-products from non-ruminant origins (that is, processed animal protein from pig and poultry production, here blood meal, hydrolysed feather meal, meat and bone meal, poultry by-product meal, and poultry oil); and (4) fisheries and aquaculture processing by-products, hereafter referred to as fish by-products, processed into fishmeal and fish oil. The total availability of food system by-products was estimated by multiplying the production quantities of primary products^{2,33} by conversion factors for different by-products and residues^{10,33}, or applying global statistics³ or other literature (Methods). The feed use of these by-products and residues was then subtracted from their total availability to estimate the potential availability of materials not already used as feed.

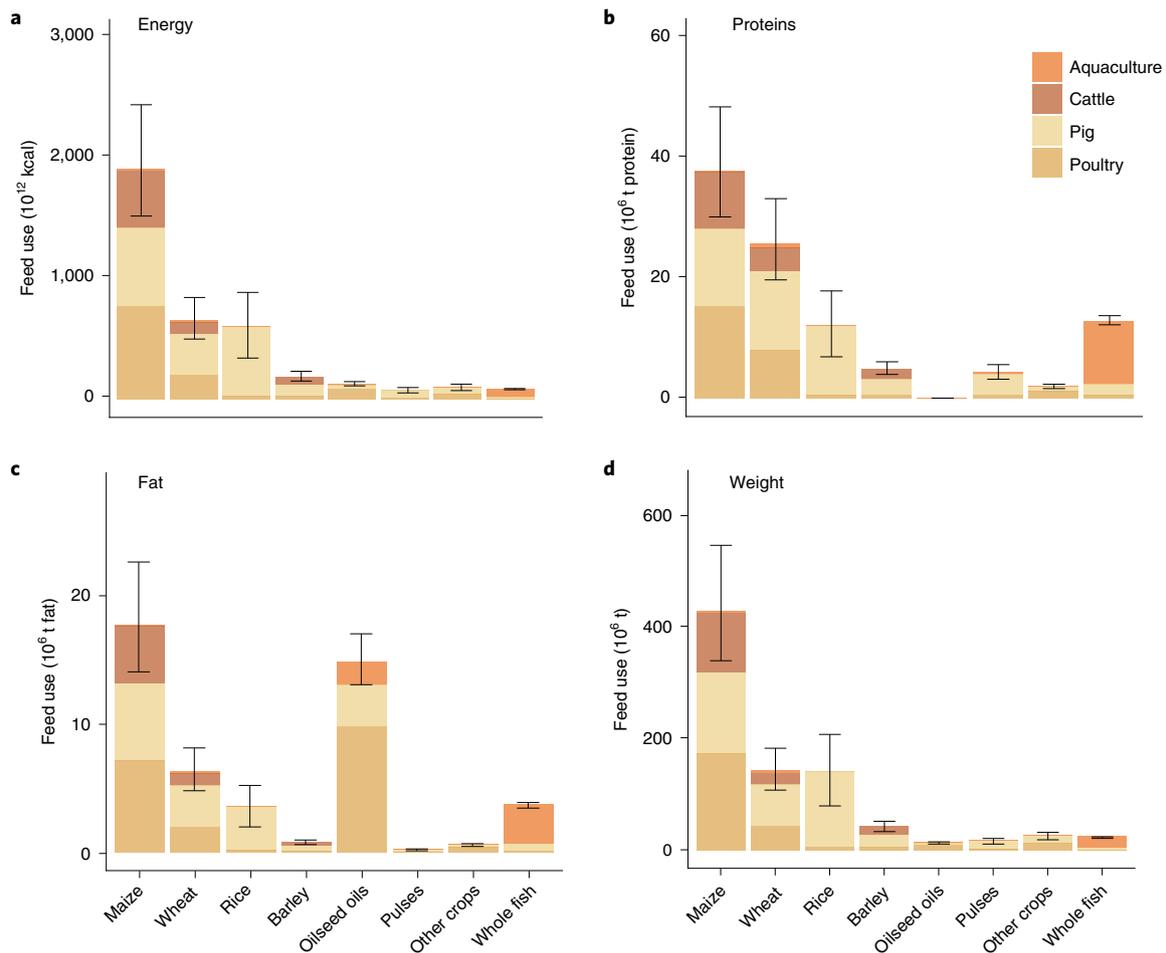


Fig. 3 | Global feed use of food-competing feedstuff. a–d. The values represent averages over 2016–2018 for energy content (kcal) (**a**), protein content (**b**), fat content (**c**) and quantities (dry matter weight) (**d**). The error bars represent the total uncertainty range for different feedstuffs (Methods). The use of the feed is colour-coded to each feed group.

Only relatively small shares of crop residues and livestock by-products are currently used as feed, while nearly all oilseed meals (that is, oilseed meals and cakes, here grouped together under meals) and more than half of the total potential of crop processing by-products, such as sugar beet pulp and cereal bran, are already used as feeds (Fig. 4). It should be noted that while only a small share of crop residues are used for feed, these resources also have other uses such as biofuels or bedding material for livestock (Discussion). Here the use of crop residues in maintaining soil quality was taken into account in sustainable harvest ratios (Methods), but other uses were excluded, assuming that all by-products not already used for feed would be available to replace the human-edible feeds in animal diets. Despite their multiple uses, the highest theoretical potential in utilizing by-products as feed still lies in crop residues, as their theoretical availability exceeds the availability of other by-products (Fig. 5).

The availability of crop residues and livestock by-products is directly related to the volume of crop and livestock production in a country; hence, countries with higher agricultural production show the highest potential availability (Fig. 5a,g). For crop processing by-products, such as cereal bran, which have higher variation in their production and higher feed use, South Asia, Russia and North America show high availability (Fig. 5e), while for sugar processing by-products, Brazil and India show particular potential for increased feed use (Fig. 5b). Brazil is also the largest producer of citrus pulp (Fig. 5c). The United States, China and Brazil are the largest

producers of distiller's grains from both biofuel production and beer brewing, showing also the highest availability (Fig. 5d). Oilseed meals are highly valued feed materials, which shows in nearly all oilseed meals being used as feed at the global level (Fig. 5f). For fishmeal from fish by-products, countries with the most fisheries and aquaculture production (such as China and Indonesia) show the highest availability and the largest potential to increase the production of fishmeal and fish oil from fish by-products, either for local needs or for export to other countries (Fig. 5h).

Replacement potential. Once we had estimated the current food system's feed flows and the availability of by-products, we were able to assess the potential of replacing food-competing feedstuff with by-products, including both the livestock and aquaculture sectors. Animal-specific nutritional requirements and regulations regarding the feed use of animal by-products were considered in the replacement potential (Methods). The regional availability of by-products was also considered, assuming that all by-products that are not currently used as feed were utilizable in animal production (Methods and Discussion). For a detailed analysis, we selected by-products that are currently used as feed but that also have a large potential to increase their feed use at the global level. Hence, we focused on the potential to replace food-competing feeds (that is, cereals, oilseed oils, pulses, fishmeal from whole fish and fish oil from whole fish) with by-products having similar nutritional profiles (Table 1).

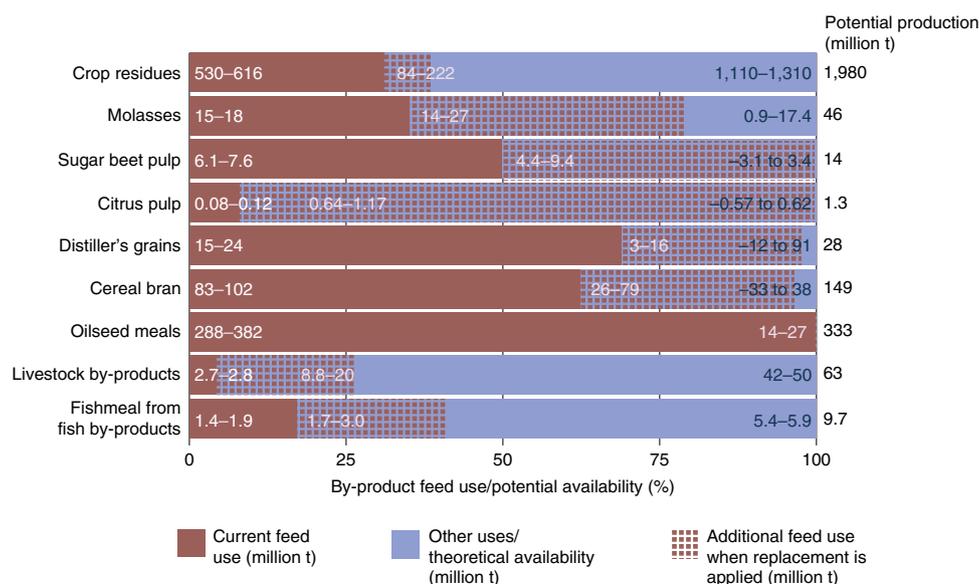


Fig. 4 | Feed use and theoretical availability of food system by-products, including the uncertainty range. The increased feed use of by-products when applying the replacement potential analysed in this study. Uncertainty range for current feed use (left), additional feed use when replacement is applied (middle) and other uses/theoretical availability (right) is shown. Negative values refer to the feed use exceeding potential availability. For the individual products included in the combined categories, see Supplementary Table 4.

Although the potential availability of some by-products or residues is much higher than their current feed use (Fig. 4), animal-specific nutritional requirements constrain their use in diets of livestock and aquaculture (Supplementary Table 6). For example, although crop residues are abundant, their fibrousness and lack of protein and readily utilizable carbohydrates limit their inclusion potential in diets that maintain animal productivity (Supplementary Table 8). The same applies for some other feedstuffs: for example, livestock by-products could replace all fish use, but to maintain the essential fatty acid profile required in aquaculture production³⁴, not all fish oil in aquafeeds can be substituted with processed animal fats from livestock (Supplementary Tables 6 and 7).

Here the replacement potential was estimated on the basis of literature on feed experiments, applying the maximum replacement ratios with no observed impact on productivity (Methods). The only exception was considered for the replacement of cereals with crop residues in cattle production, as negative impacts on productivity are probably unavoidable even with low substitution rates (Supplementary Tables 6 and 8). Therefore, for feed cereal use, two cases were analysed: first, without the inclusion of crop residues in the replacement, and second, including also crop residues and taking the consequent reduction in cattle productivity into account (Table 1).

When considering the replacement constraints (Supplementary Table 6) and the total availability of the selected by-products, up to 11–12% of the food-competing feedstuff could be globally replaced with the selected by-products without negatively impacting animal productivity. The replacement share could be as high as 25–29% when also considering the replacement of cereals with crop residues and consequently allowing some decrease in animal productivity (Table 1). The highest total feed replacement potential lies in cereals, as these are integral feedstuffs in all animal production systems (Fig. 2). However, the share of potential replacement is the highest for fishmeal and fish oil made from whole fish, indicating that nearly all whole fish used to produce fishmeal and fish oil could be replaced with by-products (Table 1).

Applying the maximum replacement potential of food-competing feedstuff with by-products could free up altogether

430–650 × 10¹² kcal and 17–26 million tons of protein for humans, corresponding to 5–7% and 7–11% of the current global food supply, respectively. The current global food supply refers to the average food supply for the global population in 2016–2018 (ref. ²), taking into account food losses and waste from the supply chain, excluding the production and consumption stages³⁵. More specifically, up to 72–103 million tons of cereals (almost 10% of their feed use), up to 3.8–6.0 million tons of vegetable oils from oilseeds (~31–42% of their feed use), 8–19 million tons of pulses (~50–88% of their feed use) and 2.9–3.9 million tons of fishmeal made from whole fish, corresponding to more than 17 million tons of whole fish (~11% of the current seafood supply) could be directed to human food use. When also considering crop residues as potential replacement materials, up to 25–28% of cereal feed use could be replaced; but this would impact animal productivity, which should be balanced and assessed carefully (Table 1). When applying world average yields for the replaced feed crop groups, the replacement would free up to 31–54 million ha of cropland. If also considering crop residues as replacement materials, the replacement would free more than 100 million ha of cropland, corresponding to 7% of the world total arable land use in 2018 (ref. ²).

In the maximum replacement potential scenario, the majority of the available cereal and sugar processing by-products are utilized as feeds. In contrast, fishmeal from fish by-products, livestock by-products and crop residues remain largely unutilized, and the majority of their biomass would still be available for other uses than feed, such as energy use (Fig. 4).

Discussion

We have demonstrated the considerable potential of increasing the feed use of food system by-products in the current food system. Our analysis extends and complements existing scenario-based assessments, which have found that it is possible to keep the global food supply adequate by restricting livestock feed use to only non-food-competing feedstuffs, combined with changes in livestock production levels and thus diet changes^{8–11,29}. By quantifying the potential to reduce the feed use of food-competing feedstuffs across the current global food system, we were able to estimate how

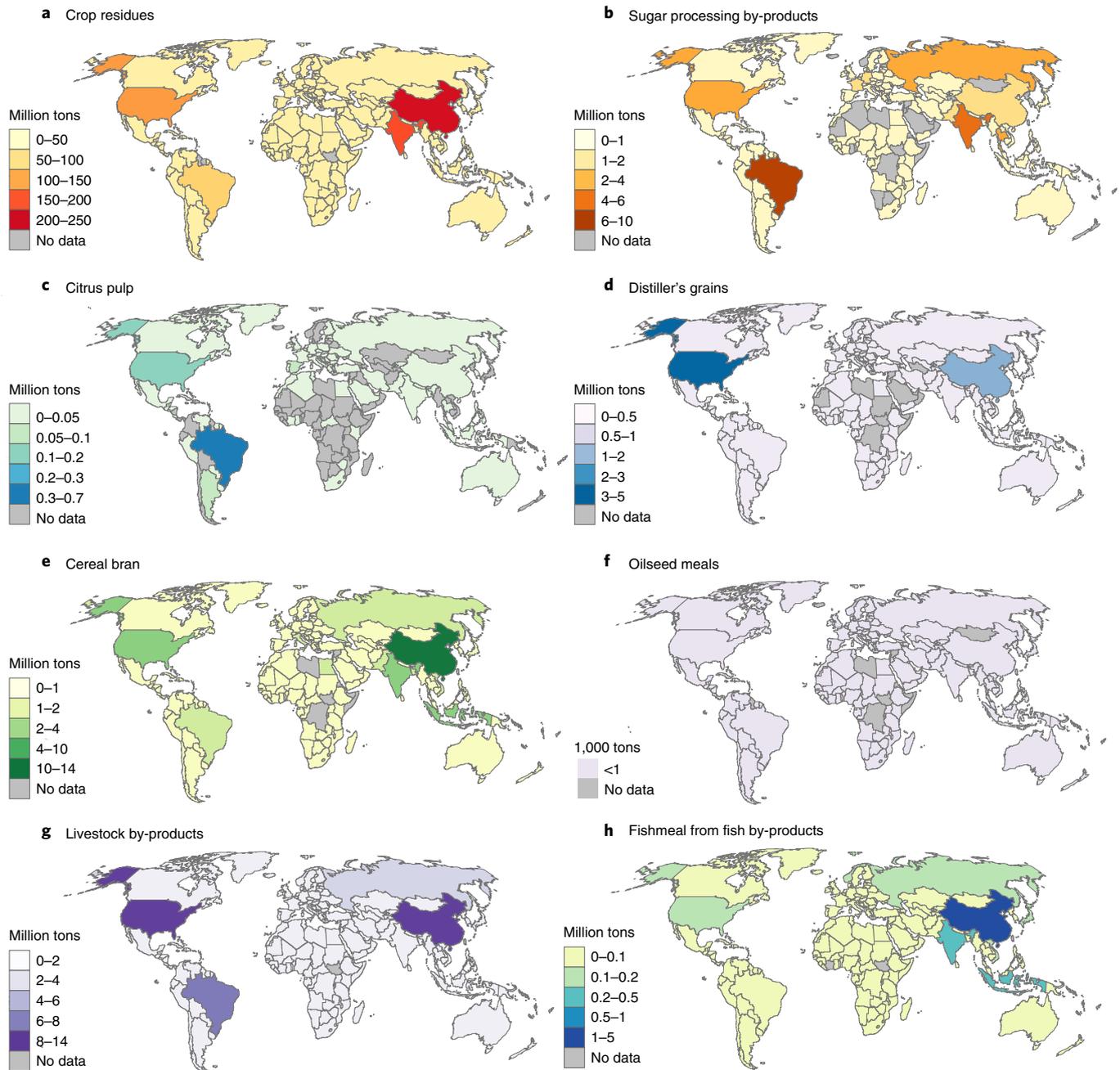


Fig. 5 | Theoretical availability of by-products and residues. **a**, Crop residues include residues from rice, cereals, sugar cane and pulses. **b**, Sugar processing by-products include molasses from sugar beet and sugar cane, as well as sugar beet pulp. **c**, Citrus pulp includes the by-products from citrus juice processing. **d**, Distiller's grains include the by-products from corn ethanol production and barley beer brewing. **e**, Cereal bran includes bran of barley, buckwheat, maize, millet, oats, pulses, rice, rye, sorghum, wheat, fonio, triticale and other cereals. **f**, Oilseed meals include rapeseed, soybean, sunflower seed, palm kernel, sesame seed, cottonseed, groundnut and other oilseed meals. **g**, Livestock by-products include by-products of non-ruminant origin, including blood meal, hydrolysed feather meal, meat meal and poultry by-product meal and poultry oil. **h**, Fishmeal from fish by-products includes by-products from processing of both aquaculture and capture fish. The values were computed by subtracting the current global feed use from potential by-product production and then rescaling the available by-products on the basis of each country's share of global production.

to increase the global food supply without consuming additional natural resources (Table 1).

We found that reducing the feed use of cereals presents the highest potential for increasing the global food supply. However, the increased supply of whole fish, pulses and oilseed oils can also contribute substantially to human nutrition, especially in terms of protein and fat (Fig. 3). Notably, we also showed that these

potentials vary across the globe (Fig. 5). Global trade can increase the availability of food system by-products—and therefore the replacement potential—in some regions, but in this analysis, only intra-region trade was allowed. The replacement potential of food-grade feed use could be further increased by also considering food waste¹⁰ and former foods—that is, foodstuff manufactured for human consumption but not consumed by humans for practical

Table 1 | Replacement potential and increased food supply

Feedstuff	Feed use (million t)	Replacement material	Replacement potential (%)	Increased food supply					
				10 ¹² kcal	Percentage of current supply (%)	10 ¹² g of protein	Percentage of current supply (%)	10 ¹² g of fat	Percentage of current supply (%)
Cereals	894 (742–1060)	Cereal bran, sugar beet pulp, molasses, distiller's grains, citrus pulp	9.8 (9.7–9.8)	376 (307–440)	3.6–5.2	9.70 (7.93–11.4)	3.3–4.7	2.65 (2.16–3.10)	0.9–1.2
Cereals including replacement with crop residues ^a		Cereal bran, sugar beet pulp, molasses, distiller's grains, citrus pulp, crop residues	26 (25–28)	940 (753–1,180)	8.9–13.8	24.3 (19.4–30.4)	8.1–12.6	6.62 (5.30–8.28)	2.1–3.3
Oilseed oils	13.1 (12.2–14.2)	Poultry oil, fish oil from fish by-products	37 (31–42)	45.6 (36.0–56.5)	0.4–0.7	0	0	4.86 (3.83–6.02)	1.5–2.4
Pulses	18.7 (15.0–22.6)	Oilseed meals, livestock by-products, fishmeal from fish by-products	59 (50–88)	48.9 (33.0–87.1)	0.4–1.0	2.61 (1.76–4.64)	0.7–1.9	0.16 (0.11–0.28)	0.0–0.1
Fishmeal from whole fish	3.46 (3.30–3.64)	Livestock by-products, fishmeal from fish by-products	99 (91–100)	61.9 (53.7–70.2)	0.6–0.8	9.08 (7.87–10.3)	3.3–4.3	2.60 (2.25–2.94)	0.9–1.2
Fish oil from whole fish	0.55 (0.50–0.59)	Poultry oil, fish oil from fish by-products	100 (92–100)	48.9 (41.3–56.5)	0.5–0.7	7.17 (6.06–8.29)	2.5–3.4	2.05 (1.73–2.36)	0.7–1.0
Total	930 (772–1103)		12 (11–12)	532 (430–654)	6.2 (5.1–7.7)	21.4 (17.6–26.3)	8.9 (7.3–11.0)	10.3 (8.4–12.3)	4.1 (3.4–5.0)
Total including replacement with crop residues			27 (25–29)	1,100 (875–1,390)	12.9 (10.3–16.3)	35.9 (29.1–45.3)	15.0 (12.1–18.8)	14.2 (11.5–17.5)	5.7 (4.6–7.1)

The values represent the replacement potential with selected food system by-products and residues, given replacement constraints (Supplementary Tables 6–8) and regional availability of by-products and residues (Methods). The median, 5th percentile and 95th percentile values of the uncertainty range are presented. Two replacement scenarios for cereals were considered: (1) cereals replaced with by-products that do not have an impact on livestock productivity and (2) cereals replaced also with crop residues considering the reduced productivity (40–80%) in cattle meat and dairy production. Fishmeal and fish oil were converted to whole fish to estimate the increased food supply using the conversion factors 0.2 for fishmeal and 0.04 for fish oil (Methods). Since fishmeal and fish oil can be produced simultaneously from the same fish, the increased food supply from replacing fishmeal and fish oil alternatives is calculated by considering only the one with the higher replacement potential to avoid double-accounting, in this case fishmeal. ^aThis is excluded in the 'Total' computation but is included in 'Total including replacement with crop residues'.

or logistical reasons^{36–39}. Post-consumer food waste can be safe and nutritious for pigs when treated properly⁴⁰, and pre-consumer, plant-based food waste can also be fed to ruminants⁴¹. Replacing food-competing feedstuff with food waste could save up to 8.8 million tons of human-edible grains in the European Union⁴², in addition to our estimates of 14.7–18.6 million tons on the replacement potential of cereals with by-products and crop residues in Europe. Moreover, food system by-products not yet considered in this study (such as by-products from dairy or bakery industries) have shown considerable feedstuff potential in case studies with little or no reductions in productivity³⁸. Their replacement potential should therefore be incorporated and assessed in future global studies. Further research is warranted on the replacement potential of food-competing feedstuffs with different by-products and residues in animal nutrition.

Despite the high potential, the prospects of replacing part of food-competing feedstuffs with food system by-products and residues are faced by various challenges. For example, the production of alternative feeds can be limited by the availability of by-products and residues or by existing regulations, such as bans on intra-species feed recycling in farmed animal production in the European Union^{43–45}. Nutritional aspects can also limit the potential. Some by-products

are of lower nutritional quality and can contain antinutritive compounds or high amounts of fibre that can lead to decreased animal production, especially in monogastric animals^{46,47}. This is particularly the case with crop residues, which show the highest potential availability (Fig. 4). Replacing high-quality feeds with alternative biomass materials could result in lower livestock and aquaculture productivity or reduced nutritional content (for example, fatty acid composition) of the commodities produced^{48,49}. Raising livestock or fish species that can consume lower-quality feeds (such as crop residues) can increase the feed use potential of these by-products and residues^{10,50}. If the use of lower-quality feeds is considered beneficial from a larger circular systems perspective—for example, supported by policy incentives—reductions in productivity could be acceptable to producers. Furthermore, processing by-products through, for example, fermentation or other chemical treatments or additives can improve their nutritional value^{18,51–53}. Yet, as shown in the different feed experiment studies reviewed here (Supplementary Tables 7 and 8), crop processing and animal by-products are of particularly valuable nutritional quality, and they can replace food-grade feed use while maintaining productivity (Supplementary Table 8)^{37,39}. Especially in cattle nutrition, it is possible to formulate diets entirely based on non-food-competing feedstuffs even at very high animal

production levels²⁰. Furthermore, many by-products (especially those generated in livestock and fish processing) have high water content and are highly perishable, or their production is seasonal (as is also the case with crop residues). Hence, they require proper infrastructure and know-how for stabilization, collecting, transportation, storage and processing⁴⁷, which are currently not in place.

When increasing the feed use of food system by-products and residues, it is important to consider the impact of reduced raw materials available for other competitive uses, such as bioenergy, pharmaceuticals and fertilizer production. Yet, even when applying the maximum replacement potential shown in this study, much of crop residues and fish and livestock by-products would remain available for other uses (Fig. 3). The issue of competitive uses is therefore more critical for other by-product groups, such as crop processing by-products. It can be argued, however, that food production should be prioritized over other uses of these biomass flows, as the other uses can typically utilize multiple alternative materials, whereas food can be produced only within food systems^{13,54}. Furthermore, if aiming to totally decouple animal production from arable land use and consequently limit the production of by-products only to food production, the availability of feed-use-driven by-products such as soybean meals would be considerably lower. The complexity in utilizing food system by-products highlights that a broad systems perspective is required⁵⁵, complemented by further research to fully understand the replacement potential, practical challenges and trade-offs related to realizing this potential.

Increasing the human consumption of food-grade feedstuff also presents challenges. First, not all feed cereals meet the food quality standards set by manufacturers or government agencies, and changing from feed crop production to food crop production might require additional inputs, such as increased fertilization. Second, consumer preferences such as cultural and taste aspects need to be considered. For example, whole fish used in fishmeal and fish oil industries (that is, forage fish) consists mainly of bony and small pelagic fish species, other low-value by-catch fish or juvenile individuals. These are often not preferred for direct human consumption, and they might require processing and preserving (for example, in canned, cured or dried form) for wider acceptance and uses in human diets³⁶. However, these small fish are often low-cost and highly nutritious, and they can serve as valuable dietary additions, especially in regions where more expensive fish products are not accessible for many people⁵⁷.

The data in this study were gathered from various sources, databases, reports and models, each of which contain limitations of their own. An uncertainty analysis was performed for the estimation of livestock and aquaculture feed use, as well as for the potential availability of different by-products (Methods). Despite the uncertainties involved, our estimates for livestock and aquaculture feed use and the availability of by-products are in accordance with previous studies (see the comparison in the Supplementary Information). While our study provides preliminary quantifications, a wider range of by-products and their replacement potential should be assessed in future studies, also including a more comprehensive trade model. Specifically, some food-competing feedstuff categories excluded in this study, such as roots and tubers, might present additional replacement opportunities. Moreover, estimating the replacement potential constraints in animal nutrition is challenging since animal nutritional needs differ in different growth stages and production levels. The estimates used in this study were based on feed experiment studies that consider each replacement material individually (Methods). In practice, animal diets would probably be designed to include several different replacement materials simultaneously (for example, brans, sugar beet pulp and oilseed meals). Their combined effect would, however, need more careful consideration, as it could affect the nutritional value and palatability of the final product or animal health. On the basis of these limitations, our results should

be considered as the theoretical potential of a biophysical change. These findings should be combined with more local-level studies on the practical replacement potential, which also accounts for social and economic factors.

More efficient use of food system by-products and residues can reduce food–feed competition and increase the global food supply without increasing the use of valuable natural resources. This, in combination with other measures, is an urgently needed action in the transition towards more sustainable and circular food systems, which are prominent objectives in many national and European Union–level strategies^{58,59}. However, harnessing the untapped potential of food system by-products and residues would require a paradigm shift that puts more value on the efficient use of materials and the capacity of the livestock and aquaculture sectors to circulate non-food-grade biomass back to food systems through feed use. Policy interventions and regulation would be needed in managing the feed resources and to provide incentives for feed industries to develop and innovate solutions for increased use of the materials least used as feed, as highlighted by this study.

Methods

The material flows of feed use and the production of by-products and residues in the global food system were mapped to understand the links and dependencies between the three subsectors of crop, livestock and aquaculture production. The analysis consisted of four main steps (Fig. 1). First, we quantified the global food system flows, including the national levels of feed use in both the livestock and aquaculture sectors and the potential production of by-products. Second, the regional availability of by-products and residues was analysed by subtracting the quantities used as feed from the potential production. Third, using existing literature on feed experiments, we considered how much of the food-competing feedstuff can be replaced with food system by-products, considering the nutritional requirements of the production animals as well as regulations. Fourth, the replacement potential was analysed, combining the regional availability of the by-products and residues with the nutritional requirements. Finally, the potential increase in the global food supply was calculated, assuming that all feedstuffs freed by this replacement were redirected to human consumption. The analysis was performed for a three-year average of 2016–2018.

Here the focus was on replacing human-edible feed use, including cereals, oilseed oils, pulses, sugar crops and whole fish used in producing fish oil and fishmeal, with by-products and residues. Although some of the feedstuffs in these categories are produced with varieties classified as not suitable for human food (for example, fodder maize), and not all of them meet the quality criteria for food use, we allocated them to the food-competing feedstuff category since they are produced on arable land that can instead be used for the production of varieties suitable for human consumption. Also, other forage feeds (for example, alfalfa or grass hay) may compete with food production when produced on arable land, but unlike fodder maize, they are less demanding and are often produced in marginal lands^{60,61}; therefore, they were not treated as food-competing feedstuff in this study. All feed use of oilseeds was converted into meals/cakes and oils. While some unprocessed oilseeds (for example, soybeans) are consumed by humans, here only the oil fraction was considered human edible. The economic importance of different oilseed meals varies greatly, and especially with soybean, the meal fraction constitutes a major part of the production value. Here we still aggregate all oilseed meals as by-products from the food system perspective, as they are fractions of food crops but require the animal sector to return to the human food supply. Roughages, crop residues and crop processing by-products (such as oilseed meals and cereal bran) were not considered food-competing (Supplementary Table 4). Although some of them (for example, brans) can also be used as food, they are considered co-products of primary food commodities (for example, flour); therefore, they were not considered to be in direct competition with food use.

Feed use material flows. For the total feed use in livestock production, we first multiplied the yearly national cattle (meat and dairy), poultry (meat and eggs) and pork (meat) production from the statistics from the Food and Agriculture Organization of the United Nations (FAO)² by the ratios of different production systems from FAO GLEAM²¹. The production numbers were multiplied by the regional feed conversion ratios (FCRs) (kg dry matter feed per kg output), combining the FCRs from three global studies: Mekonnen and Hoekstra⁶² (all commodities), Mottet et al.³ (all commodities) and Herrero et al.²³ (only for cattle). The FCR values reported as dry matter feed use per protein content were converted into dry matter feed use per product by applying data on protein content of the different end products from ref. ⁶³. These sources, although being the most up-to-date ones covering all world regions, are limited and include uncertainties (for example, due to the lack of data). In this study, the FCRs for the years 2000 (refs. ^{23,62}) and 2010 (ref. ¹) were applied. It is very likely that the FCRs

have improved since, with more efficient production systems. At the same time, the development of livestock FCRs in the past decade has been rather minor; for example, the FCRs for finishing pigs in the European Union improved by only 1% between 2013 and 2019 (refs. ^{64,65}). Nevertheless, updated and more precise FCRs, particularly for low-income countries—where the development might be faster and collecting data can be challenging—could yield somewhat different results. There is therefore a need for studies that work with the uncertainties related to the data applied and address potential changes in feed use material flows owing to production systems' development. The country- and species-specific feed use was multiplied by the ratio of different feedstuffs from ref. ²¹. These feed use data are presented for different production systems for ten world regions, including the feed use of both non-food-competing feedstuff (such as roughages and by-products) and the feed use of food-competing feedstuff (such as cereals and other food crops) for the different livestock species. This procedure resulted in higher estimates of total fishmeal use in poultry and pig production compared with the official data reported in ref. ⁶⁶ and was thus corrected by applying the fishmeal inclusion rates for pig and poultry from ref. ²⁶. In addition, the aggregated feed use category of grains in ruminant feed was divided into individual commodities (maize, wheat and barley) on the basis of global feed use ratios of these materials.

For the total feed use in aquaculture, for both commercial and farm-made feeds, we multiplied the production of each fed aquaculture production group (carps, tilapias, catfishes, other freshwater fishes, salmon, trouts, milkfish, eels, other marine fishes, shrimps and other freshwater crustaceans) by their respective FCRs. The FCRs for commercial feeds were derived from ref. ²⁵, and the FCRs for farm-made feeds were assumed to be 50% higher than those for commercial ones on the basis of ref. ⁶⁷. Diet compositions for the major fed aquaculture groups were taken from country-specific survey data from ref. ³¹ and extrapolated to country-level diets according to ref. ³². The diet composition data were provided in ranges of inclusion for each ingredient (minimum, maximum and average), and to estimate a diet composition that sums to 100%, the proportion of each ingredient for the average diet composition was used to scale the diet to it, as explained in more detail in the Supplementary Information. The amounts of fishmeal and fish oil produced from by-products of fish processing were estimated to be 25–35% of the total quantities produced³.

The livestock and aquaculture feed data were combined, the different feed categories were unified and the totals were validated and harmonized with the estimates of global feed use from FAO Supply and Utilization Accounts² for the years 2016–2018 for the feed groups for which the data were available (cereals, pulses, vegetable oils and molasses). Comparisons between our feed use estimates and published data are available in the Supplementary Information.

Availability of by-products and residues. To estimate the availability of food system by-products and residues, we first estimated their global production and subtracted current feed use from the totals. We then assigned the available by-products to countries on the basis of their share of global production of each feedstuff. Four categories of food system by-products were considered: (1) crop residues; (2) cereal, sugar, citrus fruit and oilseed processing by-products; (3) livestock by-products; and (4) fish by-products processed into fishmeal and fish oil. The focus was on the by-products of primary crop and animal production and crop processing by-products already used as feed in important quantities at the global scale; therefore, food waste from retail or consumption, for example, was not considered here.

To estimate the potential availability of crop residues, the yearly crop production³ was multiplied by crop-specific residues-to-production ratios from ref. ⁶⁸ and S. Wirsenius et al. (manuscript in preparation). Here we considered only crop residues from cereals, rice, sugar cane and pulses that are most used as feedstuff^{7,69}. Crop residues left on fields have an important impact on soil fertilization and moisture retention²⁸. We therefore accounted for the crop residues that will be left on fields by multiplying the crop production by the ratios of maximum sustainable harvest, ranging from 0% to 50% (refs. ^{28,70}).

Crop processing by-products are the co-products that result from a multifunctional process that is driven by the demand of the main product. The by-products considered in this study included cereal bran, distiller's grains from biofuel and brewing industries, sugar beet pulp, sugarcane and sugar beet molasses, citrus pulp, and oilseed meals. The average quantities of cereal bran and molasses produced between 2016 and 2018 were adopted from FAO Supply and Utilization Accounts². The amounts of distiller's grains from corn ethanol production were applied from ref. ⁷¹ for the four highest-production countries, covering 97% of the global corn ethanol production. Brewer's grains from beer brewing were estimated assuming that 21–22 kg of spent grains are produced per hectolitre of brewed beer⁷² and multiplying the country-level barley beer production³ by this conversion factor. The amounts of sugar beet pulp and oilseed meals were calculated from the average amounts of sugar beet and oilseeds processed between 2016 and 2018 (ref. ²) and multiplied by the conversion factors⁷³ reducing the amounts of waste created in the processing stage⁷⁴. The production of citrus pulp was estimated by multiplying the amounts of citrus fruits (lemons and limes, oranges, tangerines, mandarins, clementines and satsumas) processed²¹ by the conversion factor⁷³ and subtracting waste and losses from processing⁷⁴.

To estimate the potential availability of livestock by-products, we first converted the production quantities of end products (cattle, pig and poultry meat)² to live weight using dressing percentages²¹ and then multiplied those by the ratios of the processed by-products (poultry by-product meal, poultry oil, blood meal, hydrolysed feather meal, meat meal from pork meat production and poultry oil)³³. To estimate the poultry by-products from egg production, the amounts of slaughtered hen were calculated. This was estimated by dividing the numbers of laying hens² by the average age at slaughtering and multiplying by their average weight at the end of the laying period²¹. Here the meat from laying hens was not assumed to be consumed by humans.

To estimate the availability of by-products from fish production, we first gathered the aquaculture production and capture fisheries data from FishStatJ³⁰. The fisheries production was multiplied by the average ratios of human consumption and non-food use from refs. ^{75,76}, which presented the average ratios for developed and developing countries separately. The data were corrected for certain captured fish species for which the literature indicates a higher ratio going to non-food use^{77,78}. The amounts of fish destined for non-food uses were then multiplied by the ratios going to reduction (that is, fishmeal and fish oil production) and the ratios of fish fed directly to aquaculture^{75,76}. The amounts of potential fish by-products were estimated by multiplying the amounts of fish for human consumption from capture fisheries and aquaculture by the ratios processed^{75,76} and multiplying the processed quantities by the average ratio of 41.5% of fish consisting of by-products (such as trimmings)⁷⁹, subtracting 2% blood that is not used in reduction and finally assuming 2% losses at the primary fish processing stage⁷⁸. The share of by-products in fish varies among different fish species and even among the same species. The value applied in this study (41.5%) was estimated for salmon⁷⁹ and is probably a conservative estimate for most other fish species. However, it was applied here as a proxy, to avoid an overly optimistic estimation of fish by-product availability. To account for the uncertainty inherent in applying these conversion factors, we performed a sensitivity analysis (see below). The amounts of fishmeal and fish oil that could be produced from these by-products were then estimated by using the conversion ratios of 0.2 for fishmeal and 0.04 for fish oil, values a bit lower than the conversion ratios for fishmeal and fish oil from whole fish⁷⁷. Comparisons between our estimates and assessments from previous studies of food system by-product availability are available in the Supplementary Information. The production of by-products was converted to dry matter using the dry matter contents of the different feedstuffs^{22,80,81}.

Replacement constraints. The replacement constraints estimating the share of by-products that can replace food-competing feedstuff in animal feed were derived from feed experiment studies, assuming no reductions in productivity. The only exception for this was the replacement of cereals with crop residues in cattle feeds, which reduced productivity by 40–80%. This reduced productivity was taken into account later when estimating the increased food supply.

Fishmeal and fish oil are included in livestock feeds and aquafeeds because of their protein content, favourable amino acid and fatty acid profiles, effects on growth and the immune system, and high digestibility⁸². However, they are not essential to pig and poultry, and here we assumed that 75–100% of the fishmeal in pig and poultry feeds is replaceable with oilseed meals, fishmeal made from fish by-products or livestock by-products of non-ruminant origin (blood meal and hydrolysed feather meal) without negatively impacting their productivity^{83,84} (Supplementary Table 7).

On the basis of previous alternative feed experiments for various fish species, 27–79% of the fishmeal (dry matter) and 51–79% of the fish oil in aquafeeds can be replaced with processed by-products from livestock production (Supplementary Table 7). Fishmeal and fish oil made from fish by-products differ from those produced from whole fish as they on average contain less protein and have a higher ash content⁸⁵. Despite this, they provide essential fatty acids and have been successfully applied in aquafeeds⁸⁵. Here we assume that they are viable alternatives and can replace 75–100% of the fishmeal and fish oil made from whole fish in aquafeeds. Distiller's grains have also been applied in aquafeeds, but they require further processing to remove fibre and increase their protein content to be viable alternatives for fishmeal⁸⁶; therefore, they were not included as fishmeal replacement for fish feed in this study.

Crop processing by-products, including cereal by-products (brans and distiller's grains), citrus pulp and sugar by-products (sugar beet pulp and molasses), were considered here as potential replacements for cereal use, and oilseed meals as potential replacements for pulse use in livestock feed. Cereal by-products such as bran have been applied in pig feeding (Supplementary Table 8). They typically contain less starch and more fibre than whole cereals, due to endosperm removal during processing⁸⁷. Although the high fibre content of these feedstuffs can produce satiety and have beneficial impacts on gut health in pig production, their inclusion is sometimes limited because of the reduced digestibility of dietary energy and protein, which can reduce the overall production performance⁸⁸, including also environmental performance (e.g. waste and overall greenhouse gas emissions). Sugar beet pulp contains readily digestible fibre such as pectin, has a low lignin concentration and thus has a high energy value for ruminant nutrition⁸⁹, making it a well-suited substitute for cereals²⁰. The nutritive value of sugar beet pulp can be further improved with added molasses⁸⁹. Crop residues

(straws and leaves) that are high in fibre can replace part of the cereals used in ruminant feeding, but with negative impacts on productivity (Supplementary Tables 6 and 8). They are better suited for replacing conventional roughage, such as grass silage, in ruminant diets. However, the potential use of crop residues for monogastric animals such as pigs and poultry is much lower due to the limited ability of monogastrics to digest feedstuffs with high fibre concentrations and low digestibility⁹⁰ (Supplementary Table 6). Oilseed meals and cakes (derived from soy and rapeseed, for example) are high-quality protein feeds with balanced amino acid composition and high nutrient digestibility for livestock⁸⁰. The animal production responses of oilseed meals and cakes are typically superior or less often equal to those of pulses (for example, faba bean, pea, lupin and lentils) in diets of lactating dairy cows^{90–92}, pigs^{90,93} and poultry^{94,95}. The use of oilseed meals and cakes as protein feed in livestock diets is currently the prevailing practice, whereas pulses are considered as the alternative. The substitution rates of pulses with rapeseed meal and cake and soybean meal were 100% on all livestock diets according to our literature review (Supplementary Table 8). However, as literature about substitution rates of pulses with other oilseed by-products was lacking, the substitution rate of all oilseed by-products was assumed to be 75–100%, taking into account possible differences in nutritive value. For ruminants, only the mixed and feedlot production systems²¹ that contained cereals in their feed were considered in the replacement, since the ruminant diets in grazing systems are mainly based on forages and typically contain no or only low amounts of cereal-based concentrates.

Legislation and regulation also constrain the use of livestock by-products as feed. A comprehensive review of animal by-product regulations in all countries was out of scope for this study, so to follow a precautionary approach and avoid overly optimistic by-product availability estimates, we applied the European Union regulations globally, since they can be considered among the strictest ones. Feeding farmed animals on materials originating from the same species is forbidden^{43–45}; in addition, the use of processed by-products from bovine animals is banned in livestock or aquaculture feed to avoid the spread of transmissible diseases^{43,44}. The safety issues regarding the feed use of by-products of ruminant origin are also acknowledged in US regulations⁹⁶ as well as the more broad feed use recommendations by the FAO⁹⁷. Livestock by-products of bovine origin were therefore not considered as feed replacements in this study. However, livestock-derived protein of non-ruminant origin (meat and bone meal, blood meal, hydrolysed feather meal and poultry meal assessed in this study) is allowed for pig, poultry and aquaculture feeds, considering the intra-species recycling ban⁴⁵.

Replacement potential. The replacement potential of cereals, fishmeal and fish oil with food system by-products and residues was estimated by considering (1) the potential availability of the replacement materials within the 19 world regions (see Supplementary Table 5 for the division of countries into subregions) and (2) the replacement constraints including the nutritional requirements of livestock and aquaculture as well as the regulation of the use of different animal-derived by-products and residues in livestock and aquaculture feeds (Supplementary Tables 6–8). Environmental performance was, however, not considered.

First, the feed use of each of the food-competing feedstuffs selected was multiplied by the replacement constraints to estimate the maximum and minimum replacement potentials for each animal production group and replacement material individually. Second, the maximum and minimum replacement potentials were corrected with the availability of the selected replacement material in the region. Third, the combined replacement potential of the different replacement materials for one animal production group was estimated by summing the individual replacement potentials and normalizing them to avoid exceeding the total feed use of the animal production group in a region. Finally, the combined potential of the different replacement materials and animal production groups were summed to derive the total replacement potential (see Supplementary Section 3 for a more detailed description of the method).

The increased food supply was estimated by multiplying the replaced food-competing feedstuff amounts by their energy (kcal), protein and fat contents^{63,80,81}. Since fishmeal and fish oil can be produced simultaneously from the same fish, the increased food supply from replacing fishmeal and fish oil alternatives was not summed to avoid double-accounting; instead, only the one with the higher replacement potential was considered.

For the replacement of cereals in feed use, two cases were estimated: one applying only the replacement materials (cereal bran, sugar beet pulp, molasses, distiller's grains and citrus pulp) and constraints with no estimated impact on productivity (Supplementary Table 6) and a second case adding crop residues as a potential replacement material in addition to the first case. In the latter case, the replacement with crop residues implies a 40–80% decrease in cattle meat and dairy production (Supplementary Table 6), which was then calculated with a simplified approach assuming that the reduced production would be proportional to the share of feed replaced and subtracted from the estimated increase in the food supply.

Since the selected by-products are typically low-value commodities, inter-regional trade of by-products and residues was excluded, but materials were assumed to be freely traded within each region. Oilseed meals and fishmeal are exceptions, being highly traded and valued products in the global feed markets. Here, as we did not account for inter-regional trade, the feed use of these highly

traded commodities exceeds the potential production for some regions. In those regions, the replacement potential is assumed to be zero for the by-products with negative availability.

Uncertainty analysis. To assess the combined uncertainties related to the estimation of livestock and aquaculture feed use and the production of food system by-products, we performed Monte Carlo simulations for the input data. First, we searched the literature to find the most suitable ranges for each of the input parameters and variables. We then used these ranges in Monte Carlo simulations ($n = 500$) to perform an uncertainty analysis.

For the analysis, we generated 500 values of potential livestock and aquaculture feed use on the basis of a truncated normal distribution. We used the minimum, maximum and mean values and the standard deviation of the reported FCRs from the literature (described in the 'Feed use material flows' section) to derive the truncated normal distributions for the different production systems and regions.

Next, we followed a similar approach to derive the uncertainty intervals for the availability of by-products and residues. Five hundred randomly sampled values were taken from uniform distributions of different conversion factors with a coefficient of variation (CV) of 0.1. This CV was chosen because it represents the variation in the FAO technical conversion factors⁷³ for many of the crop processing by-products. Due to the lack of more detailed data, the same distribution and CV were assumed to also represent the uncertainty in the availability of crop residues and livestock by-products. Finally, we applied the range for replacement potentials identified in the literature (Supplementary Table 6) and generated 500 values of potential replacement constraints on the basis of a uniform distribution to estimate the uncertainty related to the replacement potential (Supplementary Information).

Data availability

All the data used in this study are publicly available; see the Supplementary Data and Methods for descriptions of the source data.

Code availability

The analysis was performed using RStudio (R version 4.0.5)⁹⁸. The code is available at <https://github.com/vcsandstrom/byprod>.

Received: 18 October 2021; Accepted: 10 August 2022;
Published online: 19 September 2022

References

- Mottet, A. et al. Livestock: on our plates or eating at our table? A new analysis of the feed/food debate. *Glob. Food Sec.* **14**, 1–8 (2017).
- Food and Agriculture Data Statistics (FAOSTAT)* (FAO, 2022).
- The State of World Fisheries and Aquaculture: Sustainability in Action* (FAO, 2020).
- Bowles, N., Alexander, S. & Hadjikakou, M. The livestock sector and planetary boundaries: a 'limits to growth' perspective with dietary implications. *Ecol. Econ.* **160**, 128–136 (2019).
- Foley, J. A. et al. Solutions for a cultivated planet. *Nature* **478**, 337–342 (2011).
- Godfray, H. C. J. et al. Food security: the challenge of feeding 9 billion people. *Science* **327**, 812–818 (2010).
- Van Kernebeek, H. R., Oosting, S. J., Van Ittersum, M. K., Bikker, P. & De Boer, I. J. Saving land to feed a growing population: consequences for consumption of crop and livestock products. *Int. J. Life Cycle Assess.* **21**, 677–687 (2016).
- Schader, C. et al. Impacts of feeding less food-competing feedstuffs to livestock on global food system sustainability. *R. Soc. Interface* **12**, 20150891 (2015).
- Röös, E. et al. Greedy or needy? Land use and climate impacts of food in 2050 under different livestock futures. *Glob. Environ. Change* **47**, 1–12 (2017).
- van Hal, O. et al. Upcycling food leftovers and grass resources through livestock: impact of livestock system and productivity. *J. Clean. Prod.* **219**, 485–496 (2019).
- Van Zanten, H. H. E. et al. Defining a land boundary for sustainable livestock consumption. *Glob. Change Biol.* **24**, 4185–4194 (2018).
- Billen, G. et al. Reshaping the European agro-food system and closing its nitrogen cycle: the potential of combining dietary change, agroecology, and circularity. *One Earth* **4**, 839–850 (2021).
- Van Zanten, H. H., Van Ittersum, M. K. & De Boer, I. J. The role of farm animals in a circular food system. *Glob. Food Sec.* **21**, 18–22 (2019).
- Van Kernebeek, H. R. J., Oosting, S. J., Van Ittersum, M. K., Ripoll-Bosch, R. & De Boer, I. J. M. Closing the phosphorus cycle in a food system: insights from a modelling exercise. *Animal* **12**, 1755–1765 (2018).
- Van Selm, B. et al. Circularity in animal production requires a change in the EAT–Lancet diet in Europe. *Nat. Food* **3**, 66–73 (2022).
- Govoni, C. et al. Global assessment of natural resources for chicken production. *Adv. Water Res.* **154**, 103987 (2021).

17. Devendra, C. & Sevilla, C. C. Availability and use of feed resources in crop–animal systems in Asia. *Agric. Syst.* **71**, 59–73 (2002).
18. Luciano, A., Espinosa, C. D., Pinotti, L. & Stein, H. H. Standardized total tract digestibility of phosphorus in bakery meal fed to pigs and effects of bakery meal on growth performance of weanling pigs. *Anim. Feed Sci. Technol.* **284**, 115148 (2021).
19. Ertl, P., Zebeli, Q., Zollitsch, W. & Knaus, W. Feeding of by-products completely replaced cereals and pulses in dairy cows and enhanced edible feed conversion ratio. *J. Dairy Sci.* **98**, 1225–1233 (2015).
20. Karlsson, J., Spörndly, R., Lindberg, M. & Holtenius, K. Replacing human-edible feed ingredients with by-products increases net food production efficiency in dairy cows. *J. Dairy Sci.* **101**, 7146–7155 (2018).
21. *Global Livestock Environmental Assessment Model Version 2.0* (FAO, 2017).
22. Wirseni, S. *Human Use of Land and Organic Materials: Modeling the Turnover of Biomass in the Global Food System* (Chalmers Univ. of Technology, 2000).
23. Herrero, M. et al. Biomass use, production, feed efficiencies, and greenhouse gas emissions from global livestock systems. *Proc. Natl Acad. Sci. USA* **110**, 20888–20893 (2013).
24. Tacon, A. G. J. & Hasan, M. R. *Feed Ingredients and Fertilizers for Farmed Aquatic Animals: Sources and Composition* (FAO, 2009).
25. Tacon, A. G. J. & Metian, M. Feed matters: satisfying the feed demand of aquaculture. *Rev. Fish. Sci. Aquac.* **23**, 1–10 (2015).
26. Froehlich, H. E., Runge, C. A., Gentry, R. R., Gaines, S. D. & Halpern, B. S. Comparative terrestrial feed and land use of an aquaculture-dominant world. *Proc. Natl Acad. Sci. USA* **115**, 5295–5300 (2018).
27. Karlsson, J. O. & Rööös, E. Resource-efficient use of land and animals—environmental impacts of food systems based on organic cropping and avoided food–feed competition. *Land Use Policy* **85**, 63–72 (2019).
28. Scarlet, N., Martinov, M. & Dallemard, J. F. Assessment of the availability of agricultural crop residues in the European Union: potential and limitations for bioenergy use. *Waste Manage. (Oxf.)* **30**, 1889–1897 (2010).
29. Karlsson, J. et al. *Future Nordic Diets: Exploring Ways for Sustainably Feeding the Nordics* Vol. 2017566 (Nordic Council of Ministers, 2017).
30. FishStatJ—Software for Fishery and Aquaculture Statistical Time Series, version 3.04.12. (FAO Fisheries and Aquaculture Department, 2020).
31. Tacon, A. G. J., Hasan, M. R. & Metian, M. *Demand and Supply of Feed Ingredients for Farmed Fish and Crustaceans: Trends and Prospects* FAO Fisheries and Aquaculture Technical Paper No. 564 (FAO, 2011).
32. Troell, M. et al. Does aquaculture add resilience to the global food system? *Proc. Natl Acad. Sci. USA* **111**, 13257–13263 (2014).
33. van Hal, O. *Upcycling Biomass in a Circular Food System: The Role of Livestock and Fish* (Wageningen Univ., 2020).
34. Monteiro, M., Matos, E., Ramos, R., Campos, I. & Valente, L. M. P. A blend of land animal fats can replace up to 75% fish oil without affecting growth and nutrient utilization of European seabass. *Aquaculture* **487**, 22–31 (2018).
35. Kumm, M. et al. Lost food, wasted resources: global food supply chain losses and their impacts on freshwater, cropland, and fertiliser use. *Sci. Total Environ.* **438**, 477–489 (2012).
36. Pinotti, L., Giromini, C., Ottoboni, M., Tretola, M. & Marchis, D. Review: insects and former foodstuffs for upgrading food waste biomasses/streams to feed ingredients for farm animals. *Animal* **13**, 1365–1375 (2019).
37. Pinotti, L. et al. Recycling food leftovers in feed as opportunity to increase the sustainability of livestock production. *J. Clean. Prod.* **294**, 126290 (2021).
38. Liu, Y., Jha, R., Stein, H. H. & North Central Coordinating Committee on Swine Nutrition (NCCC-42). Nutritional composition, gross energy concentration, and in vitro digestibility of dry matter in 46 sources of bakery meals. *J. Anim. Sci.* **96**, 4685–4692 (2018).
39. Giromini, C. et al. Nutritional evaluation of former food products (ex-food) intended for pig nutrition. *Food Addit. Contam. A* **34**, 1436–1445 (2017).
40. Shurson, G. C., Urriola, P. E. & Ligt, J. L. Can we effectively manage parasites, prions, and pathogens in the global feed industry to achieve One Health? *Transbound. Emerg. Dis.* **69**, 4–30 (2022).
41. Dou, Z., Galligan, D. & Shurson, G. Food waste as untapped resources for climate mitigation. In *The Role of Agricultural Science and Technology in Climate 21 Project Implementation*, pp. 14–17 (Council for Agricultural Science and Technology, 2021).
42. Zu Ermgassen, E. K., Phalan, B., Green, R. E. & Balmford, A. Reducing the land use of EU pork production: where there's will, there's a way. *Food Policy* **58**, 35–48 (2016).
43. *EC 1069/2009 Commission Regulation (EC) No. 1069/2009 of the European Parliament and of the Council Laying Down Health Rules as Regards Animal By-products and Derived Products Not Intended for Human Consumption and Repealing Regulation (EC) No. 1774/2002 (Animal By-products Regulation)* (European Commission, 2009).
44. *EC 142/2011 Commission Regulation (EU) No. 142/2011 Implementing Regulation (EC) No. 1069/2009 of the European Parliament and of the Council Laying Down Health Rules as Regards Animal By-products and Derived Products Not Intended for Human Consumption and Implementing Council Directive 97/78/EC as Regards Certain Samples and Items Exempt from Veterinary Checks at the Border under That Directive* (European Commission, 2011).
45. *EC 1372/2021 Commission Regulation (EU) 2021/1372 of 17 August 2021 Amending Annex IV to Regulation (EC) No. 999/2001 of the European Parliament and of the Council as Regards the Prohibition to Feed Non-ruminant Farmed Animals, Other Than Fur Animals, with Protein Derived from Animals* (European Commission, 2021).
46. Bindelle, J., Leterme, P. & Buldgen, A. Nutritional and environmental consequences of dietary fibre in pig nutrition: a review. *Biotechnol. Agron. Soc. Environ.* **12**, 69–80 (2008).
47. Colović, D., Rakita, S., Banjac, V., Đuragić, O. & Čabarkapa, I. Plant food by-products as feed: characteristics, possibilities, environmental benefits, and negative sides. *Food Rev. Int.* **35**, 363–389 (2019).
48. Fry, J. P. et al. Environmental health impacts of feeding crops to farmed fish. *Environ. Int.* **91**, 201–214 (2016).
49. Cottrell, R. S., Blanchard, J. L., Halpern, B. S., Metian, M. & Froehlich, H. E. Global adoption of novel aquaculture feeds could substantially reduce forage fish demand by 2030. *Nat. Food* **1**, 301–308 (2020).
50. Zijlstra, R. T. & Beltranena, E. Swine convert co-products from food and biofuel industries into animal protein for food. *Anim. Front.* **3**, 48–53 (2013).
51. Shi, C., Zhang, Y., Lu, Z. & Wang, Y. Solid-state fermentation of corn–soybean meal mixed feed with *Bacillus subtilis* and *Enterococcus faecium* for degrading antinutritional factors and enhancing nutritional value. *J. Anim. Sci. Biotechnol.* **8**, 50 (2017).
52. Dawood, M. A. O. & Koshio, S. Application of fermentation strategy in aquaculture for sustainable aquaculture. *Rev. Aquac.* **12**, 987–1002 (2019).
53. Pires, A. J. V., Carvalho, G. G. P. D. & Ribeiro, L. S. O. Chemical treatment of roughage. *Rev. Bras. Zootec.* **39**, 192–203 (2010).
54. Muscat, A., Olde, E. M., Boer, I. J. & Ripoll-Bosch, R. The battle for biomass: a systematic review of food–feed–fuel competition. *Glob. Food Sec.* **25**, 100330 (2020).
55. Herrero, M. et al. Articulating the effect of food systems innovation on the Sustainable Development Goals. *Lancet Planet. Health* **5**, e50–e62 (2021).
56. Tacon, A. G. J. & Metian, M. Fishing for aquaculture: non-food use of small pelagic forage fish—a global perspective. *Rev. Fish. Sci.* **17**, 305–317 (2009).
57. Cashion, T., Le Manach, F., Zeller, D. & Pauly, D. Most fish destined for fishmeal production are food-grade fish. *Fish Fish.* **18**, 837–844 (2017).
58. *EC COM/2020/98 Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions: A New Circular Economy Action Plan for a Cleaner and More Competitive Europe* (European Commission) (2020).
59. *Government Resolution on the Strategic Programme for Circular Economy* (Ministry of the Environment, Finland, 2021).
60. Mehmood, M. A. et al. Biomass production for bioenergy using marginal lands. *Sustain. Prod. Consum.* **9**, 3–21 (2017).
61. Valentine, J. et al. Food vs. fuel: the use of land for lignocellulosic 'next generation' energy crops that minimize competition with primary food production. *GCB Bioenergy* **4**, 1–19 (2012).
62. Mekonnen, M. M. & Hoekstra, A. Y. A global assessment of the water footprint of farm animal products. *Ecosystems* **15**, 401–415 (2012).
63. *Food Balance Sheets: A Handbook* (FAO, 2001).
64. *Pig Cost of Production in Selected Countries* (ADHB Market Intelligence, 2015).
65. *Pig Cost of Production in Selected Countries* (ADHB Market Intelligence, 2019).
66. Jackson, A. Fish in–fish out ratios explained. *Aquac. Eur.* **34**, 5–10 (2009).
67. *On-Farm Feeding and Feed Management in Aquaculture* (FAO, 2013).
68. García-Condado, S. et al. Assessing lignocellulosic biomass production from crop residues in the European Union: modelling, analysis of the current scenario and drivers of interannual variability. *GCB Bioenergy* **11**, 809–831 (2019).
69. Gertenbach, W. D. & Dugmore, T. J. Crop residues for animal feeding. *S. Afr. J. Anim. Sci.* **5**, 49–51 (2004).
70. Ronzon, T., Piotrowski, S. & Carus, M. *DataM—Biomass Estimates (v3): A New Database to Quantify Biomass Availability in the European Union* (Institute for Prospective and Technological Studies, 2015).
71. Iram, A., Cekmeçelioglu, D. & Demirci, A. Distillers' dried grains with solubles (DDGS) and its potential as fermentation feedstock. *Appl. Microbiol. Biotechnol.* **104**, 6115–6128 (2020).
72. Lynch, K. M., Steffen, E. J. & Arendt, E. K. Brewers' spent grain: a review with an emphasis on food and health. *J. Inst. Brew.* **122**, 553–568 (2016).
73. *Technical Conversion Factors for Agricultural Commodities: Commodity Trees* (FAO, 1996).
74. *Global Food Losses and Food Waste—Extent, Causes and Prevention* (FAO, 2011).
75. *FAO Yearbook: Fishery and Aquaculture Statistics 2008* (FAO, 2010).
76. *FAO Yearbook: Fishery and Aquaculture Statistics 2019* (FAO, 2019).
77. Shepherd, C. J. & Jackson, A. J. Global fishmeal and fish-oil supply: inputs, outputs and markets—global production of fishmeal and fish-oil. *J. Fish Biol.* **83**, 1046–1066 (2013).

78. Cao, L. et al. China's aquaculture and the world's wild fisheries. *Science* **347**, 133–135 (2015).
79. Stevens, J. R., Newton, R. W., Tlustý, M. & Little, D. C. The rise of aquaculture by-products: increasing food production, value, and sustainability through strategic utilisation. *Mar. Policy* **90**, 115–124 (2018).
80. *Animal Feed Resources Information System* (Feedipedia, 2021).
81. *Feedtables* (INRA-CIRAD-AFZ, 2021).
82. Cho, J. H. & Kim, I. H. Fish meal—nutritive value. *J. Anim. Physiol. Anim. Nutr.* **95**, 685–692 (2011).
83. Frempong, N. S., Nortey, T. N., Paulk, C. & Stark, C. R. Evaluating the effect of replacing fish meal in broiler diets with either soybean meal or poultry by-product meal on broiler performance and total feed cost per kilogram of gain. *J. Appl. Poult. Res.* **28**, 912–918 (2019).
84. Zier, C. E., Jones, R. D. & Azain, M. J. Use of pet food-grade poultry by-product meal as an alternate protein source in weanling pig diets. *J. Anim. Sci.* **82**, 3049–3057 (2004).
85. Hua, K. et al. The future of aquatic protein: implications for protein sources in aquaculture diets. *One Earth* **1**, 316–329 (2019).
86. Hardy, R. W. Utilization of plant proteins in fish diets: effects of global demand and supplies of fishmeal. *Aquac. Res.* **41**, 770–776 (2010).
87. Woyengo, T. A., Beltranena, E. & Zijlstra, R. T. Nonruminant nutrition symposium: controlling feed cost by including alternative ingredients into pig diets—a review. *J. Anim. Sci.* **92**, 1293–1305 (2014).
88. Jarrett, S. & Ashworth, C. J. The role of dietary fibre in pig production, with a particular emphasis on reproduction. *J. Anim. Sci. Biotechnol.* **9**, 1–11 (2018).
89. Fadel, J. G., DePeters, E. J. & Arosemena, A. Composition and digestibility of beet pulp with and without molasses and dried using three methods. *Anim. Feed Sci. Technol.* **85**, 121–129 (2000).
90. Puhakka, L., Jaakkola, S., Simpura, I., Kokkonen, T. & Vanhatalo, A. Effects of replacing rapeseed meal with fava bean at 2 concentrate crude protein levels on feed intake, nutrient digestion, and milk production in cows fed grass silage-based diets. *J. Dairy Sci.* **99**, 7993–8006 (2016).
91. Ramin, M., Höjer, A. & Hetta, M. The effects of legume seeds on the lactation performance of dairy cows fed grass silage-based diets. *Agric. Food Sci.* **26**, 129–137 (2017).
92. Lamminen, M., Halmemies-Beauchet-Filleau, A., Kokkonen, T., Vanhatalo, A. & Jaakkola, S. The effect of partial substitution of rapeseed meal and faba beans by *Spirulina platensis* microalgae on milk production, nitrogen utilization, and amino acid metabolism of lactating dairy cows. *J. Dairy Sci.* **102**, 7102–7117 (2019).
93. Degola, L. & D, J. The influence of dietary inclusion of peas, faba bean and lupin as a replacement for soybean meal on pig performance and carcass traits. *Agron. Res.* **16**, 389–397 (2018).
94. Koivunen, E., Tuunainen, P., Valkonen, E., Rossow, L. & Valaja, J. Use of faba beans (*Vicia faba* L.) in diets of laying hens. *Agric. Food Sci.* **23**, 165–172 (2014).
95. Koivunen, E. et al. Digestibility and energy value of pea (*Pisum sativum* L.), faba bean (*Vicia faba* L.) and blue lupin (narrow-leaf) (*Lupinus angustifolius*) seeds in broilers. *Anim. Feed Sci. Technol.* **218**, 120–127 (2016).
96. *Code of Federal Regulations Title 21: Food and Drugs, Chapter I: Food and Drug Administration, Department of Health and Human Services, Subchapter E: Animal Drugs, Feeds and Related Products, Part 589: Substances Prohibited from Use in Animal Food or Feed, Subpart B: Listing of Specific Substances Prohibited from Use in Animal Food or Feed, Sec. 589.2001: Cattle Materials Prohibited in Animal Food or Feed to Prevent Transmission of Bovine Spongiform Encephalopathy* (US Food and Drug Administration, 2020).
97. *Good Practices for the Feed Sector—Implementing the Codex Alimentarius Code of Practice on Good Animal Feeding: FAO Animal Production and Health Manual* (FAO and IFIF, 2020); <https://doi.org/10.4060/cb1761en>
98. R Core Team. R: A Language and Environment for Statistical Computing v.4.0.5 (R Foundation for Statistical Computing, 2021).

Acknowledgements

This study was funded by the European Research Council under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 819202), the Aalto University School of Engineering Doctoral Programme, Maa- ja vesiteknikan tukiry and the project TREFORM funded by the Academy of Finland (grant no. 339834).

Author contributions

V.S., A.C. and M.K. designed the study. V.S. and A.C. gathered the data and performed the analysis with the help of J.P.M.L. reviewed the literature related to livestock feed experiments. M.T. provided the data for the aquafeed calculations. V.S., V.V. and M.K. created the illustrations. All authors discussed the methods and results and helped shape the research and analysis. V.S. and A.C. took the lead in writing the manuscript with important contributions from all authors.

Funding

Open Access funding provided by Aalto University

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s43016-022-00589-6>.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s43016-022-00589-6>.

Correspondence and requests for materials should be addressed to Vilma Sandström or Matti Kumm.

Peer review information *Nature Food* thanks Hannah Van Zanten, Zhengxia Dou and Luciano Pinotti for their contribution to the peer review of this work.

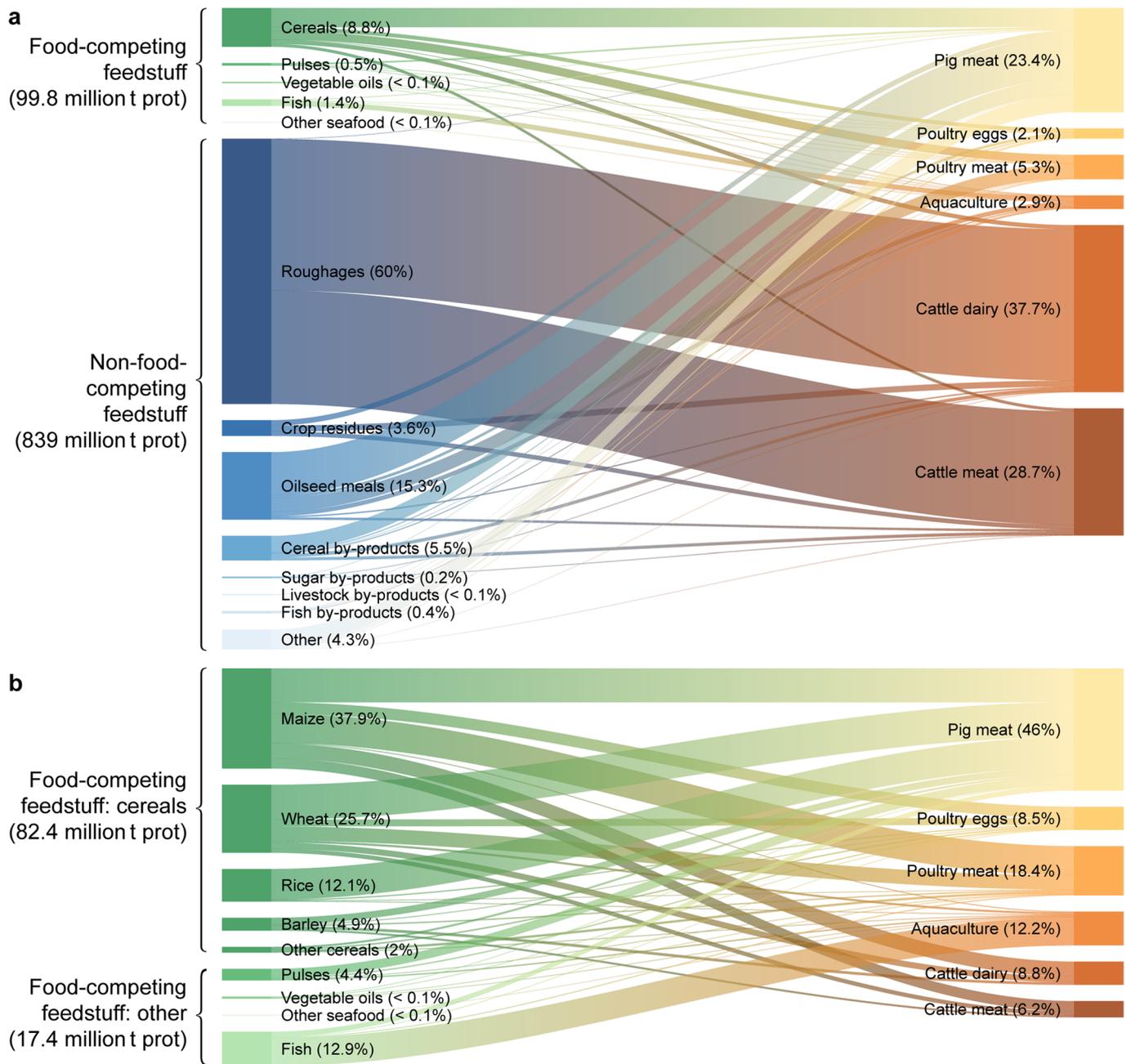
Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2022



Extended Data Fig. 1 | Feed use material flows in the global food system (feed use in tons of protein). (a) all feed flows; (b) flows only for food-competing feedstuff. The percentages refer to the share of the feed use categories (on the left) and the share of the feed use in a specific animal production group (on the right) of the total global feed use. Feedstuff included in each category are described in Supplementary Tables 3 and 4. See data sources used in Methods.