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# Rising rural body-mass index is the main driver of the global obesity epidemic in adults

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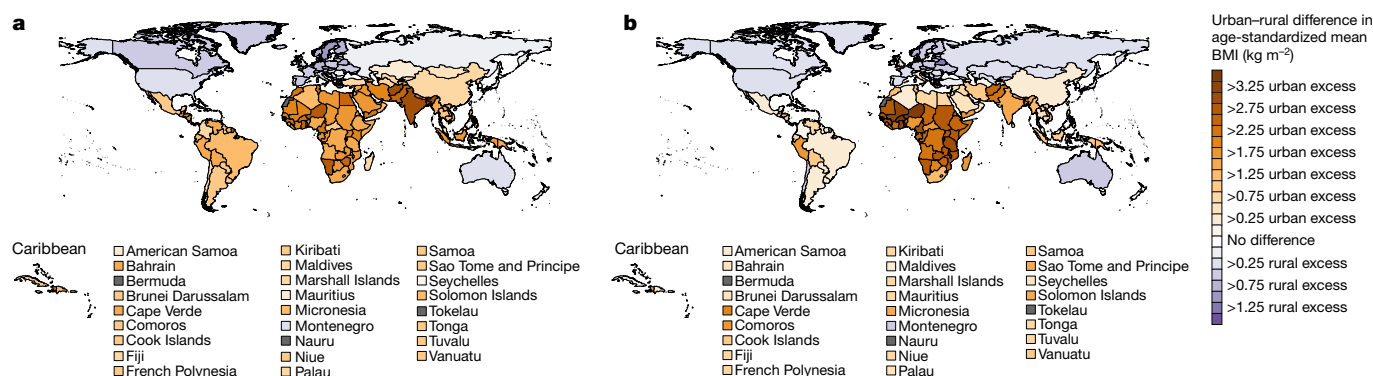
Body-mass index (BMI) has increased steadily in most countries in parallel with a rise in the proportion of the population who live in cities<sup>1,2</sup>. This has led to a widely reported view that urbanization is one of the most important drivers of the global rise in obesity<sup>3–6</sup>. Here we use 2,009 population-based studies, with measurements of height and weight in more than 112 million adults, to report national, regional and global trends in mean BMI segregated by place of residence (a rural or urban area) from 1985 to 2017. We show that, contrary to the dominant paradigm, more than 55% of the global rise in mean BMI from 1985 to 2017—and more than 80% in some low- and middle-income regions—was due to increases in BMI in rural areas. This large contribution stems from the fact that, with the exception of women in sub-Saharan Africa, BMI is increasing at the same rate or faster in rural areas than in cities in low- and middle-income regions. These trends have in turn resulted in a closing—and in some countries reversal—of the gap in BMI between urban and rural areas in low- and middle-income countries, especially for women. In high-income and industrialized countries, we noted a persistently higher rural BMI, especially for women. There is an urgent need for an integrated approach to rural nutrition that enhances financial and physical access to healthy foods, to avoid replacing the rural undernutrition disadvantage in poor countries with a more general malnutrition disadvantage that entails excessive consumption of low-quality calories.

Being underweight or overweight can lead to adverse health outcomes. BMI—a measure of underweight and overweight—is rising in most countries<sup>2</sup>. It is commonly stated that urbanization is one of the most important drivers of the worldwide rise in BMI because diet and lifestyle in cities lead to adiposity<sup>3–6</sup>. However, such statements are typically based on cross-sectional comparisons in one or a small number of countries. Only a few studies have analysed how BMI is changing over time in rural and urban areas. The majority have been in one country,

over short durations, and/or in one sex and narrow age groups. The few studies that covered more than one country<sup>7–12</sup> used at most a few dozen data sources and hence could not systematically estimate trends, and focused primarily on women of child-bearing age.

Data on how BMI in rural and urban populations is changing are needed to plan interventions that address underweight and overweight. Here, we report on mean BMI in rural and urban areas of 200 countries and territories from 1985 to 2017. We used 2,009 population-based studies of human anthropometry conducted in 190 countries (Extended Data Fig. 1), with measurements of height and weight in more than 112 million adults aged 18 years and older. We excluded data based on self-reported height and weight because they are subject to bias. For each sex, we used a Bayesian hierarchical model to estimate mean BMI by year, country and rural or urban place of residence. As described in the Methods, the estimated trends in population mean BMI represent a combination of (1) the change in the health of individuals due to change in their economic status and environment, and (2) the change in the composition of individuals that make up the population (and their economic status and environment).

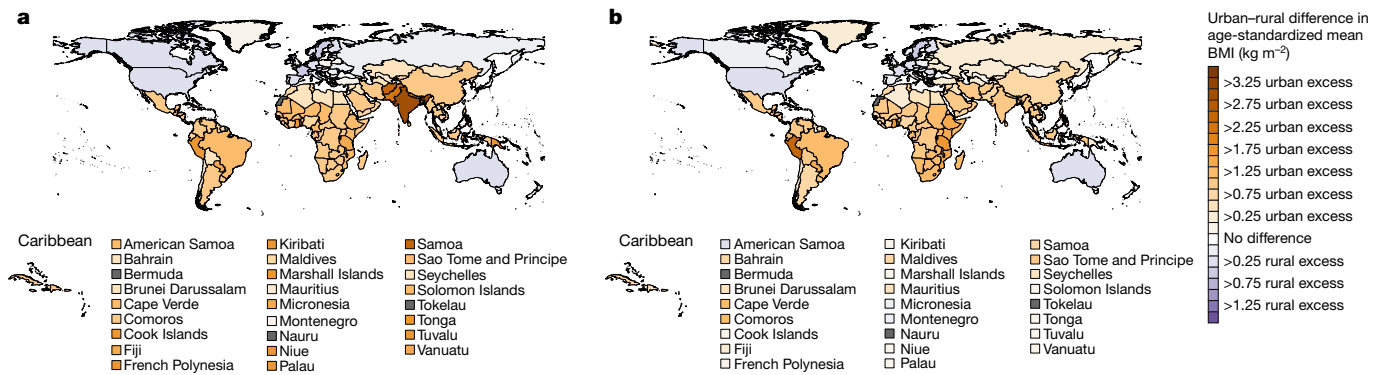
From 1985 to 2017, the proportion of the world's population who lived in urban areas<sup>1</sup> increased from 41% to 55%. Over the same period, global age-standardized mean BMI increased from 22.6 kg m<sup>-2</sup> (95% credible interval 22.4–22.9) to 24.7 kg m<sup>-2</sup> (24.5–24.9) in women, and from 22.2 kg m<sup>-2</sup> (22.0–22.4) to 24.4 kg m<sup>-2</sup> (24.2–24.5) in men. The increase in mean BMI was 2.09 kg m<sup>-2</sup> (1.73–2.44) and 2.10 kg m<sup>-2</sup> (1.79–2.41) among rural women and men, respectively, compared to 1.35 kg m<sup>-2</sup> (1.05–1.65) and 1.59 kg m<sup>-2</sup> (1.33–1.84) in urban women and men. Nationally, change in mean BMI ranged from small decreases among women in 12 countries in Europe and Asia Pacific, to a rise of >5 kg m<sup>-2</sup> among women in Egypt and Honduras. The lowest observed sex-specific mean BMI over these 33 years was that of rural women in Bangladesh of 17.7 kg m<sup>-2</sup> (16.3–19.2) and rural men in



**Fig. 1 | The difference between rural and urban age-standardized mean BMI in women. a**, Difference in age-standardized mean BMI in 1985. **b**, Difference in age-standardized mean BMI in 2017. We did not estimate the difference between rural and urban areas for countries and territories in which the entire population live in areas classified as urban (Singapore,

Hong Kong, Bermuda and Nauru) or rural (Tokelau)—shown in grey. See Extended Data Fig. 2 for mean BMI at the national level and in rural and urban populations in 1985 and 2017. See Extended Data Fig. 6 for comparisons of the results between women and men.

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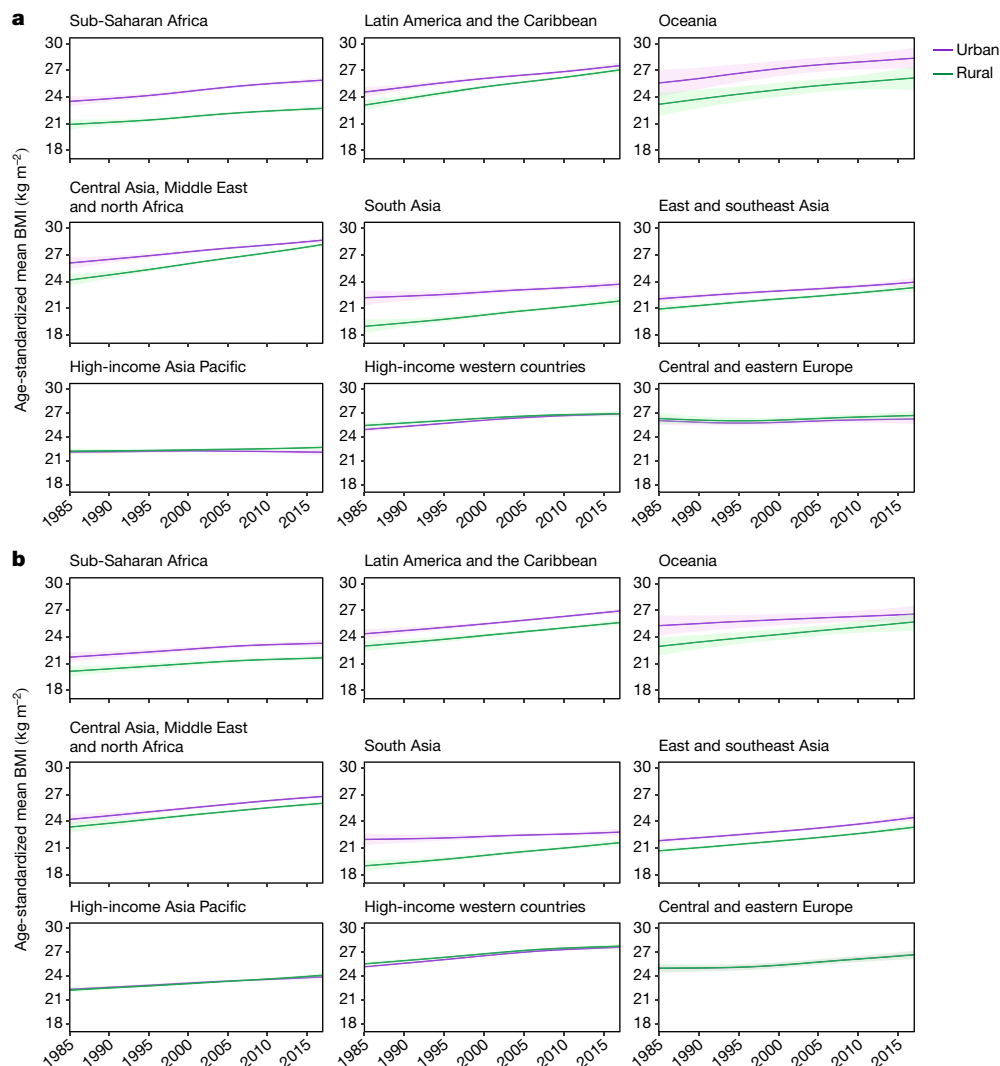


**Fig. 2 | The difference between rural and urban age-standardized mean BMI in men. a, Difference in age-standardized mean BMI in 1985. b, Difference in age-standardized mean BMI in 2017. We did not estimate the difference between rural and urban areas for countries and territories in which the entire population live in areas classified as urban (Singapore,**

Hong Kong, Bermuda and Nauru) or rural (Tokelau)—shown in grey. See Extended Data Fig. 3 for mean BMI at the national level and in rural and urban populations in 1985 and 2017. See Extended Data Fig. 6 for comparison of results between women and men.

Ethiopia of 18.4 kg m<sup>-2</sup> (17.0–19.9), both in 1985; the highest were 35.4 kg m<sup>-2</sup> (33.7–37.1) for urban women and 34.6 kg m<sup>-2</sup> (33.1–35.9) for rural men in American Samoa in 2017 (Extended Data Figs. 2, 3), representing a twofold difference.

In 1985, urban men and women in every country in east, south and southeast Asia, Oceania, Latin America and the Caribbean and a region that comprises central Asia, the Middle East and north Africa had a higher mean BMI than their rural peers (Figs. 1, 2). The urban–rural



**Fig. 3 | Trends in age-standardized mean BMI by rural and urban place of residence. a, Trends are shown for women in each region. b, Trends are shown for men in each region. The lines show the posterior mean estimates and the shaded areas show the 95% credible intervals.**

**Table 1 | Contributors to the rise in mean BMI from 1985 to 2017**

		Rural component		Urban component		Urbanization component		
		Absolute contribution (kg m <sup>-2</sup> )	Percentage contribution (%)	Absolute contribution (kg m <sup>-2</sup> )	Percentage contribution (%)	Absolute contribution (kg m <sup>-2</sup> )	Percentage contribution (%)	
<b>Emerging economies</b>								
Central Asia, Middle East and north Africa	Men	1.30 (0.96–1.64)	48 (41–54)	1.33 (1.02–1.65)	49 (44–54)	0.09 (0.06–0.12)	3 (2–5)	
	Women	1.96 (1.57–2.33)	59 (54–64)	1.31 (0.95–1.69)	39 (34–44)	0.06 (0.03–0.09)	2 (1–3)	
East and southeast Asia	Men	1.99 (1.62–2.37)	67 (63–71)	0.66 (0.53–0.80)	22 (20–24)	0.33 (0.26–0.39)	11 (9–14)	
	Women	1.81 (1.36–2.26)	73 (67–80)	0.47 (0.32–0.64)	19 (16–22)	0.18 (0.10–0.26)	7 (4–11)	
Latin America and the Caribbean	Men	0.86 (0.63–1.09)	31 (26–37)	1.73 (1.31–2.16)	63 (58–67)	0.17 (0.13–0.20)	6 (5–8)	
	Women	1.29 (1.07–1.51)	38 (34–43)	2.01 (1.56–2.49)	60 (55–63)	0.06 (0.03–0.10)	2 (1–3)	
Oceania	Men	2.24 (1.12–3.37)	90 (80–102)	0.24 (–0.03–0.51)	10 (–2–20)	0.00 (0.00–0.00)	0 (0–0)	
	Women	2.41 (0.89–3.98)	81 (69–90)	0.53 (0.18–0.89)	19 (10–31)	0.00 (0.00–0.00)	0 (0–0)	
South Asia	Men	1.99 (1.42–2.54)	86 (79–94)	0.20 (0.00–0.40)	8 (0–15)	0.12 (0.09–0.15)	5 (3–8)	
	Women	2.18 (1.46–2.87)	80 (73–87)	0.36 (0.13–0.60)	13 (6–19)	0.19 (0.16–0.23)	7 (5–11)	
<b>Sub-Saharan Africa</b>								
Sub-Saharan Africa	Men	1.14 (0.64–1.63)	64 (53–73)	0.39 (0.22–0.55)	22 (15–28)	0.23 (0.19–0.27)	14 (10–21)	
	Women	1.37 (0.90–1.83)	57 (49–63)	0.58 (0.42–0.74)	24 (21–28)	0.45 (0.42–0.49)	19 (15–25)	
<b>High-income and other industrialized regions</b>								
Central and eastern Europe	Men	0.59 (0.35–0.82)	35 (26–44)	1.10 (0.70–1.50)	65 (57–73)	0.00 (–0.01–0.01)	0 (–1–1)	
	Women	0.14 (–0.19–0.45)	NR	0.13 (–0.45–0.69)	NR	–0.02 (–0.03–0.00)	NR	
High-income Asia Pacific	Men	0.48 (0.37–0.59)	31 (25–37)	1.15 (0.84–1.46)	72 (68–75)	–0.04 (–0.08–0.00)	–2 (–6–0)	
	Women	0.12 (–0.01–0.27)	NR	–0.02 (–0.38–0.36)	NR	–0.10 (–0.15 to –0.06)	NR	
High-income western countries	Men	0.58 (0.47–0.69)	24 (22–27)	1.80 (1.53–2.07)	76 (74–78)	–0.01 (–0.02–0.00)	0 (–1–0)	
	Women	0.39 (0.24–0.54)	21 (15–26)	1.44 (1.09–1.79)	79 (74–84)	0.00 (–0.02–0.01)	0 (–1–1)	
<b>World</b>								
World	Men	1.24 (1.06–1.43)	57 (53–60)	0.65 (0.54–0.75)	30 (27–32)	0.30 (0.28–0.32)	14 (12–16)	
	Women	1.22 (1.01–1.43)	60 (56–64)	0.56 (0.44–0.69)	28 (24–31)	0.25 (0.23–0.27)	13 (11–15)	

Contributions of the rise in mean BMI in rural and urban populations and of urbanization to the rise in mean BMI from 1985 to 2017, by region. Urbanization is defined as an increase in the proportion of the population who live in urban areas. Percentage contributions were calculated as described in the Methods. The reported values are the means and 95% credible intervals. The three percentages sum to 100%. When one component causes an increase in BMI in a region and another does the opposite, the components can be negative or greater than 100%. Urban and rural mean BMI and the percentage of the population who live in urban areas in 1985 and 2017 for each region are provided in Extended Data Table 1. NR, percentage contribution was not reported, because the regional change in mean BMI (which appears in the denominator of the percentage contribution) was small (<0.5 kg m<sup>-2</sup>), leading to unstable estimates.

gap was as large as 3.25 kg m<sup>-2</sup> (2.57–3.96) in women and 3.05 kg m<sup>-2</sup> (2.44–3.68) in men in India. Over time, the BMI gap between rural and urban women shrank in all of these regions by at least 40%, as BMI rose faster in rural areas than in cities (Fig. 3). In 14 countries in these regions, including Armenia, Chile, Jamaica, Jordan, Malaysia, Taiwan and Turkey, the ordering of rural and urban female BMI reversed over time and rural women had higher BMI than their urban peers in 2017 (Fig. 1 and Extended Data Fig. 4).

The mean BMI of rural men also increased more than the mean BMI of urban men in south Asia and Oceania, shrinking the urban–rural BMI gap by more than half (Figs. 2, 3). In east and southeast Asia, Latin America and the Caribbean, and central Asia, the Middle East and north Africa, men in both rural and urban areas experienced a similar BMI increase and, therefore, the urban excess BMI did not change substantially over time.

In contrast to emerging economies, excess BMI among urban women became larger in sub-Saharan Africa (Fig. 3): from 2.59 kg m<sup>-2</sup> (2.21–2.98) in 1985 to 3.17 kg m<sup>-2</sup> (2.93–3.42) in 2017 (posterior probability of the observed increase being a true increase >0.999). This occurred because female BMI rose faster in cities than in rural areas in sub-Saharan Africa. This led to women in sub-Saharan African countries, especially those in west Africa, having the largest urban excess BMI of any country in 2017—for example, more than 3.35 kg m<sup>-2</sup> in Niger, Burkina Faso, Togo and Ghana (Fig. 1 and Extended Data Fig. 4). BMI increased at a similar rate in rural and urban men in sub-Saharan Africa, with the difference in 2017 (1.66 kg m<sup>-2</sup>; 1.37–1.94) being similar to 1985 (1.60 kg m<sup>-2</sup>; 1.13–2.07) (Fig. 2 and Extended Data Fig. 4).

BMI was previously lower in rural areas of low- and middle-income countries than in cities, both because rural residents had higher energy expenditure in their daily work—especially agriculture—and domestic activities, such as fuelwood and water collection<sup>13,14</sup>, and because lower incomes in rural areas restricted food consumption<sup>15</sup>. In middle-income countries, agriculture is increasingly mechanized, cars are used for rural transport as income increases and road infrastructure improves, service and administrative jobs have become more common for example, because homes have a water connection and use commercial fuels<sup>16</sup>. Furthermore, higher incomes as a result of economic growth allow more spending on food and hence higher caloric intake, disproportionately more in rural areas, where a substantial share of income was previously spent on food. Additionally, the consumption of processed carbohydrates may have increased disproportionately in rural areas where such foods have become more readily available through national and transnational companies<sup>9,17–21</sup>. These changes, referred to as ‘urbanization of rural life’ by some researchers<sup>6</sup>, have contributed to a larger increase in rural BMI<sup>22,23</sup>.

In contrast to other regions, urbanization in sub-Saharan Africa preceded significant economic growth<sup>24</sup>. Subsistence farming remains common in Africa, and agriculture remains mostly manual; fuelwood—usually collected by women—is still the dominant fuel in rural Africa; and the use of cars for transportation is limited by poor infrastructure and poverty. In African cities, many people have service and office jobs, and mobility has become less energy-intensive owing to shorter travel distances and the use of cars and buses. Furthermore, urban markets where fresh produce is sold are increasingly replaced by commercially prepared and processed

foods from transnational and local industries and street vendors<sup>25–27</sup>. These effects are exacerbated by limited time and space for cooking healthy meals and possibly perceptions of large weight as a sign of affluence<sup>28,29</sup>.

In contrast to low- and middle-income regions, urban women in high-income western and Asia Pacific regions, and in central and eastern Europe, had slightly lower mean BMI than their rural peers in 2017 (Fig. 3). The rural excess BMI for women in these regions changed little from 1985 to 2017. Nationally, the excess BMI of rural women was largest in central and eastern European countries (for example, around 1 kg m<sup>-2</sup> or more in Belarus, Latvia and Czech Republic; Fig. 1 and Extended Data Fig. 4). Rural men in high-income western countries also had an excess BMI compared to urban men throughout the analysis period. The largest rural excess BMI for men in 2017 was seen in Sweden, Czech Republic, Ireland, Australia, Austria and the United States, which all had an excess BMI of 0.35 kg m<sup>-2</sup> or larger. In the high-income Asia Pacific region and in central and eastern Europe, rural and urban men had almost identical BMI throughout these three decades (Fig. 2 and Extended Data Fig. 4).

The lower urban BMI in high-income and industrialized countries reflects a growing rural economic and social disadvantage, including lower education and income, lower availability and higher price of healthy and fresh foods<sup>30,31</sup>, less access to, and use of, public transport and walking than in cities<sup>32,33</sup>, and limited availability of facilities for sports and recreational activity<sup>34</sup>, which account for a significant share of overall physical activity in high-income and industrialized countries.

We also estimated how much of the overall rise in mean BMI since 1985 has been due to increases in BMI of rural and urban populations versus those attributable to urbanization (defined as an increase in the proportion of the population who live in urban areas), in each region and in the world as a whole. At the global level, 60% (56–64) of the rise in mean BMI from 1985 to 2017 in women and 57% (53–60) in men was due to increases in the BMI of rural populations; 28% (24–31) in women and 30% (27–32) in men due to the rise in BMI in urban populations; and 13% (11–15) and 14% (12–16) due to urbanization (Table 1). The contribution of the rise in rural BMI ranged from around 60% to 90% in the mostly rural regions of sub-Saharan Africa, east, south and south-east Asia and Oceania. The contribution of urbanization was small in all regions of the world, with maximum values of 19% (15–25) among women and 14% (10–21) among men in sub-Saharan Africa.

Our results show that, contrary to the prevailing view<sup>3–6</sup>, BMI is rising at the same rate or faster in rural areas compared to cities, particularly in low- and middle-income countries except among women in sub-Saharan Africa. These trends have resulted in a rural–urban convergence in BMI in most low- and middle-income countries, especially for women. This convergence mirrors the experience of high-income and industrialized countries, where we found a persistently higher BMI in rural areas. The rising rural BMI is the largest contributor to the BMI rise in low- and middle-income regions and in the world as a whole over the last 33 years, which challenges the current paradigm of urban living and urbanization as the key driver of the global epidemic of obesity.

In poor societies, urban areas historically had lower levels of undernutrition<sup>35,36</sup>, possibly because infrastructure such as roads and electricity facilitate food trade, transport and storage in cities, which can in turn reduce the impacts of agricultural shocks and seasonality. As economic growth and rural nutrition programmes reduce rural caloric deficiency, the rural undernutrition disadvantage may be replaced with a more general and complex malnutrition that entails excessive consumption of low-quality calories. To avoid such an unhealthy transition, the fragmented national and international responses to undernutrition and obesity should be integrated, and the narrow focus of international aid on undernutrition should be broadened, to enhance access to healthier foods in poor rural and urban communities.

## Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41586-019-1171-x>.

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**Author contributions** M.E. designed the study and oversaw research. H.B. led the data collection and statistical analysis, and prepared results. The other authors contributed to study design; collected, reanalysed, pooled and checked

data; analysed pooled data; and prepared results. M.E. and H.B. wrote the first draft of the manuscript with input from the other authors.

**Competing interests** M.E. reports a charitable grant from the AstraZeneca Young Health Programme, and personal fees from Prudential, Scor and Third Bridge, outside the submitted work. The other authors declare no competing interests.

**Additional information**

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## NCD Risk Factor Collaboration (NCD-RisC)

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## METHODS

Our aim was to estimate trends in mean BMI from 1985 to 2017 by rural and urban place of residence for 200 countries and territories (Supplementary Table 2). To achieve this aim, we pooled cross-sectional population-based data on height and weight in adults aged 18 years and older. Therefore, by design, our results measure total change in BMI in each country's rural and urban populations, which consists of (1) change in the BMI of individuals due to change in their economic status and environment, and (2) change in the composition of individuals that make up the population (and their economic status and environment). Change in population composition occurs naturally owing to fertility and mortality, as well as owing to migration. Therefore, our results should not be interpreted as solely a change in the BMI of individuals. Both components of change are relevant for policy formulation because policies should address the environment and nutrition of the contemporary population.

We used mean BMI as the primary outcome, rather than prevalence of overweight or obesity, because the relationship between BMI and disease risk is continuous, with each unit lower BMI being associated with a constant proportional reduction in disease risk until a BMI of around 21–23 kg m<sup>-2</sup>, which is below the cut-offs used to define overweight and obesity<sup>37–39</sup>. Therefore, the largest health benefits of weight management are achieved by lowering the population distribution of BMI. Mean BMI is the simplest summary statistic of the population distribution. Nonetheless, mean BMI and prevalence of overweight and obesity are closely associated (Extended Data Fig. 5).

**Data sources.** We used a database on cardiometabolic risk factors collated by the Non-Communicable Disease Risk Factor Collaboration (NCD-RisC). NCD-RisC is a worldwide network of health researchers and practitioners, that systematically documents the worldwide trends and variations in risk factors for non-communicable diseases. The database was collated through multiple routes for identifying and accessing data. We accessed publicly available population-based measurement surveys—for example, Demographic and Health Surveys, Global School-based Student Health Surveys, the European Health Interview and Health Examination Surveys and those available via the Inter-University Consortium for Political and Social Research. We requested, through the World Health Organization (WHO) and its regional and country offices, help with identification and access to population-based surveys from ministries of health and other national health and statistical agencies. Requests were also sent by the World Heart Federation to its national partners. We made similar requests to the co-authors of an earlier pooled analysis of cardiometabolic risk factors<sup>40–43</sup> and invited them to reanalyse data from their studies and join NCD-RisC. Finally, to identify major sources not accessed through the above routes, we searched and reviewed published studies as described previously<sup>44</sup> and invited all eligible studies to join NCD-RisC.

Anonymized individual record data from sources included in NCD-RisC were reanalysed according to a common protocol. Within each survey, we included participants aged 18 years and older who were not pregnant. We dropped participants with implausible BMI levels (defined as BMI < 10 kg m<sup>-2</sup> or BMI > 80 kg m<sup>-2</sup>) or with implausible height or weight values (defined as height < 100 cm, height > 250 cm, weight < 12 kg or weight > 300 kg; <0.2% of all subjects). We also dropped participants whose urban and rural status was unknown in surveys that had recorded place of residence (0.05% of all participants). We calculated mean BMI and its standard error by sex, age group (18 years, 19 years, 10-year age groups from 20–29 years to 70–79 years and 80+ years) and rural or urban place of residence. All analyses incorporated appropriate sample weights and complex survey design, when applicable, in calculating summary statistics. Countries typically use the rural and urban classification of communities designated by their statistical offices at any given time both for survey design and for reporting of population to the United Nations Population Division. The classification can change, for example as previously rural areas grow and industrialize and hence become, and are (re)designated as, de novo cities. To the extent that the reclassifications keep up with changes in the real status of each community, survey and population data reflect the status of each community at the time of measurement. For surveys without information on place of residence, we calculated age- and sex-stratified summary statistics for the entire sample, which represented the population-weighted sum of rural and urban means.

To ensure summaries were prepared according to the study protocol, computer code was provided to NCD-RisC members who requested assistance. All submitted data were checked by at least two independent reviewers. Questions and clarifications were discussed with NCD-RisC members and resolved before data were incorporated into the database.

Finally, we incorporated all nationally representative data from sources that were identified but not accessed through the above routes, by extracting summary statistics from published reports. Data were also extracted for nine WHO STEPwise approach to Surveillance (STEPS) surveys, one Countrywide Integrated Non-communicable Diseases Intervention (CINDI) survey, and five sites of the

WHO Multinational MONItoring of trends and determinants in Cardiovascular disease (MONICA) project that were not deposited in the MONICA Data Centre. Data were extracted from published reports only when reported by sex and in age groups no wider than 20 years. We also used data from a previous global data pooling study<sup>45</sup> when such data had not been accessed through the routes described.

All NCD-RisC members are asked periodically to review the list of sources from their country, to suggest additional sources not in the database, and to verify that the included data meet the inclusion criteria listed below and are not duplicates. The NCD-RisC database is continuously updated through this contact with NCD-RisC members. For this paper, we used data from the NCD-RisC database for years 1985 to 2017 and ages 18 years and older. A list of the data sources that we used in this analysis and their characteristics is provided in Supplementary Table 1.

**Data inclusion and exclusion.** Data sources were included in the NCD-RisC database if: (1) measured data on height, weight, waist circumference or hip circumference were available; (2) study participants were 5 years of age and older; (3) data were collected using a probabilistic sampling method with a defined sampling frame; (4) data were from population samples at the national, sub-national (that is, covering one or more sub-national regions, more than three urban communities or more than five rural communities) or community level; and (5) data were from the countries and territories listed in Supplementary Table 2.

We excluded all data sources that were based solely on self-reported weight and height without a measurement component, because these data are subject to biases that vary by geography, time, age, sex and socioeconomic characteristics<sup>45–47</sup>. Owing to these variations, approaches to correcting self-reported data leave residual bias. We also excluded data sources on population subgroups whose anthropometric status may differ systematically from the general population, including: (1) studies that included or excluded people based on their health status or cardiovascular risk; (2) studies whose participants were only ethnic minorities; (3) specific educational, occupational, or socioeconomic subgroups, with the exception noted below; (4) those recruited through health facilities, with the exception noted below; and (5) women aged 15–19 years in surveys which sampled only ever-married women or measured height and weight only among mothers.

We used school-based data in countries, and in age–sex groups, with school enrolment of 70% or higher. We used data for which the sampling frame was health insurance schemes in countries in which at least 80% of the population were insured. Finally, we used data collected through general practice and primary care systems in high-income and central European countries with universal insurance, because contact with the primary care systems tends to be as good as or better than response rates for population-based surveys.

**Conversion of BMI prevalence metrics to mean BMI.** In 2% of our data points—mostly extracted from published reports or from a previous pooling analysis<sup>43</sup>—mean BMI was not reported, but data were available for the prevalence of one or more BMI categories, for example, BMI ≥ 30 kg m<sup>-2</sup>. In order to use these data, we used previously validated conversion regressions<sup>2</sup> to estimate the missing primary outcome from the available BMI prevalence metric(s). All sources of uncertainty in the conversion—including the sampling uncertainty of the original data, the uncertainty of the regression coefficients and random effects, and the regression residuals—were carried forward by using repeated draws from their joint posterior distribution, accounting for the correlations among the uncertainties of regression coefficients and random effects.

**Statistical analysis of BMI trends by rural and urban place of residence.** We used a Bayesian hierarchical model to estimate mean BMI by country, year, sex, age and place of residence. The statistical model is described in detail in a statistical paper and related substantive papers<sup>2,35,40–44,48–51</sup>, and in the Supplementary Information. In summary, we organized countries into 21 regions (Supplementary Table 2), mostly based on geography and national income. The exception was high-income English-speaking countries (Australia, Canada, Ireland, New Zealand, the United Kingdom and the United States), grouped together in one region because BMI and other cardiometabolic risk factors have similar trends in these countries, which can be distinct from other countries in their geographical regions<sup>2,49,50,52</sup>. Regions were in turn organized into nine super-regions.

The model had a hierarchical structure in which estimates for each country and year were informed by their own data, if available, and by data from other years in the same country and from other countries, especially those in the same region with data for similar time periods. The extent to which estimates for each country-year were influenced by data from other years and other countries depended on whether the country had data, the sample size of the data, whether they were national, and the within-country and within-region variability of the available data. The model incorporated nonlinear time trends comprising linear terms and a second-order random walk, all modelled hierarchically. The age association of BMI was modelled using a cubic spline to allow nonlinear age patterns, which could vary across countries. The model accounted for the possibility that BMI in sub-national and community samples might differ systematically from nationally

representative ones and have larger variation than in national studies. These features were implemented by including data-driven fixed-effect and random-effect terms for sub-national and community data. The fixed effects adjusted for systematic differences between sub-national or community studies and national studies. The random effects allowed national data to have larger influence on the estimates than sub-national or community data with similar sample sizes.

Here, we extended the model to make estimates for rural and urban populations following a previously published approach<sup>35,51</sup>. This model includes a parameter representing the urban–rural BMI difference, which is estimated empirically and allowed to vary by country and year. The model uses all of the data—those stratified by rural and urban place of residence as well as those reported for the entire population. If data for a country-year were not stratified by place of residence, the estimated urban–rural BMI difference was informed by stratified data from other years and countries, especially those in the same region with data from similar time periods.

We fitted the statistical model with the Markov chain Monte Carlo (MCMC) algorithm and following burn-in obtained 5,000 samples (or draws) from the posterior distribution of model parameters, which were in turn used to obtain the posterior distributions of our primary outcomes—mean urban BMI, mean rural BMI and mean urban–rural BMI difference. Posterior estimates were made in 1-year age groups for ages 18 and 19 and 5-year age groups for those aged 20 years and older. We generated age-standardized estimates by taking weighted means of age-specific estimates, using age weights from the WHO standard population. Regional and global rural and urban mean BMI estimates were calculated as population-weighted averages of rural and urban mean for the constituent country estimates by age group and sex. National mean BMI was calculated as population-weighted averages of the rural and urban means. All analyses were done separately by sex because geographical and temporal patterns of BMI differ between men and women<sup>2</sup>.

The reported credible intervals represent the 2.5th and the 97.5th percentiles of the posterior distributions. We report the posterior probability that the estimated urban–rural BMI difference is a true difference in the same direction as the posterior mean estimate. We also report the posterior probability that the estimated change in the rural–urban BMI difference over time represents a true increase or decrease.

**Validation of statistical model.** We calculated the difference between the posterior estimates from the model and data from national studies. Median errors were very close to zero (0.03 kg m<sup>-2</sup> for women and -0.02 kg m<sup>-2</sup> for men) and median absolute errors were 0.32 kg m<sup>-2</sup> for women and 0.26 kg m<sup>-2</sup> for men, indicating that the estimates were unbiased and had small deviations relative to national studies. The differences were indistinguishable from zero at the 5% level of statistical significance.

We also tested how well our statistical model predicts missing data, known as external predictive validity or cross-validation, in two different tests. In the first test, we held out all data from 10% of countries with data (that is, created the appearance of countries with no data for which we actually had data). The countries for which the data were withheld were selected randomly from the following three groups: data rich (8 or more data sources for women and 7 or more data sources for men), data poor (1–3 data sources for women and 1–2 for men) and average data availability (4–7 data sources for women and 3–6 for men). All data-rich countries had at least one data source after 2000 and at least one source with data stratified on rural and urban place of residence. We fitted the model to the data from the remaining 90% of countries and made estimates of the held-out observations. In the second test, we assessed other patterns of missing data by holding out 10% of our data sources, again from a mix of data-rich, data-poor and average-data countries, as defined above. For a given country, we either held out a random one third of the country's data or all of the country's 2000–2017 data to determine, respectively, how well we filled in the gaps for countries with intermittent data and how well we estimated in countries without recent data. We fitted the model to the remaining 90% of the dataset and made estimates of the held-out observations. We repeated each test five times, holding out a different subset of data in each repetition. In both tests, we calculated the differences between the held-out data and the estimates. We also calculated the 95% credible intervals of the estimates; in a model with good external predictive validity, 95% of held-out values would be included in the 95% credible intervals.

Our statistical model performed very well in the external validation tests, that is, in estimating mean BMI when data were missing. The estimates of mean BMI were unbiased, as evidenced with median errors that were zero or close to zero globally (0.03 and -0.03 kg m<sup>-2</sup> for women and -0.15 and 0.00 kg m<sup>-2</sup> for men in the first and second tests, respectively), and less than  $\pm 0.20$  kg m<sup>-2</sup> in every subset of withheld data except 1985–1999 data in the first test for men, for which the median error was -0.24 kg m<sup>-2</sup> (Extended Data Table 2). Most of the median errors were indistinguishable from zero at the 5% level of statistical significance.

The 95% credible intervals of estimated mean BMI covered 94–98% of true data globally; coverage was >93% in all but one subset of withheld data. Median absolute errors ranged from 0.52 to 1.09 kg m<sup>-2</sup> globally and were at most 1.29 kg m<sup>-2</sup> in all subsets of withheld data. Median absolute errors were smaller in the second test, in which subsets of data sources from some countries were withheld, than in the first test, in which all data from some countries were withheld. Given that we had data for 190 out of 200 countries for women and 183 out of 200 countries for men, the second test is a better reflection of data availability in our analysis. For comparison, median absolute differences for mean BMI between pairs of nationally representative surveys done in the same country and in the same year was 0.46 kg m<sup>-2</sup>, indicating that our estimates perform almost as well as running two parallel surveys in the same country and year.

**Contributions of urbanization and rural and urban BMI change to changes in population mean BMI.** We calculated the contributions of the following components to change in population mean BMI from 1985 to 2017: the contribution of change in BMI in rural areas, the contribution of change in BMI in urban areas, and the contribution of urbanization (that is, increase in the proportion of people living in urban areas). The first two parts were calculated by fixing the proportion of people living in rural and urban areas to 1985 levels and allowing BMI to change as it did in the respective population. The contribution of urbanization was calculated by fixing BMI in rural and urban areas to 2017 levels and allowing the proportion of people living in cities to change as it did. Percentage contributions were calculated using posterior draws, with reported credible intervals representing the 2.5th and the 97.5th percentiles of their posterior distributions. The change in mean BMI from 1985 to 2017 was then calculated as (contribution of change in rural BMI + contribution of change in urban BMI + contribution of change in the proportion of the population living in urban areas) = ((change in BMI<sub>rural1985–2017</sub>) (percentage living in rural areas<sub>1985</sub>) + (change in BMI<sub>urban1985–2017</sub>) (percentage living in urban areas<sub>1985</sub>) + (change in percentage living in urban areas<sub>1985–2017</sub>) (BMI<sub>urban2017</sub> - BMI<sub>rural2017</sub>)).

**Strengths and limitations.** Urbanization is regarded as one of the most important contributors to the global obesity epidemic, but this perspective is based on limited data. We present the first comparable estimates of mean BMI for rural and urban populations worldwide over three decades using, to our knowledge, the largest and most comprehensive global database of human anthropometry with information on urban or rural place of residence. We used population-based measurement data from almost all countries, with information on participants' urban or rural place of residence for the majority of data sources. We maintained a high level of data quality through repeated checks of study characteristics against our inclusion and exclusion criteria, which were verified by NCD-RisC members, and did not use any self-reported data to avoid bias in height and weight. Data were analysed according to a common protocol to obtain mean BMI by age, sex and place of residence. We used a statistical model that used all available data, while giving more weight to national data than sub-national and community studies and took into account the epidemiological features of BMI by using nonlinear time trends and age associations. The model used information on the urban–rural difference in BMI where available and estimated this difference hierarchically and temporally in the absence of stratified data.

Despite our large-scale data collation effort, some countries and regions had fewer data sources, particularly the Caribbean, and Polynesia and Micronesia. There were also fewer data sources before 2000. This temporal and geographical sparsity of data led to wider uncertainty intervals for these countries, regions and years. Although health surveys commonly use the rural and urban classification of national statistical offices, cities and rural areas in different countries vary in their demographic characteristics (for example, population size or density), economic activity, administrative structures, infrastructure and environment. These differences appropriately exist because countries themselves differ in terms of their demography, geography and economy. For example, a country with a smaller population may use a lower threshold for urban designation than one with a larger population, because its cities are naturally smaller even if they serve the same functions. Official rural and urban classifications are used for resource allocation and planning for nutrition and health<sup>53–58</sup>, which makes them the appropriate unit for tracking outcomes. Nonetheless, understanding the causes of change in rural and urban areas can be enriched with use of more complex and multi-dimensional measures of urbanicity involving size, density, economic and commercial activities and infrastructures<sup>59,60</sup>. Finally, urbanization could arise from a variety of mechanisms: (1) natural increase due to excess births over deaths in cities compared to rural areas, (2) rural to urban migration (often related to opportunities for work and education) and (3) reclassification of previously rural areas as they grow and industrialize and hence become, and are (re)designated as, *de novo* cities. The contributions of these mechanisms to urbanization vary across countries. The use of time-varying rural versus urban classification of communities ensures that in any year, the rural and urban strata represent the actual status of each community.

However, each of these mechanisms may have different implications for changes in nutrition and physical activity and, therefore, BMI.

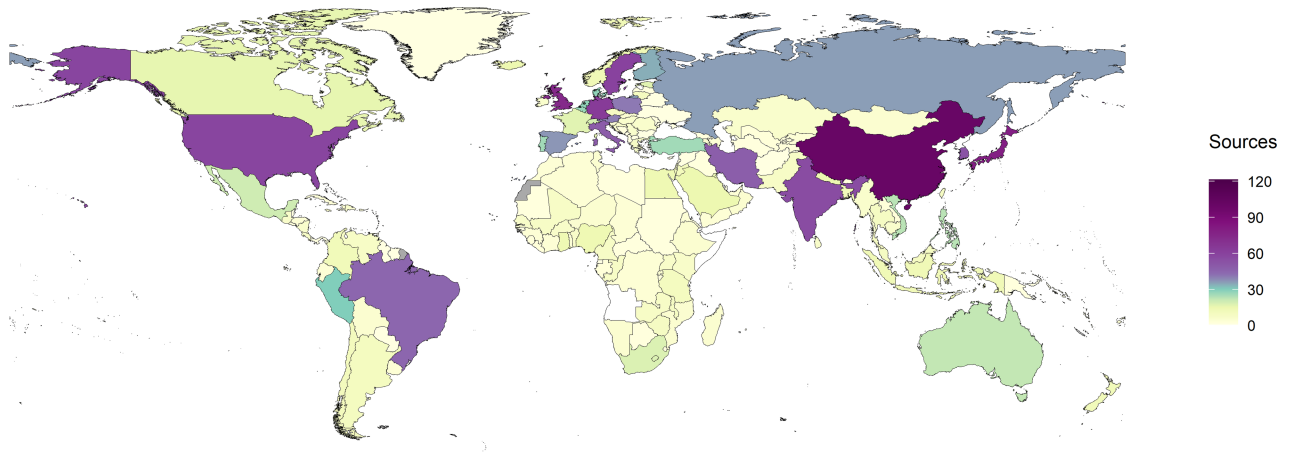
### Data availability

Estimates of mean BMI by country, year, sex and urban and rural place of residence are available from <http://www.ncdrisc.org/>. Input data from publicly available sources can also be downloaded from <http://www.ncdrisc.org/>. For other data sources, contact information for data providers can be obtained from <http://www.ncdrisc.org/>.

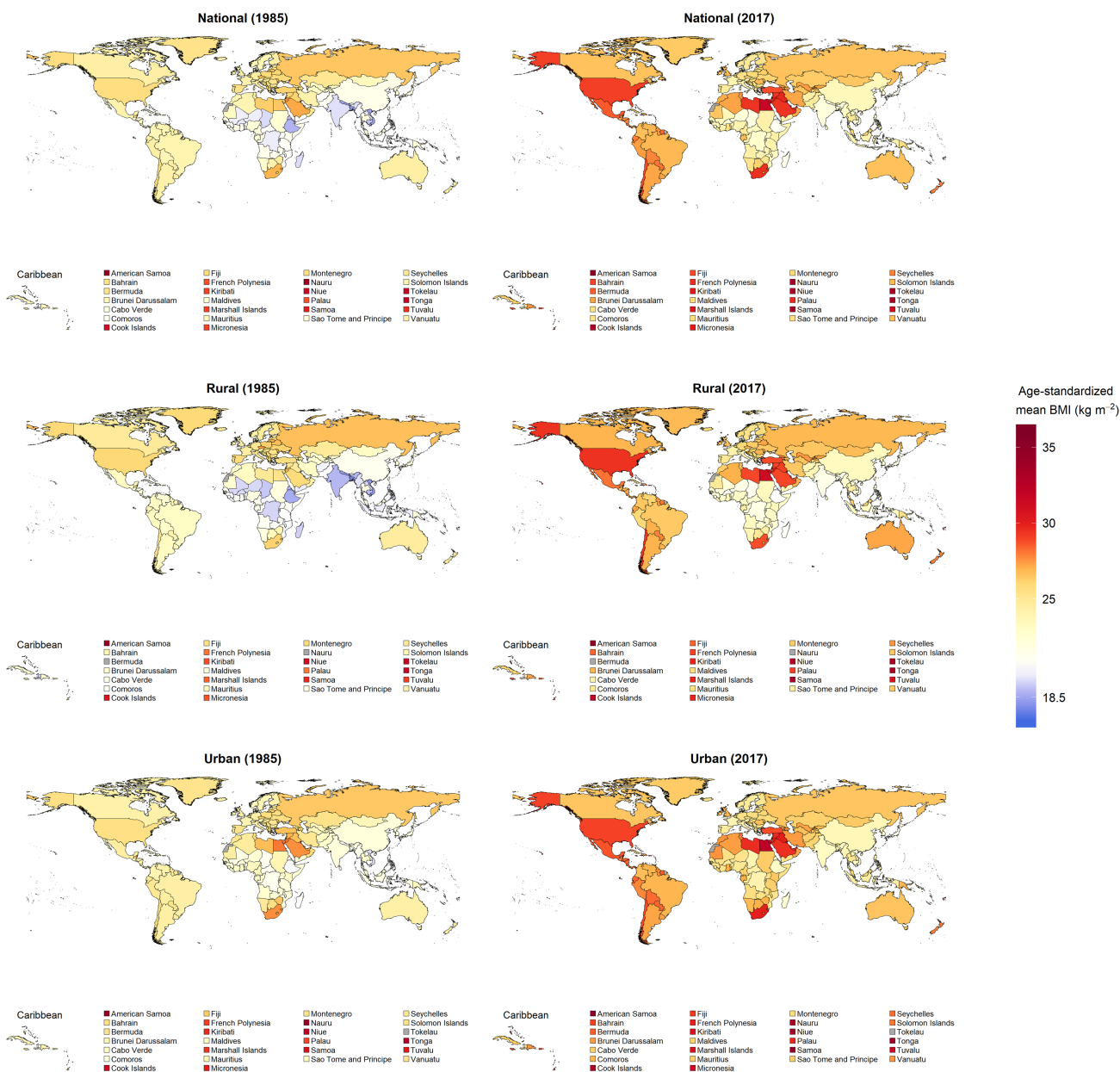
### Code availability

The computer code for the Bayesian hierarchical model used in this work is available at <http://www.ncdrisc.org/>.

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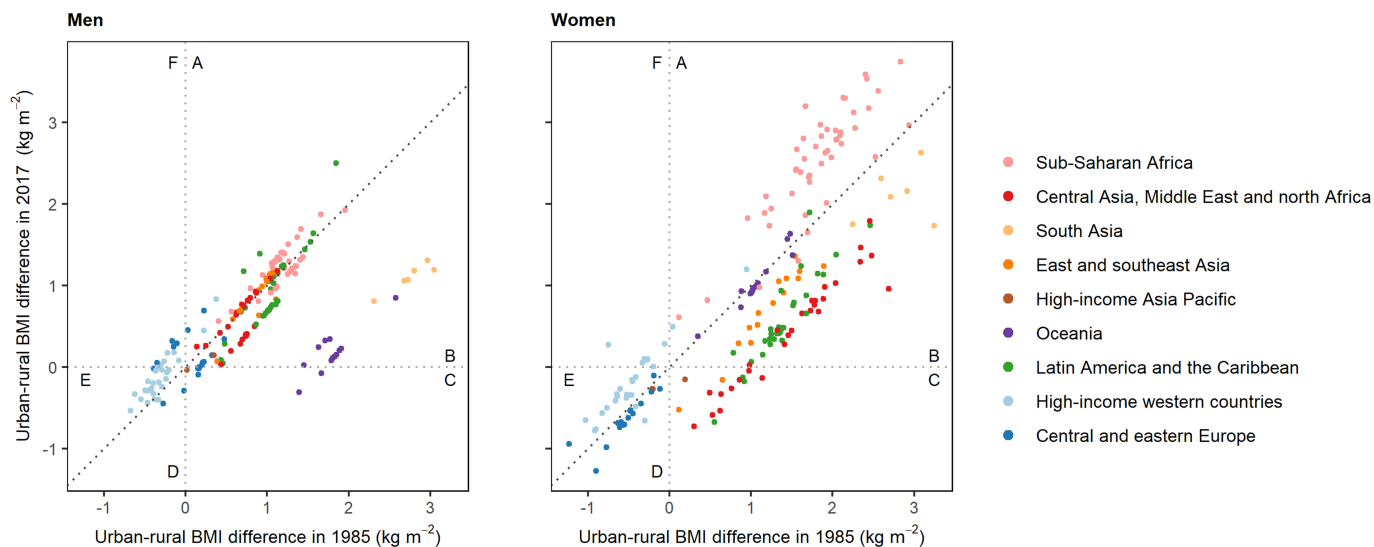
**Extended Data Fig. 1 | Number of data sources by country.** The colour indicates the number of population-based data sources used in the analysis for each country. Countries and territories not included in the analysis are coloured in grey.



Extended Data Fig. 2 | Age-standardized national, rural and urban mean BMI in women aged 18 years and older in 1985 and 2017 by country. The numerical values are provided in Supplementary Table 3 and can be downloaded from <http://www.ncdrisc.org>.

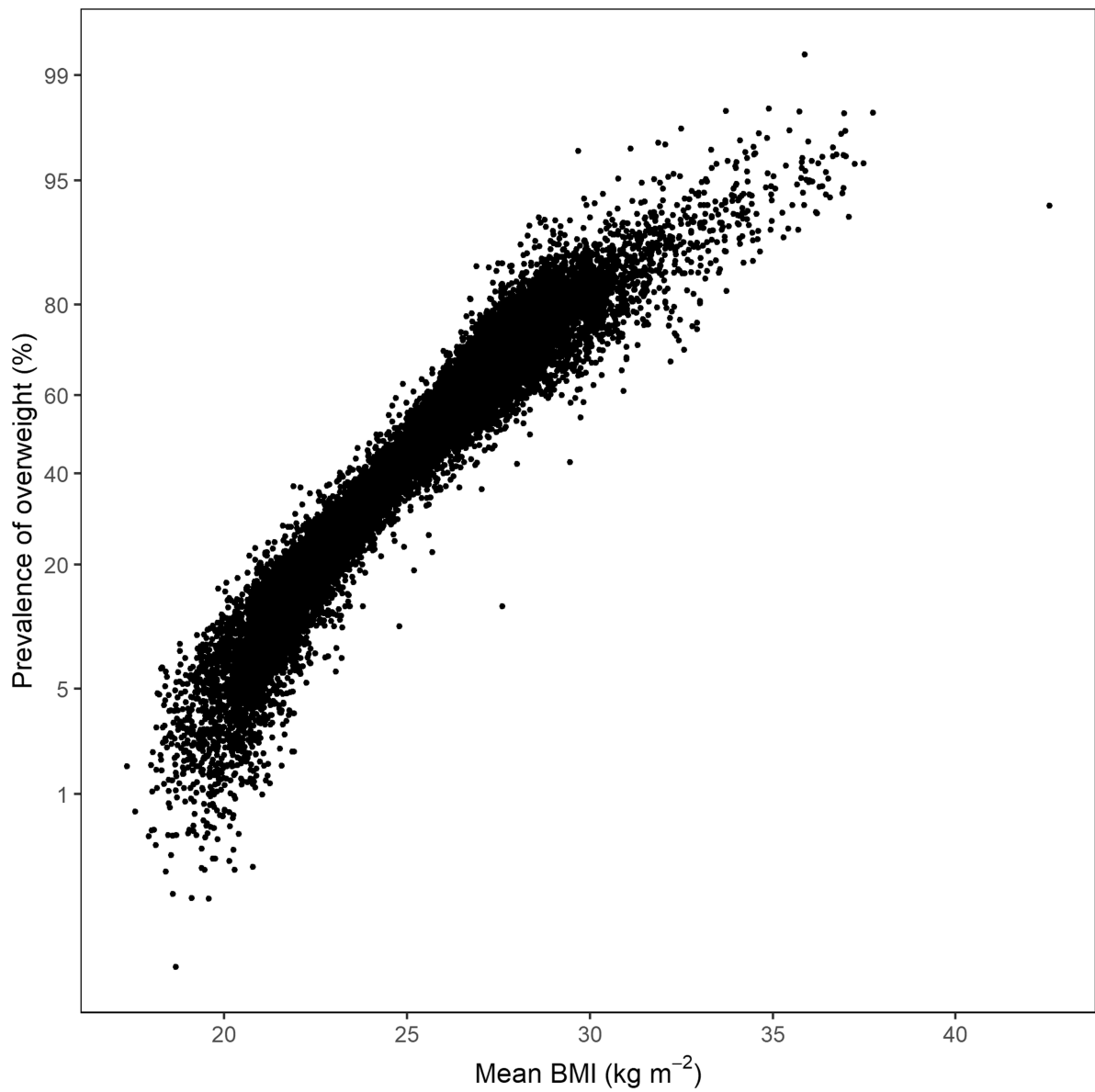






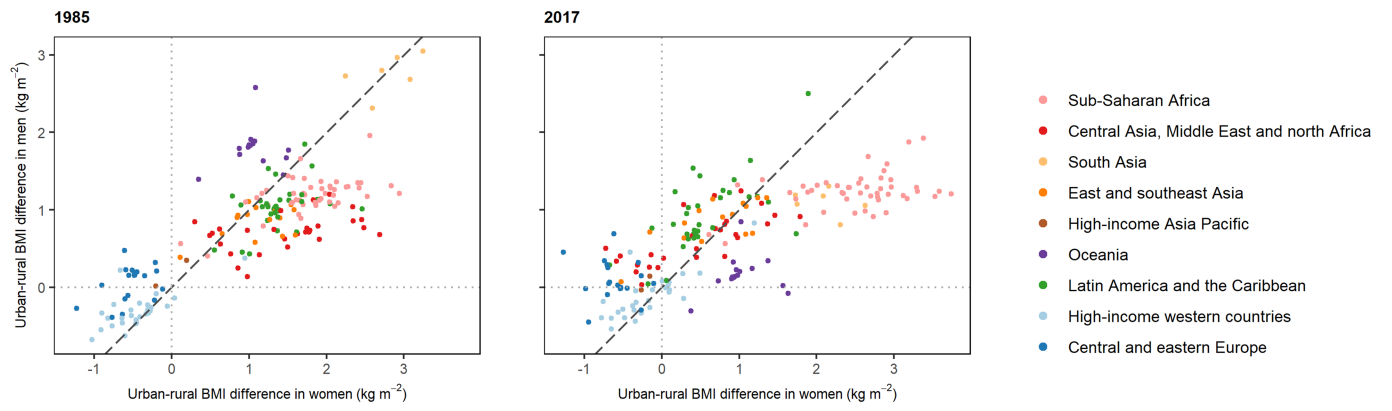
**Extended Data Fig. 4 | The difference between rural and urban age-standardized mean BMI in 1985 compared to 2017.** Each point shows one country and colours indicate region. A positive number indicates a higher urban mean BMI and a negative number indicates a higher rural mean BMI. Different sections labelled A–F indicate the following categories of countries. A, countries with an urban excess BMI that

increased from 1985 to 2017. B, countries with an urban excess BMI that decreased from 1985 to 2017. C, countries with an urban excess BMI in 1985 that changed to a rural excess BMI in 2017. D, countries with a rural excess BMI that increased from 1985 to 2017. E, countries with a rural excess BMI that decreased from 1985 to 2017. F, countries with a rural excess BMI in 1985 that changed to an urban excess BMI in 2017.



**Extended Data Fig. 5 | The relationship between mean BMI and prevalence of overweight.** Overweight is defined as BMI  $\geq 25$  kg m<sup>-2</sup>. Prevalence is plotted on a probit scale, which changes in an approximately linear manner as the mean changes. Each point represents an age group-

and sex-specific mean, stratified by place of residence as described in the Methods and with more than 25 participants, from data sources in the NCD-RisC database.



**Extended Data Fig. 6 | Comparison of the difference between rural and urban age-standardized mean BMI in women and men aged 18 years and older in 1985 and 2017. Each point shows one country and colours indicate region.**

Extended Data Table 1 | Mean BMI and percentage of the population by urban and rural place of residence

Region	Sex	Percentage of the population living in urban areas		Age-standardized mean BMI (kg m <sup>-2</sup> )			
				Rural		Urban	
				1985	2017	1985	2017
<b>Emerging economies</b>							
Central Asia, Middle East and north Africa	Men	51%	63%	23.4 (22.7-24.0)	26.0 (25.8-26.3)	24.2 (23.6-24.8)	26.8 (26.6-27.0)
	Women			24.2 (23.5-24.9)	28.2 (27.9-28.4)	26.1 (25.4-26.8)	28.7 (28.4-28.9)
East and southeast Asia	Men	25%	55%	20.7 (20.4-21.0)	23.3 (23.0-23.7)	21.8 (21.5-22.1)	24.4 (24.0-24.9)
	Women			20.9 (20.5-21.3)	23.3 (22.9-23.8)	22.1 (21.7-22.4)	23.9 (23.4-24.4)
Latin America and the Caribbean	Men	68%	80%	23.0 (22.4-23.6)	25.6 (25.3-25.9)	24.4 (23.8-24.9)	26.9 (26.6-27.2)
	Women			23.1 (22.5-23.7)	27.1 (26.7-27.4)	24.6 (24.0-25.1)	27.5 (27.2-27.9)
Oceania	Men	21%	20%	22.9 (21.9-24.0)	25.7 (24.7-26.7)	25.3 (24.2-26.4)	26.6 (25.7-27.5)
	Women			23.2 (21.9-24.5)	26.2 (24.8-27.5)	25.6 (24.1-27.1)	28.4 (27.2-29.6)
South Asia	Men	24%	34%	19.0 (18.4-19.6)	21.6 (21.2-22.0)	22.0 (21.3-22.6)	22.8 (22.4-23.2)
	Women			19.0 (18.2-19.7)	21.8 (21.4-22.3)	22.2 (21.3-23.0)	23.7 (23.3-24.2)
<b>Sub-Saharan Africa</b>							
Sub-Saharan Africa	Men	25%	39%	20.1 (19.6-20.7)	21.7 (21.3-22.0)	21.7 (21.2-22.3)	23.3 (22.9-23.7)
	Women			20.9 (20.4-21.5)	22.7 (22.4-23.0)	23.5 (23.0-24.1)	25.9 (25.6-26.2)
<b>High-income and other industrialized regions</b>							
Central and eastern Europe	Men	65%	68%	25.0 (24.4-25.6)	26.7 (26.2-27.2)	25.0 (24.5-25.5)	26.7 (26.1-27.3)
	Women			26.3 (25.6-27.0)	26.7 (26.1-27.2)	26.0 (25.4-26.6)	26.2 (25.6-26.9)
High-income Asia Pacific	Men	74%	91%	22.3 (22.0-22.6)	24.1 (23.9-24.4)	22.4 (22.1-22.6)	23.9 (23.6-24.2)
	Women			22.2 (21.8-22.6)	22.7 (22.3-23.0)	22.1 (21.8-22.4)	22.1 (21.7-22.5)
High-income western countries	Men	74%	80%	25.6 (25.3-25.8)	27.8 (27.5-28.1)	25.2 (24.9-25.4)	27.6 (27.4-27.9)
	Women			25.4 (25.0-25.8)	26.9 (26.5-27.3)	24.9 (24.6-25.2)	26.9 (26.5-27.2)
<b>World</b>							
World	Men	41%	55%	21.1 (20.9-21.3)	23.2 (23.0-23.4)	23.7 (23.5-23.9)	25.3 (25.2-25.5)
	Women			21.5 (21.3-21.8)	23.6 (23.4-23.8)	24.2 (23.9-24.4)	25.5 (25.3-25.7)

For each region, the table shows age-standardized mean BMI for urban and rural populations and the percentage of the population living in urban areas in 1985 and 2017. See Supplementary Table 2 for a list of countries in each region. Numbers in parentheses show 95% credible intervals.

Extended Data Table 2 | Results of model validation

Validation	Sex	Data		No. of held-out observations	Percent covered	Error (kg m <sup>-2</sup> ) <sup>†</sup>				Absolute error (kg m <sup>-2</sup> )			
						Median	Q1	Q3	(p*)	Median	Q1	Q3	(p*)
Test 1	Women	All		7022	98	0.03	-1.09	1.08	0.08	1.09	0.50	1.88	0.08
		Study representativeness	Community	1589	98	0.30	-0.89	1.31	0.48	1.16	0.54	1.95	0.48
			Sub-national	1197	98	-0.09	-1.30	1.25	0.03	1.29	0.61	2.04	0.03
			National	4236	97	-0.03	-1.09	0.95	0.06	1.00	0.47	1.78	0.06
		Years	1985-1999	480	96	0.00	-1.33	0.86	0.14	1.06	0.47	1.69	0.14
	2000-2017		6542	98	0.03	-1.07	1.10	0.17	1.09	0.50	1.90	0.17	
	Men	All		6392	97	-0.15	-0.98	0.74	0.00	0.86	0.43	1.54	0.00
		Study representativeness	Community	1409	98	-0.15	-0.92	0.63	0.01	0.78	0.39	1.37	0.01
			Sub-national	1233	98	-0.11	-0.85	0.87	0.18	0.86	0.40	1.56	0.18
			National	3750	96	-0.16	-1.06	0.74	0.00	0.89	0.45	1.59	0.00
Years		1985-1999	627	99	-0.24	-0.90	0.50	0.02	0.72	0.36	1.21	0.02	
	2000-2017	5765	97	-0.13	-1.00	0.76	0.00	0.88	0.44	1.58	0.00		
Test 2	Women	All		7680	94	-0.03	-0.67	0.58	0.29	0.62	0.28	1.19	0.29
		Study representativeness	Community	1480	88	0.10	-0.75	0.92	0.83	0.84	0.38	1.59	0.83
			Sub-national	1330	93	-0.07	-0.73	0.58	0.38	0.65	0.30	1.19	0.38
			National	4870	96	-0.05	-0.63	0.50	0.27	0.57	0.26	1.08	0.27
		Years	1985-1999	1472	94	-0.02	-0.56	0.55	0.71	0.56	0.25	1.15	0.71
	2000-2017		6208	94	-0.03	-0.69	0.58	0.21	0.64	0.29	1.20	0.21	
	Men	All		6608	95	0.00	-0.54	0.51	0.23	0.52	0.24	1.01	0.23
		Study representativeness	Community	1559	93	0.01	-0.65	0.65	0.71	0.65	0.32	1.23	0.71
			Sub-national	1137	94	0.03	-0.51	0.56	0.93	0.54	0.25	1.06	0.93
			National	3912	96	-0.01	-0.51	0.45	0.19	0.48	0.21	0.91	0.19
Years		1985-1999	1190	97	-0.04	-0.52	0.37	0.68	0.45	0.20	0.84	0.68	
	2000-2017	5418	95	0.01	-0.55	0.53	0.28	0.54	0.25	1.05	0.28		

Q1, first quartile; Q3, third quartile; p, p value.

†Estimated values minus held-out values.

\*p values for model error comparisons were calculated using the non-parametric Wilcoxon signed-rank test for paired data. The p values are calculated assuming independence of the held-out observations. They should therefore be interpreted as an approximation because there is some dependence among the held-out observations, within each of the five repetitions for example.

## Reporting Summary

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### Statistical parameters

When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

n/a Confirmed

- The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement
- An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided  
*Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistics 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)
- For null hypothesis testing, the test statistic (e.g.  $F$ ,  $t$ ,  $r$ ) with confidence intervals, effect sizes, degrees of freedom and  $P$  value noted  
*Give  $P$  values as exact values whenever suitable.*
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's  $d$ , Pearson's  $r$ ), indicating how they were calculated
- Clearly defined error bars  
*State explicitly what error bars represent (e.g. SD, SE, CI)*

*Our web collection on [statistics for biologists](#) may be useful.*

### Software and code

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

Data collection Processing of secondary data was conducted using the statistical software R (version 3.5.1).

Data analysis All analyses were conducted using the statistical software R (version 3.5.1). The code for national analysis of mean risk factor trends is available at [www.ncdrisc.org](http://www.ncdrisc.org). The code for analysis of trends in urban and rural subgroups is available from [www.ncdrisc.org](http://www.ncdrisc.org).

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/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [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 list of figures that have associated raw data
- A description of any restrictions on data availability

This is a data-pooling study that brings together almost 2000 disparate data sources and uses a Bayesian hierarchical model to estimate population risk factor trends. Estimates of mean BMI by country, year, sex and place of residence (urban and rural) are available from [www.ncdrisc.org](http://www.ncdrisc.org). Estimates of mean BMI by

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

For a reference copy of the document with all sections, see [nature.com/authors/policies/ReportingSummary-flat.pdf](https://www.nature.com/authors/policies/ReportingSummary-flat.pdf)

## Behavioural & social sciences study design

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

Study description	We pooled and re-analysed population-based data on height and weight in adults to estimate trends in mean BMI from 1985 to 2017 by urban and rural place of residence from 200 countries and territories, using a Bayesian hierarchical model.
Research sample	We pooled data from 2,009 population-based studies of human anthropometry conducted in 190 countries, with measurement of height and weight in over 112 million adults aged 18 years and older. Studies were representative of a national, subnational or community population.
Sampling strategy	We included data collected using a probabilistic sampling method with a defined sampling frame. We therefore included studies with simple random and complex survey designs but excluded convenience samples.
Data collection	We used data on measured height and weight to calculate body-mass index. We excluded self-reported data.
Timing	We pooled data collected from 1985 to 2017. We also included national studies for the 3 years prior to 1985 (n=17), assigning them to 1985, so that they can inform the estimates in countries with slightly earlier national data.
Data exclusions	<p>We excluded all data sources that were solely based on self-reported weight and height without a measurement component because these data are subject to biases that vary by geography, time, age, sex and socioeconomic characteristics. Due to these variations, approaches to correcting self-reported data leave residual bias. We also excluded data sources on population subgroups whose anthropometric status may differ systematically from the general population, including:</p> <ul style="list-style-type: none"> <li>• studies that had included or excluded people based on their health status or cardiovascular risk;</li> <li>• studies whose participants were only ethnic minorities;</li> <li>• specific educational, occupational, or socioeconomic subgroups, with the exception noted below;</li> <li>• those recruited through health facilities, with the exception noted below; and</li> <li>• women aged 18-19 years in surveys which sampled only ever-married women or measured height and weight only among mothers.</li> </ul> <p>Our exclusion criteria were established at the initiation of the study to ensure all data were representative.</p>
Non-participation	Our inclusion/exclusion criteria were designed to ensure participants of the surveys included were representative of the general population from which each sample was drawn.
Randomization	Our study is descriptive, and we did not carry out experiments.

## Reporting for specific materials, systems and methods

### Materials & experimental systems

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Unique biological materials
<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
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants

### Methods

n/a	Involvement 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