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An optimized crop–livestock system can achieve a safe and just planetary boundary for phosphorus at the sub-basin level in China

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The contribution of crop and livestock production to the exceedance of the planetary boundary for phosphorus (P) in China is still unclear, despite the country's well-known issues with P fertilizer overuse and P-related water pollution. Using coupled models at sub-basin scales we estimate that livestock production increased the consumption of P fertilizer fivefold and exacerbated P losses twofold from 1980 to 2017. At present, China's crop–livestock system is responsible for exceeding what is considered a 'just' threshold for fertilizer P use by 30% (ranging from 17% to 68%) and a 'safe' water quality threshold by 45% (ranging from 31% to 74%) in 25 sub-basins in China. Improving the crop–livestock system will keep all sub-basins within safe water quality and just multigenerational limits for P in 2050.

Phosphorus (P) is an essential element for modern agriculture and is crucial to maintaining a stable ecosystem for humanity[1,2]. The application of P fertilizers has contributed to around 30% of food production in Africa[3], 60% of food production in China[4] and 80% of food production in France[5]. Sufficient application of P fertilizer would double the productivity of smallholder farms and ensure that the Zero Hunger target is achieved in sub-Saharan Africa in 2030[6]. However, losses of P used in agriculture to watercourses in the past few decades have led to severe water quality degradation and exceeded the so-called 'safe' and 'just' operating space, or threshold value for the ecosystem[1,7]. This threshold is also known as the planetary boundary for the biogeochemical cycling of P or the P planetary boundary (PPB)[2,8].

A few studies have reported that the low use efficiency of fertilizer P for crop and feed production has accelerated the unsustainability of P use[9–11] and is responsible for the exceedance of P concentrations in the water; that is, the PPB[7,12,13]. Livestock production has been largely neglected in analyses of the PPB and in strategies to keep the biogeochemical cycle of P within the PPB despite the great increase in livestock populations and rapid changes in production systems seen recently[14]. As a key driving force of the rapidly increasing crop production and use of synthetic P fertilizer, livestock production contributes not only to indirect P losses to watercourses, but also to the direct discharge of manure P to watercourses as a result of poor manure management and loose regulations[14–16]. Given the current importance of livestock production to the safe and just PPB, and the increasing role of livestock production in global food production in the future, it is necessary to fill these knowledge gaps[17,18]. Determining the impacts of livestock production on the safe and just PPB is particularly important at regional and basin scales, where the deterioration of water quality takes place and P losses to watercourse must be managed. Few studies directly

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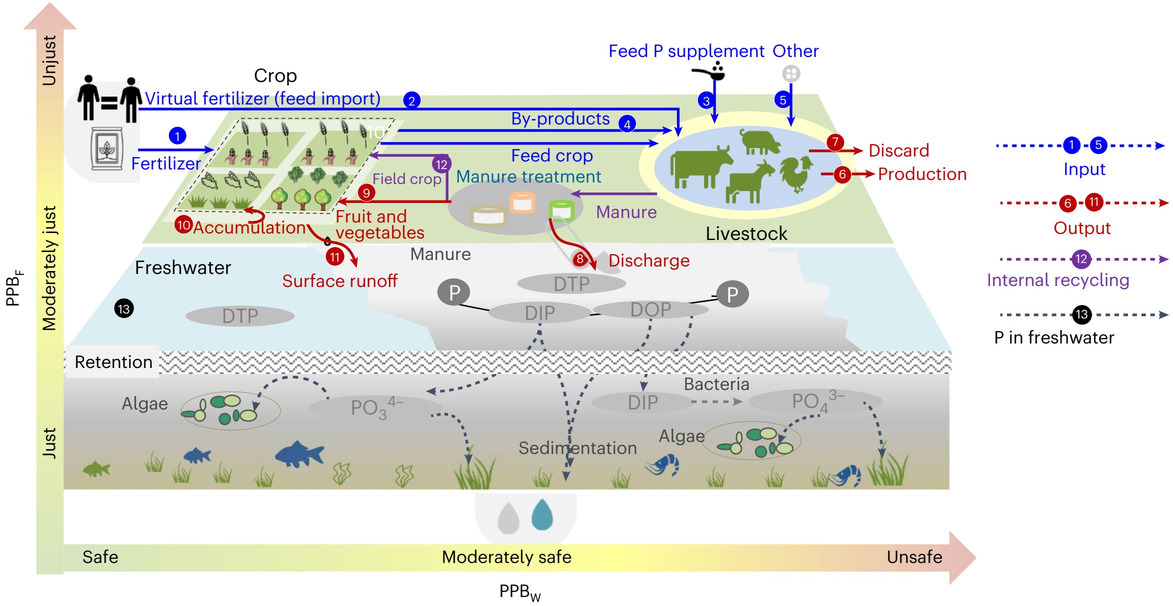

Fig. 1 | Illustration of P flow in the crop–livestock production system and its affect on a safe and just PPB. Black dashed arrows represent the transformation of P in waterbody. See Table 1 for an explanation of the numbers 1–11. DTP, total dissolved P; DIP, dissolved inorganic P; DOP, dissolved organic P; PO_4^{3-}, phosphates.

downscale the PPB to regions or consider justice indicators (such as equal human rights and historical responsibilities)[19–21]. The water-quality-based approach commonly used in previous assessments provides precise environmental limits[22] and recommendations for achieving safe water quality at the local scale[23], but does not fully consider the fairness aspect. Here we design a framework to analyse the effect of China's crop–livestock system on the exceedance of a safe and just PPB at sub-basin scale (Fig. 1). A safe PPB (PPB_W, where W is water quality) was defined as the threshold for P concentrations in surface water from the perspective of safe water available for all, whereas a just PPB (PPB_F, where F is fertilizer use) was defined as equal P fertilizer use per capita under the threshold of total P fertilizer use required to avoid freshwater eutrophication and ocean anoxic events[21].

We use China as an example to systematically quantify the contribution of crop–livestock production to the transgression of the safe and just PPB at a sub-basin scale owing to its overuse of P fertilizer and severe water quality issues. We combined two models—Nutrient flow in Food chains, Environment and Resources use (NUFER) and the Model to Assess River Inputs of Nutrients to seas (MARINA)—to analyse China's crop–livestock production and its impacts on the transgression of the PPB at a sub-basin scale. We explore the differences between the safe and just PPB to generate new insights into P sustainability and planetary boundary research. In addition, we explore ways to find a balance between ensuring a sufficient supply of animal-sourced food and a safe and just PPB in 2050.

Results

Contribution of the livestock transition to P input and losses

P input. The total P input to the crop–livestock production system increased by a factor of 6.3 from around 1,126 Gg P in 1980 to 7,120 Gg P in 2017 (Fig. 2a and Table 1). This increase is relatively large compared with the total synthetic P fertilizer input to the entire crop production system (from 1,208 Gg P in 1980 to 5,262 Gg P in 2017) in China[24]. Extra P inputs, such as synthetic P fertilizers (1,534 Gg P), feed P supplements (mainly dicalcium phosphate, 1,013 Gg P) and imported feed (mainly soybeans, 375 Gg P), contributed 42% of the total P input to the crop–livestock system in 2017 (Fig. 2a,e). A few studies have also reported that extra P inputs accounted for 46% of total P input to livestock production systems in 2010[25,26]. In contrast, the contribution of the extra P inputs in 1980 was 29% of the total P input, two-thirds of that in 2017, which indicates that the crop–livestock system has become increasingly reliant on these extra P inputs during the transition (Fig. 2a,e). This trend is similar to the reliance on extra nitrogen inputs to the crop–livestock production system in China[14].

Virtual P fertilizer use, which refers to the P fertilizer that needs to be consumed for the production of feed for export to China, has also greatly increased (Fig. 2d). A large increase in imported feed P from 1949 to 2018 has also been observed due to the rapid increase in livestock production[27]. This is partly due to the increase in feed imports[28] and partly due to the low efficiency of P use in countries producing soybean (for example, Brazil, where the soil has high P absorption capability)[29]. The remaining P input to the crop–livestock system was through grass, crop residues and by-products of food processing, which require no cropland, are not in competition with food for humans (Fig. 2e) and provide a good example of recycling food waste to support livestock production[30].

P output as product and losses. The total P output as products (such as meat, milk and eggs) increased by a factor of 7.0 from 116 Gg in 1980 to 813 Gg in 2017 (Fig. 2b and Table 1). This increase indicates an improvement in P use efficiency for the entire crop–livestock system due to the greater increase in P output as products than the total P input during the period (Fig. 2a,b). The total P loss of the crop–livestock system to surface water exhibited a different trend from those of the P input and output: the total P loss reached a peak of 2,554 Gg in 2010 then decreased to 1,088 Gg in 2017 (Fig. 2c) due to stricter environmental regulations in China after 2013[15,31]. The recent decline in P losses from livestock production was consistent with the findings of previous studies[27]. Most of the changes in the total P loss were attributed to changes in the direct discharge of manure to watercourses or manure landfill without treatment (Fig. 2f). Detailed information about the changes in the average P budget to produce each unit of P or protein in products and livestock units is illustrated in Extended Data Fig. 1, and the detailed contributions of different livestock categories to P flows are shown in Extended Data Fig. 2.

Contributions of different production systems. Between 1980 and 2017, there were large shifts in the P flows between different crop–livestock systems, namely traditional small-scale mixed crop–livestock systems (mixed), grassland-based grazing systems (grazing) and modern

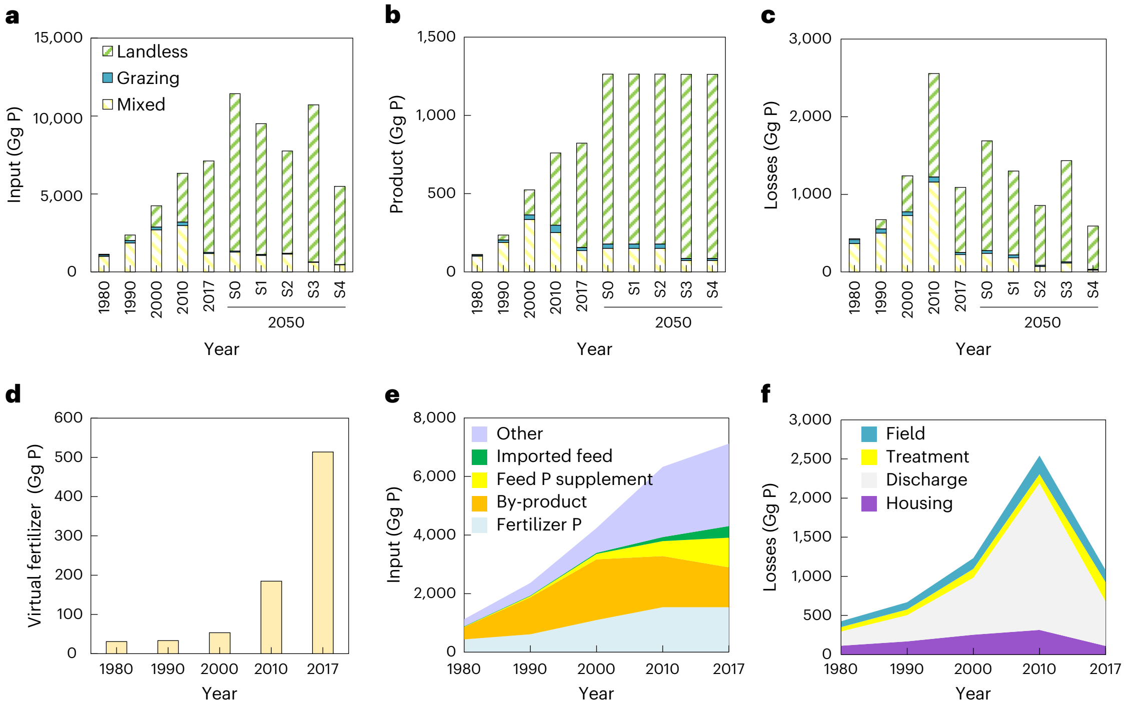

Fig. 2 | Changes in P flows for the crop–livestock system from 1980 to 2017 and scenarios in 2050. a–**c**, P input (**a**), production output (**b**) and losses (**c**) for mixed, grazing and landless livestock production systems. **d**, Virtual P fertilizer input (P fertilizer consumed by countries for the production of feed for export to China). **e**, P input for different sectors. **f**, P loss pathways. Four scenarios for 2050 were considered: S0, business as usual; S1, improved feed P management; S2, improved manure P management; S3, improved herd and structure management; S4, S1–S3 combined.

large-scale landless crop–livestock systems (landless). In contrast to its negligible impact in 1980, the total P input to landless systems increased by a factor of 130 between 1980 and 2017, making it the dominant contributor to the overall P input in 2017 (Fig. 2a). Similarly, landless systems have played an important role in P outputs and losses to the environment, although their contributions to the total losses were found to be slightly lower in 2017 than in 2010 (Fig. 2b,c). Improvements in P use efficiency[10] and the ban on direct manure discharge to the environment since 2010 were the main causes of the decrease in overall P losses in 2017 (Fig. 3).

Driving forces of changes in P flows. Several reasons account for the changes in the P flows. The first reason is the rapid increase in the total livestock population, which tripled from 1980 to 2010 and increased by another 5.0% between 2010 and 2017 (Extended Data Fig. 3). The second reason is the large shift in the structure of livestock production from mixed systems to landless systems. Between 1980 and 2017, the number of animals in landless systems increased by a factor of 130 (Extended Data Fig. 3a). The substantial changes in P flows over the past 40 years have also been attributed to the large differences in the average total P input, new P input and P losses corresponding to the delivery of 1 kg of P among the various livestock production systems (Extended Data Fig. 4a–c) and livestock categories (Extended Data Fig. 4d–f). The third reason is the large increase in P overfertilization of crop production during the examined period. Cropland has become increasingly overfertilized with P fertilizers, leading to a continuous decrease in the P use efficiency of crop production from 1980 to 2010[32,33]. The fourth reason is the large increase in the amount of inorganic P feed supplement used between 1980 and 2017. The concentrations of total P and available P in livestock diets in China were higher than those required by livestock[10,34], resulting in the overconsumption of P supplements, mainly in the form of dicalcium phosphate.

Policies (referring in this work to government guidance, regulations and standards) have also played important roles in reshaping P flows in the crop–livestock system in China (Fig. 3). By examining the changes in policies and the production of P fertilizer since 1980, we found that policies had shifted from supporting P fertilizer production and applications to protecting limited P rock reserves and ensuring balanced fertilization. Before 2010, many policies (mainly government guidance) were implemented to reduce taxation of the fertilizer industry and subsidize the production, transportation and sale of fertilizers (Fig. 2a). Most of these policies have a direct and simple target: to produce more P fertilizer to ensure food security. These policies led to the overfertilization of P in crop production between 1980 and 2010. After 2010, many policies aimed to both improve P fertilizer application and protect the environment or save P rock reserves (Fig. 3a). Compared with 980–2000, policies became more multifunctional after 2010 (Fig. 3a). For example, the Zero Fertilizer Increase policy (which aimed to control fertilizer use[35,36]) together with other policies such as formulated fertilization by soil testing[37] reduced the application of P fertilizer in China by 23% between 2015 and 2020[24].

Similarly, policies related to livestock production mainly focused on the support of livestock production without strict environmental protection policies before 2010 (Fig. 3b), such as the direct subsidy policies implemented between 1980–2000 and 2001–2010. Few policies were related to environmental protection before 2010. However, most of these policies were technological recommendations or specifications, which lacked effective enforcement compared with government guidance and regulations. This led to large losses of manure P to the environment from 1980 to 2010 (Fig. 2c). Similarly, P management policies related to livestock production were also becoming more multifunctional. Since 2013, the Action Plan for Prevention and Treatment of Water Pollution and the Action Plan for Manure Recycling have been implemented, which aim to control pollution, increase resource use efficiency and enhance crop–livestock production[31]. These regulations

Table 1 | P flows in the crop–livestock system for the period 1980–2050

	P flow code	P flow	1980	2017	2050	
					S0	S4
Input	(1)	Fertilizer P (Gg P)	436	1,534	3,957	0
	(2)	Feed import (Gg P)	16	397	521	429
	(3)	Feed P supplement (Gg P)	8	1,013	1,372	915
	(4)	By-product (Gg P)	423	1,362	1,805	1,599
	(5)	Other (Gg P)	243	2,814	3,791	2,548
		Total (Gg P)	1,126	7,120	11,446	5,491
Output	(6)	Production (Gg P)	116	813	1,263	1,263
	(7)	Discard (Gg P)	24	82	85	79
	(8)	Manure P loss (Gg P)	352	940	1,441	162
	(9)	Manure export (Gg P)	374	3,464	5,429	176
	(10)	Soil accumulation (Gg P)	185	1,673	2,983	3,385
	(11)	Field P loss (Gg P)	75	148	245	427
		Total (Gg P)	1,126	7,120	11,446	5,491
Feed (Gg P)			1,561	6,311	9,515	6,935
Manure (Gg P)			1,420	5,415	8,166	5,594
Manure P applied (Gg P)			408	830	626	5,157

See Fig. 1 for the conceptual flows of P in the crop–livestock production system. S0 is the business-as-usual scenario. S4 is the scenario that combines improved feed, manure and structure management.

were responsible for the decrease in P losses to the environment since 2010 (Fig. 2c).

Exceedance of PPB at a sub-basin scale

PPB$_F$. We considered two just boundaries of PPB$_F$ for global fertilizer use: loose and strict[2]. Loose and strict PPB$_F$ refer to the limits on P fertilizer required to keep surface water and coastal water clean, which were 11.2 Tg P and 6.2 Tg P fertilizer at the global level, respectively. This strict PPB$_F$ may substantially impact crop yields, and is unlikely to be achieved in the short term when the technologies (sustaining high crop productivity with little P fertilizer use) were not available yet. The loose PPB$_F$ could be achieved through better nutrient management practices. In this study we mainly considered the fertilizer P used in (1) domestic feed crop production, (2) imported feed crop production in other countries and (3) other domestic crop production (Fig. 4). The fertilizer P use associated with imported and domestic feed crop production was attributed to crop–livestock production in China.

In 1980, 7 out of 25 sub-basins exceeded the strict PPB$_F$ and no basins exceeded the loose PPB$_F$ (Fig. 4a). The average of the potential contribution of the crop–livestock sector to the exceedance of PPB$_F$ for all sub-basins was 38% compared with the rest of crops and imported feed crops. In 1980, the crop–livestock production system did not lead to the exceedance of the loose PPB$_F$ or the strict PPB$_F$ in the sub-basins (Fig. 4a), and the use of virtual P fertilizer was negligible compared with the total use of P fertilizer (Fig. 4a).

In contrast to their status in 1980, all 25 sub-basins exceeded the strict PPB$_F$ and loose PPB$_F$ for fertilizer P use in 2017. The crop–livestock system contributed 30% (17–68%) to the exceedance of PPB$_F$ (Fig. 4) due to greater P overfertilization in China[38]. Contributions from the crop–livestock system were much larger in 2017 than in 1980. P fertilizer use related to feed production led to all sub-basins exceeding the strict PPB$_F$, except for three sub-basins of the Pearl River and the Yangtze delta. In total, three sub-basins exceeded the loose PPB$_F$ for fertilizer P used for crop feed production, which included Liao River, Toudaoguai and Lanzhou in the Yellow River basin (Fig. 4d). This trend was similar to that identified by the Ministry of Ecology and Environment of China, which reported a higher concentration of nutrients and lower water quality standards in these regions[39]. The contribution of virtual P fertilizer consumption increased by 50% between 1980 and 2017 (Fig. 4c).

Safe PPB for water quality. The safe PPB for water quality provided a threshold for P loss to surface water (PPB$_W$) and is critical to evaluating the eutrophication potential. Here we also set two levels of PPB$_W$ (loose and strict) based on the water quality status and hydrogeology of the different sub-basins. The loose PPB$_W$ was based on the water quality Class III standard[40], which requires a P concentration below 0.2 mg l^{-1}. The strict PPB$_W$ was based on the water quality Class II standard[40], which requires a P concentration below 0.1 mg l^{-1} (Fig. 5). The loose PPB$_W$ refers to a short-term target, while the strict PPB$_W$ refers to a long-term target, for example in 2050, given the recent improvement in water quality in China.

In 1980, 15 out of the 25 sub-basins exceeded the strict PPB$_W$ and 10 sub-basins exceeded the loose PPB$_W$ (Fig. 5a). The contribution of the crop–livestock system to the total P over the loose PPB$_W$ ranged from 27% to 68% among the sub-basins (Extended Data Table 1). The crop–livestock system also played a major role in some of the sub-basins, such as Lanzhou in the Yellow River basin and Mintuo and Jinsha in the Yangtze River basin. The locations where the crop–livestock system itself exceeded the strict PPB$_W$ in 1980 were mainly located in river deltas (Fig. 5a).

Twenty-three of the 25 sub-basins (excluding Wu and Lanzhou) exceeded the strict PPB$_W$ in 2017 (Fig. 5d) and 19 sub-basins exceeded the loose PPB$_W$ in 2017 (Fig. 5d). The contribution of livestock production to total P loss was 45% (31–74%) in 2017 (Extended Data Table 1). The contribution of the crop–livestock system itself exceeded the strict PPB$_W$ for 17 sub-basins and exceeded the loose PPB$_W$ for 11 sub-basins in 2017 (Fig. 5d). In 2017, the three sub-basins with the largest contributions of P in the crop–livestock system to exceeding PPB$_W$ were the Yellow delta (52%), Huayuankou (54%) and Hai (51%). The exceedance rate was higher in the Yellow and Pearl River basins than in the Yangtze River basin in both 1980 and 2017 (Fig. 5a,d). For example, the highest exceedance rate of the crop–livestock system in 2017 occurred in the Pearl delta, which was 21 times higher than the strict PPB$_W$ and 10 times higher than the loose PPB$_W$.

The river length with water quality below the Class III standard accounted for 16% of the total river length, and was mainly distributed in the Yangtze delta, Poyang and Dongting[39]. More than 30% of Yellow River basins exceeded the Class III standard, most of the sub-basin of the Pearl basins were in good condition and over 55% of Liao basins exceeded the Class III standard and were classified as mildly contaminated[39]—all of which agreed with the findings of this study.

Factors driving exceedance of the PPB at sub-basin scales. In addition to the total P fertilizer use and P loss (Figs. 4 and 5), spatial–temporal heterogeneity of the sub-basins also contributed to the exceedance of the PPB. This was partly due to the spatial heterogeneity of livestock populations and production structures at sub-basin scales (Supplementary Figs. 1 and 2). A similar situation exists for P losses: the sub-basins with the highest P losses may have lower exceedance rates than the other sub-basins. This indicates that other factors impact the transgression of the PPB in sub-basins in addition to the changes in the crop–livestock production structure and the related policies, as described above (Fig. 3 and Supplementary Fig. 1). For example, the use of P fertilizer for other crops had a stronger impact than that used by livestock production on the exceedance of PPB$_F$ under the just PPB in 1980 and 2017 (Supplementary Fig. 1). This was caused by a combination of factors, including China's high feed import rate[28] and the country's expanded output of fruit and vegetables, which consumed ten times more P fertilizer than grain crop production[41]. The average amount of discharge water per capita had a substantial negative impact on the transgression of PPB$_W$ under the safe PPB in both years (Extended Data Fig. 5), consistent with the findings of other studies[42].

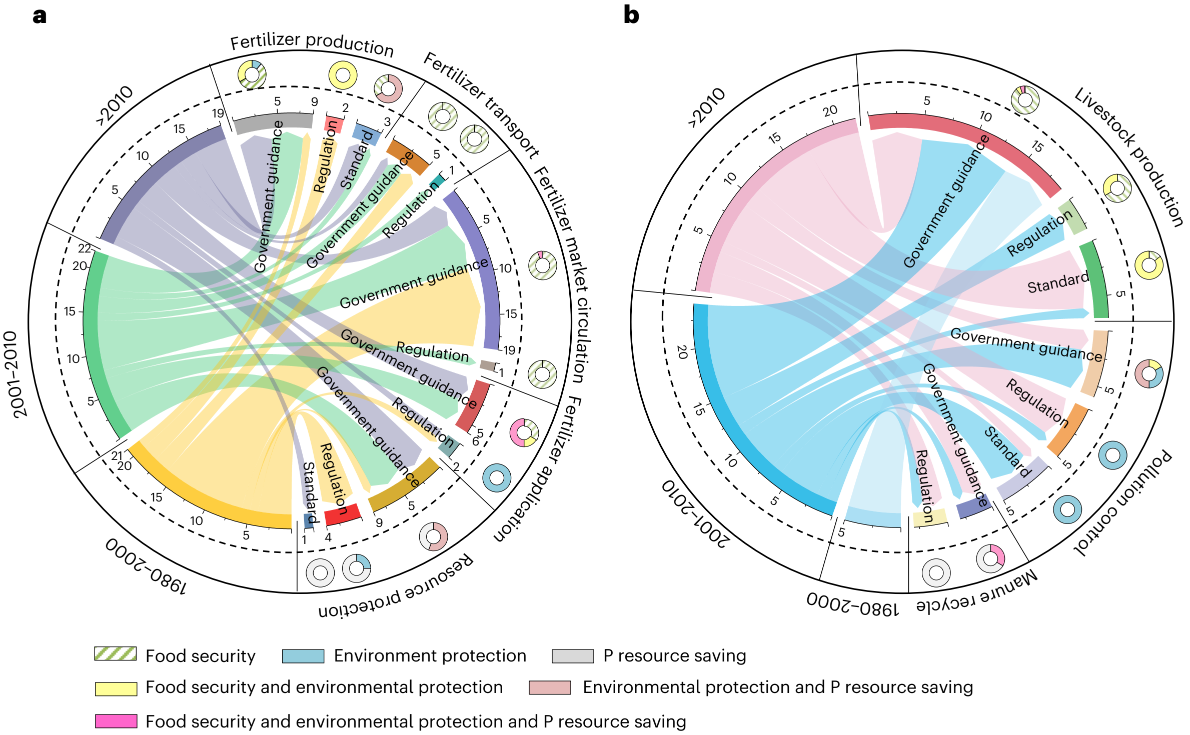

Fig. 3 | Changes and impacts of policies related to crop and livestock production since 1980. a, Targets and objectives of policies for P fertilizer production and use in crop production ($n = 62$ policies); **b**, Targets and objectives of policies for livestock production ($n = 51$ policies). The widths of the arrows represent the number of policies. The doughnut charts in the outer ring represent the distribution of policies between different functions (see the legend). The periods studied were based on the economic development of China. Government guidance comprised formal statements or guidelines that outline how the government intends to conduct its operations and manage its resources. Regulations were rules established by the government that were enforced by law. Standards were developed by standards organizations and ensured that the established criteria or specifications were achieved. The impacts of policies on crop production, livestock production, environment protection and P resource saving were based on the aims of policies given. These policies were collected from government websites and literature. The colours used for the shaded ring segments represent different functions (such as crop production, livestock production, environment protection and P resource saving) of polices.

Uncertainties in exceedance of the PPB at sub-basin scales. Several studies downscaled PPB to a per-capita basis, considering equal rights for all human beings[21,43]. Other studies used different criteria to downscale the PB to smaller scales on the basis, for example, historical emissions of greenhouse gases[44,45]. We argue that the PPB should be different among sub-basins if we intend to achieve multigenerational equal use of P fertilizer across the country. Here we used surface water quality criteria as a required threshold value for safe water quality. However, nutrient threshold values may differ among water bodies. For example, in some cases, nutrient concentrations that were set at the threshold differ by more than tenfold between countries[46]. This was in part due to inconsistency in the reported forms of P, such as total P content and dissolved inorganic P content[47], and in part due to the different approaches used to set threshold of P concentrations[46]. Thus, the exceedance of safe water quality at the sub-basin may show large variance when different criteria of water quality are used.

In addition, P losses may also be underestimated. For example, there were losses of 556 Gg P from mining processes[48,49] and 594 Gg P from P fertilizer manufacturing to environment per year in recent decades[25]. These P losses were together almost equal to the total P losses from the crop–livestock system. If all these losses are considered, then the exceedance of the safe water quality may be even greater, especially for the Yangtze River basin and sub-basins, which greatly contribute to P mining and manufacturing of P fertilizer.

Effects of improving the crop–livestock system

We developed a series of options to optimize the crop–livestock P system to keep P within the PPB. In the business-as-usual scenario (S0), we assumed a linear increase in livestock production along with increases in wealth and urbanization rates. The feed and manure management practices were kept the same as in 2017. However, we assumed that urban and rural wastewater would all be connected to sewage treatment systems and then properly treated based on the recent development of treatment plants and the ambitious rural revitalization policy[50] (Extended Data Fig. 6). The S1 scenario focused on improved feed use efficiency through lower diet P contents, using more highly water soluble P supplements and precise feeding. The S2 scenario focused on improving manure management via increasing the collection of manure, solid–liquid separation and 4R (right source, right rate, right time and right place) manure application technologies (Extended Data Fig. 6). The S3 scenario aimed to improve the livestock production structure, with most of the additional requirement for livestock products being fulfilled by the landless industrial production system owing to its high feed use efficiency. S4 was the combination of S1–S3, and represents the integrated improved management of the feed, the manure and the livestock production system (Extended Data Fig. 6).

S0. According to S0, the total P input of the crop–livestock system is projected to increase by 61% between 2017 and 2050 as a result of the sharply rising demand for food derived from animals[14]. Similarly, compared with 2017, the total P output as products and the P loss to the environment are predicted to increase by 53% and 55% under S0, respectively (Fig. 2a–c). These increases will be contributed by the landless production system and ruminant animals (Fig. 2). The much higher increase in total P input than total P output and losses was partly attributed to more fertilizer P required for feed production, and partly

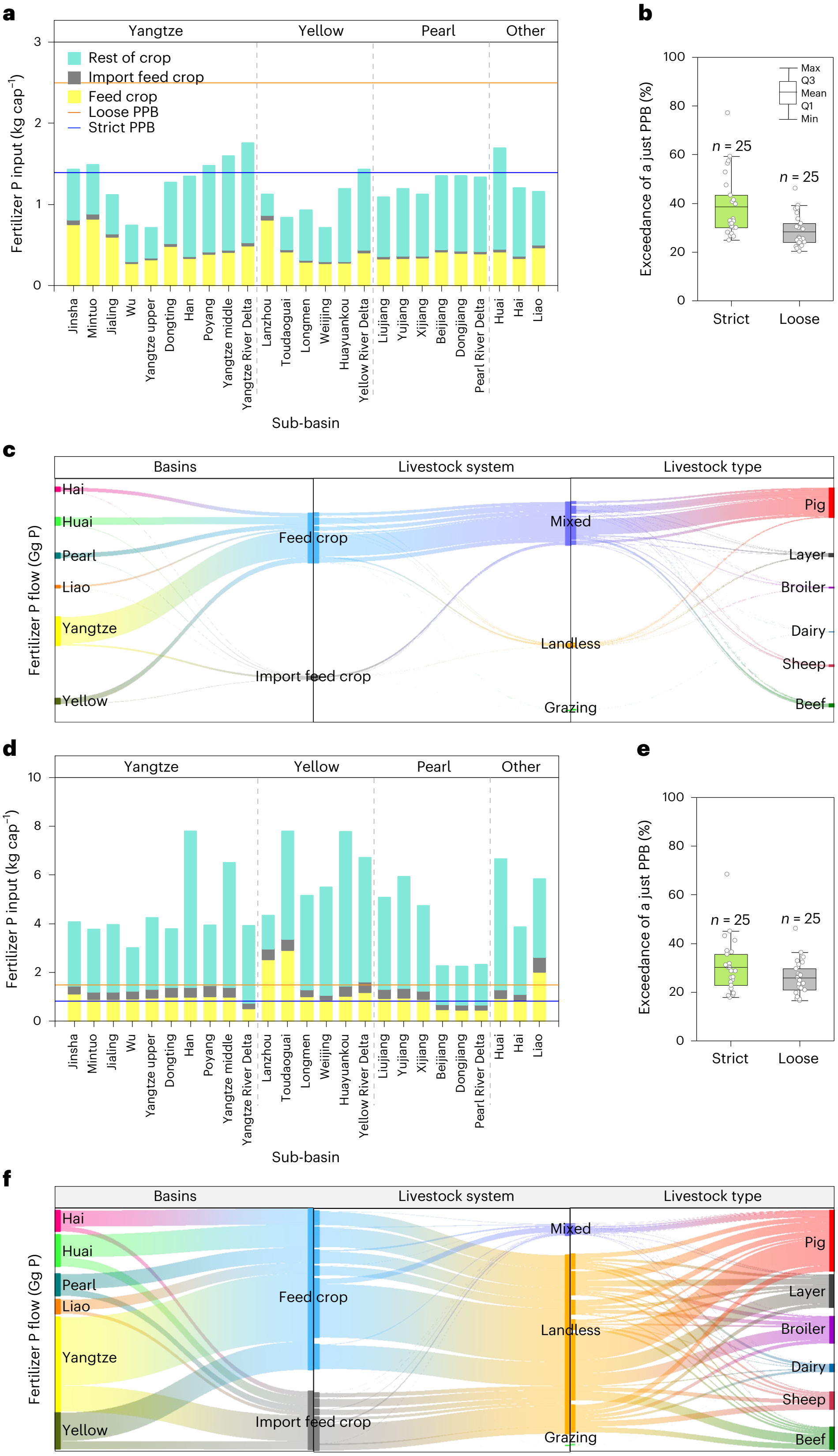

Fig. 4 | Exceedance of a just planetary boundary and flows of P fertilizer use. **a**–**c**, Exceedance of a just planetary boundary for P fertilizer use (**a**), contribution of crop–livestock system to exceeding a just planetary boundary for P fertilizer use (**b**) and flows of P fertilizer use between different livestock production systems and categories (**c**) at a sub-basin scale in 1980. **d**–**f**, Exceedance of just planetary boundary for P fertilizer use (**d**), contribution of crop–livestock system to exceeding a just planetary boundary for P fertilizer use (**e**) and flows of P fertilizer use between different livestock production systems and categories (**f**) at a sub-basin scale in 2017. In **b** and **e** *n* is the sample size used to observe the contribution of the crop–livestock system to exceeding a just planetary boundary. The legend in **a** also applies to **d**. Colours represent different basins, livestock systems and animal categories.

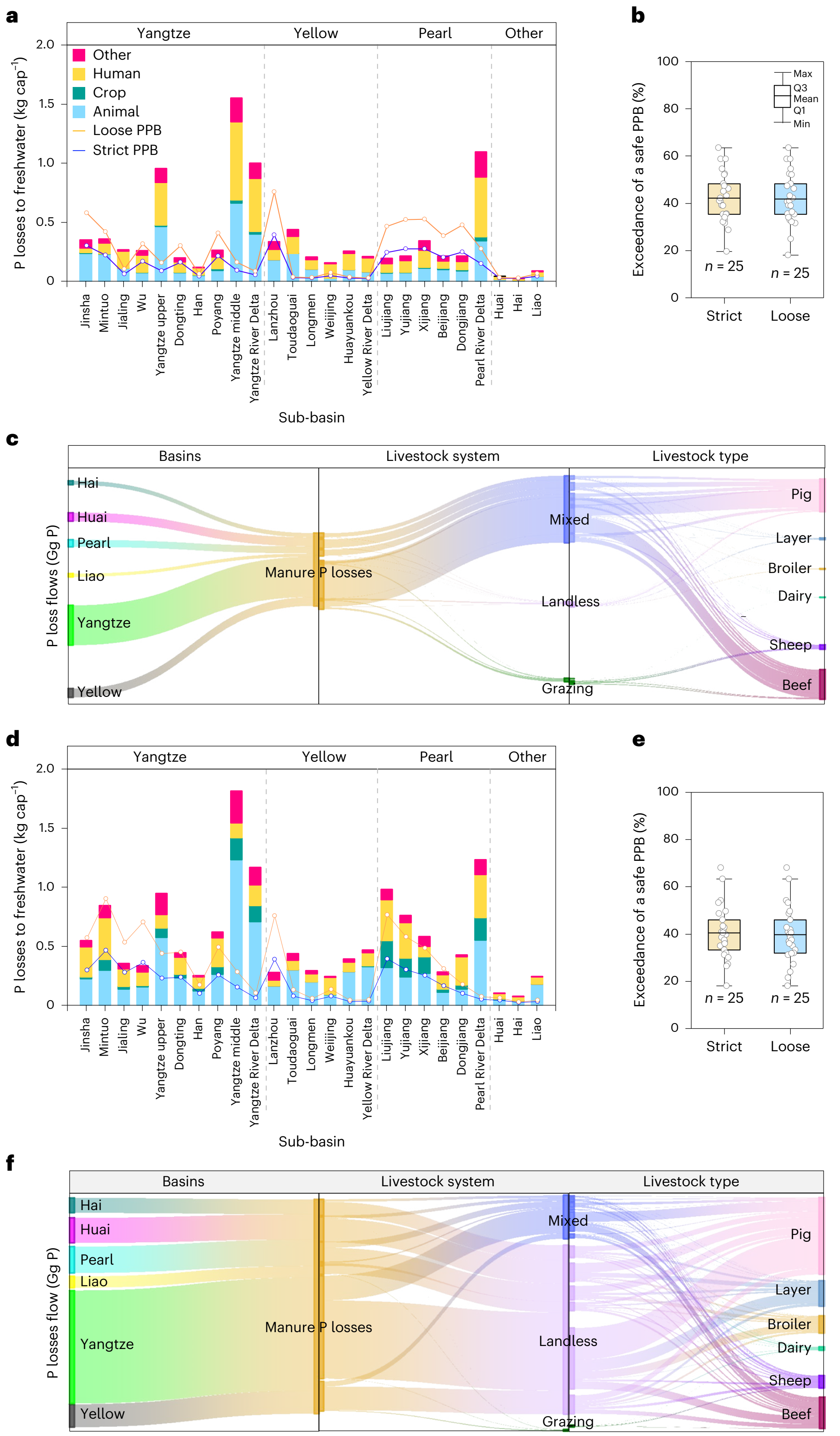

Fig. 5 | Exceedance of a safe planetary boundary for water quality and the distribution of P losses. a–c, Exceedance of a safe planetary boundary for water quality for different sources (**a**), contributions of crop–livestock system to exceeding a safe planetary boundary (**b**) and P losses between different livestock production systems and categories (**c**) at a sub-basin scale in 1980. **d–f**, Exceedance of a safe planetary boundary for water quality for different sources (**d**), contributions of crop–livestock system to exceeding a safe planetary boundary (**e**) and P losses between different livestock production systems and categories (**f**) at a sub-basin scale in 2017. In **b** and **e** *n* is the sample size used to observe the contribution of the crop–livestock system to exceeding a safe planetary boundary. The legend in **a** also applies to **d**. Colours represent P losses in different basins, livestock systems and categories.

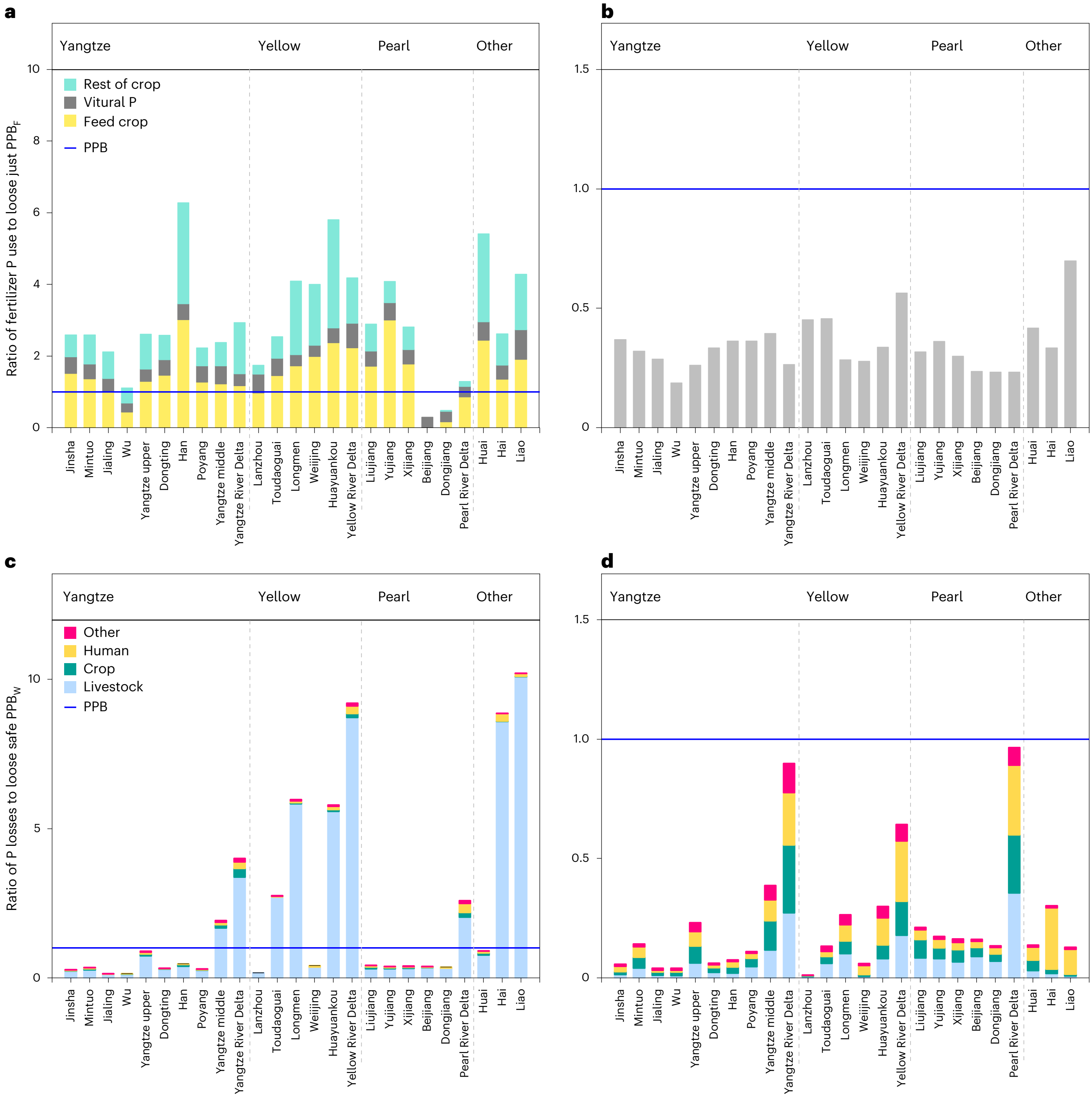

Fig. 6 | Contributions of improvements in livestock production to ensure P remains within the PPB at sub-basin scales. a–b, Potential improvements under S0 (**a**) and S4 (**b**) to ensure that P remains within the loose PPB_F in 2050 in the 25 sub-basins. **c**–**d**, Potential improvements under S0 (**c**) and S4 (**d**) to ensure that P remains within the loose PPB_W in 2050 in the 25 sub-basins. The legend in **c** also applies to **d**.

to no large increases in the P use efficiency of crop–livestock systems between S0 and 2017. Detailed information about the P budgets of the different scenarios in 2050 is given in Extended Data Fig. 7 and Supplementary Fig. 3.

S0 results in the crop–livestock sector continuing to transgress PPB_F for fertilizer P use in China (Fig. 6a). For example, the domestic feed production alone will exceed the loose PPB_F by a factor of 1–3 across all 25 sub-basins under the just PPB under S0 (Fig. 6a). The crop–livestock system will exceed the loose PPB_W by a factor of 2–10 under the safe PPB across the 25 sub-basins (Fig. 6c). Interestingly, 23 sub-basins will exceed the loose limit of PPB_F under the just PPB for fertilizer P use, but only 9 sub-basins will exceed PPB_W under the safe PPB for water quality (Fig. 6a,c). This is partly due to the increase in the new P input being larger than the reduction in the P loss to water resulting from stricter water quality protection policies (Fig. 3b) and partly due to the smaller threshold values of PPB_F under a just PPB resulting from the population increase between 2017 and 2050[51].

Improvement strategies in 2050. The optimal feed management strategy (S1) would decrease the new P input and P loss to water by 1% and 22% compared with the values under S0, respectively (Fig. 2). However, S1 cannot ensure that P fertilizer consumption remains within PPB_F and PPB_W for all sub-basins under the loose and strict limits (Extended Data Figs. 8 and 9). An appropriate manure management strategy (S2) will decrease the mineral P consumption of the crop–livestock system by 55% compared with that for S0. S2 also successfully kept all sub-basins within PPB_F under the loose standard and 23 out of 25 sub-basins within PPB_F under the strict standard (Extended Data Figs. 8 and 9). However, S2 resulted in 20–22 of the 25 sub-basins remaining within PPB_W under the loose or strict standards, which is less promising than the result for PPB_F (Extended Data Fig. 8–9). The optimal livestock production structure strategy (S3) produced livestock products more efficiently but without large improvements in terms of the exceedance of PPB_F and PPB_W.

The whole-chain livestock P management strategy (S4) contributed to reducing the demand for mineral P by 90% and resulted in almost all sub-basins remaining within the loose and strict PPB_F for fertilizer P use compared with S0 (Fig. 6b and Extended Data Fig. 9). S4 would also reduce manure P loss to surface water by 49–90% relative to S0, and ensure that all sub-basins remain within PPB_W, particularly under the loose standards (Fig. 6d). Therefore, S4 would keep P within the planetary boundary at a sub-basin scale, and ensure to the achievement of a safe and just operating space of the P cycle for China.

Future P management and policy implications. Improved P management in the crop–livestock system has the potential to increase P network resilience, as it will increase the internal recycling of manure P, which may substantial reduce the requirement for mineral P fertilizer—the major factor that has driven the decline of P network resilience in recent years in China[52]. However, our results revealed that the effect of the combined options on the PPB was heterogeneous; we therefore recommend that P management in the crop–livestock system should depend on the local conditions causing the transgression. Here we consider various strategies for regions with different PPB transgression levels, considering both fertilizer P use and P losses to water.

Regions where the PPB was maintained. The safe regions were defined as the regions that remained within the strict PPB limit. Such regions were mainly located in the sub-basins of the Yangtze River (such as Jinsha, Jialing and Wujiang). Livestock farms should be considered in the management of P at the whole-system level, and practices should be continually improved. In the safe regions, the use of soil P reserves must be considered in feed cropland because the residual soil P can supply plant-available P[53]. To maintain water quality, it is necessary to monitor the environmental impacts of combined strategies, and changes in the water web distribution and local livestock production should be considered[54]. Policymakers should encourage farmers to adopt combined options and give feedback, for example, by holding technical training and knowledge competitions and cultivating expert farmers[55]. Policymakers and researchers should also monitor the willingness of farmers to adopt these options and give appropriate advice.

Regions where the PPB was moderately exceeded. Moderately safe regions were defined as being between the loose and strict limits of the PPB. In these regions, such as Yellow River Delta, the carrying capability of livestock should first be considered. Second, the numbers of livestock should match the local feed production. Third, the dependence of the livestock system on virtual crop feed should be reduced by using new protein feed[56]. We also recommend that the P balance between crop uptake and manure application is focused on for crop feed cropland[57]. Policymakers should encourage measures that close the P loop in livestock systems. For example, the government should encourage farms to adopt landless system recirculation and the reuse of P[58]. Government investment should be focused on technologies for manure P recovery and application.

Regions where the PPB was greatly exceeded. Unsafe regions were defined as those that transgressed or grew near to the loose limit of the PPB. For unsafe regions, such as the middle courses of the Yangtze River Delta and Pearl River Delta, P management should involve a combined strategy based on the production and consumption of livestock. As a production-based strategy, the numbers of livestock should be reduced in unsafe regions. One possible measure is reducing the numbers of monogastric animals because of their higher P requirement than those of ruminants[34]. In addition, as is done in the Netherlands, manure policies and manure export should be developed and made mandatory[58]. As a consumption-based strategy, trade should be recommended as a means of meeting requirements for livestock production, with the import of livestock produced in high-efficiency regions[59].

Management of the P cycle in crop–livestock systems based on a regionally safe and just planetary boundary would contribute to improved P fertilizer resilience in China by reducing the dependence on P fertilizer use in the crop–livestock system, given that the crop–livestock system accounted for 25% of fertilizer P use. Recycling livestock manure would thus replace fertilizer use and contribute to P resource saving, and offer the opportunity to make P more sustainable in China.

Improvements in other sectors (such as crops and human waste[60]) are also necessary. For the crop system, policy options include precise fertilization, increasing the tax on fertilizer use and using the residual soil P[61]. The application of manure P according to crops' P requirment is particularly important among these options. This is because the manure P comprised various P forms and can easily be lost to the environment[62]. For the food system, lower meat consumption and a lower-P diet should be encouraged[63,64]. Advanced technologies for wastewater treatment include wet-chemical leaching and wet-oxidative options[65], which are more achievable and effective in reducing excess P export to freshwater than watershed conservation practices[50,66–68]. These advanced recovery technologies for recycling human waste P in the food system therefore have the greatest potential to reduce P losses.

Methods

We combined the NUFER animal model and the MARINA 1.0[69] model to analyse China's crop–livestock transition and its impacts on transgressing the PPB. The NUFER animal model was used to analyse P flows in the crop–livestock system (Supplementary Fig. 4) and MARINA 1.0 was used to quantify the effect of China's crop–livestock transition on water quality at the sub-basin scale. The NUFER animal model provided the agricultural P balance data as input to the MARINA 1.0 model (Supplementary Fig. 4).

NUFER animal model

The NUFER animal model was developed from the NUFER model and focused on crop–livestock production between 1980 and 2017 in China. This model included six different animal categories (pig, layer, broiler, dairy, beef and sheep) and three crop–livestock production systems (mixed, grazing and landless). In the NUFER animal model, P was input through the application of fertilizer and the import of feed and detailed calculations based on the feed dry matter intake first. P was output as livestock products and losses during feed production and manure management, as described in detail in ref. 14 and in Supplementary Table 1. In this study the model was applied over the period 1980–2050 at decadal intervals for each province and each sub-basin.

P input in crop–livestock system. The P input in the crop–livestock system was the sum of the P in fertilizer, imported feed, by-products from food production, feed supplements and other sources. P input is expressed as:

$$P_I = P_{CF} + P_{IM} + P_{SUPP} + P_{By\_pro} + P_{Oth} \quad (1)$$

where P_{CF} is the quantity of fertilizer P applied for domestic crop feed production, P_{IM} is the quantity of crop feed imported from abroad, P_{SUPP} is the quantity of P supplemented in livestock feed, $P_{\mathrm{By\_pro}}$ is the quantity of by-products used in livestock feed and P_{Oth} is the quantity of other feed (such as grass, forage) used in livestock feed. All quantities are in gigagrams of P.

Fertilizer P input for crop feed. For the crop–livestock system, the input quantities were calculated based on feed dry matter intake ($\mathrm{DM_{IN}}$, Gg) using the following equations:

$$P_{\mathrm{CF}} = \frac{\mathrm{DM_{IN}} \times R_{\mathrm{Crop\ feed}} \times P^{\mathrm{c}}_{\mathrm{Crop\ feed}} \times (1 - R_{\mathrm{IM}})}{\mathrm{PFP_{Domestic}}} \quad (2)$$

$$P_{\mathrm{IM}} = \mathrm{DM_{IN}} \times R_{\mathrm{Crop\ feed}} \times P^{\mathrm{c}}_{\mathrm{Crop\ feed}} \times R_{\mathrm{IM}} \quad (3)$$

$$P_{\mathrm{SUPP}} = \mathrm{DM_{IN}} \times R_{\mathrm{SUPP}} \times P^{\mathrm{c}}_{\mathrm{SUPP}} \quad (4)$$

$$P_{\mathrm{By\_pro}} = \mathrm{DM_{IN}} \times R_{\mathrm{By\_pro}} \times P^{\mathrm{c}}_{\mathrm{By\_pro}} \quad (5)$$

$$P_{\mathrm{Oth}} = P_{\mathrm{Feed}} - P_{\mathrm{Crop\ feed}} - P_{\mathrm{IM}} - P_{\mathrm{SUPP}} - P_{\mathrm{By\_pro}} \quad (6)$$

where $R_{\mathrm{Crop\ feed}}$, R_{SUPP} and $R_{\mathrm{By\_pro}}$ are the ratios of crop feed, feed P supplements and by-products to livestock feed, respectively (in %). $P^{\mathrm{c}}_{\mathrm{Crop\ feed}}$, $P^{\mathrm{c}}_{\mathrm{SUPP}}$, $P^{\mathrm{c}}_{\mathrm{By\_pro}}$ are the P contents of crop feed, feed P supplement and by-products, respectively (in g kg^{-1}). The superscript c representsis content. $\mathrm{PFP_{Domestic}}$ is the partial fertilizer P productivity for produce per unit domestic crop feed (in kg kg^{-1}). R_{IM} is the rate of crop feed imported from abroad (in %).

$R_{\mathrm{Crop\ feed}}$, R_{SUPP} and $R_{\mathrm{By\_pro}}$ were obtained from Chinese livestock feed recommendations[70]. $P^{\mathrm{c}}_{\mathrm{Crop\ feed}}$, $P^{\mathrm{c}}_{\mathrm{SUPP}}$, $P^{\mathrm{c}}_{\mathrm{By\_pro}}$ and R_{IM} were obtained from the literature (Supplementary Tables 2 and 3). $\mathrm{PFP_{Domestic}}$ was obtained from the literature (Supplementary Table 4).

$$\mathrm{DM_{IN}} = \mathrm{DM^{e}_{IN}} \times N_{\mathrm{AN}} \times D_{\mathrm{Feeding}} \quad (7)$$

$$P_{\mathrm{Feed}} = \mathrm{DM_{IN}} \times P^{\mathrm{c}}_{\mathrm{Feed}} \quad (8)$$

$\mathrm{DM_{IN}}$ is per year (in Gg), $\mathrm{DM^{e}_{IN}}$ is feed DM intake per day (e) (in kg day^{-1}), N_{AN} is the number of animals (in head)[60], D_{Feeding} is the animal feeding days and $P^{\mathrm{c}}_{\mathrm{Feed}}$ is the total P concentration in each animal's diet during 1980–2017 (in %).

$\mathrm{DM^{e}_{IN}}$ was obtained from ref. 71. N_{AN} was obtained from ref. 72 and ref. 28. D_{Feeding} was obtained from ref. 73. $P^{\mathrm{c}}_{\mathrm{Feed}}$ is shown in Supplementary Table 5.

P output in the crop–livestock system. The P output in the crop–livestock system was the sum of P in livestock production, manure loss and manure recycled to crops, and was calculated as:

$$P_{\mathrm{O}} = P_{\mathrm{Prod}} + P_{\mathrm{Losses}} + P_{\mathrm{Recycle}} \quad (9)$$

where P_{Prod} is the amount of livestock production (in Gg P), P_{Losses} is the total amount of manure losses (in Gg P) and P_{Recycle} is the amount of manure recycled to crops (in Gg P).

$$P_{\mathrm{Prod}} = Q_{\mathrm{Prod}} \times N_{\mathrm{AN}} \times P^{\mathrm{a}}_{\mathrm{Pro}} \quad (10)$$

$$P_{\mathrm{Losses}} = P^{\mathrm{H}}_{\mathrm{Losses}} + P^{\mathrm{D}}_{\mathrm{Losses}} + P^{\mathrm{T}}_{\mathrm{Losses}} + P^{\mathrm{F}}_{\mathrm{Losses}} \quad (11)$$

$$P_{\mathrm{Recycle}} = P_{\mathrm{Man}} - P^{\mathrm{H}}_{\mathrm{Losses}} - P^{\mathrm{D}}_{\mathrm{Losses}} - P^{\mathrm{T}}_{\mathrm{Losses}} \quad (12)$$

where Q_{Prod} is the amount of livestock production (in Gg) and $P^{\mathrm{a}}_{\mathrm{Pro}}$ denotes the P content for each type of livestock production (in g kg^{-1}); these values were obtained from the literature (Supplementary Table 6). $P^{\mathrm{H}}_{\mathrm{Losses}}$, $P^{\mathrm{D}}_{\mathrm{Losses}}$, $P^{\mathrm{T}}_{\mathrm{Losses}}$ and $P^{\mathrm{F}}_{\mathrm{Losses}}$ are the P losses in the crop–livestock system via animal housing, storage and direct discharge/landfill, treatment and field application, respectively (in Gg P). P_{Man} is the amount of livestock manure (in Gg P) calculated as the difference between feed P consumption and manure P excretion.

Manure P recycled. The quantity of manure P recycled was calculated as the difference between manure P excretion and losses. The manure P was recycled to cereal crops (such as maize, rice and wheat) and cash crops (such as fruit and vegetables). This was calculated as follows:

$$P^{\mathrm{C}}_{\mathrm{Recycle}} = P_{\mathrm{Recycle}} \times R^{\mathrm{C}}_{\mathrm{Recycle}} \quad (13)$$

$$P^{\mathrm{E}}_{\mathrm{Recycle}} = P_{\mathrm{Recycle}} - P^{\mathrm{C}}_{\mathrm{Recycle}} \quad (14)$$

Where $R^{\mathrm{C}}_{\mathrm{Recycle}}$ is defined as the ratio of manure recycle to cropland (in %; Supplementary Table 7).

P losses to surface water. The NUFER animal model accounts for the whole chain of livestock manure management (for example, housing and storage, discharge, treatment and application losses). The calculation of P losses to surface water included: (1) $P^{\mathrm{H}}_{\mathrm{Losses}}$ calculated by multiplying the manure P excretion by the rate of manure P losses; (2) $P^{\mathrm{D}}_{\mathrm{Losses}}$ quantified by $P^{\mathrm{H}}_{\mathrm{Losses}}$ and the rate of manure P discharge directly; (3) $P^{\mathrm{T}}_{\mathrm{Losses}}$ calculated from $P^{\mathrm{H}}_{\mathrm{Losses}}$, $P^{\mathrm{D}}_{\mathrm{Losses}}$ and the rate of P loss during manure treatment; (4) $P^{\mathrm{F}}_{\mathrm{Losses}}$ based on $P^{\mathrm{H}}_{\mathrm{Losses}}$, $P^{\mathrm{D}}_{\mathrm{Losses}}$, $P^{\mathrm{T}}_{\mathrm{Losses}}$ and the rate of P loss via runoff, erosion and leaching. All loss parameters in the NUFER animal model were derived from ref. 71 (Supplementary Table 8).

MARINA 1.0 model

The MARINA 1.0 model was applied to quantify the annual river export of P in different forms at the sub-basin scale. In this study, six large river basins (the Yellow, Liao, Hai, Yangtze, Huai and Pearl rivers) in China were explicitly represented within the model, which covered 25 sub-basins. The MARINA 1.0 model included point and diffuse sources[69]. Point sources of P were expressed as direct discharge of animal manure and human sewage to rivers. Diffuse sources of P were the sum of manure P, fertilizer P applied to cropland, P due to the leaching of organic matter and P weathering. The results were expressed as the river export of total dissolved phosphorus (TDP) to the mouth of each river.

In this study, the MARINA 1.0 model was updated and modified to 1980, 2017 and 2050, respectively. For 1980 and 2017, we updated direct discharge of animal manure and human sewage to rivers. For 2050, we updated only the direct discharge of animal manure. An overview of the MARINA 1.0 model input and update is given in Supplementary Table 9. The overall equation of the MARINA 1.0 model is expressed as:

$$M_{Fyj} = \mathrm{RS}_{Fyj} \times \mathrm{FE}_{\mathrm{riv}F\mathrm{outlet}j} \times \mathrm{FE}_{\mathrm{riv}F\mathrm{mouth}j} \quad (15)$$

where M_{Fyj} is the river export of P in form F (DIP and DOP) from source y from sub-basin j (in kg yr^{-1}); RS_{Fyj} is the P input in form F to rivers (surface water) from diffuse and point sources y in sub-basin j (in kg yr^{-1}); $\mathrm{FE}_{\mathrm{riv}F\mathrm{outlet}j}$ is the fraction of P in form F exported to the outlet of sub-basin j (0–1) and $\mathrm{FE}_{\mathrm{riv}F\mathrm{mouth}j}$ is the fraction of P in form F exported from the outlet of sub-basin j to the river mouth (0–1). RS_{Fyj}, $\mathrm{FE}_{\mathrm{riv}F\mathrm{outlet}j}$ and $\mathrm{FE}_{\mathrm{riv}F\mathrm{mouth}j}$ are calculated as follows.

P inputs to surface waters from diffuse and point sources. RS_{Fyj} included P input from diffuse (RSdif_{Fyj}; in kg yr^{-1}) and point sources (RSpnt_{Fyj}; in kg yr^{-1}), calculated as follows:

$$\mathrm{RSdif}_{Fyj} = \mathrm{WSdif}_{Pyj} \times G_{Fj} \times \mathrm{FE}_{\mathrm{ws}Fj} \tag{16}$$

$$\mathrm{WSdif}_{\mathrm{P}yj} = \mathrm{WSdif}_{\mathrm{Pfe}j} + \mathrm{WSdif}_{\mathrm{Pman}j} + \mathrm{WSdif}_{\mathrm{Phumuncon}j} \tag{17}$$

$$G_{Fj} = 1 - \frac{\mathrm{WSdif}_{\mathrm{Pex}j}}{\mathrm{WSdif}_{\mathrm{P}yj}} \tag{18}$$

$$\mathrm{RSpnt}_{Fyj} = \mathrm{RSpnt}_{\mathrm{P}yj} \times \mathrm{FEpnt}_{Fy} \tag{19}$$

where $\mathrm{WSdif}_{\mathrm{P}yj}$ is the P input to agricultural land in sub-basin j from diffuse sources y (in kg yr^{-1}); G_{Fj} is the fraction of P forms F applied to agricultural land that remained in soils of sub-basin j after animal grazing and crop harvesting (0–1); $\mathrm{FE}_{\mathrm{ws}Fj}$ is the export fraction of P form F entering surface water of sub-basins j (0–1); and $\mathrm{WSdif}_{\mathrm{Pfe}j}$, $\mathrm{WSdif}_{\mathrm{Pman}j}$ and $\mathrm{WSdif}_{\mathrm{Phumuncon}j}$ are the amounts of fertilizer P, animal manure and human excretion applied to agricultural land in sub-basin j, respectively (in kg yr^{-1}). $\mathrm{WSdif}_{\mathrm{Pex}j}$ is the export of P from agricultural areas by animal grazing and crop harvesting (in kg yr^{-1}); $\mathrm{RSpnt}_{\mathrm{P}yj}$ is P inputs to surface waters in sub-basin j from point source y (in kg yr^{-1}); FEpnt_{Fy} is the fraction of P form F entering surface waters in sub-basin j from point source y (0–1). See Supplementary Tables 10–13 for detailed calculations and sources of $\mathrm{WSdif}_{\mathrm{Pfe}j}$, $\mathrm{WSdif}_{\mathrm{Pman}j}$ and $\mathrm{WSdif}_{\mathrm{Phumuncon}j}$, $\mathrm{WSdif}_{\mathrm{Pex}j}$, $\mathrm{RSpnt}_{\mathrm{P}yj}$ and FEpnt_{Fy}.

P fractions reaching the outlet and mouth from sub-basins *j*. $\mathrm{FE}_{\mathrm{riv}F\mathrm{outlet}j}$ and $\mathrm{FE}_{\mathrm{riv}F\mathrm{mouth}j}$ represent the export fractions of P reaching the outlet and mouth of sub-basin j, respectively, calculated as:

$$\mathrm{FE}_{\mathrm{riv}F\mathrm{outlet}j} = (1 - D_{Fj}) \times (1 - L_{Fj}) \times \left(1 - \mathrm{FQrem}_{\ j}\right) \tag{20}$$

$$\begin{aligned}\mathrm{FE}_{\mathrm{riv}F\mathrm{mouth}j} = {} & \left(1 - \left(D_{F\mathrm{jdc}} \times \mathrm{jucA}_{\mathrm{jdc}}\right)\right) \times \left(1 - \left(L_{F\mathrm{jdc}} \times \mathrm{jucA}_{\mathrm{jdc}}\right)\right) \\ & \times \left(1 - \left(\mathrm{FQrem}_{F\mathrm{jdc}} \times \mathrm{jucA}_{\mathrm{jdc}}\right)\right)\end{aligned} \tag{21}$$

D_{Fj} is the fraction of P form (DIP) retained in reservoirs and lakes in sub-basin j (0–1). L_{Fj} is the fraction of P form (DIP) retained in or/and lost from water systems. FQrem_j is the fraction of P (DIP, DOP) removed from water systems in sub-basin j via water consumption (0–1). $D_{F\mathrm{jdC}}$ is the fraction of nutrient form F (DIP) retained in reservoirs of down-stream (jdC) sub-basins with the main channel (C) (0–1). $L_{F\mathrm{jdC}}$ is the fraction of nutrient form (F) that is lost from surface waters of down-stream (jdC) sub-basins with the main channel (C) (0–1). $\mathrm{jucA}_{\mathrm{jdC}}$ is drainage area (A) of the main channel (C) in down-stream (jdC) sub-basins that exports nutrients from the outlet of middle-stream main channel (jmC) (0–1). $\mathrm{FQrem}_{F\mathrm{jdC}}$ is the fractions of P form F that is lost from surface waters of down-stream (jdC) sub-basins with the main channel (C) via water consumption (0–1). The detailed calculations and sources of FQrem_j, $D_{F\mathrm{jdC}}$, $\mathrm{jucA}_{\mathrm{jdC}}$ and $\mathrm{FQrem}_{F\mathrm{jdC}}$ are shown in Supplementary Table 13.

Safe and just PPB

We used the just P fertilizer use per capita and safe-water-quality-based P concentration limited water quality requirement (Supplementary Fig. 5). The just PPB considered multigenerational equal use of P fertilizer per capita and was used to establish $\mathrm{PPB}_{\mathrm{F}}$. The boundary of P fertilizer use was allocated to each person from the perspective of fairness; thus, the boundary was expressed as fertilizer P use per capita[20,21] (Fig. 4). The safe PPB was used to establish $\mathrm{PPB}_{\mathrm{W}}$ from the perspective of safe water quality for the entire population. An overview of the just and safe PPB is given in Supplementary Fig. 5.

Just planetary boundary for fertilizer P use. Two boundary of global fertilizer P use (11.2 and 6.2 Tg P) were used, which correspond to the prevention of ocean anoxic events and freshwater eutrophication[2,19], respectively. Here we refer to the thresholds of 11.2 and 6.2 Tg P as loose and strict boundaries, respectively. Aiming to achieve human equity and fairness, we divided the global uniform fertilizer P application boundary by the global population. Then we used the downscaled boundary as the threshold (PPBF in kg cap–^{1}) for P fertilizer use at the sub-basin scale, which is given by:

$$\mathrm{PPB}_{\mathrm{F}} = \mathrm{PPB}^{\mathrm{global}}_{\mathrm{fertilizer\ P}} \div \mathrm{Pop}^{\mathrm{global}} \tag{22}$$

where $\mathrm{PPB}^{\mathrm{global}}_{\mathrm{fertilizer\ P}}$ is the threshold of global fertilizer P applied (in Tg P) and $\mathrm{Pop}^{\mathrm{global}}$ is the global population[40]. $\mathrm{PPB}_{\mathrm{F}}$ values are given in Supplementary Table 14.

Safe planetary boundary for water quality P

We calculated $\mathrm{PPB}_{\mathrm{w}}$ for each sub-basin in China. First, in accordance with the current water quality standard for P[39,74,75], we set the two aimed total phosphorus (TP) concentrations (Class II and III) for each sub-basin. Class II and III represent the current and future situations, respectively. Second, we calculated the water quality P threshold for each sub-basin based on actual water discharged in the five most recent years at the sub-basin scale in China[76]. Third, we calculated $\mathrm{PPB}_{\mathrm{w}}$ on a per-capita basis for comparison with the threshold for fertilizer P use as follows:

$$\mathrm{PPB}_{\mathrm{W}} = (C_i \times Q_i) \div \mathrm{Pop}^{i} \tag{23}$$

where C_i denotes the class of the water quality standard for sub-basin i (Class II and III with values of 0.1 and 0.2 mg P l^{-1}, respectively). We defined Class II and III as the strict and loose thresholds, respectively. Q_i is the quantity of water actual discharge for sub-basin i (in 10^8 m^3) (Supplementary Table 15). PPBW values are listed in Supplementary Table 16.

Impacts of policies

We collected relevant policies from the websites of different ministries using keywords such as fertilizer production, fertilizer transportation, fertilizer application, livestock production, manure management and pollution, and manure recycling from 1980 to 2017 (Supplementary Table 17). We divided all the years into three different periods, namely 1980–2000, 2001–2010 and post 2010, based on the economic and agricultural development level. According to the strictness and legal force, all of the policies were categorized into government guidance, regulations and standards. Government guidance refers to a series of announcements by different ministries or central government. These opinions were not as comprehensive and system as regulations, but in practice, they are often as strong as regulations in a certain period. Regulations are normative documents formulated by the central government or ministries with strong legal force. Standards are a set of guidelines and documents for specific aspects of a product, service, organization or process formulated by professional standardization agencies.

Given our main objective, all the policies were further classified into three functions: promoting crop or livestock production to ensure food security, cancelling subsidies or adjusting taxes to protect the environment and save limited P resources. For example, to promote crop production, policies such as electricity subsidies and natural gas subsidies were used to encourage P fertilizer production, railway subsidies were used to ensure P fertilizer transportation and tax exemptions were applied to ensure P fertilizer supply (Supplementary Table 17).

Few policies positively ensure food security while reinforcing environmental protection and preserving P resources (Fig. 3).

Scenarios for optimizing P use and losses in the crop–livestock system in 2050

Five scenarios, the business-as-usual scenario and four mitigation scenarios, were designed to improve P management of crop–livestock production and to ensure that P remains within the PPB at the sub-basin scale. We set 2017 as the reference year and 2050 as the target year, because agriculture will gradually enter a new era and the structure of demand for agricultural products will change greatly by 2050[77,78]. These scenarios were based on the Shared Socio-economic Pathways-2 (SSP2) baseline for China[77]. SSP2 for China assumes that food demand and livestock product consumption will increase because of rapid urbanization. For example, the urban population is predicted to increase by 34%, and the requirements for pork, milk, beef and mutton are predicted to increase by 68%, 30%, 38% and 27%, respectively, compared with 2017 (Supplementary Table 18). Animal production is expected to become increasingly intensive, with more recycling of manure to cropland. We assumed that all wastewater both in rural and urban areas will be connected to sewage systems. P removal by advanced technologies during treatment will reach more than 90%. Some improvements in resource use efficiency and environmental policies are expected, but only to reduce local pollution. Each scenario is described in detail in Extended Data Fig. 6 and Supplementary Table 19.

S0. S0 reflected current livestock production and environmental policies combined with the increased urbanization, population and food demand of SSP2 for China. In this scenario, we assumed that the additional animal production requirement will be produced by a landless system for each animal category, following the historical trend. However, feed, herd and manure management practices remain the same as those in 2017.

S1. This scenario was based on S0 but with feed P optimized and precision feeding adopted. It is assumed that the normal feed P supplement will be entirely replaced with a high-P water supplement (monodicalcium phosphate) and that the amount of feed P will be reduced by 5% (ref. 10). In addition, according to the P requirements of different animals, phase feeding with individualized requirements is provided during growth, resulting in a decrease in the feed conversion ratio of 9%.

S2. This scenario assumed that all manure in housing or storage is collected with no discharge of manure P, particularly from landless systems. A concrete floor was assumed in the animal production systems, resulting in no leaching in the housing or storage sector. We also assumed that manure is applied on the basis of the P requirement for the feed crop, thus decreasing the amount of fertilizer P used. The mineral fertilizer equivalency value of P in the livestock manure was assumed to be 100% (ref. 59).

S3. S3 was based on S0, but it was assumed that the numbers of animals in mixed and grazing systems would be halved. The landless system was assumed to be the dominant system providing animal products to meet human requirements. In addition, the mortality rate in the landless system is reduced by 6%.

S4. S4 combined the measures in S1–S3 and reflected optimal management in the crop–livestock system. For the livestock system, we assumed that precise P manure management and a landless system will be used in 2050. For the feed crop system, we assumed no application of chemical fertilizers and that a balance was maintained between crop uptake and fertilizer P input. S4 is thus a combination of improved feed P management and manure P management with an appropriate livestock feeding structure.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Records of fertilizer P application and production of livestock are from China's National Bureau of Statistics. Data for crop feed imports are from FAOSTAT. Population data (global and Chinese) are from the United Nations. Data for discharge losses of livestock manure are from China's Ministry of Ecology and Environment. Major parameters related to the P content of feed crops and livestock production, P recommendations for livestock feed, P losses of different crop–livestock systems and PPBs were collected from the literature cited in the manuscript. Source data are provided with this paper.

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Author contributions

L.M. and Z.B. conceived the study. L.L. conducted the modelling and wrote and revised the first draft. Z.B. wrote and revised the manuscript. J.Y. conducted the water pollution modelling. Z.Y., F.L., Z.C. and X.C. participated in the result discussions. M.W., M.S. and C.K. provided support for data collection and processing.

Competing interests

The authors declare no competing interests.

Additional information

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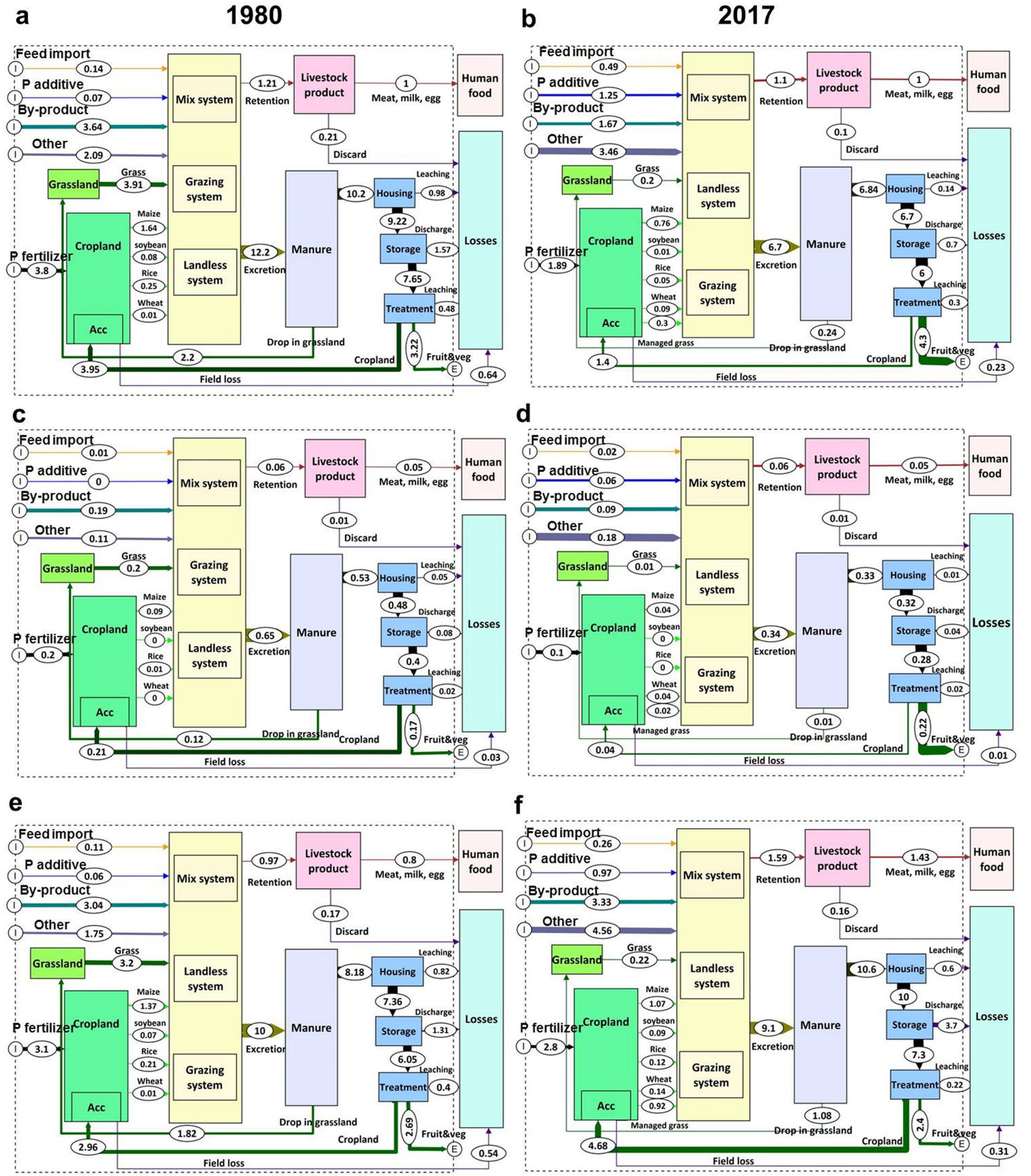
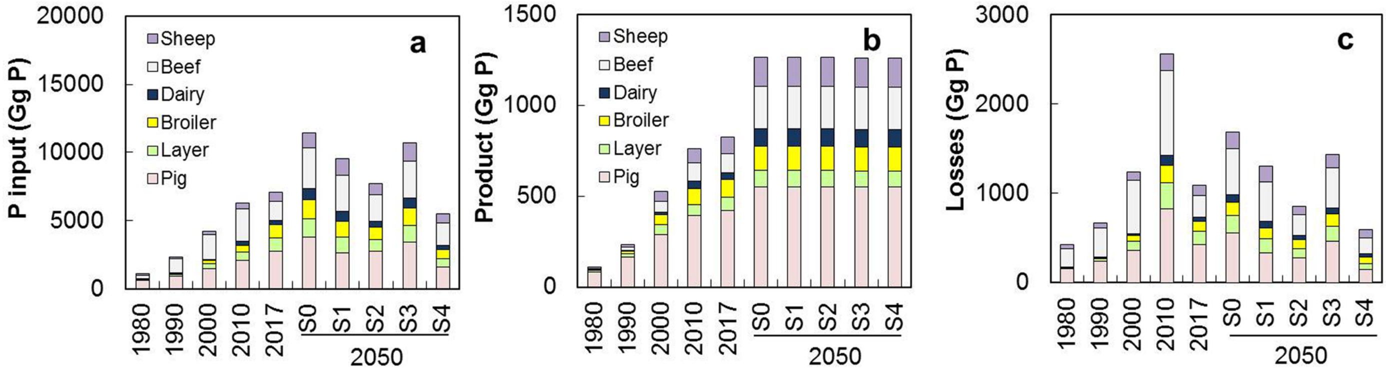
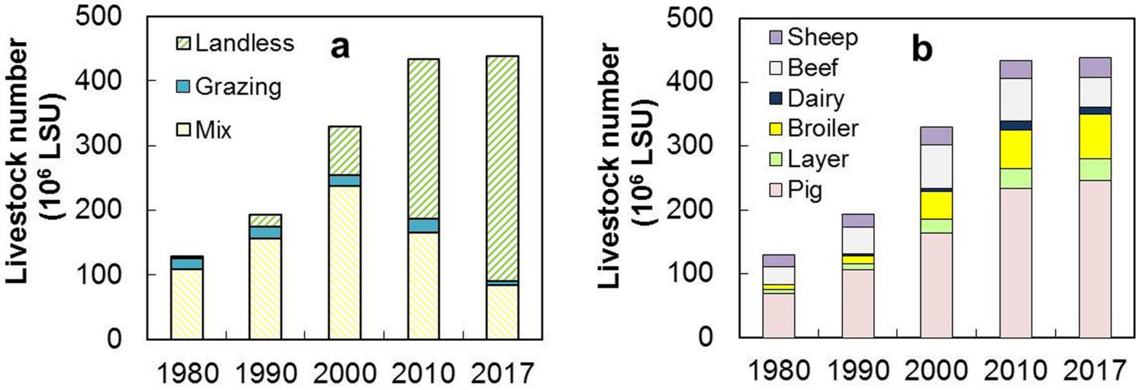


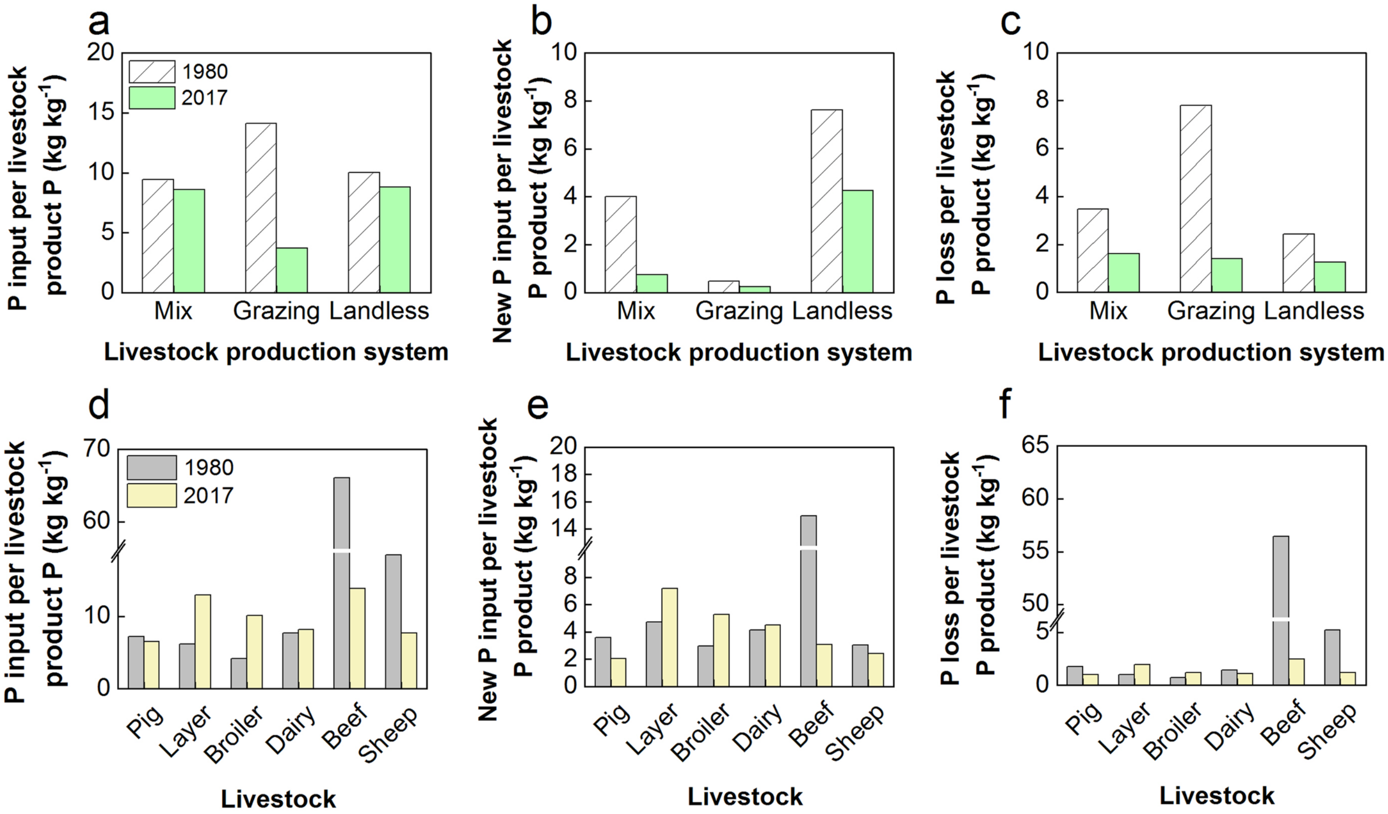
Extended Data Fig. 1 | P budget of crop-livestock production system. P flow in kg of P output as product (**a**), protein (**c**) and standard livestock unit (**e**) in 1980. P flow in kg of P output as product (**b**), protein (**d**) and standard livestock unit (**f**) in 2017.



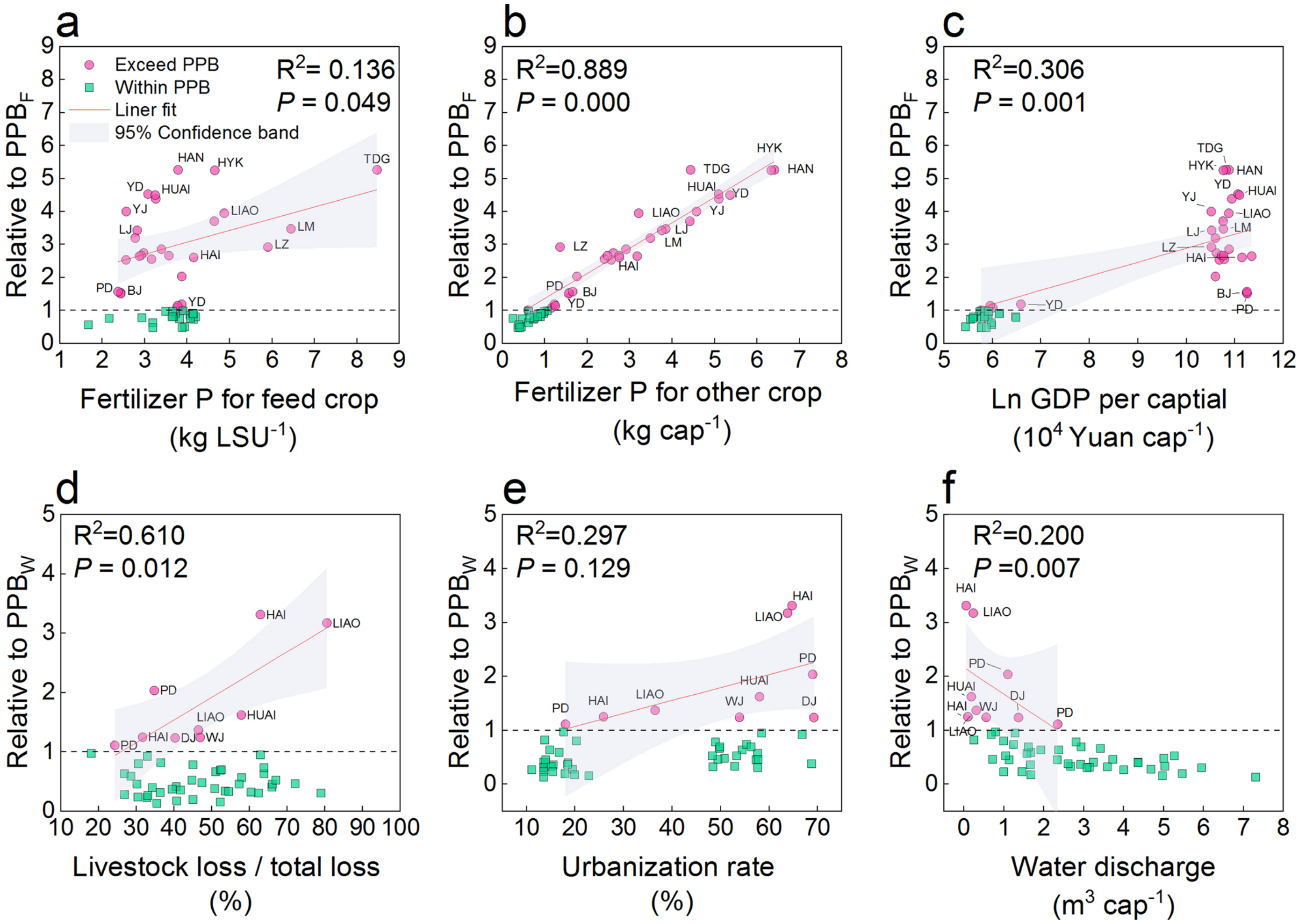
Extended Data Fig. 2 | Phosphorus input, output and losses in the crop-livestock production system from 1980 to 2017 and under different scenarios in 2050 (S0-S4). **a**, P input; **b**, livestock product P output; **c**, environmental losses.



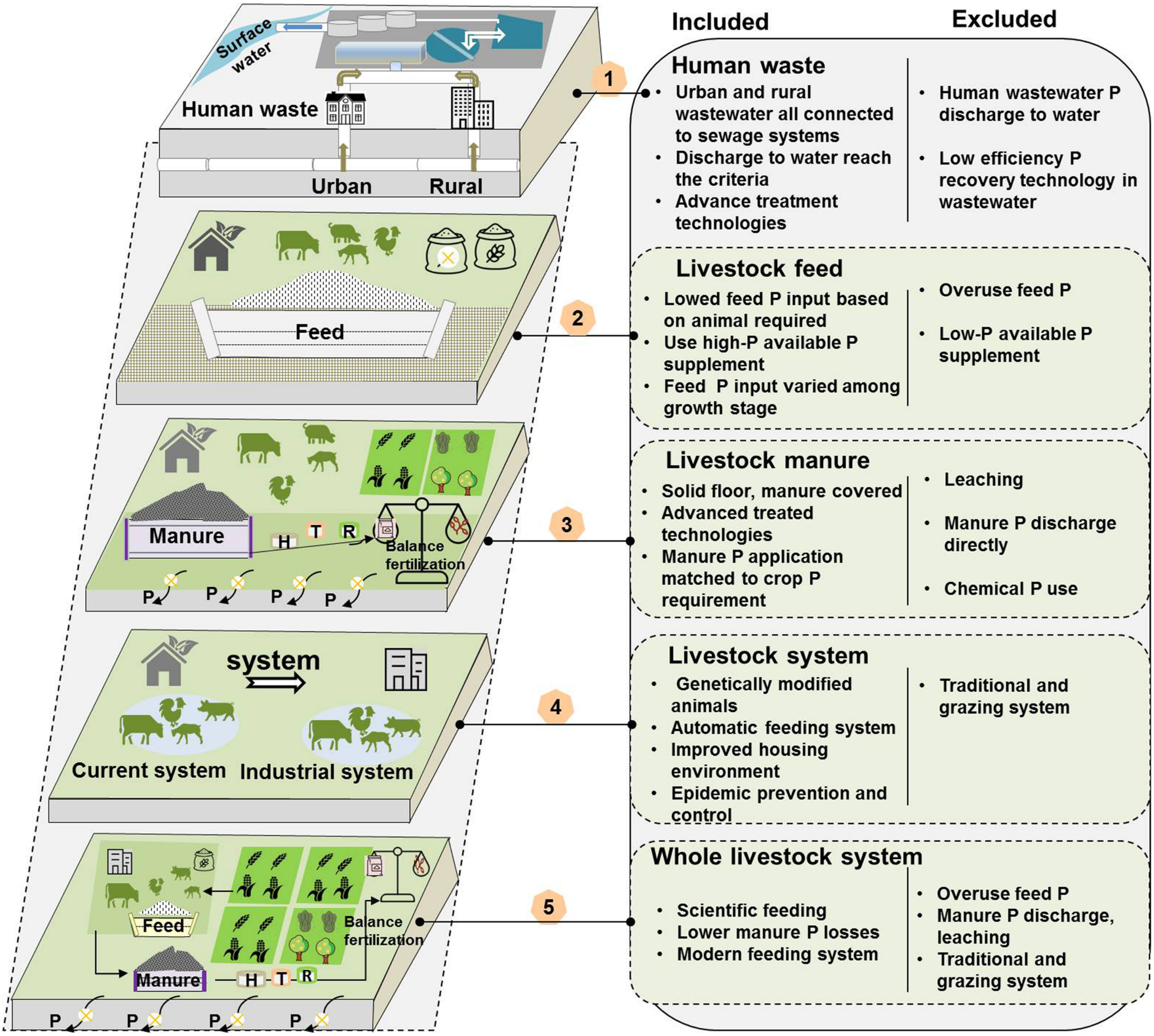
Extended Data Fig. 3 | Changes of crop-livestock production structure from 1980 to 2017 in China. **a**, crop-livestock production systems; **b**, livestock categories.



Extended Data Fig. 4 | Phosphorus input, losses per livestock product in different systems and animal categories in 1980 and 2017. a-c, Changes of total P input (**a**), "new" P input (**b**), and P losses (**c**) per livestock product in different crop-livestock production systems. **d-f**, Changes of total P input (**d**), "new" P input (**e**), P losses (**f**) per livestock product in different crop-livestock production systems. In Extended Data Fig. 4d, the y axis is broken from 18.8 to 56.3; In Extended Data Fig. 4e, the y axis is broken from 10.0 to 12.3; In Extended Data Fig. 4f, the y axis is broken from 6.0 to 48.8.

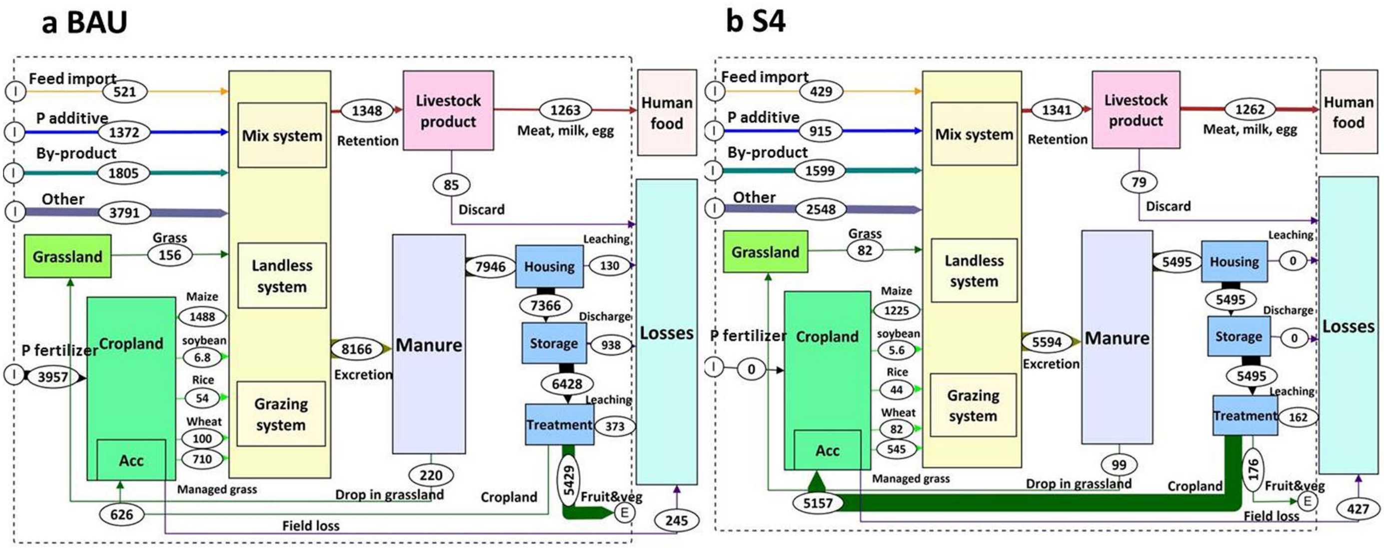


Extended Data Fig. 5 | Factors affected phosphorus exceeding its planetary boundary. **a-c**, Relationship of excedace of just fertilizer P use between fertilizer P use for crop feed (**a**), fertilizer P use for other crop (**b**), GDP per capital (**c**) at sub-basin scale between 1980 and 2017. **d-f**, Relationship of excedace of safe water quality between livestock manure P loss (**d**), urbanization rate (**e**), water discharge per capita (**f**) at sub-basin scale between 1980 and 2017.

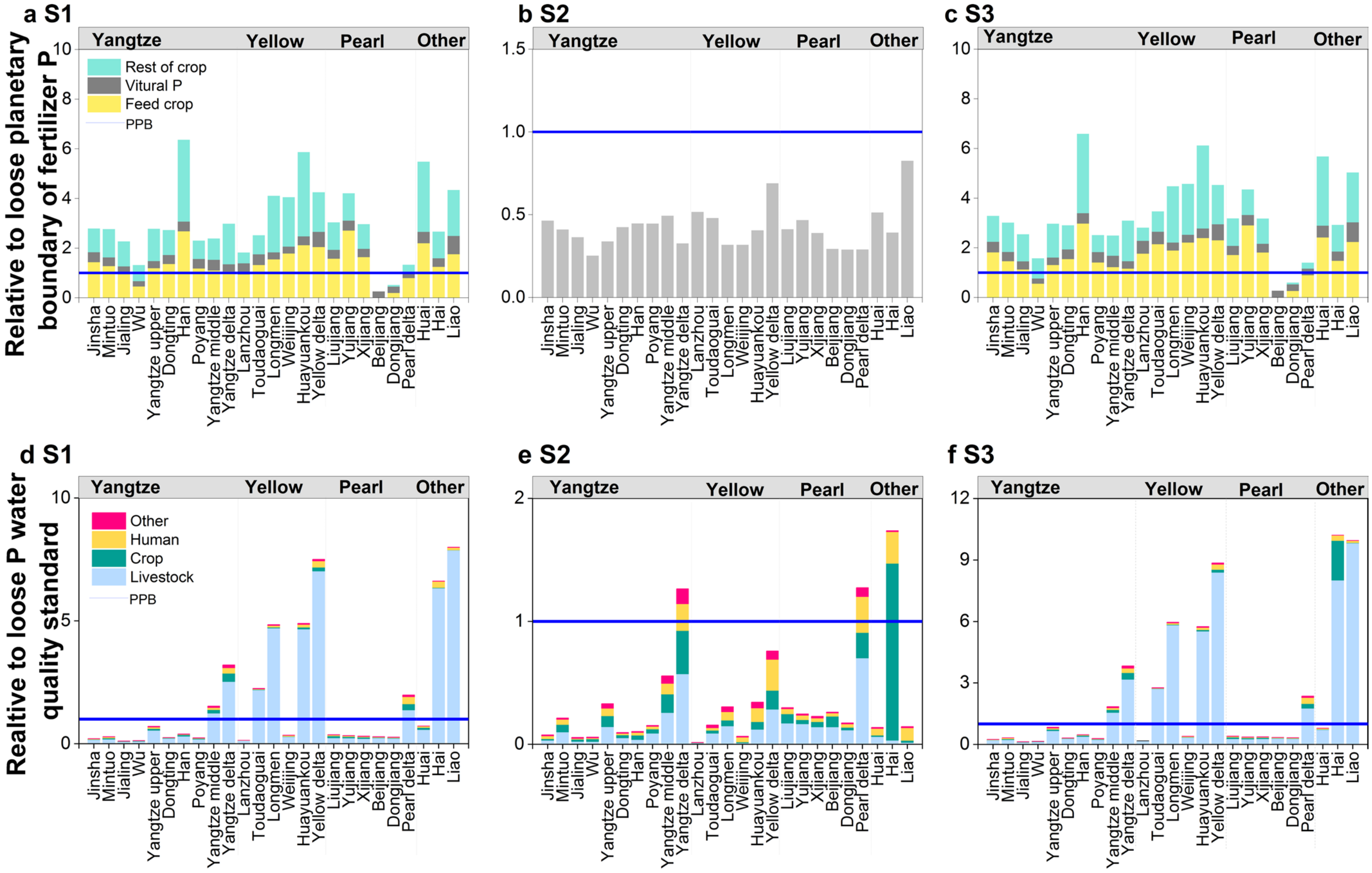


	Included	Excluded
Human waste	Urban and rural wastewater all connected to sewage systems Discharge to water reach the criteria Advance treatment technologies	Human wastewater P discharge to water Low efficiency P recovery technology in wastewater
Livestock feed	Lowed feed P input based on animal required Use high-P available P supplement Feed P input varied among growth stage	Overuse feed P Low-P available P supplement
Livestock manure	Solid floor, manure covered Advanced treated technologies Manure P application matched to crop P requirement	Leaching Manure P discharge directly Chemical P use
Livestock system	Genetically modified animals Automatic feeding system Improved housing environment Epidemic prevention and control	Traditional and grazing system
Whole livestock system	Scientific feeding Lower manure P losses Modern feeding system	Overuse feed P Manure P discharge, leaching Traditional and grazing system

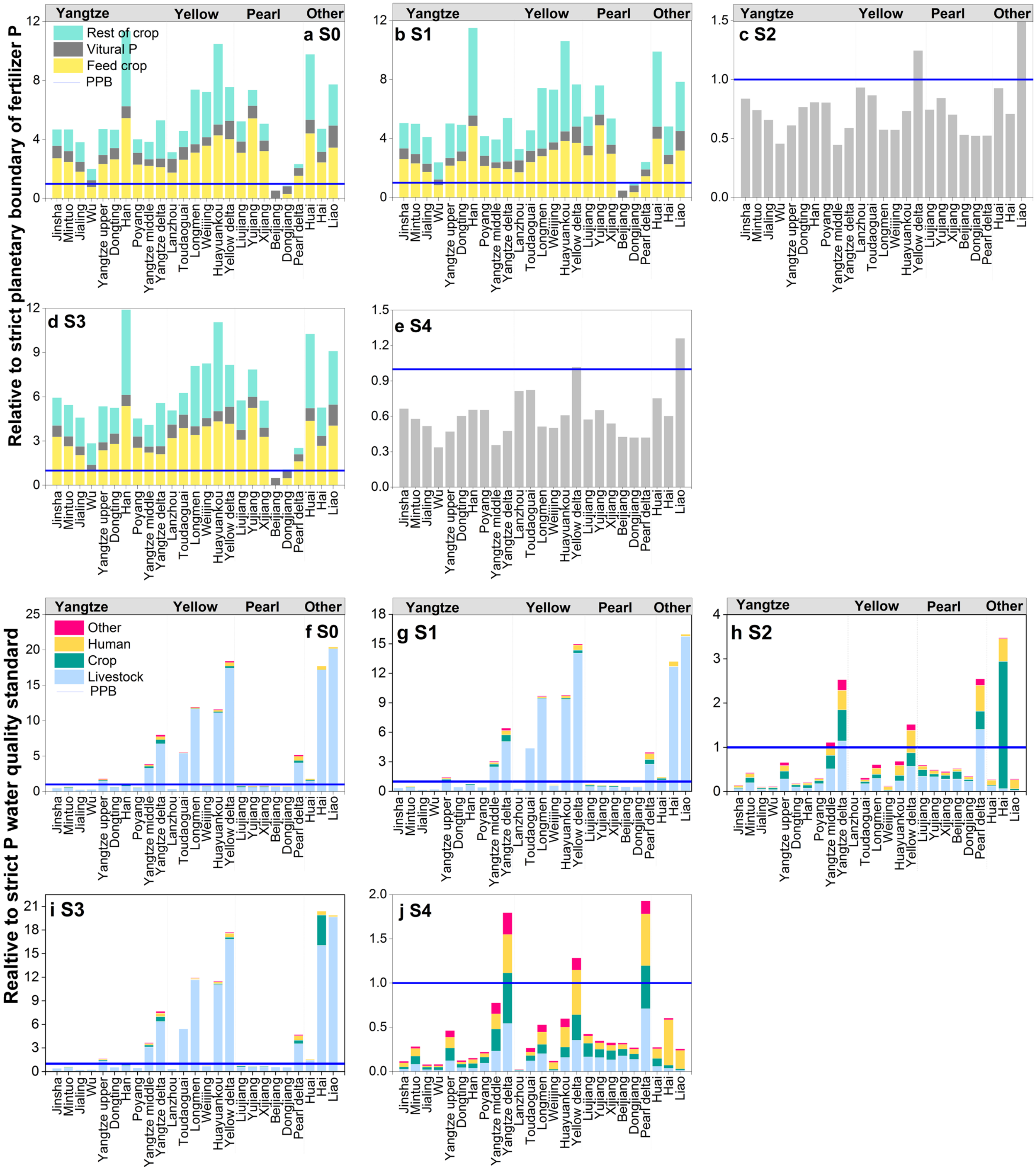
Extended Data Fig. 6 | Overview of steps to optimize crop-livestock P management to ensure that P remain within the PPB. The icons of animal/crop/people/building icons were obtained from Office material library.



Extended Data Fig. 7 | Total P budget of crop-livestock system. a, Business as usual; **b**, Combined scenario in 2050. Unit: Gg P.

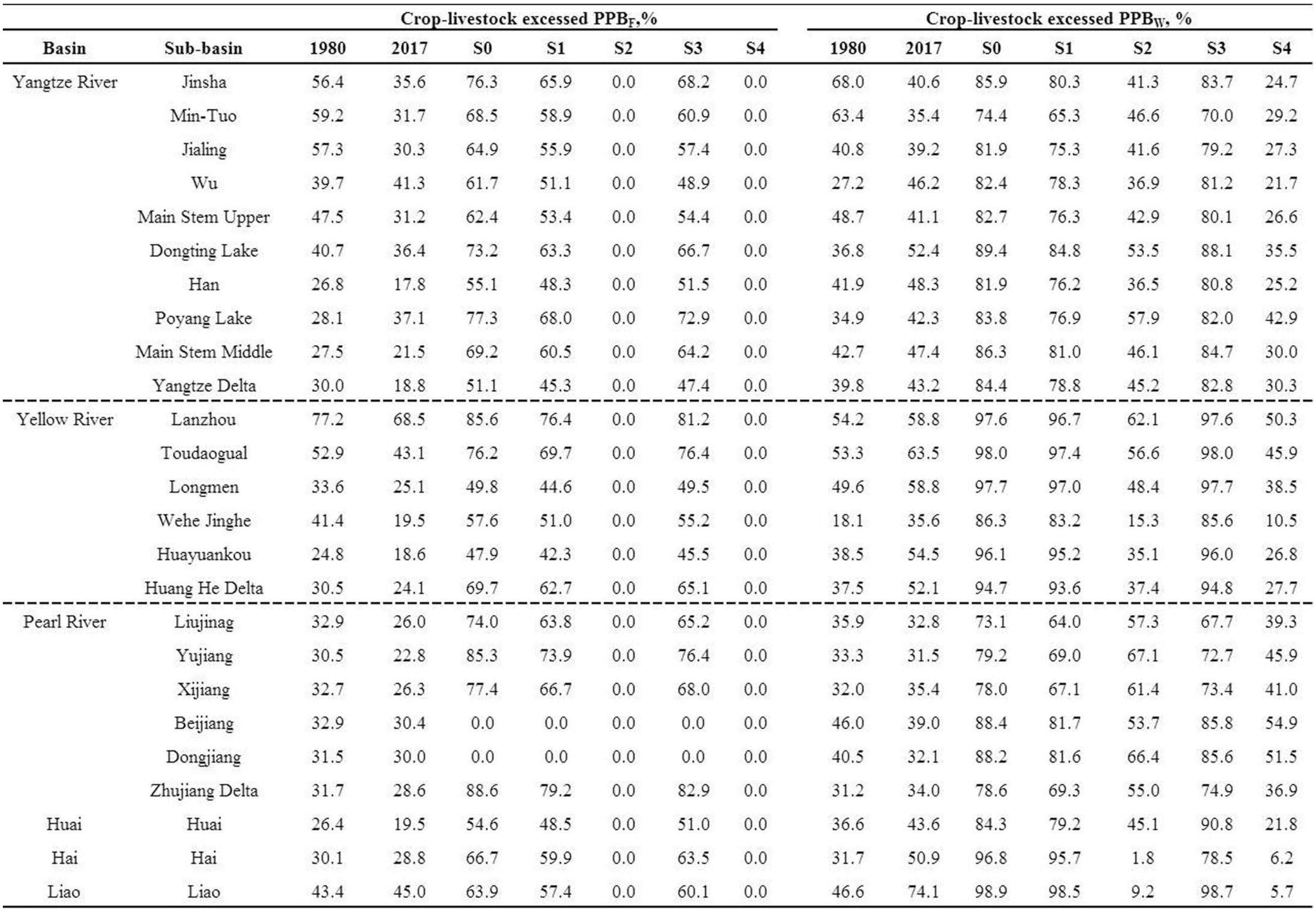


Extended Data Fig. 8 | Contribution of improvements in livestock production to ensure P within loose planetary boundary. **a**–**c**, Contribution of S1 (**a**),S2 (**b**) and S3 (**c**) in livestock production to ensure P within loose just fertilizer P use boundary; **d**-**f**, Contribution of S1 (**d**),S2 (**e**) and S3 (**f**) in livestock production to ensure P within loose safe water quality threshold. S1, improved feed P management; S2, improved manure management; S3, improved herb and structure management.



Extended Data Fig. 9 | Contribution of improvements in livestock production to ensure P within strict planetary boundary. **a**–**e**, Contribution of S0 (**a**), S1 (**b**), S2 (**c**), S3 (**d**) and S4 (**e**) in livestock production to ensure P within strict just fertilizer P use boundary; **f**-**j**, Contribution of S0 (**f**), S1 (**g**), S2 (**h**), S3 (**i**) and S4 (**j**) in livestock production to ensure P within strict safe water quality threshold. S0, business as usual; S1, improved feed P management; S2, improved manure management; S3, improved herb and structure management. S4, the scenario that combination of improved feed, manure and structure management.

Extended Data Table 1 | he rate of crop-livestock contributed to P flow excess PPB for just fertilizer P use (PPB_F) and safe water quality (PPB_W)



		Crop-livestock excessed PPB_F,%							Crop-livestock excessed PPB_W, %						
Basin	**Sub-basin**	**1980**	**2017**	**S0**	**S1**	**S2**	**S3**	**S4**	**1980**	**2017**	**S0**	**S1**	**S2**	**S3**	**S4**
Yangtze River	Jinsha	56.4	35.6	76.3	65.9	0.0	68.2	0.0	68.0	40.6	85.9	80.3	41.3	83.7	24.7
	Min-Tuo	59.2	31.7	68.5	58.9	0.0	60.9	0.0	63.4	35.4	74.4	65.3	46.6	70.0	29.2
	Jialing	57.3	30.3	64.9	55.9	0.0	57.4	0.0	40.8	39.2	81.9	75.3	41.6	79.2	27.3
	Wu	39.7	41.3	61.7	51.1	0.0	48.9	0.0	27.2	46.2	82.4	78.3	36.9	81.2	21.7
	Main Stem Upper	47.5	31.2	62.4	53.4	0.0	54.4	0.0	48.7	41.1	82.7	76.3	42.9	80.1	26.6
	Dongting Lake	40.7	36.4	73.2	63.3	0.0	66.7	0.0	36.8	52.4	89.4	84.8	53.5	88.1	35.5
	Han	26.8	17.8	55.1	48.3	0.0	51.5	0.0	41.9	48.3	81.9	76.2	36.5	80.8	25.2
	Poyang Lake	28.1	37.1	77.3	68.0	0.0	72.9	0.0	34.9	42.3	83.8	76.9	57.9	82.0	42.9
	Main Stem Middle	27.5	21.5	69.2	60.5	0.0	64.2	0.0	42.7	47.4	86.3	81.0	46.1	84.7	30.0
	Yangtze Delta	30.0	18.8	51.1	45.3	0.0	47.4	0.0	39.8	43.2	84.4	78.8	45.2	82.8	30.3
Yellow River	Lanzhou	77.2	68.5	85.6	76.4	0.0	81.2	0.0	54.2	58.8	97.6	96.7	62.1	97.6	50.3
	Toudaogual	52.9	43.1	76.2	69.7	0.0	76.4	0.0	53.3	63.5	98.0	97.4	56.6	98.0	45.9
	Longmen	33.6	25.1	49.8	44.6	0.0	49.5	0.0	49.6	58.8	97.7	97.0	48.4	97.7	38.5
	Wehe Jinghe	41.4	19.5	57.6	51.0	0.0	55.2	0.0	18.1	35.6	86.3	83.2	15.3	85.6	10.5
	Huayuankou	24.8	18.6	47.9	42.3	0.0	45.5	0.0	38.5	54.5	96.1	95.2	35.1	96.0	26.8
	Huang He Delta	30.5	24.1	69.7	62.7	0.0	65.1	0.0	37.5	52.1	94.7	93.6	37.4	94.8	27.7
Pearl River	Liujinag	32.9	26.0	74.0	63.8	0.0	65.2	0.0	35.9	32.8	73.1	64.0	57.3	67.7	39.3
	Yujiang	30.5	22.8	85.3	73.9	0.0	76.4	0.0	33.3	31.5	79.2	69.0	67.1	72.7	45.9
	Xijiang	32.7	26.3	77.4	66.7	0.0	68.0	0.0	32.0	35.4	78.0	67.1	61.4	73.4	41.0
	Beijiang	32.9	30.4	0.0	0.0	0.0	0.0	0.0	46.0	39.0	88.4	81.7	53.7	85.8	54.9
	Dongjiang	31.5	30.0	0.0	0.0	0.0	0.0	0.0	40.5	32.1	88.2	81.6	66.4	85.6	51.5
	Zhujiang Delta	31.7	28.6	88.6	79.2	0.0	82.9	0.0	31.2	34.0	78.6	69.3	55.0	74.9	36.9
Huai	Huai	26.4	19.5	54.6	48.5	0.0	51.0	0.0	36.6	43.6	84.3	79.2	45.1	90.8	21.8
Hai	Hai	30.1	28.8	66.7	59.9	0.0	63.5	0.0	31.7	50.9	96.8	95.7	1.8	78.5	6.2
Liao	Liao	43.4	45.0	63.9	57.4	0.0	60.1	0.0	46.6	74.1	98.9	98.5	9.2	98.7	5.7

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Records of fertilizer P application and production of livestock are from China’s National Bureau of Statistics. Data of crop feed imports are from FAOSTAT. Population data – global and Chinese – are from the United Nations. Data on discharge losses of livestock manure are from China’s Ministry of Ecology and Environment. Major parameters related to the phosphorus (P) content of feed crops and livestock production, P recommendations for livestock feed, P losses of different crop-livestock systems, as well as P planetary boundaries were collected from the literature referenced in the manuscript.

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	not applicable.
Population characteristics	not applicable.
Recruitment	not applicable.
Ethics oversight	not applicable.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	*Describe how sample size was determined, detailing any statistical methods used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient.*
Data exclusions	*Describe any data exclusions. If no data were excluded from the analyses, state so OR if data were excluded, describe the exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.*
Replication	*Describe the measures taken to verify the reproducibility of the experimental findings. If all attempts at replication were successful, confirm this OR if there are any findings that were not replicated or cannot be reproduced, note this and describe why.*
Randomization	*Describe how samples/organisms/participants were allocated into experimental groups. If allocation was not random, describe how covariates were controlled OR if this is not relevant to your study, explain why.*
Blinding	*Describe whether the investigators were blinded to group allocation during data collection and/or analysis. If blinding was not possible, describe why OR explain why blinding was not relevant to your study.*

Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	*Briefly describe the study type including whether data are quantitative, qualitative, or mixed-methods (e.g. qualitative cross-sectional, quantitative experimental, mixed-methods case study).*
Research sample	*State the research sample (e.g. Harvard university undergraduates, villagers in rural India) and provide relevant demographic information (e.g. age, sex) and indicate whether the sample is representative. Provide a rationale for the study sample chosen. For studies involving existing datasets, please describe the dataset and source.*
Sampling strategy	*Describe the sampling procedure (e.g. random, snowball, stratified, convenience). Describe the statistical methods that were used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient. For qualitative data, please indicate whether data saturation was considered, and what criteria were used to decide that no further sampling was needed.*
Data collection	*Provide details about the data collection procedure, including the instruments or devices used to record the data (e.g. pen and paper, computer, eye tracker, video or audio equipment) whether anyone was present besides the participant(s) and the researcher, and whether the researcher was blind to experimental condition and/or the study hypothesis during data collection.*
Timing	*Indicate the start and stop dates of data collection. If there is a gap between collection periods, state the dates for each sample cohort.*

Data exclusions	*If no data were excluded from the analyses, state so OR if data were excluded, provide the exact number of exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.*
Non-participation	*State how many participants dropped out/declined participation and the reason(s) given OR provide response rate OR state that no participants dropped out/declined participation.*
Randomization	*If participants were not allocated into experimental groups, state so OR describe how participants were allocated to groups, and if allocation was not random, describe how covariates were controlled.*

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The safe and just planetary boundary of phosphorus(P) needs to be achieved at sub-national level, to ensure a stability and resilience Earth system. However, how livestock production contributes to the exceedance of the planetary boundary of P at sub-basin scale was still unclear in China, where P fertilizer were overused and P related water pollution was severe. Our results indicate that the livestock production increased the fertilizer P consumption by 5-fold and P losses by 2-fold from 1980 to 2017. Currently, the crop-livestock system responsible for the exceedance of just fertilizer P use threshold by 30%, and safe water quality threshold by 45% for 25 sub-basins in China. Improving the crop-livestock system will keep all sub-basins within water quality safe and multi-generation just requirements for P in 2050. Our results may generate new insights into guiding policies supporting sustainable livestock production to achieve safe and just planetary at country level.
Research sample	(1) five different animal categories (pig, layer, broiler, dairy, beef, and sheep). (2) three different crop-livestock production system(mixed, grazing, and landless). (3) six large river basins (Yellow, Liao, Hai, Yangtze, Huai, and Pearl Rivers), which covered 25 sub- basins.
Sampling strategy	(1) This study analyzed the P flow in different crop-livestock system for 25 sub-basins in China using NUFER(NUtrient flow in Food chains, Environment and Resources use) animal model; (2) the effect of livestock production on water quality was assessed by MARINA(Model to Assess River Inputs of Nutrients to seAs) 1.0 model; (3) the impact of the crop-livestock system production on safe and just planetary boundary were examined by bottom-up and top-down approach, respectively.
Data collection	Data were collected from National Bureal of Statistics of China and FAOSTAT. Population data of China and global were from the United Nations. The discharge losses of livestock manure are from Ministry of Ecology and Environment of China. The major of the parameters related to P content of crop feed and livestock production, feed P recommend for livestock, P recycle to field of different crop-livestock system, planetary boundary for P were collected from literatures.
Timing and spatial scale	The P flow in different crop-livestock system were analyzed for each sub-basin during 1980-2050 in China. The effect of livestock production on water quality were assessed during 1980, 2017 and 2050. The impacts of the crop-livestock system production on safe and just planetary boundary were examined in 1980, 2017 and 2050.
Data exclusions	Not applicable to this study.
Reproducibility	Not applicable to this study.
Randomization	Not applicable to this study.
Blinding	Not applicable to this study.

Did the study involve field work? ☐ Yes ☒ No

Field work, collection and transport

Field conditions	*Describe the study conditions for field work, providing relevant parameters (e.g. temperature, rainfall).*
Location	*State the location of the sampling or experiment, providing relevant parameters (e.g. latitude and longitude, elevation, water depth).*
Access & import/export	*Describe the efforts you have made to access habitats and to collect and import/export your samples in a responsible manner and in compliance with local, national and international laws, noting any permits that were obtained (give the name of the issuing authority, the date of issue, and any identifying information).*
Disturbance	*Describe any disturbance caused by the study and how it was minimized.*

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☒	☐	Animals and other organisms
☒	☐	Clinical data
☒	☐	Dual use research of concern

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging

Antibodies

Antibodies used	*Describe all antibodies used in the study; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Validation	*Describe the validation of each primary antibody for the species and application, noting any validation statements on the manufacturer's website, relevant citations, antibody profiles in online databases, or data provided in the manuscript.*

Eukaryotic cell lines

Policy information about cell lines and Sex and Gender in Research

Cell line source(s)	*State the source of each cell line used and the sex of all primary cell lines and cells derived from human participants or vertebrate models.*
Authentication	*Describe the authentication procedures for each cell line used OR declare that none of the cell lines used were authenticated.*
Mycoplasma contamination	*Confirm that all cell lines tested negative for mycoplasma contamination OR describe the results of the testing for mycoplasma contamination OR declare that the cell lines were not tested for mycoplasma contamination.*
Commonly misidentified lines (See ICLAC register)	*Name any commonly misidentified cell lines used in the study and provide a rationale for their use.*

Palaeontology and Archaeology

Specimen provenance	*Provide provenance information for specimens and describe permits that were obtained for the work (including the name of the issuing authority, the date of issue, and any identifying information). Permits should encompass collection and, where applicable, export.*
Specimen deposition	*Indicate where the specimens have been deposited to permit free access by other researchers.*
Dating methods	*If new dates are provided, describe how they were obtained (e.g. collection, storage, sample pretreatment and measurement), where they were obtained (i.e. lab name), the calibration program and the protocol for quality assurance OR state that no new dates are provided.*

☐ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

Ethics oversight	*Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	*For laboratory animals, report species, strain and age OR state that the study did not involve laboratory animals.*
Wild animals	*Provide details on animals observed in or captured in the field; report species and age where possible. Describe how animals were caught and transported and what happened to captive animals after the study (if killed, explain why and describe method; if released, say where and when) OR state that the study did not involve wild animals.*
Reporting on sex	*Indicate if findings apply to only one sex; describe whether sex was considered in study design, methods used for assigning sex.*

Reporting on sex	*Provide data disaggregated for sex where this information has been collected in the source data as appropriate; provide overall numbers in this Reporting Summary. Please state if this information has not been collected. Report sex-based analyses where performed, justify reasons for lack of sex-based analysis.*
Field-collected samples	*For laboratory work with field-collected samples, describe all relevant parameters such as housing, maintenance, temperature, photoperiod and end-of-experiment protocol OR state that the study did not involve samples collected from the field.*
Ethics oversight	*Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Clinical data

Policy information about clinical studies

All manuscripts should comply with the ICMJE guidelines for publication of clinical research and a completed CONSORT checklist must be included with all submissions.

Clinical trial registration	*Provide the trial registration number from ClinicalTrials.gov or an equivalent agency.*
Study protocol	*Note where the full trial protocol can be accessed OR if not available, explain why.*
Data collection	*Describe the settings and locales of data collection, noting the time periods of recruitment and data collection.*
Outcomes	*Describe how you pre-defined primary and secondary outcome measures and how you assessed these measures.*

Dual use research of concern

Policy information about dual use research of concern

Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes	
☐	☐	Public health
☐	☐	National security
☐	☐	Crops and/or livestock
☐	☐	Ecosystems
☐	☐	Any other significant area

Experiments of concern

Does the work involve any of these experiments of concern:

No	Yes	
☐	☐	Demonstrate how to render a vaccine ineffective
☐	☐	Confer resistance to therapeutically useful antibiotics or antiviral agents
☐	☐	Enhance the virulence of a pathogen or render a nonpathogen virulent
☐	☐	Increase transmissibility of a pathogen
☐	☐	Alter the host range of a pathogen
☐	☐	Enable evasion of diagnostic/detection modalities
☐	☐	Enable the weaponization of a biological agent or toxin
☐	☐	Any other potentially harmful combination of experiments and agents

ChIP-seq

Data deposition

☐ Confirm that both raw and final processed data have been deposited in a public database such as GEO.

☐ Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

Data access links *May remain private before publication.*	*For "Initial submission" or "Revised version" documents, provide reviewer access links. For your "Final submission" document, provide a link to the deposited data.*

Files in database submission	*Provide a list of all files available in the database submission.*
Genome browser session (e.g. UCSC)	*Provide a link to an anonymized genome browser session for "Initial submission" and "Revised version" documents only, to enable peer review. Write "no longer applicable" for "Final submission" documents.*

Methodology

Replicates	*Describe the experimental replicates, specifying number, type and replicate agreement.*
Sequencing depth	*Describe the sequencing depth for each experiment, providing the total number of reads, uniquely mapped reads, length of reads and whether they were paired- or single-end.*
Antibodies	*Describe the antibodies used for the ChIP-seq experiments; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Peak calling parameters	*Specify the command line program and parameters used for read mapping and peak calling, including the ChIP, control and index files used.*
Data quality	*Describe the methods used to ensure data quality in full detail, including how many peaks are at FDR 5% and above 5-fold enrichment.*
Software	*Describe the software used to collect and analyze the ChIP-seq data. For custom code that has been deposited into a community repository, provide accession details.*

Flow Cytometry

Plots

Confirm that:

☐ The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).

☐ The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).

☐ All plots are contour plots with outliers or pseudocolor plots.

☐ A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparation	*Describe the sample preparation, detailing the biological source of the cells and any tissue processing steps used.*
Instrument	*Identify the instrument used for data collection, specifying make and model number.*
Software	*Describe the software used to collect and analyze the flow cytometry data. For custom code that has been deposited into a community repository, provide accession details.*
Cell population abundance	*Describe the abundance of the relevant cell populations within post-sort fractions, providing details on the purity of the samples and how it was determined.*
Gating strategy	*Describe the gating strategy used for all relevant experiments, specifying the preliminary FSC/SSC gates of the starting cell population, indicating where boundaries between "positive" and "negative" staining cell populations are defined.*

☐ Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

Magnetic resonance imaging

Experimental design

Design type	*Indicate task or resting state; event-related or block design.*
Design specifications	*Specify the number of blocks, trials or experimental units per session and/or subject, and specify the length of each trial or block (if trials are blocked) and interval between trials.*
Behavioral performance measures	*State number and/or type of variables recorded (e.g. correct button press, response time) and what statistics were used to establish that the subjects were performing the task as expected (e.g. mean, range, and/or standard deviation across subjects).*

Acquisition

Imaging type(s)	*Specify: functional, structural, diffusion, perfusion.*
Field strength	*Specify in Tesla*
Sequence & imaging parameters	*Specify the pulse sequence type (gradient echo, spin echo, etc.), imaging type (EPI, spiral, etc.), field of view, matrix size, slice thickness, orientation and TE/TR/flip angle.*
Area of acquisition	*State whether a whole brain scan was used OR define the area of acquisition, describing how the region was determined.*

Diffusion MRI ☐ Used ☐ Not used

Preprocessing

Preprocessing software	*Provide detail on software version and revision number and on specific parameters (model/functions, brain extraction, segmentation, smoothing kernel size, etc.).*
Normalization	*If data were normalized/standardized, describe the approach(es): specify linear or non-linear and define image types used for transformation OR indicate that data were not normalized and explain rationale for lack of normalization.*
Normalization template	*Describe the template used for normalization/transformation, specifying subject space or group standardized space (e.g. original Talairach, MNI305, ICBM152) OR indicate that the data were not normalized.*
Noise and artifact removal	*Describe your procedure(s) for artifact and structured noise removal, specifying motion parameters, tissue signals and physiological signals (heart rate, respiration).*
Volume censoring	*Define your software and/or method and criteria for volume censoring, and state the extent of such censoring.*

Statistical modeling & inference

Model type and settings	*Specify type (mass univariate, multivariate, RSA, predictive, etc.) and describe essential details of the model at the first and second levels (e.g. fixed, random or mixed effects; drift or auto-correlation).*
Effect(s) tested	*Define precise effect in terms of the task or stimulus conditions instead of psychological concepts and indicate whether ANOVA or factorial designs were used.*

Specify type of analysis: ☐ Whole brain ☐ ROI-based ☐ Both

Statistic type for inference (See Eklund et al. 2016)	*Specify voxel-wise or cluster-wise and report all relevant parameters for cluster-wise methods.*
Correction	*Describe the type of correction and how it is obtained for multiple comparisons (e.g. FWE, FDR, permutation or Monte Carlo).*

Models & analysis

n/a	Involved in the study
☐	☐ Functional and/or effective connectivity
☐	☐ Graph analysis
☐	☐ Multivariate modeling or predictive analysis

Functional and/or effective connectivity	*Report the measures of dependence used and the model details (e.g. Pearson correlation, partial correlation, mutual information).*
Graph analysis	*Report the dependent variable and connectivity measure, specifying weighted graph or binarized graph, subject- or group-level, and the global and/or node summaries used (e.g. clustering coefficient, efficiency, etc.).*
Multivariate modeling and predictive analysis	*Specify independent variables, features extraction and dimension reduction, model, training and evaluation metrics.*