





# Labour market evolution is a key determinant of global agroeconomic and environmental futures

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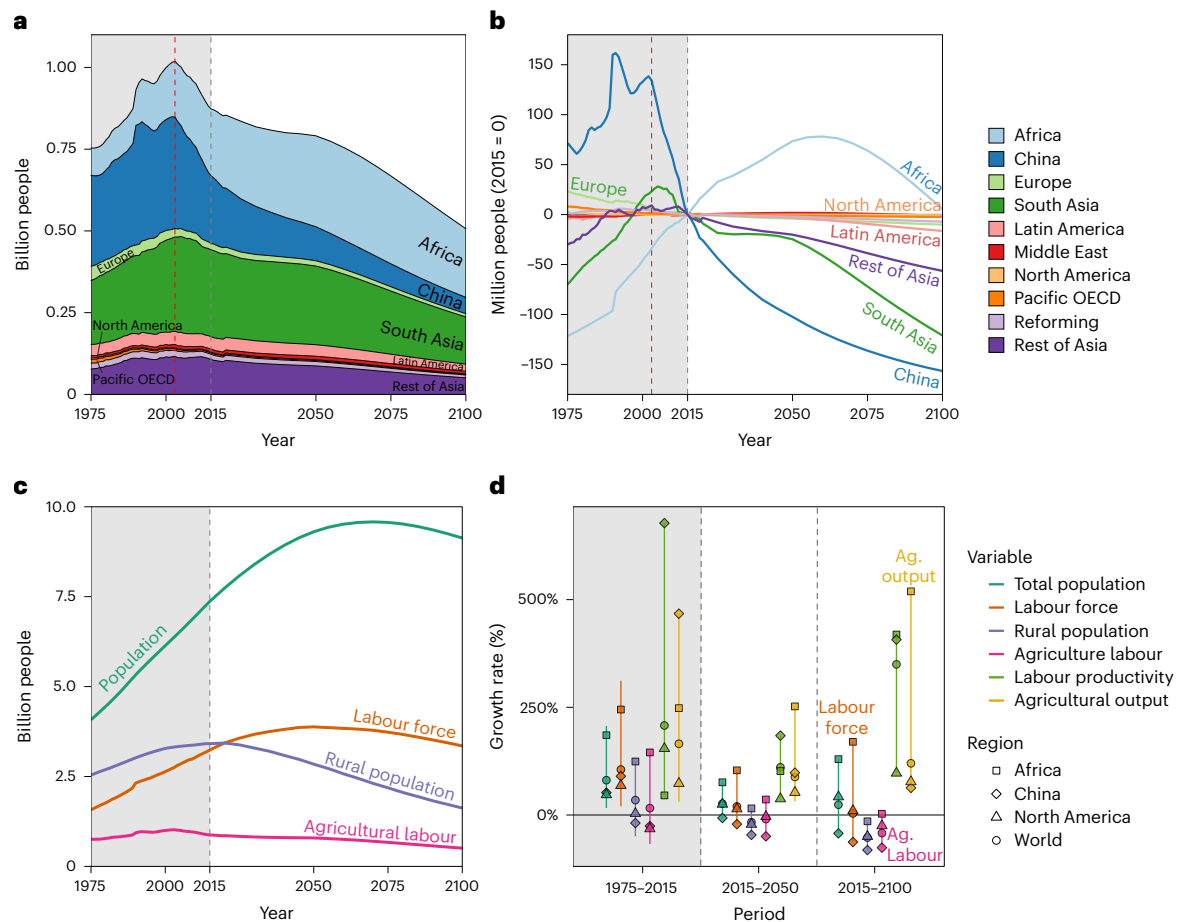
Long-term labour market evolution shapes agricultural transformation through labour productivity growth and labour market transitions. Despite its importance in agricultural production, labour has been overlooked when exploring the agrifood–water–environment–climate nexus. Here we incorporate evolving labour markets into multisector dynamic modelling to examine their agroeconomic and environmental implications. Our projections show that the recent decline of global agricultural employment persists, with an estimated decadal decrease of 43 million people by 2100, strengthening the decoupling of labour from production. Exploring scenarios with varying labour productivity and supply factors, we also show a positive relationship between productivity-adjusted labour supply and agricultural emissions, with more pronounced and heterogeneous regional and sectoral responses. While highlighting the pressing need to capture labour dynamics in integrated human–Earth systems, our study lays the foundation for further investigation into labour market responses and feedback in broader scenarios.

The long-term evolution of the agricultural labour market is characterized by the growth of labour productivity and transitions in labour markets<sup>1</sup>. This evolution has fuelled agricultural transformation, facilitated sectoral integration between agriculture and non-agriculture sectors, and, consequently, contributed to economic development<sup>2,3</sup>. Globally, labour engaged in primary agriculture peaked in the early 2000s at approximately 1.1 billion people and has since declined by 20% to 0.88 billion in 2019, despite the continuously increasing population, total labour force and agricultural output<sup>4</sup> (see historical periods in Fig. 1). The global decoupling, both between agricultural labour demand and output and between agricultural labour supply and the total labour force is likely to continue in the foreseeable future, especially in developing economies<sup>5</sup>.

In developed regions, the structural changes in agriculture, largely driven by the ‘labour pull’ from industrialization, have been completed, as evidenced by the low agricultural employment share. For example, the United States reached 10%—a milestone of agricultural

transformation defined by Alvarez-Cuadrado and Poschke<sup>6</sup>—in the 1950s (and 2% in the 1990s), a substantial drop from 75% in 1800. The recent global decline in agricultural employment has been greatly driven by urbanization and the ‘labour push’ from education and mechanization in emerging markets and developing economies, for example, China, India and Brazil<sup>7–9</sup>. For instance, China witnessed a decrease of over 150 million agricultural workers in the past two decades, concurrently with substantial growth in agricultural output. Conversely, the least developed countries are still experiencing growth in agricultural labour. Currently, over 50% of the labour force in sub-Saharan Africa works in primary agriculture, while the world average is around 25%.

Despite their critical role in shaping global agricultural transformation, labour market dynamics have long been overlooked in global economic and multisector dynamic modelling (Supplementary Discussion, section 1 and Supplementary Table 1). On the one hand, most partial equilibrium models, such as GLOBIOM, IMAGE, IMPACT, MagPIE and GCAM, do not explicitly represent agricultural labour markets<sup>10</sup>.



**Fig. 1 | Historical trends and future projections of agricultural labour-related metrics. a, b,** Agricultural labour input by region (stacked areas; see Supplementary Table 2 for the IPCC R10 region mapping) (**a**), and the corresponding changes (lines) over time relative to 2015 (**b**). **c,** Changes in population and labour-related metrics at the world level. **d,** The growth rate of key variables by region and period. The point-range plots show values for key regions (shape of the point) and the R10 region ranges (whiskers). Vertical dotted lines, where applicable, highlight 2003 (red) and 2015 (grey). Data from 1975

to 2015 (grey background areas) are historical observations compiled based on USDA and ILO data. Annotation is added for key regions (**a, b**) and variables (**c, d**). Data after 2015 are projections from the 'Evolving' scenario (GCAM) in the current study (agricultural labour, labour productivity and value output) or the SSP database (population and labour force). The agricultural labour data presented encompass labour in primary crop, livestock and forestry production, while labour in the fishery sector (3% globally) is not included.

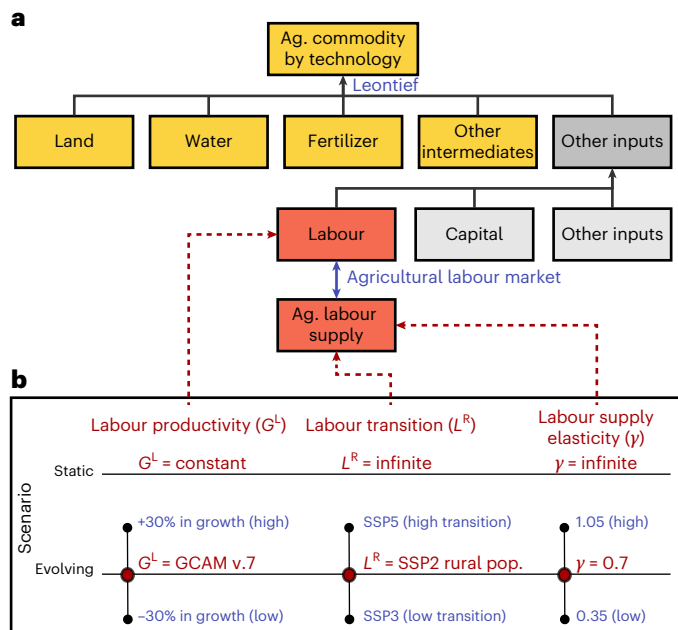
On the other hand, general equilibrium models, such as AIM, ENVISAGE, EPPA, MAGNET and FARM, encompass the entire economy adhering to macroeconomic closures but face challenges in tracing physical labour units<sup>11</sup>, further complicating the connection between labour supply and the labour force or population<sup>12,13</sup>. Notably, the models mentioned above are workhorses in evaluating long-run socioeconomic and climate scenarios, contributing the majority of the vetted pathways to the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report (AR6) Scenario Database<sup>14</sup>. The limited representation of agricultural labour in these models may hinder a comprehensive understanding of the complex interplay between agriculture, economy, environment and broader Earth systems.

Existing studies on agricultural labour, whether empirical analysis or economic equilibrium modelling, tend to be region or sector specific<sup>15–17</sup> or comparatively static<sup>18,19</sup>, and usually encompass limited environmental outcomes<sup>20</sup>. Besides labour, agricultural production also demands inputs with more direct environmental implications, such as land, water and fertilizer, and serves as a key source of greenhouse gas emissions (GHG) through activities such as rice cultivation, synthetic fertilizer application, waste burning, enteric fermentation and land-use change<sup>21</sup>. Thus, dynamic changes in labour markets may have critical environmental implications through market-mediated

impacts on agricultural production, factor input substitution and international trade<sup>17,20,22</sup>. However, the role of agricultural labour has been neglected in existing studies that explore the agrifood–water–environment–climate nexus<sup>23–27</sup>.

In this article, we explore the sensitivity of agro-economic and environmental outcomes to key factors depicting future agricultural labour market evolution. We employ an open-source multisector dynamic model, the Global Change Analysis Model (GCAM)<sup>28</sup>, to compare systematically designed sensitivity scenarios around assumptions related to agricultural labour market evolution (Methods). Specifically, we modify a recent version of GCAM (v.7.0) to represent agricultural labour input demand in production technologies and incorporate a wage-responsive labour supply that is linked to labour transition assumptions (Fig. 2). The updated model captures the dynamics of future agricultural labour market evolution, including changes in labour productivity, labour transitions and the labour force. Thus, it expands historical agricultural labour inputs and related metrics to future periods endogenously within the integrated human–Earth system modelling framework.

Considering assumptions of agricultural labour productivity growth, labour transition (implied by rural population changes) and labour supply elasticity, the reference projections are updated and



**Fig. 2 | Agricultural labour market representation and scenario design.**

**a**, Schematic illustrating changes in a generic agricultural production structure at the technology level (Leontief production function) to depict labour input demand and its connection to labour supply in the GCAM. The yellow boxes represent endogenous variables in the model, and ‘other intermediates’ depict cross-sectoral transitions, such as crop feed inputs in the livestock sector. ‘Other inputs’ is an aggregation of exogenously represented inputs, which is further disaggregated into labour, capital and the remaining ‘other inputs’. **b**, Scenarios for the evolution of the agricultural labour market by varying key factors, including agricultural labour productivity, availability and supply elasticity. Dotted line arrows depict the connections between these factors and the labour market in **a**. The ‘Static’ scenario represents the original GCAM scenario without explicit representations of the labour market. The ‘Evolving’ scenario is the updated reference scenario with explicit representations of the labour market and its evolution factors. Sensitivity scenarios around the market evolution assumptions are displayed.

referred to as the ‘Evolving’ scenario in this study. For comparison, we include a scenario with constant labour productivity and perfectly elastic labour supply, denoted as the ‘Static’ scenario. It is noteworthy that the Static scenario, while extreme, provides a sufficient interpretation for the labour market implied by original assumptions when agricultural labour was not explicitly represented in the modelling because the effective labour supply, that is, productivity-adjusted labour (Supplementary Discussion, section 2.4), and other agro-economic projections would be identical. Thus, the scenario comparison between Evolving and Static also reveals the impact of neglecting agricultural labour dynamics in modelling. In addition, relative to the Evolving scenario, we also examine three sets of sensitivity scenarios with varying agricultural labour productivity, labour transition or labour supply elasticity, respectively. By comparing Evolving with Static and other sensitivity scenarios, our results provide fundamentally new insights into understanding the critical labour market linkage across sectors and demonstrate the sensitivity of agro-economic responses and the corresponding environmental consequences to future labour market evolution assumptions, highlighting the importance of capturing labour dynamics in the multisector dynamic modelling framework.

## Results

### Labour inputs in agricultural production

By capturing the drivers of future labour market evolution, the results from the Evolving scenario reveal a 42% decrease in global agricultural

labour, or 366 million people (not including fishery), from 2015 to 2100 (Fig. 1a,b), primarily through reductions in China (157 million), South Asia (121 million) and the rest of Asia (56 million). The overall global decrease is less pronounced by the mid-century (9% or 82 million), as Africa adds 73 million people in agriculture by 2050. After peaking around 2060, the increasing trend in Africa reverses, dropping back to its 2020 value by 2100. With a substantial increase in agricultural value output across regions, for example, +60% in China to +520% in Africa by 2100, the results demonstrate a strengthening global decoupling between agricultural labour input and output (Fig. 1d). The global agricultural employment share decreases to about 15% by 2100, with a trend of regional convergence as developing regions accelerate agricultural transformation (Fig. 1c and Supplementary Fig. 8).

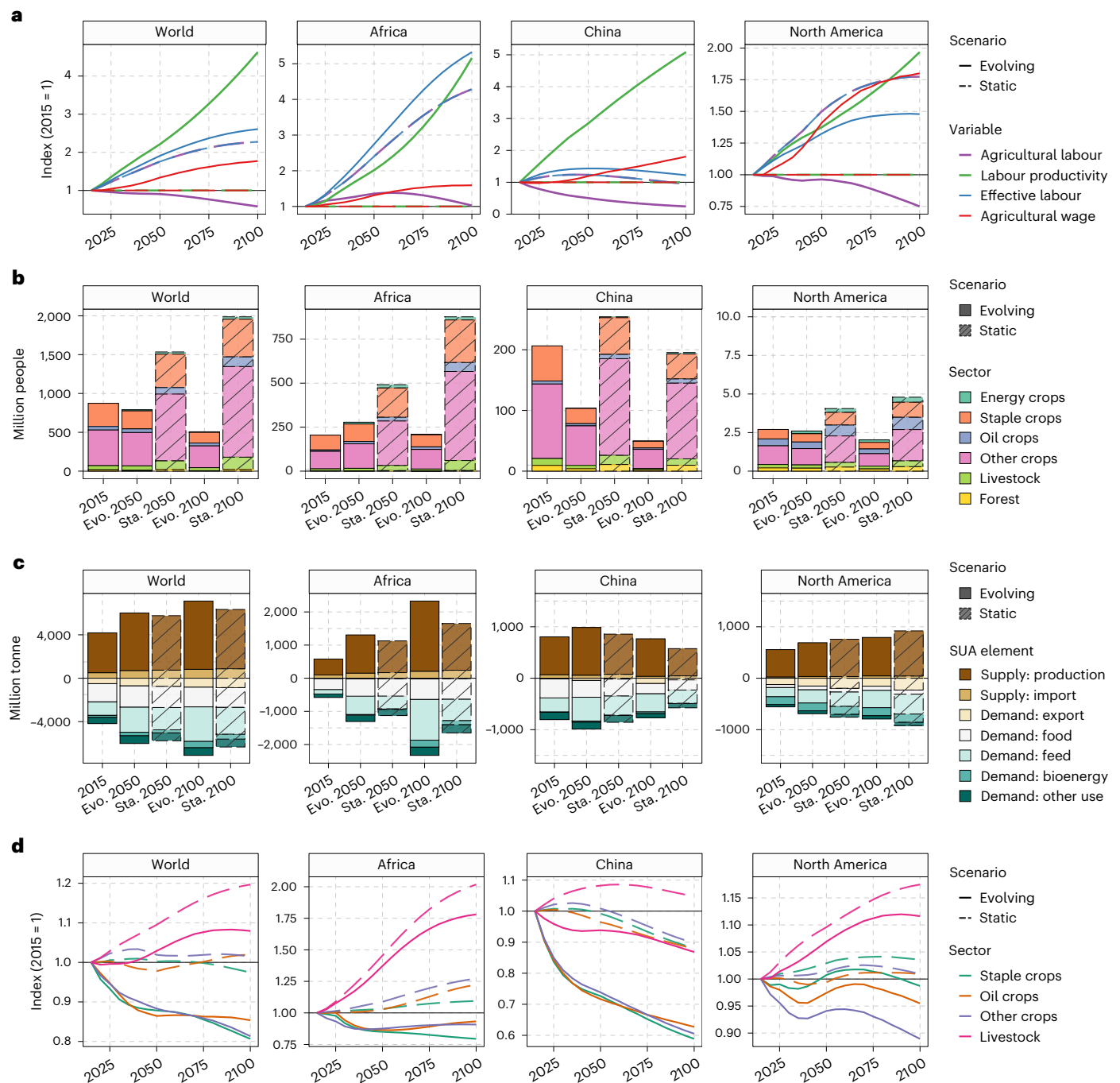
The decline in labour input over time in the Evolving scenario is observed in all agricultural sectors except for purpose-grown energy crops (Fig. 3b). The expansion of energy crops is expected to commence after 2025, and by 2100, about 1.5% of agricultural labour globally works in this sector, with a more substantial share in developed regions, for example, 8% (0.16 million) in North America. The majority of the agricultural labour decrease occurred in crop sectors (43% or 348 million). A faster labour decline is seen in staple crops (54% or 161 million) compared with oil and other crops (37% or 189 million) or livestock (16% or 14 million) because non-staple food and non-food consumptions are more elastic and livestock sectors tend to be relatively less labour-intensive.

In the Static scenario, with no productivity change and unlimited labour supply, that is, fixed wage rates, agricultural labour input more than doubles globally (+127%), more than quadruples in Africa (+329%), increases considerably in North America (+77%) and slightly decreases in China (−5%) by 2100 (Fig. 3a and Supplementary Fig. 10). This is in stark contrast to the Evolving scenario, which estimates an overall 1.5 billion fewer people employed in agriculture (lower in all agricultural sectors) by the end of the century compared to Static.

However, the difference is less pronounced when looking at productivity-adjusted labour, that is, effective labour, because the impact of labour productivity and labour supply factors may offset each other. Consequently, labour market evolution in the Evolving scenario encourages a moderate global effective labour increase (+15%) by 2100 compared to the Static assumptions (Fig. 3a). In other words, when considering labour market evolution in Evolving, labour productivity growth outweighs the labour supply constraints in determining effective labour inputs at the world level. The impact is also regionally heterogeneous, ranging from −16% in North America to +29% in China, driven by regional differences in labour productivity, transitions and the consequential change in international trade patterns. Additionally, with more productive labour and an elastic labour supply, the agricultural wage rate also follows a growing trend in all regions, for example, +77% globally by 2100, ranging from +33% in the rest of Asia to +116% in Reforming Economies (Supplementary Fig. 8).

### Agroeconomic implications of labour market evolution

The future evolution of the labour market directly affects agricultural production, leading to a cascading effect in agricultural markets. In the Evolving scenario, for staple crops, world production is projected to increase by 71% from 3,685 Mt in 2015 to 6,300 Mt in 2100 (Fig. 3c), partly driven by a more substantial labour yield increase (+270%) from 12.3 to 45.9 t per person in the same period. The corresponding demand-side changes include large increases in feed (+1,925 Mt) and bioenergy (+400 Mt) consumption and relatively moderate increases in food (+150 Mt) and other uses (+130 Mt) (Fig. 3c). Labour market evolution influences agricultural markets from both the supply and demand sides. On the supply side, higher staple crop production (+15% or +820 Mt) is encouraged by the similar increase in global effective labour (+15%) in Evolving versus Static (Fig. 3c). As labour yield growth is considerably faster than wage rate growth in the Evolving scenario,



**Fig. 3 | Impact of agricultural labour market evolution on key agroeconomic outcomes. a–d.** Projections from the Evolving and Static scenarios are presented for various agricultural labour market variables (**a**), labour by sector (**b**), supply utilization accounts (SUAs) for staple crops (**c**) and agricultural prices (**d**). **a**, Key agricultural labour market variables by region (world and three key regions in subpanels) and scenario. **b**, Stacked bars decomposing the agricultural labour in **a** by sector across scenarios, Evolving (Evo.) versus Static (Sta.), for

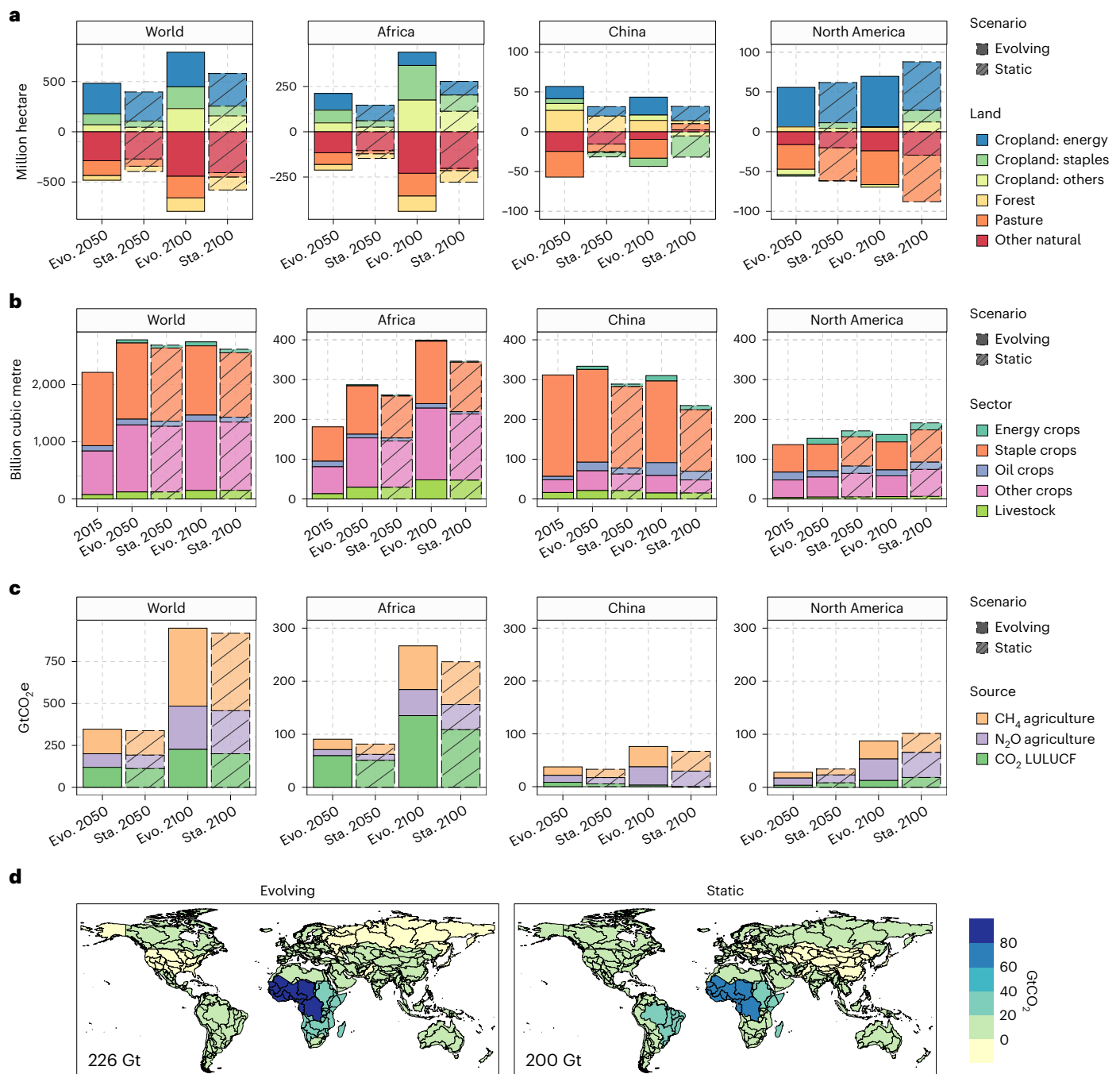
2050 and 2100. **c**, Stacked bars depicting the supply (positive values) and demand (negative values) balance (total supply offsets total demand) by region and scenario for 2050 and 2100. Staple crops include GCAM commodities of Wheat, Rice, Corn, OtherGrain, and RootTuber (Supplementary Table 3). **d**, The agricultural producer price index (2015 = 1) with breakdowns by region, sector and scenario. Data source: GCAM simulation results.

the labour cost share in production decreases, further driving down prices of staple crops by 17% globally compared with Static (Fig. 3d). Thus, on the demand side, the relatively lower crop prices encourage higher consumption of feed (+694 Mt), bioenergy (+120 Mt), and food (+6 Mt) (Fig. 3c).

Regionally, impacts on the supply utilization accounts for staple crops reflect the global responses for regions with higher effective labour due to labour market evolution, such as Africa and China,

and move in opposite directions for regions with smaller effective labour, such as North America. In Africa, the net import of staple crops in 2100 decreases by 37 Mt (16%), and the corresponding net import-to-production ratio also decreases from 16% to 9%, indicating a decline in the region's trade dependency under the Evolving scenario. The net export-to-production ratio decreases from 21% to 15% in North America but increases from 3% to 9% in China. Changes in international trade also play a critical role in regional results, due to





**Fig. 4 | Impact of agricultural labour market evolution on key environmental outcomes. a–d.** Projections from the Evolving and Static scenarios for land-use change (a), agricultural water withdrawal (b), cumulative emissions from agriculture and LULUCF (c), along with maps illustrating the cumulative LULUCF emissions (d). a, Stacked bars depict land-use change (relative to 2015), decomposed by land type across scenarios, Evolving (Evo.) versus Static (Sta.), by

region (world and three key regions in subpanels) for 2050 and 2100. b, Stacked bars representing agricultural water withdrawal by sector. c, Cumulative GHG emissions by source for the periods 2020–2050 and 2020–2100. d, The spatial decomposition of the 2020–2100 cumulative LULUCF carbon emissions by 32 GCAM regions, with net total values labelled (for example, 226 GtCO<sub>2</sub> in the Evolving scenario). Data source: GCAM simulation results.

labour market evolution and its effect on the comparative advantage across regions.

Similar supply utilization account responses are observed for other crops and livestock sectors even though impacts on livestock sectors are more complicated and regionally heterogeneous. Notably, livestock sectors tend to be less labour-intensive than crops, so the price decrease in livestock products under the Evolving scenario is smaller than that of crops, for example, –10% versus –18% in 2100 globally, and a more pronounced difference is seen in Africa (–12%

versus –28%) (Fig. 3d). This difference in price responses encourages dietary substitutions, that is, lower livestock consumption induced by relatively more expensive livestock products. The substitution effect (relatively lower livestock consumption) offsets the effect from the positive effective labour supply shift (lower production cost), resulting in minimal changes in global livestock production, for example, –1% in beef. In addition, as labour market evolution leads to lower crop prices but has no direct impact on pasture (no labour inputs), our results also show stronger substitutions between

feed crops and pasture in supplying feedstuff for ruminant livestock sectors.

### Environmental implications of labour market evolution

Global changes in agricultural production, triggered by dynamic changes in labour markets, impact other agricultural inputs such as land, water and fertilizer, with resulting environmental impacts. In the Evolving scenario, with global agricultural production growing from 2015 to 2100, cropland expands by about 790 Mha to 2,420 Mha, nitrogen fertilizer use grows by 80 to 190 MtN, and agricultural water withdrawal increases by 530 billion cubic metres (bcm) to 2,750 bcm (Fig. 4 and Supplementary Fig. 9). Compared with the Static scenario, the considerably higher overall production in the Evolving scenario entails increased consumption of agricultural inputs globally, for example, by 2100, +10% (+215 Mha) in cropland, +6% (+10 MtN) in fertilizer, and +5% (+130 bcm) in agricultural water withdrawal. In addition, the expanded cropland mainly replaces pasture (−175 Mha), forest (−5 Mha) and other natural land (−35 Mha) (Fig. 4a).

Changes in agricultural production technologies, including irrigation and fertilizer applications, and the redistribution of supply across regions, play pivotal roles in determining the environmental impacts of labour market evolution. In the case of staple crops, considering labour market evolution, the +15% increase in global production (Fig. 3c) and effective labour (Fig. 3a) is associated with disproportionate changes in other inputs: +16% (+120 Mha) in staple cropland, +5% (+4 MtN) in fertilizer and +7% (+85 bcm) in water withdrawal (Fig. 4a,b and Supplementary Fig. 7). Notably, the results indicate a global agricultural extensification, as the marginal staple crop yield is  $6.9 \text{ t ha}^{-1}$ , 7% lower than the yield in the Static scenario, bringing down the overall yield by 1% in the Evolving scenario ( $7.3 \text{ t ha}^{-1}$ ). This extensification is partly driven by the production shift from higher-yield and higher-inputs developed regions, such as North America, to relatively lower-yield and lower-inputs developing regions, such as Africa. Meanwhile, the intensity of fertilizer and water use is also decreased due to the weaker price-induced yield response, as agricultural prices are relatively lower in the Evolving scenario.

In the Evolving scenario, agricultural activities and land-use change lead to global cumulative (2020–2100) emissions of 465 gigatons of carbon dioxide equivalent ( $\text{GtCO}_2\text{e}$ ) methane ( $\text{CH}_4$ ), 260  $\text{GtCO}_2\text{e}$  nitrous oxide ( $\text{N}_2\text{O}$ ) and 260  $\text{GtCO}_2\text{e}$   $\text{CO}_2$  from land use, land-use change and forestry (LULUCF). Compared to the Static scenario, changes in methane and nitrous oxide emissions due to labour market evolution align with agricultural production changes, for example, in 2100, +9% (+0.07  $\text{GtCO}_2\text{e}$ ) in methane from rice cultivation, +6% (+0.19  $\text{GtCO}_2\text{e}$ ) in nitrous oxide from corn production and −1% (−0.03  $\text{GtCO}_2\text{e}$ ) in methane from beef production (Supplementary Fig. 12). Despite regional and sectoral variations, when comparing aggregated cumulative GHG emissions, which are more relevant to climate outcomes<sup>29</sup>, the impacts are relatively small, +2  $\text{GtCO}_2\text{eq}$  in methane and +1  $\text{GtCO}_2\text{e}$  in nitrous oxide (Fig. 4c). In contrast, the impact on LULUCF is more substantial, +13% (+26  $\text{GtCO}_2\text{e}$ ), mainly driven by the additional forest and natural land decreases in Africa (Fig. 4d).

### Sensitivity to labour market evolution assumptions

The cascading effects of labour market evolution on agricultural markets and the environment are further validated in the broader sensitivity scenarios (Fig. 5). In general, higher labour productivity, weaker transitions to non-agricultural sectors and a more elastic agricultural labour supply (with a backdrop of increasing wage rates in the Evolving scenario) result in higher effective labour, and vice versa, consistent with theoretical expectations. Labour productivity delineates the gap between physical labour and effective labour (Fig. 5a). Moreover, higher effective labour leads to lower labour costs, encouraging higher production (mainly crops) at lower agricultural producer prices, which consequently leads to higher inputs (cropland, fertilizer and water) and emissions, and vice versa (Supplementary Fig. 15).

The sensitivity scenarios depict a 5.8% scenario-wise variation at the world level in end-of-century effective labour changes, measured as the standard deviation of (logarithmic) differences relative to the Evolving scenario (Supplementary Table 6). This variation ripples to the global agricultural market, resulting in a corresponding variation of 36% in wage rates, 8% in staple crop prices and 6% in livestock prices. The corresponding variation in land-use change responses is 82 Mha in pasture, 34 Mha in staple cropland and 4 Mha in forest. Consequently, the variation in cumulative emission impacts is 1.4  $\text{GtCO}_2\text{e}$  in agricultural methane, 2.2  $\text{GtCO}_2\text{e}$  in nitrous oxide and 11.8  $\text{GtCO}_2\text{e}$  in LULUCF carbon dioxide emissions.

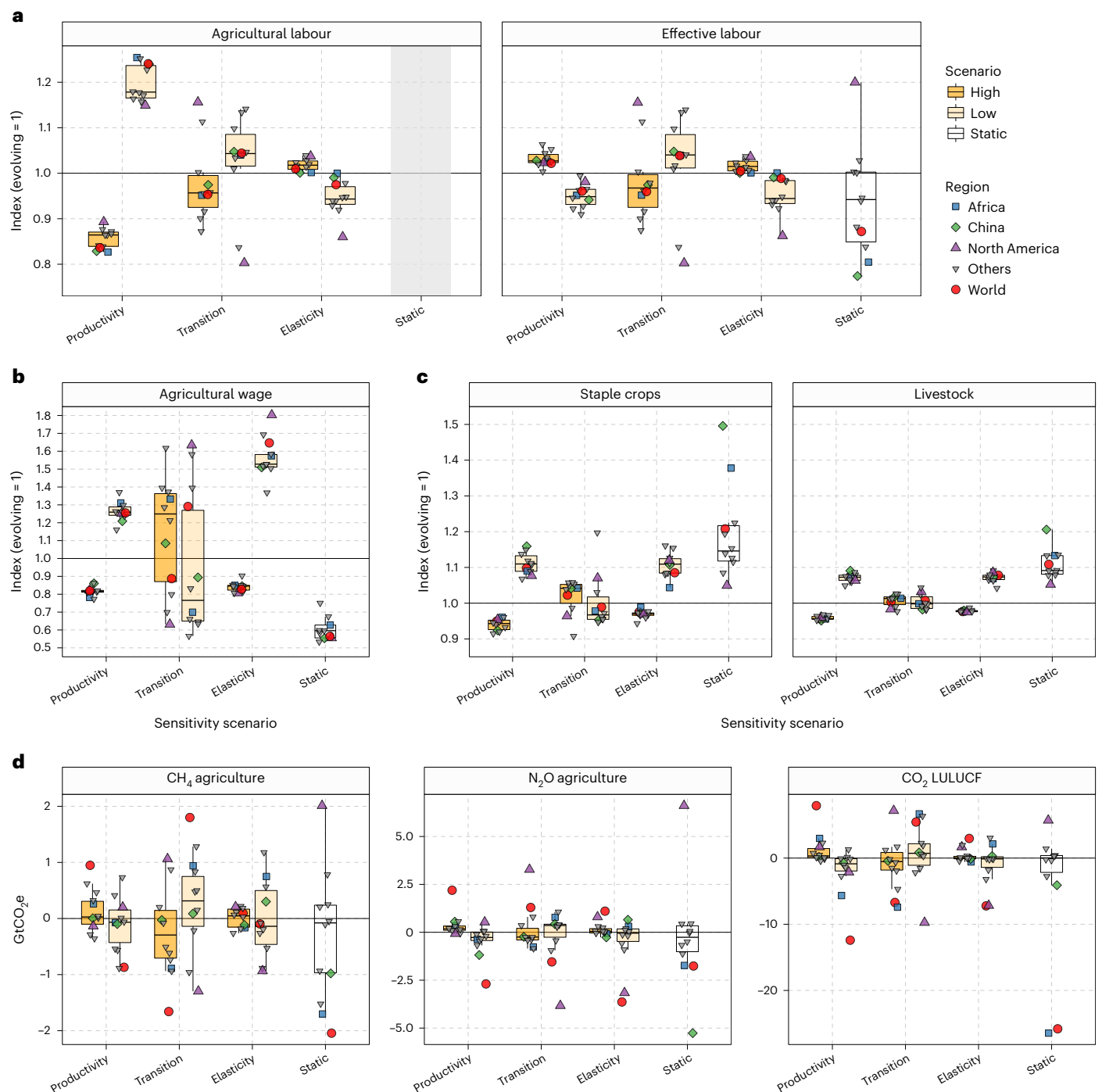
In general, wage rates and staple crop prices demonstrate higher sensitivity than livestock prices to labour market dynamics. Similarly, LULUCF emissions exhibit greater sensitivity than agricultural methane and nitrous oxide emissions. Further exploration reveals that agricultural labour market changes (effective labour) account for 44% and 59% of the variations in the responses of staple cropland and other cropland, respectively, showing a robust and positive relationship in all regions (Supplementary Table 7). As expected, the corresponding relationship with pasture responses is significantly negative. Moreover, agricultural labour market changes explain 52% of the variations in cumulative LULUCF emission impacts, with a strong positive relationship indicating a marginal effect ranging from +0.3 (Africa) to +2.2 (Latin America)  $\text{GtCO}_2\text{e}$  LULUCF emissions per 1% increase in effective labour.

### Discussion

While the role of humans in integrated human–Earth systems has been emphasized<sup>30</sup>, modelling efforts have primarily concentrated on the demand side, for example, demographic changes<sup>31</sup> and behavioural changes<sup>32,33</sup>. Our study underscores the human role as labour input in agricultural production, a factor that has been largely overlooked previously. By representing labour markets in the multisector dynamic modelling of GCAM and incorporating future labour market evolution into our reference scenario, we find that the recent trend of declining employment in global primary agriculture will persist. Our results project a net average global decadal decrease of 21 million people by mid-century and 43 million by the end of the century, in stark contrast to the decadal increase of over 90 million people observed in 1961–2003 (peak year)<sup>4</sup>. The results demonstrate a strengthening decoupling of labour from future agricultural production. A thorough comparison of our scenarios with varying assumptions regarding agricultural labour productivity and labour supply has yielded several key insights.

First, there exists a complex and critical linkage between labour market dynamics and global environmental change. Specifically, dynamic changes in future labour market evolution directly impact the equilibrium of the physical labour market; the impact is then transmitted to agro-economic variables such as agricultural prices, production, trade and land use, consequently influencing global agricultural emissions. In general, a stronger ‘labour push’, characterized by higher agricultural labour productivity growth, or a weaker ‘labour pull’, that is, a slower transition of agricultural labour to industrial and service sectors, promotes higher overall agricultural production and increased GHG emissions from the production activities and land-use change. Conversely, the opposite trend is observed when these factors are reversed. Hence, these responses and potential feedbacks must be considered for relevant decision-making processes<sup>34,35</sup>.

Second, agricultural labour market evolution encourages changes of comparative advantage across regions, resulting in pronounced regional implications on production and trade patterns. Differential changes in regional agricultural labour market evolution factors lead to relative price adjustments and subsequent shifts in global production and trade patterns<sup>19,36</sup>. For instance, a trend of closing the labour yield gap<sup>37</sup> across regions, as implied in our Evolving scenarios, contributes to a global production shift from developed to developing regions,



**Fig. 5 | Sensitivity of end-of-century agroeconomic and emission implications to labour market assumptions. a–d.** End-of-century (2100) projections from the sensitivity scenario, relative to the Evolving scenario, for agricultural labour (a), wage rate (b), agricultural prices (c) and cumulative (2020–2100) emissions from agriculture and LULUCF (d). In all panels, boxplots (Tukey style) depict

the median values (line), the interquartile ranges (IQR; boxes), the minimum/maximum of  $1.5 \times$  IQR ranges and the minimum/maximum values (whiskers) across the IPCC R10 regions ( $n = 10$ ), organized by scenario. Points display values for key regions. Physical agricultural labour results for the Static scenario are not shown in a,b. Data source: GCAM simulation results.

alleviating the dependency on imports in currently importing regions with low factor productivity, such as Africa. However, such a production shift driven by higher effective labour yield has a trade-off with land yield, which is typically lower in developing regions and has more direct environmental implications<sup>38,39</sup>. Notably, potential changes in regional factor rewards and trade balance, probably inducing macroeconomic feedback<sup>40</sup>, were not included in our analysis and should be explored in future work. Nevertheless, it is important to broadly acknowledge the

varying productivity changes both across factor inputs (for example, labour and land) and regions, and the potential trade-offs involved.

Third, labour market evolution impacts agricultural sectors differently, resulting in complex responses and feedback mechanisms. Agricultural sectors may respond differently to changes in wage rates due to their varying labour intensity. For instance, crops are typically more labour-intensive than livestock sectors, while pasture requires little to no labour. In our scenarios with lower labour costs (that is,

lower effective wage rates), we observed a strong land shift away from pasture, driven by the faster decrease in the cost of feed crops relative to grazing. These results, more pronounced under an evolving labour market, echo recent evidence of globally plateaued pasture area<sup>41</sup> and the shift of livestock production from pastoral to mixed systems<sup>42</sup>. Similarly, crops are more responsive to wage rate changes compared to livestock products, potentially leading to consumption substitutions. Overall, our findings suggest that agricultural sector-wide labour market changes may result in mediated agroeconomic responses and environmental implications.

More broadly, our scenarios also imply potentially substantial labour market feedback when exploring alternative pathways. For example, transitions to low-externality diets, often involving a dietary shift away from animal-based foods<sup>43,44</sup>, will impact labour markets, probably reducing livestock labour while fostering transitions within crop sectors, in addition to any potential health and environment outcomes. Moreover, as widely recognized, land and water constraints may limit the large-scale production of purpose-grown bioenergy crops<sup>26,45</sup>. Similarly, labour input in energy crop production cannot be overlooked, potentially requiring a major labour shift into the sector, for example, an estimated 1.5% of global agricultural employment in 2100 in our Evolving scenario. More importantly, beyond the climate-bioenergy crop (land) yield feedback emphasized in Xu et al.<sup>46</sup>, future labour supply shocks, such as heat stress, could also alter the dynamics of bioenergy supply and climate feedback.

Our study also provides insights relevant to developers of global economic and multisector dynamic models. Notably, labour productivity growth ('labour push') and labour market transition ('labour pull') have opposite impacts on effective labour and agroeconomic outcomes. Neglecting both factors indeed results in relatively mediated global impacts, while regional impacts could still be substantial when one factor is dominating. Recent model intercomparison projects have revealed notable disparities in long-term agroeconomic projections, particularly at the regional level<sup>10,47,48</sup>. Discrepancies in the representation and parameterization of agricultural labour markets across these models probably have contributed to the uncertainty in the projections. In addition, multisector dynamic models have been used to investigate the environmental impact of urbanization, fuelling a debate on whether urbanization (1) frees up rural built-up areas and reduces fragmentation, thus benefiting large-scale farming and the environment<sup>49</sup>, or (2) displaces agricultural and natural land, leading to potentially large land-use change emissions<sup>50</sup>. It is crucial to recognize that alongside urban and rural area changes, urbanization-induced labour market changes probably also play an important role, as evidenced by our exploration of agricultural labour transition parameters.

In sum, our study establishes a foundation for further exploration of scenarios in which agricultural labour market evolutions may play a role, including those examining demographic or other socioeconomic changes<sup>51,52</sup>, heat-stress-induced labour productivity shocks<sup>53</sup>, or broader agroeconomic–environment interactions<sup>47,54</sup> (see Supplementary Information, section 4 for additional discussions of limitations and future work). More interdisciplinary collaboration is needed to integrate agricultural labour dynamics into existing approaches and enhance our understanding of the interactions between agriculture, the economy and the environment.

## Methods

### GCAM description

The GCAM<sup>28</sup> is a multisector dynamic model that integrates representations of both human and physical Earth systems. The model has been widely used to explore future agroeconomic projections<sup>10,27,47</sup> and generate pathways under various climate futures<sup>55</sup>, such as those in the IPCC AR6 Scenario Database<sup>56</sup>. Here we provide a brief overview of the model with a focus on the agriculture sector. More details can be

found in the online documentation (<http://jgcri.github.io/gcam-doc/>) or recent model applications<sup>25,26,57,58</sup>.

Our study utilizes a recently released version of GCAM (v.7.0)<sup>59</sup>. The model is calibrated to the base year of 2015 and runs dynamically up to 2100 in 5 year steps, driven by future socioeconomic and technological changes. The reference scenario utilizes population and income projections in the Shared Socioeconomic Pathway 2 (SSP2) 'Middle-of-the-Road' scenario<sup>51,60</sup> and biophysical yield (land productivity) growth assumptions based on Food and Agriculture Organization (FAO) projections<sup>61,62</sup>. GCAM encompasses 32 world regions, and agricultural production is modelled at the intersection of 235 water basins and the 32 geopolitical regions (Supplementary Table 2). In the base year, GCAM represents the supply and utilization accounts of 21 crop commodities, 6 livestock commodities and a primary forestry product (Supplementary Table 3), providing aggregated representations of all agricultural commodities included in the FAOSTAT database<sup>63,64</sup>. Additionally, purpose-grown energy crops are introduced in 2025. The model includes all land covers and employs a nested logit approach to model their competition, while crop yield at the technology level (that is, by irrigation and inputs) connects cropland to production. Agricultural GHG emissions in GCAM are activity-based. In particular, CH<sub>4</sub> and N<sub>2</sub>O are traced endogenously as their emission factors are linked to sectoral activities in the agriculture system. The accounting for LULUCF emissions relies on emission factors of soil organic carbon<sup>65</sup> and vegetation carbon<sup>66</sup>, which are dynamically applied to land-use change results<sup>26</sup>. Additional model descriptions, including recent developments, are provided in Supplementary Discussion, sections 2.1 and 2.2.

In the main results, we primarily discuss end-of-the-century implications due to their climate relevance in the literature, with additional results provided in the Supplementary Information. Where applicable, GCAM regions are aggregated into IPCC R10 regions (Supplementary Table 2) to communicate the results.

### Representing agricultural labour markets

A schematic of the labour market changes in GCAM is provided in Fig. 2a. Here we illustrate the agroeconomic linkages to the labour market with detailed derivations of the market equilibrium. In GCAM, representative profit-maximizing agricultural producers in crop, livestock and forestry sectors make production and management decisions by determining input uses given constant-return-to-scale technologies and a vector of input and output prices. For the production of crop  $k$ , the land rental profit, denoted as  $P^A$ , received by landowners from land use in  $k$  using irrigation technology  $i$  (irrigation or rainfed) and management practice  $m$  (high fertilizer or low fertilizer) in water basin  $b$ , region  $r$  and period  $t$  is derived in equation (1)<sup>27,28</sup>. Here  $P$  represents output prices,  $P^W$  and  $P^F$  denote input prices for water and fertilizer, respectively,  $g^A$ ,  $g^W$  and  $g^F$  represent output yields relative to land, water and fertilizer inputs, and  $h$  is an aggregate of other input costs.

$$P^A_{k,i,m,b,r,t} = \left( P_{k,r,t} - \frac{P^W_{k,b,r,t}}{g^W_{k,i,b,r,t}} - \frac{P^F_{k,r,t}}{g^F_{k,m,b,r,t}} - h_{k,b,r,t} \right) \times g^A_{k,i,m,b,r,t} \quad (1)$$

Land-use allocation is governed by a nested logit structure, which specifies a relationship between land shares and relative rental profits (see Supplementary Information, section 2.2 for details). This structure enables endogenous price-induced yield responses through technology transitions and competition between agricultural land and natural land.

In GCAM v.7.0, labour costs in agricultural production are embedded in  $h$ , which has been held constant over time, that is,  $h_{k,b,r,t} = h_{k,b,r,t_0}$  where  $t_0$  is the base calibration year. In our study, we explicitly represent labour and capital in agricultural production technologies, and the corresponding costs are separated from  $h$  (equation (2) and Fig. 2a). Here  $P^L$  and  $P^K$  denote the wage rate and capital price, respectively,



$g^L$  and  $g^K$  represent output yields relative to labour and capital inputs, and  $h'$  accounts for the remaining other input costs.

$$h_{k,b,r,t} = \frac{P_{r,t}^L}{g_{k,i,m,b,r,t}^L} + \frac{P_{r,t}^K}{g_{k,i,m,b,r,t}^K} + h'_{k,b,r,t} \quad (2)$$

Note that  $g^L$  and  $g^K$  are differentiated across technologies ( $i$  and  $m$ ), allowing for endogenous labour-capital substitution via technology transition (Supplementary Information, section 2.3). The global mean labour cost share in primary agricultural production in the base year is 35% for crop sectors and 24% for livestock sectors, while the corresponding capital cost shares are 14% and 10%, respectively<sup>67</sup>. While the remaining other cost ( $h'$ ) is still held constant, it becomes considerably smaller after the separation of labour and capital. By substituting equation (2) into equation (1), expressing labour yield as the ratio between output ( $Q$ ) and the effective labour input ( $G^L \times Q^L$ ), and rearranging terms, the labour demand at the technology level is derived in equation (3). Note that effective labour is a product of the physical labour input ( $Q^L$ ) and the corresponding technical shifter ( $G^L$ ) governing labour productivity changes ( $G_{r,\text{base year}}^L = 1$ ) (Supplementary Discussion, section 2.4).

$$Q_{k,i,m,b,r,t}^L = \left( P_{k,r,t} - \frac{P_{k,i,m,b,r,t}^K}{g_{k,i,m,b,r,t}^K} - \frac{P_{k,i,b,r,t}^W}{g_{k,i,b,r,t}^W} - \frac{P_{k,r,t}^E}{g_{k,m,b,r,t}^E} - \frac{P_{k,r,t}^K}{g_{k,i,m,b,r,t}^K} - h'_{k,b,r,t} \right) \times \frac{Q_{k,i,m,b,r,t}}{G_{r,t}^L P_{r,t}^L} \quad (3)$$

The labour demand derived is consistent for forestry sectors, where water and fertilizer inputs are not utilized and can be extended to the livestock sectors, which are represented by mixed and pastoral technologies at the regional level and encompass intermediate costs of feedstuff. Labour demand in the fishery sector, which accounted for 3% of agricultural labour in 2015, is not considered in our study. Thus, the aggregate regional wage-responsive agricultural labour demand ( $Q_{r,t}^{\text{demand}}$ ) can be derived as the sum total of the labour demand across GCAM agricultural sectors ( $k$ ), technological combinations ( $n$ ) and subregion scales ( $b$ ),  $Q_{r,t}^{\text{demand}} = \sum_{k,b} Q_{k,n,b,r,t}^L = f(P_{r,t}^L)$ .

The supply of agricultural labour is typically intertwined with the broader economy-wide labour force,  $L^F$ , which serves as a key socio-economic factor closely tied to population and demographic shifts. Furthermore, the availability of agricultural labour can be influenced by transitions between agricultural and non-agricultural sectors, driven by agricultural transformation and manifested through processes such as urbanization. Thus, we construct an exponential agricultural labour supply function, specifying the relationship between agricultural labour share in the total labour force and wage rates, with a supply elasticity of  $\gamma$ , in equation (4), where  $\alpha$  is the calibration parameter and  $\beta$  is an expansion parameter to consider sectoral transitions.

$$\frac{Q_{r,t}^{\text{supply}}}{L_{r,t}^F} = \alpha_r \times P_{r,t}^L{}^\gamma \times \beta_{r,t} \quad (4)$$

We rely on rural population changes to drive the future sectoral transition<sup>31</sup> by specifying  $\beta$  as a wedge between the labour force and rural population ( $L^R$ ), that is,  $\beta = \frac{L^R}{L^F}$ . Particularly,  $\beta$  is initially observed in the base year, while future changes are driven by external assumptions in SSP scenarios. Thus, the agricultural labour supply can be derived as  $Q_{r,t}^{\text{supply}} = \alpha_r \times P_{r,t}^L{}^\gamma \times L_{r,t}^R$ . Regional labour markets are cleared by connecting labour demand and supply,  $Q_{r,t}^{\text{demand}} = Q_{r,t}^{\text{supply}}$ , and  $P_{r,t}^L$  is solved.

Because our study focuses on the labour market, we assume a perfectly elastic capital supply, that is,  $\frac{P_{r,t}^K}{g_{k,i,m,b,r,t}^K} = \frac{P_{r,t_0}^K}{g_{k,i,m,b,r,t_0}^K}$ . All agricultural input and output markets in the model, including labour markets, are calibrated to observations in the model base year. For this study, we compiled a dataset that includes regional and sectoral labour input

information in primary agriculture. We gathered and synthesized data from various sources, including the International Labour Organization (ILO)<sup>68</sup>, the US Department of Agriculture (USDA)<sup>69</sup>, the FAO Statistical Database<sup>70</sup> and the Global Trade Analysis Project (GTAP) Version 10 Database<sup>67</sup> (Supplementary Discussion, section 2.5). The calibration of the agro-economic equilibrium in GCAM for the base year is considerably enhanced because the data enable the capture of labour intensity heterogeneity across regions and agricultural sectors.

### Experimental design

Consistent with expectations, the theoretical model of agricultural labour markets highlights the important role of labour productivity changes ( $G_{r,t}^L$ ), labour transition implied by rural population changes ( $L_{r,t}^R$ ) and labour supply elasticity ( $\gamma$ ) in determining the future agricultural market equilibrium (Fig. 2b). All three factors collectively capture the drivers of future labour market evolution in our study, with the latter two referred to as labour supply factors.

In GCAM v.7.0, a factor productivity trajectory was calibrated for the Material sector (representing the rest of the economy), based on the GDP path in SSP2. This factor productivity trajectory serves as the default path for agricultural labour productivity growth in the Evolving scenario. By the end of the century, labour productivity is approximately 4.6 times higher at the global level compared with the base year, ranging from 2 times in North America to 5.2 times in Africa (Supplementary Fig. 6). For rural population changes, we rely on projections from SSP2<sup>51</sup> for consistency in the Evolving scenario. It is estimated that the global rural population will decrease by 1.8 billion people (or -47%) from 2015 (3.4 billion) to 2100 (1.6 billion), with considerable regional variation in the decrease, for example, 0.6 billion (-53%) in South Asia, 0.5 billion (-81%) in China, 0.1 billion (-15%) in Africa, and 0.03 billion (-50%) in North America (Supplementary Fig. 7). Additionally, we adopt a long-term agricultural labour supply elasticity of  $\gamma = 0.7$  based on Hill et al.<sup>71</sup> in the Evolving scenario.

It is important to note that assuming a constant term ( $\frac{P_{r,t}^L}{g_{k,i,m,b,r,t}^L} + \frac{P_{r,t}^K}{g_{k,i,m,b,r,t}^K}$ ) in equation (2), as commonly done when agricultural labour is not explicitly represented, would lead equation (3) to collapse to equation (1), making the specification identical to that of GCAM v.7.0. In our Static scenario, we assume a perfectly elastic physical labour supply ( $P_{r,t}^L = P_r^L$ ) with constant productivity ( $g_{k,i,m,b,r,t}^L = g_{k,i,m,b,r}^L$  or  $G_{r,t}^L = G_r^L$ ), providing a sufficient but not necessary interpretation of GCAM v.7.0 specifications (no explicit agricultural labour). Perfectly elastic physical labour supply implies an unlimited rural population and infinite supply elasticity. That is, the Static scenario can be viewed as a sensitivity scenario relative to the Evolving scenario, with extreme changes in all factors. Comparing the Evolving and Static scenarios also reveals the impact of incorporating agricultural labour market dynamics into the modelling. Additionally, another extreme scenario we could consider testing involves fixing the effective labour supply at the base year. However, implementing this scenario posed challenges as the model struggled to solve for all future periods due to its dynamic nature.

Based on the Evolving scenario, we also respectively examine the sensitivity of the three key labour market evolution factors. For labour productivity, we test a 30% range of growth rates around the default values. That is, agricultural productivity at the world level is about 3.5 (low) to 5.7 (high) times higher compared with the base year (Supplementary Fig. 6). For the rural population, we examine projections from SSP3 (low transition) and SSP5 (high transition) scenarios, which estimate 2.4 billion and 1.2 billion rural populations in 2100, respectively. These figures represent a 47% increase and a 24% decrease compared to SSP2 (1.6 billion) (Supplementary Fig. 7). Note that regional rural populations could change differently across scenarios. For instance, developed regions, including North America, Europe and the Pacific OECD, have a different order across scenarios compared with other regions or globally, as depicted in the narrative

of the corresponding SSPs. In addition, for agricultural labour supply elasticity, we test a 50% range of the default elasticity of 0.7, that is, 0.35 (low) and 1.05 (high).

While the sensitivity scenarios are exploratory in nature, these additional tests enhance our understanding of the cascading effects of labour market shocks on agricultural markets and environmental outcomes. They also validate that the insights gleaned from our main scenario comparison remain robust across the tested parameter ranges. Furthermore, the results discussed in the main text focus on the global level, and on key regions including Africa, China and North America. Additional results are presented in Supplementary Discussion, section 3.

### Reporting summary

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

### Data availability

The GCAM simulation results and processed data generated in this study are available via Zenodo at <https://doi.org/10.5281/zenodo.13852194> (ref. 72). Source data are provided with this paper.

### Code availability

GCAM is an open-source model available via GitHub at [github.com/JGCRI/gcam-core](https://github.com/JGCRI/gcam-core), and the specific version of the model used in this study is archived at [github.com/realxinzhao/paper-nfood2024-AgLaborEvolution-GCAM](https://github.com/realxinzhao/paper-nfood2024-AgLaborEvolution-GCAM) and available via Zenodo at <https://doi.org/10.5281/zenodo.13852265> (ref. 73). The R code for generating the main figures is archived at [github.com/realxinzhao/paper-nfood2024-AgLaborEvolution-DisplayItems](https://github.com/realxinzhao/paper-nfood2024-AgLaborEvolution-DisplayItems) and available via Zenodo at <https://doi.org/10.5281/zenodo.13852236> (ref. 74).

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## Author contributions

X.Z., J.A.E. and D.S. conceptualized the research. D.S., X.Z. and P.P. contributed to the modelling and simulations. D.S. and X.Z. led the visualization and wrote the first draft of the manuscript. All authors (D.S., J.A.E., P.P., S.T.W., B.C.O., M.A.W. and X.Z.) contributed to the interpretation of the results and writing the paper.

## Competing interests

The authors declare no competing interests.

## Additional information

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| <input type="checkbox"/>            | <input checked="" type="checkbox"/> The statistical test(s) used AND whether they are one- or two-sided<br><i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i>                                                               |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> A description of all covariates tested                                                                                                                                                                                                                                |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons                                                                                                                                                   |
| <input type="checkbox"/>            | <input checked="" type="checkbox"/> A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals) |
| <input type="checkbox"/>            | <input checked="" type="checkbox"/> For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i> ) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted<br><i>Give P values as exact values whenever suitable.</i>                     |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings                                                                                                                                                                      |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes                                                                                                                                                |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Estimates of effect sizes (e.g. Cohen's <i>d</i> , Pearson's <i>r</i> ), indicating how they were calculated                                                                                                                                                          |

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

|                 |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|-----------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Data collection | Simulations were run using a modified version of GCAM 7.0 and GCAM data system. Both GCAM model and data system are publicly available. The instructions on running GCAM and the data system are available at: <a href="https://github.com/JGCRI/gcam-core">https://github.com/JGCRI/gcam-core</a> . The specific version of the model used in this study is archived at <a href="https://github.com/realxinzhao/paper-nfood2024-AgLaborEvolution-GCAM">github.com/realxinzhao/paper-nfood2024-AgLaborEvolution-GCAM</a> ( <a href="https://doi.org/10.5281/zenodo.13852265">https://doi.org/10.5281/zenodo.13852265</a> ). The R code for generating the main figures is available at <a href="https://github.com/realxinzhao/paper-nfood2024-AgLaborEvolution-DisplayItems">github.com/realxinzhao/paper-nfood2024-AgLaborEvolution-DisplayItems</a> ( <a href="https://doi.org/10.5281/zenodo.13852236">https://doi.org/10.5281/zenodo.13852236</a> ). |
| Data analysis   | R (Version 4.0.5, Windows, 64 bit) was used with custom codes.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

## Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

The GCAM simulation results and processed data generated in this study are available at Zenodo (<https://doi.org/10.5281/zenodo.13852194>).

## Human research participants

Policy information about [studies involving human research participants and Sex and Gender in Research](#).

Reporting on sex and gender

Population characteristics

Recruitment

Ethics oversight

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](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

## Ecological, evolutionary & environmental sciences study design

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

|                          |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
|--------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Study description        | This study examines the agro-economic and environmental implications of the long-term evolution of the agricultural labor market, characterized by the growth of labor productivity and transitions in labor markets. We introduce labor markets into an open-source multisector dynamic model, the Global Change Analysis Model (GCAM). Our modeling expands historical agricultural labor inputs and related metrics to future periods endogenously within the integrated human-Earth system modeling framework. Comparing systematically designed scenarios around assumptions related to agricultural labor market evolution, we highlight the cascading effects of labor market shocks on agricultural markets and environmental outcomes. |
| Research sample          | GCAM provides a reference (business as usual) scenario, which is our Static scenario (with no labor market evolution). Our study developed a Evolving scenario (with future labor market evolution) and 6 sensitivity scenarios around labor market assumptions (Fig. 2 in the Main paper). Our study does not involve sampled data. Study impacts by comparing with vs. without scenarios simulated by our model.                                                                                                                                                                                                                                                                                                                              |
| Sampling strategy        | This study did not involve statistical sampling procedure.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Data collection          | The main data used for simulations includes GCAM data system. The data used in analysis was from model simulation output. Both model input data (including FAOSTAT and USDA data) and output data are public available.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| Timing and spatial scale | Model simulations were run from 2015 to 2100 with 5-year time steps. In the modeling, the world was disaggregated into 32 geopolitical regions and agriculture was modeled at the intersection of water basin and geopolitical regions (i.e., 384 land-water regions).                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| Data exclusions          | No data was excluded.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Reproducibility          | Our analysis and results can be reproduced following the instructions in the Data and Code Statements (with links to online repositories).                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Randomization            | Not applicable.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Blinding                 | Not applicable.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |

Did the study involve field work? ☐ Yes ☒ No

## 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                                  |
|-------------------------------------|--------------------------------------------------------|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Antibodies                    |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Eukaryotic cell lines         |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Palaeontology and archaeology |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Animals and other organisms   |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clinical data                 |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Dual use research of concern  |

### Methods

| n/a                                 | Involved in the study                           |
|-------------------------------------|-------------------------------------------------|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> ChIP-seq               |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Flow cytometry         |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> MRI-based neuroimaging |