Article

Environmental plasticity in the genetics of human body size: evidence from regional-level comparisons in the CODATwins project

Karri Silventoinen [1, 2]

[1] Helsinki Institute for Demography and Population Health, University of Helsinki, Helsinki, Finland.
[2] Center for Twin Research, Osaka University Graduate School of Medicine, Osaka, Japan.

Abstract

Height and body mass index (BMI) are the most studied traits in epidemiology and human genetics. The CODATwins project is an international initiative using twin modelling to analyze how the macro-environment modifies the genetic variation of these traits. Currently, the database contains data from approximately 500,000 twin individuals, including around 1 million height and weight measurements from 57 twin cohorts across 24 countries. The countries were classified into three cultural-geographic regions: East Asia representing the low-obesogenic region, Europe the moderate-obesogenic region, and North America and Australia the high-obesogenic region. The mean height was tallest in Europe and shortest in East Asia, but height variation was largest in North America and Australia due to larger shared environmental variation. Mean BMI and BMI variation were greatest in North America and Australia and smallest in East Asia. The differences in BMI variation were mainly due to differences in additive genetic variation. In North America, Australia, and Europe, lower parental education was associated with higher mean BMI and larger BMI variation mainly due to additive genetic variation. In East Asia, parental education was not associated with mean BMI or BMI variation. These results indicate that the obesogenic environment increases BMI by reinforcing the genetic predisposition to obesity. Genetic and social susceptibility to obesity increases BMI if associated with the obesogenic macro-environment. This highlights the need for societal-level actions when coping with the global obesity pandemic.

Keywords:
BMI, cross-country comparisons, height, heritability, plasticity, twins

(Received 12 March 2025; accepted 30 April 2025; First Published online 31 July 2025)

Author for Correspondence: Karri Silventoinen, karri.silventoinen@helsinki.fi

Introduction

Anthropometric measures – especially height and body mass index (BMI) – have been crucial in demonstrating how genes and the environment influence human development. The first study on the genetics of height was conducted by Francis Galton. In his groundbreaking work "Natural Inheritance", Galton (1889) established the principles of statistical genetics by examining height correlations among relatives. This research was expanded upon by Karl Pearson (1904), who further developed Galton's ideas using larger pedigree datasets and more advanced statistical methods. However, the most significant advancement in human genetics occurred in 1918 when Ronald Fisher published a landmark paper (Fisher, 1918). Fisher showed that the Mendelian inheritance principles could be combined with the correlation patterns of quantitative traits among relatives. His work laid the mathematical foundation for quantitative genetics, which is essential in modern twin and family studies for estimating the impact of genetic and environmental factors on individual differences. Throughout these influential contributions to human genetics, height was the primary trait studied. Following these studies on height, Charles Davenport (1923) expanded statistical genetics to investigate body build and BMI. His work formed the basis for future research on the genetic influences on body weight and obesity. In recent years, advancements in molecular genetics have revealed the biological mechanisms underlying the heritability of height (Richard et al., 2025) and BMI (Silventoinen and Konttinen, 2020).

Anthropometric measures have also been crucial in demonstrating the impact of environmental factors on human development. A pioneering study by Franz Boas (1910) examined European immigrants and their American-born children, revealing that the children were taller and had different skull shapes compared to their parents. While some of his results have been criticized later (Sparks and Jantz, 2002), his study provided compelling evidence that environmental influences – such as nutrition and living conditions – play a significant role in human growth and development, as opposed to solely genetic factors. Boas' work introduced the concept of human plasticity, which suggests that body size is influenced by environmental factors. In later decades, the role of height as a population level indicator of environmental factors has been widely acknowledged. In economic history, height has been frequently used to indicate differences in the standard of living over time and between socioeconomic groups (Steckel, 2009), as well as in epidemiology as a proxy indicator of environmental stress in childhood (Silventoinen, 2015a). Recent studies that combine molecular level information, socioeconomic indicators, and disease incidence data have further supported the idea that height captures environmental variation that is important for assessing health risks (Silventoinen et al., 2023).

Therefore, from the very beginning of the scientific study of humans to the most recent developments in human genetics and epidemiology, body size has been used to demonstrate the role of genetic and environmental factors in human variability. However, there is increasing recognition that genetic and environmental factors do not act independently but instead interact with each other. Analyzing this interplay between genes and the environment requires a study design that allows for examining how environmental factors modify the genetics of body size – the environmental plasticity in genetics. One option for this approach is to utilize the classical twin design and collect information from twin pairs who have grown up under different environmental exposures. This approach was the guiding principle behind the establishment of the CODATwins project – an international effort to pool twin data from a large number of countries representing different ethnicities, geographic regions, and environmental exposures. In this article, the environmental plasticity in genetics will be explored using evidence from the CODATwins project.

Studying the interplay between genes and the environment in body size

General framework of gene-environment interactions

Studies conducted over the past 100 years have shown that both genetic and environmental factors significantly contribute to the variation in body size. Initially, the simultaneous influence of genes and the environment might seem contradictory. For instance, genetic factors account for nearly 90% of the differences in adult height within birth cohorts. These heritability estimates have remained consistent over the cohorts born over the past century, even as living standards have dramatically improved during that time (Jelenkovic et al., 2016a). This indicates that genetics play a major role in height differences, even among individuals who grew up in environments with potential growth-limiting factors. However, there are still notable differences in average height between populations that genetics alone cannot explain. For example, North Korean children aged 7 – 8 were about 13 cm shorter than their South Korean peers in 2002 – 2003 (Schwekendiek, 2009). Since both populations share a common ancestral background, this height gap cannot be attributed to genetic differences. Instead, it reflects the significant disparity in living standards between North and South Korea, which was exacerbated by the severe famine in North Korea from 1994 – 1998 – a period that affected most of the childhood years of these children (Haggard and Noland, 2007). The effect of the environment on height is also seen in the dramatic global increase in mean height over the last 100 years indicating an increase in the standard of living (NCD-RisC, 2016a).

Similarly, both genetic and environmental factors influence the variation in BMI. In early adulthood, the heritability of BMI is nearly as high as that of height, with genetic factors accounting for approximately 80% of BMI variation (Silventoinen et al., 2017). However, the development of obesity is biologically caused by an imbalance between energy intake and expenditure, highlighting the significant role of environmental factors, especially nutrition and physical exercise. The impact of environmental factors on obesity is clearly reflected in the dramatic global increase in mean BMI and obesity prevalence over the past five decades (NCD-RisC, 2016b). Despite this environmental shift toward more obesogenic conditions, the heritability of BMI has remained high, showing that genetic factors continue to play a substantial role in BMI variation (Silventoinen et al., 2017).

The complex interplay between genes and the environment influencing body size variation among individuals can be better understood by recognizing that these factors do not directly impact the human body, but rather exert their influence through physiological mechanisms. This concept is depicted in Figure 1. Physiological mechanisms are behind body development, such as growth during childhood and fat accumulation during adulthood, ultimately determining body size at different stages of life. These processes rely on nutrients and energy, which individuals acquire through their dietary intake (Bogin, 2021). Therefore, the quality and quantity of food consumed are pivotal in body development. Additionally, physical exercise can also play a significant role in maintaining energy balance and promoting muscle growth (Malina et al., 2004). Behavior, in turn, is regulated by neurophysiological mechanisms that establish feedback loops to sustain the body's homeostasis (Geary, 2023).

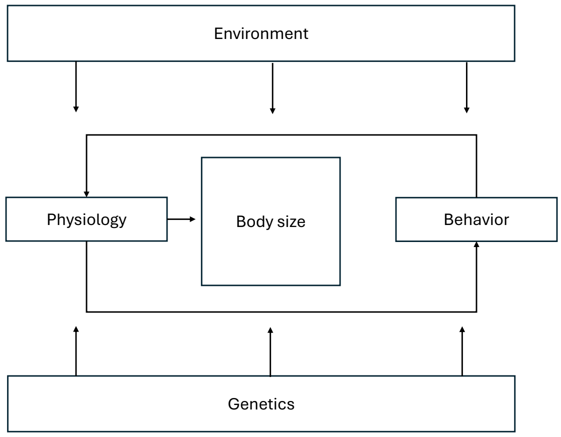

Figure 1. Schematic representation on the factors affecting body size.

However, these processes are influenced by both genetic and environmental factors. Genetic factors affect human physiology directly, as well as indirectly through behaviors like eating and physical exercise (Silventoinen and Konttinen, 2020). On the other hand, environmental factors, such as the quantity and quality of food available, also play a significant role in eating behaviors (Ulijaszek, 2023). Moreover, there are interactions between genes and the environment, as genetic factors can influence an individual's susceptibility to environmental exposures. For example, some children may be genetically more susceptible to the effects of an obesogenic environment than others. This genetic susceptibility is particularly evident in eating behavior. Therefore, children with a genetic predisposition to overeating are more likely to gain weight when exposed to an environment that promotes obesity (Llewellyn et al., 2023). This helps explain why changes in the environment can lead to an increase in the mean BMI at the population level, while individual differences within populations are largely driven by genetic variations among individuals.

Cross-country comparisons to study the role of macro-environment

Measuring environmental effects is challenging. Environmental exposures can be assessed using questionnaires and clinical markers. Similar to the effect sizes of single genetic polymorphisms, the effect sizes of environmental exposures are typically modest, but when combined, they explain a substantial proportion of variation in health outcomes (Argentieri et al., 2025). These exposome-wide studies show promise, even though measuring all exposures throughout the life course is practically impossible. However, it's important to note that these studies do not provide evidence for causal pathways, and many environmental exposures may actually serve as proxy indicators for underlying causal factors. More fundamentally, many environmental changes occur at the societal level, affecting all individuals within a population. These societal factors are particularly important from a public health perspective. An alternative approach to measuring environmental exposures is to compare different countries or geographic areas. In this case, differences between populations in health outcomes can help reveal the role of living environments behind them.

When considering body size, the food environment is especially important, as nutrient intake is the most important environmental factor affecting a child's physical development (Bogin, 2021). Furthermore, the development of obesity in adulthood is biologically driven by energy imbalance fundamentally caused by a surplus in energy intake (Geary, 2023). There are significant differences in food environments across countries, influenced by food traditions and the natural environment, such as the availability of land for cultivation, animal husbandry, and opportunities for fishing. In recent decades, food imports and national policies promoting healthy eating have also played a role in shaping food environments (Amilien and Notaker, 2019). In this context, Japan and Finland provide interesting points of comparison. Traditionally, meat consumption in Japan has been low, and until the early 2000s, fresh fish and shellfish were the primary sources of animal protein (Sasaki et al., 2022). Furthermore, soy protein consumption has historically been high in Japan (Nagata, 2021). The food environment in Japan has likely contributed to the low rates of cardiovascular diseases and the country's generally high life expectancy (Tsugane, 2021). In contrast, in Finland, the consumption of meat and dairy products has always been very high, while fish and plant-based proteins have been less commonly consumed (Mäkelä and Rautavirta, 2019).

One of the first large-scale epidemiological studies utilizing cross-country differences was The Seven Countries Study, initiated by Ancel Keys in the late 1950s to explore the relationship between diet and cardiovascular diseases (Kromhout et al., 1994). This study convincingly demonstrated that nutrition, especially a high intake of saturated fat, significantly contributed to the risk of cardiovascular diseases (Kromhout et al., 2018). Japan represented a society with a low risk of cardiovascular disease in this study, while Finland was a country with a high risk. The public health importance of this study was remarkable, and it was one of the key studies behind the North Karelia Project, which started in 1971 in Finland to improve nutrition and promote a healthier lifestyle to decrease cardiovascular risk. This project contributed to a dramatic decrease in cardiovascular mortality in Finland during the following decades (Puska et al., 2009).

Cross-country comparisons are valuable not only for demonstrating how the macro-environment influences disease incidence or other health outcomes but also for understanding how environmental factors modify the effect of other determinants on them. For example, large-scale comparative studies of European countries have shown that socioeconomic health inequalities are more pronounced in Northern Europe than in Southern Europe, primarily due to smaller socioeconomic inequalities in the incidence of cardiovascular diseases (Mackenbach, 2019). One likely explanation for this difference is the healthier traditional diet in Southern Europe compared to the diet typically consumed in Northern Europe. This indicates that the Mediterranean diet not only improves overall population health but also reduces socioeconomic health inequalities. Similarly, cross-country comparisons can be used in other study designs to analyze how environmental factors modify the impact of other determinants on various health outcomes.

The CODATwins database and geographic variability

The primary goal of the CODATwins project is to integrate a cross-country study design with genetic twin modeling. This approach allows for the examination of how macro-environmental factors impact the genetic variation that underlies height and BMI. In comparison to GWA studies, the twin design offers several advantages. Twin modeling enables the simultaneous estimation of genetic and environmental variation. Moreover, twin modeling requires a smaller sample size than GWA studies and is more cost-effective to implement. To ensure the database's representativeness, height, weight, educational attainment, and smoking were chosen as the main traits, as they can be easily obtained through questionnaires and are commonly used in surveys.

The CODATwins project was initiated in 2013 with the goal of collecting data from all twin cohorts worldwide that include information on monozygotic and dizygotic twins (Silventoinen, 2018). Most of data collection was completed in 2014 (Silventoinen et al., 2015b), with ongoing updates to the database since then (Silventoinen et al., 2019b). Currently, the CODATwins database contains data from approximately 500,000 twin individuals, including around 1 million height and weight measurements from 57 twin cohorts across 24 countries. Most of the twin cohorts are based in Europe (23 cohorts together from Belgium, Denmark, Finland, Germany, Hungary, Italy, Netherlands, Norway, Portugal, Spain, Sweden, and the United Kingdom) or North America (14 cohorts from the USA and two from Canada). There are also several cohorts from East Asia (four cohorts from Japan, three from China, two from South Korea and one from Mongolia) and Australia (three cohorts). Due to the presence of only individual cohorts from other regions (Brazil, Guinea-Bissau, Turkey, Israel, and Sri Lanka), they were excluded from regional comparisons.

The countries were reclassified into cultural-geographic regions based on average BMI. East Asia represents the low-obesogenic region, Europe the moderate-obesogenic region, and North America and Australia the high-obesogenic region (NCD-RisC, 2016b). These differences in average BMI reflect significant variations in population-level nutrition, as well as potentially other factors influencing BMI. This classification allows to analyze whether the macro-environment influences the genetic variation in height and BMI. Additionally, it was examined whether socio-economic differences in the genetic variation of height and BMI vary across these regions.

Results from the CODATwins project

Height

Figure 2 presents the mean heights, along with the additive genetic, shared environmental, and unique environmental variances of height across Europe, North America and Australia, and East Asia, categorized by sex. These results are based on previous studies from the CODATwins database for newborns (Yokoyama et al., 2018), children and adolescents aged 1 to 19 years (Jelenkovic et al., 2016b), and adults (Jelenkovic et al., 2016a). The specific values are reported in these original

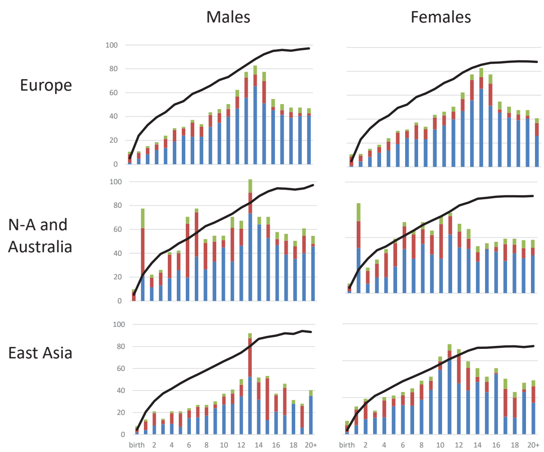

Figure 2. Additive genetic (blue), shared environmental (red), and unique environmental (green) variances of height (left Y-axis) and mean height (right Y-axis) by age (X-axis), the cultural-geographic region, and sex. Sources: Yokoyama et al. (2018), Jelenkovic et al. (2016 a), and Jelenkovic et al. (2016 b)

publications and their supplementary materials. Overall, the development of mean height and height variation was largely similar across the three cultural-geographic regions. The variation was greater during adolescence, likely reflecting individual differences in puberty-related growth. Mean height was consistently tallest in Europe and shortest in East Asia, while total variance was highest in North America. These differences in mean height and the variation of height were consistent across all ages and both sexes.

When the total height variance was decomposed into genetic and environmental components, genetic factors explained most of the variation at all ages. However, shared environmental factors also accounted for a significant proportion of the variation. The influence of shared environmental factors was particularly notable in North America and Australia, but less so in Europe and East Asia. Unique environmental factors contributed a minor proportion of the variation across all ages, cultural-geographic regions, and sexes.

Figure 3 displays the relative proportions of height variance explained by additive genetic factors with 95% confidence intervals (CI). Across all cultural-geographic regions, the heritability of height increased from infancy to mid-childhood, as the influence of shared environmental factors decreased. Heritability estimates were slightly lower in North America and Australia compared to Europe and East Asia, due to a higher proportion of shared environmental variation. These patterns were consistent for both males and females. Notably, the 95% CIs were significantly narrower in Europe, indicating larger sample sizes compared to the other regions.

Body mass index

Figure 4 presents the results for mean BMI and the variation of BMI, based on original publications for children and adolescents aged 1 to 19 years (Silventoinen et al., 2016) and adults from early adulthood through old age (Silventoinen et al., 2017). Both mean BMI and BMI variance were highest in North America and Australia and lowest in East Asia. For North American adult males, the variance was somewhat lower due to the inclusion of a cohort of World War veterans measured in the 1940s when both BMI and its variance were lower than in later periods. During childhood, shared environmental factors explained a significant proportion of BMI variation in North America and Australia, while the influence of them was minimal in the other regions across all ages. The impact of unique environmental factors was small until early adulthood but gradually increased through old age. At birth, relative weight was measured using the ponderal index, so these results are not presented in the figure due to a different scale. However, for both the ponderal index and birth weight, the results align with those for BMI in later years, showing lower

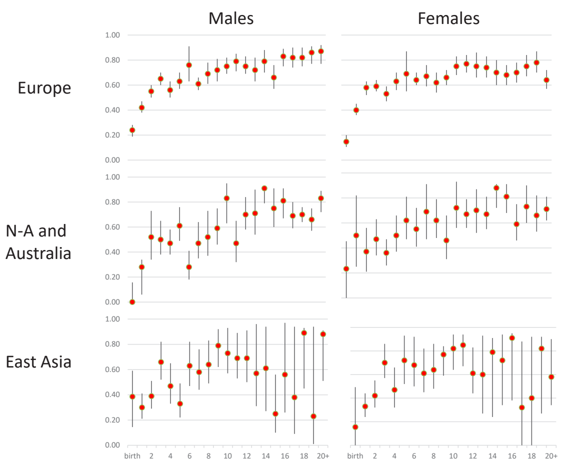

Figure 3. The proportions of variances of heigh explained by additive genetic factors with 95% confidence intervals by age (X-axis), the cultural-geographic region, and sex. Sources: Yokoyama et al. (2018), Jelenkovic et al. (2016a), and Jelenkovic et al. (2016b)

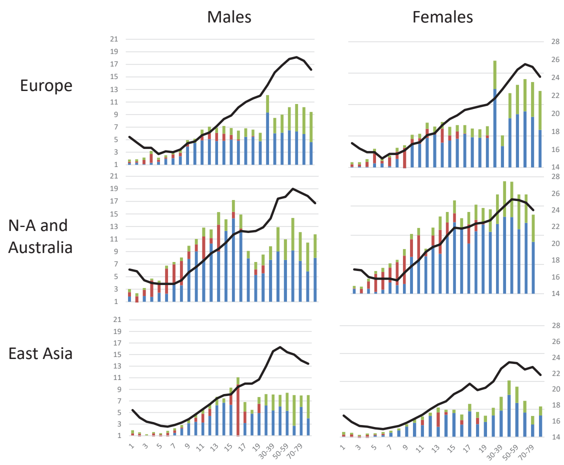

Figure 4. Additive genetic (blue), shared environmental (red), and unique environmental (green) variances of BMI (left Y-axis) and mean BMI (right Y-axis) by age (X-axis), the cultural-geographic region, and sex. Sources: Silventoinen et al. (2016), Silventoinen et al. (2017)

variation in East Asia compared to Europe and North America and Australia. The lower variance in East Asia was attributed to a smaller effect of shared environmental factors (Yokoyama et al., 2018).

Figure 5 presents the relative proportions of BMI variance explained by additive genetic factors. In all regions, the heritability of BMI followed a similar pattern: it increased from infancy and early childhood to early adulthood, then decreased into old age. This pattern was most pronounced in Europe due to narrower 95% CIs but was also observed in North America and Australia and East Asia. In childhood and adolescence, this change was primarily due to the decreasing influence of shared environmental factors, while in adulthood, it reflected the increasing influence of unique environmental factors. Heritability estimates were systematically lowest in North America and Australia, due to a larger proportion of BMI variation being explained by shared environmental factors. Overall, the heritability estimates were very similar between males and females.

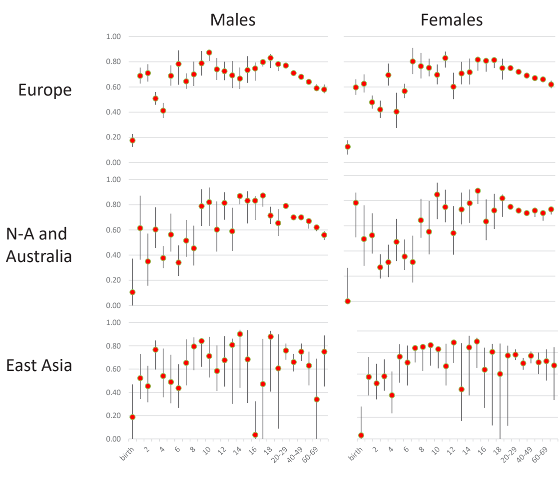

Figure 5. The proportions of variances of BMI explained by additive genetic factors with 95% confidence intervals by age (X-axis), the cultural-geographic region, and sex. Sources: Yokoyama et al. (2018), Silventoinen et al. (2016), Silventoinen et al. (2017)

Socioeconomic differences in height and BMI

The CODATwins database includes information on education, allowing for the analysis of how parental education influences the genetics of height and BMI, as well as how these effects vary across the cultural-geographic regions. When studying height, parental education was associated with taller stature in Europe and North America and Australia from infancy through old age. In contrast, this effect was small in East Asia (Jelenkovic et al., 2020). The educational differences in height variation were examined by categorizing twins into three groups: low, intermediate, and high parental education. Despite educational differences in mean height, only minor differences in the variation of height were observed between these categories. When the variance components of additive genetic, shared environmental, and unique environmental factors were analyzed using a meta-regression model, a slightly higher shared environmental variation was found in the offspring of parents with low education. However, the differences were small, and the smallest variation was found in the category of intermediate parental education. No significant differences were observed between the cultural-geographic regions when comparing the variance of height between the categories of parental education.

Similar analyses of the effect of parental education were conducted on BMI (Silventoinen et al., 2019a). In Europe, higher parental education was associated with a slightly higher BMI up to 5 years of age, but after that age, the association become negative, continuing into old age. In North America and Australia, the negative association between parental education and BMI was stronger than in Europe and persisted across all ages. In contrast, no association was found between parental education and BMI in East Asia. In North America and Australia, BMI variation was greater in the high parental education group compared to the low parental education group. A similar pattern was observed in Europe, though the differences in BMI variation between these categories were smaller than in North America and Australia. These differences in BMI variation across parental education categories were primarily due to additive genetic variation. However, in East Asia, no differences in BMI variation were observed between these categories.

Discussion

For over 100 years, anthropometric traits have played a crucial role in studying how genetic and environmental factors contribute to variations in humans. The CODATwins project is an international initiative that utilizes a cross-country study design and twin modeling to investigate how macro-environmental factors impact the genetic influences on height and BMI – two extensively studied traits in epidemiology and human genetics. To accomplish this objective, all available twin data on height and BMI were combined and analyzed using twin modeling. The variations observed between the cultural-geographic regions with diverse environmental exposures offer valuable insights into the environmental plasticity in the genetics of height and BMI.

The mean height was tallest in Europe and shortest in East Asia, consistent with previous evidence from population-based cohorts (NCD-RisC, 2016a). However, height variance was highest in North America and Australia, primarily due to a larger shared environmental variation. This is likely due to the greater ethnic diversity in North America and Australia compared to European and East Asian countries. Additionally, height was positively correlated with parental education, although this association was not observed in East Asia. Socio-economic differences in height have been documented in previous studies, typically interpreted as reflecting differences in nutrition, diseases, and other material living conditions during childhood (Steckel, 2009). However, only weak evidence was found for differences in height variation between the categories of parental education. These findings align with evidence suggesting that the heritability of height has remained unchanged across cohorts born from the late 19th century to the late 20th century, despite a dramatic increase in mean height (Jelenkovic et al., 2016a). These results suggest that environmental exposures can differ between socioeconomic categories, even if the variation of environmental exposures is largely constant within those categories. Additionally, both twin (Silventoinen et al., 2004) and GWA studies (Silventoinen et al., 2023) have provided evidence that genetic factors may also contribute to height differences across socioeconomic groups. Further research is needed to better understand the mechanisms underlying height differences between socioeconomic categories.

The average BMI was highest in North America and Australia, and lowest in East Asia, which is consistent with previous population-based studies (NCD-RisC, 2016b). Additionally, BMI variation was largest in North America and Australia and smallest in East Asia, primarily due to differences in genetic variation. This can be attributed to the impact of obesogenic environments, which can reinforce the genetic predisposition to higher BMI. Other CODATwin findings support this, showing that the genetic variance of BMI has increased during the last decades alongside rising mean BMI (Silventoinen et al., 2017). The interplay between obesogenic environments and genetics was also evident in socioeconomic disparities in BMI. In North America, Australia, and Europe, low parental education was associated with both higher mean BMI and greater genetic variance of BMI, while no such connection was found in East Asia. Previous studies have consistently identified socioeconomic differences in BMI, but these studies have mainly focused on populations following a Westernized lifestyle (McLaren, 2007), while similar associations were not observed in Japan (Silventoinen et al., 2013). This indicates that socioeconomic disparities in BMI may be a specific feature of Western societies.

Obesity is one of the biggest global health challenges today (GBD 2015 Risk Factors Collaborators, 2016), and the results from the CODATwins project can help us better understand the underlying factors contributing to this epidemic. Despite differences in mean BMI, the heritability of BMI was found to be high across all regions and socioeconomic categories. This suggests that obesogenic environments primarily influence BMI by activating genetic predispositions to higher BMI. The macro-environment plays a crucial role, as family-level factors, such as parental education, only influenced BMI in the presence of an obesogenic macro-environment. These findings highlight the importance of societal-level factors in addressing the global rise in BMI. Obesogenic macro-environments disproportionately affect individuals with genetic and social risk factors for obesity. This is reflected in greater socioeconomic disparities and higher BMI variation in obesogenic societies. Therefore, creating a healthy environment is not only vital for the overall health of populations but also crucial for addressing socioeconomic health inequalities.

In conclusion, the CODATwins project demonstrates the feasibility and value of international collaboration in twin studies. Regional comparisons using this database reveal the environmental sensitivity of the genetic factors predisposing to obesity, highlighting the significance of societal-level factors in the global obesity pandemic. In contrast, the genetics of height are less affected by environmental factors even though they can influence average height. Understanding the interplay between genes and the environment is crucial for implementing societal-level actions to enhance population health.

References

Amilien, N., Notaker, H., 2019. Health and nutritional perspectives on Nordic food traditions - an approach through food culture and history, in: Nutritional and Health Aspects of Food in Nordic Countries (Eds.) Andersen V, Bar E and Wirtanen G. Elsevier, Saint Louis.

Argentieri, M.A., Amin, N., Nevado-Holgado, A.J., Sproviero, W., Collister, J.A., Keestra, S.M., … van Duijn, C.M., 2025. Integrating the environmental and genetic architectures of aging and mortality. Nat Med. https://doi.org/10.1038/s41591-024-03483-9

Boas, F., 1910. Report Presented to the 61st Congress on Changes in Bodily Form of Descendants on Immigrants. Government Printing Office, Washington, DC.

Bogin, B., 2021. Patterns of Human Growth, 3. ed. Cambridge University Press, Cambridge.

Davenport, C.B., 1923. Body-build and its inheritance (No. 329). Carnegie Institution of Washington, Washington.

Fisher, R., 1918. The correlation between relatives on the supposition of Mendelian inheritance. Transactions of the Royal Society of Edinburgh 52, 399–433.

Galton, F., 1889. Natural Inheritance. Macmillan, London.

GBD 2015 Risk Factors Collaborators, 2016. Global, regional, and national comparative risk assessment of 79 behavioural, environmental and occupational, and metabolic risks or clusters of risks, 1990-2015: a systematic analysis for the Global Burden of Disease Study 2015. Lancet 388, 1659–1724. https://doi.org/10.1016/S0140-6736(16)31679-8

Geary, N., 2023. Energy homeostasis from Lavoisier to control theory. Phil. Trans. R. Soc. B 378, 20220201. https://doi.org/10.1098/rstb.2022.0201

Haggard, S., Noland, M., 2007. Famine in North Korea : Markets, Aid, and Reform. Columbia University Press, New York.

Jelenkovic, A., Hur, Y.-M., Sund, R., Yokoyama, Y., Siribaddana, S.H., Hotopf, M., … Silventoinen, K., 2016a. Genetic and environmental influences on adult human height across birth cohorts from 1886 to 1994. Elife 5, e20320. https://doi.org/10.7554/eLife.20320

Jelenkovic, A., Sund, R., Hur, Y.-M., Yokoyama, Y., Hjelmborg, J.V.B., Möller, S., … Silventoinen, K., 2016b. Genetic and environmental influences on height from infancy to early adulthood: An individual-based pooled analysis of 45 twin cohorts. Sci Rep 6, 28496. https://doi.org/10.1038/srep28496

Jelenkovic, A., Sund, R., Yokoyama, Y., Latvala, A., Sugawara, M., Tanaka, M., … Silventoinen, K., 2020. Genetic and environmental influences on human height from infancy through adulthood at different levels of parental education. Sci Rep 10, 7974. https://doi.org/10.1038/s41598-020-64883-8

Kromhout, D., Menotti, A., Alberti-Fidanza, A., Puddu, P.E., Hollman, P., Kafatos, A., … Jacobs, D.R., 2018. Comparative ecologic relationships of saturated fat, sucrose, food groups, and a Mediterranean food pattern score to 50-year coronary heart disease mortality rates among 16 cohorts of the Seven Countries Study. Eur J Clin Nutr 72, 1103–1110. https://doi.org/10.1038/s41430-018-0183-1

Kromhout, D., Menotti, A., Blackburn, H. (eds.), 1994. The Seven Countries Study: a Scientific Adventure in Cardiovascular Disease Epidemiology. Studio RIVM, Bilthoven.

Llewellyn, C.H., Kininmonth, A.R., Herle, M., Nas, Z., Smith, A.D., Carnell, S., Fildes, A., 2023. Behavioural susceptibility theory: the role of appetite in genetic susceptibility to obesity in early life. Philos Trans R Soc Lond B Biol Sci 378, 20220223. https://doi.org/10.1098/rstb.2022.0223

Mackenbach, J., 2019. Health Inequalities: Persistence and Change in European Welfare States. Oxford University Press, Oxford.

Mäkelä, J., Rautavirta, K., 2019. Food, nutrition, and health in Finland, in: Nutritional and Health Aspects of Food in Nordic Countries. (Eds.) Andersen V, Bar E and Wirtanen G. Elsevier, Saint Louis.

Malina, M., Bouchard, C., Bar-Or, O., 2004. Growth, Maturation and Physical Growth, 2. ed. Human Kinetics, Champaign, IL, USA.

McLaren, L., 2007. Socioeconomic status and obesity. Epidemiol Rev 29, 29–48. https://doi.org/10.1093/

epirev/mxm001
Nagata, C., 2021. Soy intake and chronic disease risk: findings from prospective cohort studies in Japan. Eur J Clin Nutr 75, 890–901. https://doi.org/10.1038/s41430-020-00744-x
NCD-RisC, 2016a. A century of trends in adult human height. Elife 5, e13410. https://doi.org/10.7554/eLife.13410
NCD-RisC, 2016b. Trends in adult body-mass index in 200 countries from 1975 to 2014: a pooled analysis of 1698 population-based measurement studies with 19·2 million participants. Lancet 387, 1377–1396. https://doi.org/10.1016/S0140-6736(16)30054-X
Pearson, K., 1904. On the laws of inheritance in man. Biometrika 3, 131–190. https://doi.org/10.1093/biomet/3.2-3.131
Puska, P., Vartiainen, E., Laatikainen, T., Jousilahti, P., Paavola, M. (eds.), 2009. The North Karelia Project: from North Karelia to National Action. National Institute for Health and Welfare, Helsinki. Available: https://www.julkari.fi/bitstream/handle/10024/80109/731beafd-b544-42b2-b853-baa87db6a046.pdf
Richard, D., Muthuirulan, P., Young, M., Yengo, L., Vedantam, S., Marouli, E., Bartell, E., Hirschhorn, J., Capellini, T.D., 2025. Functional genomics of human skeletal development and the patterning of height heritability. Cell 188, 15-32.e24. https://doi.org/10.1016/j.cell.2024.10.040
Sasaki, K., Motoyama, M., Watanabe, G., Nakajima, I., 2022. Meat consumption and consumer attitudes in Japan: An overview. Meat Science 192, 108879. https://doi.org/10.1016/j.meatsci.2022.108879
Schwekendiek, D., 2009. Height and weight differences between North and South Korea. J Biosoc Sci 41, 51–55. https://doi.org/10.1017/S002193200800299X
Silventoinen, K., 2018. Collecting an international database of twin cohorts to analyze how society modifies genetic and environmental influences, in: SAGE Research Methods Cases. SAGE, London, p. http://dx.doi.org/10.4135/9781526437549.
Silventoinen, K., 2015a. Children's anthropometrics and later disease incidence, in: Handbook of Economics and Human Biology (Eds.) Komlos J. Oxford University Press, Oxford.
Silventoinen, K, Jelenkovic, A., Latvala, A., Yokoyama, Y., Sund, R., Sugawara, M., … Kaprio, J., 2019a. Parental education and genetics of BMI from infancy to old age: a pooled analysis of 29 twin cohorts. Obesity 27, 855–865. https://doi.org/10.1002/oby.22451
Silventoinen, K., Jelenkovic, A., Sund, R., Honda, C., Aaltonen, S., Yokoyama, Y., … Kaprio, J., 2015b. The CODATwins Project: The cohort description of COllaborative Project of Development of Anthropometrical Measures in Twins to study macro-environmental variation in genetic and environmental effects on anthropometric traits. Twin Res Hum Genet 18, 348–360. https://doi.org/10.1017/thg.2015.29
Silventoinen, K., Jelenkovic, A., Sund, R., Hur, Y.-M., Yokoyama, Y., Honda, C., … Kaprio, J., 2016. Genetic and environmental effects on body mass index from infancy to the onset of adulthood: an individual-based pooled analysis of 45 twin cohorts participating in the COllaborative project of Development of Anthropometrical measures in Twins (CODATwins) study. Am J Clin Nutr 104, 371–379. https://doi.org/10.3945/ajcn.116.130252
Silventoinen, K., Jelenkovic, A., Sund, R., Yokoyama, Y., Hur, Y.-M., Cozen, W., … Kaprio, J., 2017. Differences in genetic and environmental variation in adult BMI by sex, age, time period, and region: an individual-based pooled analysis of 40 twin cohorts. Am J Clin Nutr 106, 457–466. https://doi.org/10.3945/ajcn.117.153643
Silventoinen, K., Jelenkovic, A., Yokoyama, Y., Sund, R., Sugawara, M., Tanaka, M., … Kaprio, J., 2019b. The CODATwins Project: The current status and recent findings of COllaborative Project of Development of Anthropometrical Measures in Twins. Twin Res Hum Genet 22, 800–808. https://doi.org/10.1017/thg.2019.35
Silventoinen, K., Konttinen, H., 2020. Obesity and eating behavior from the perspective of twin and genetic research. Neurosci Biobehav Rev 109, 150–165. https://doi.org/10.1016/j.neubiorev.2019.12.012
Silventoinen, K., Krueger, R.F., Bouchard, T.J., Kaprio, J., McGue, M., 2004. Heritability of body height and educational attainment in an international context: comparison of adult twins in Minnesota and Finland. Am J Hum Biol 16, 544–555. https://doi.org/10.1002/ajhb.20060
Silventoinen, K., Lahtinen, H., Davey Smith, G., Morris, T.T., Martikainen, P., 2023. Height, social position and coronary heart disease incidence: the contribution of genetic and environmental factors. J Epidemiol Community Health jech-2022-219907. https://doi.org/10.1136/jech-2022-219907
Silventoinen, K., Tatsuse, T., Martikainen, P., Rahkonen, O., Lahelma, E., Sekine, M., Lallukka, T., 2013. Occupational class differences in body mass index

and weight gain in Japan and Finland. J Epidemiol 23, 443–450. https://doi.org/10.2188/jea.je20130023

Sparks, C.S., Jantz, R.L., 2002. A reassessment of human cranial plasticity: Boas revisited. Proc Natl Acad Sci U S A 99, 14636–14639. https://doi.org/10.1073/pnas.222389599

Steckel, R.H., 2009. Heights and human welfare: recent developments and new directions. Explorations in Economic History 46, 1–23.

Tsugane, S., 2021. Why has Japan become the world's most long-lived country: insights from a food and nutrition perspective. Eur J Clin Nutr 75, 921–928. https://doi.org/10.1038/s41430-020-0677-5

Ulijaszek, S., 2023. Obesity and environments external to the body. Phil. Trans. R. Soc. B 378, 20220226. https://doi.org/10.1098/rstb.2022.0226

Yokoyama, Y., Jelenkovic, A., Hur, Y.-M., Sund, R., Fagnani, C., Stazi, M.A., … Silventoinen, K., 2018. Genetic and environmental factors affecting birth size variation: a pooled individual-based analysis of secular trends and global geographical differences using 26 twin cohorts. Int J Epidemiol 47, 1195–1206. https://doi.org/10.1093/ije/dyy081