

Hidden patterns of urban mixing across five global cities

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Here we leverage large-scale travel surveys covering over 200,000 residents across Boston, Chicago, Hong Kong, London and São Paulo. With rich individual-level data, we reveal patterns in social mixing, which cannot be identified from high-resolution mobility data alone. Inferring socioeconomic status from residential neighborhoods yields social mixing levels 16% lower than using survey data. Individuals over the age of 66 experience greater social mixing than those in late working life (aged 55–65), lending data-driven support to the ‘second youth’ hypothesis. Teenagers and women with caregiving responsibilities exhibit lower social mixing levels. Living near major transit stations reduces the influence of socioeconomic status on social mixing. Finally, inputs of home-space, activity-space and demographic attributes are embedded and fed into a supervised autoencoder, revealing that mobility shapes experienced social mixing more than sociodemographic characteristics, home environment and transit proximity. Yet, activity spaces remain stratified by income, resulting in structurally different social mixing experiences.

Human mobility plays a central role in many of the twenty-first century’s urban challenges^{1–3}, including carbon emissions^{4,5}, air pollution⁶, nonrenewable energy consumption⁷, traffic congestion^{8,9}, noise pollution^{10,11}, road fatalities and casualties¹², transport inequity⁷ and disease spread¹³.

Yet, mobility also shapes other important dimensions of urban life, such as experienced social mixing—the diversity of people an individual encounters as one moves through the city. From commutes to grocery trips, daily mobility creates opportunities for contact across socioeconomic lines. Whether and how these paths intersect matter: a broad body of research links experienced social mixing to creativity¹⁴, health outcomes¹⁵, job opportunity and economic mobility^{16,17}. The United Nations Human Settlements Program’s (UN-Habitat) Sustainable Development Goal 11 (ref. 18) specifically promotes the idea of inclusive human settlements to ensure that cities are equitable for all residents. Nevertheless, persistent patterns of social segregation remain in cities^{19,20}, and the factors that shape our everyday social exposure continue to be debated in research and in practice^{3,20,21}.

Over the past decade, the rapid growth of urban data has transformed research on segregation and mixing, especially in cities across the USA^{3,19}. However, most studies have relied on high-resolution mobility traces (such as those from mobile phones and smart cards) while inferring socioeconomic status (notably income and age) primarily from estimated home neighborhoods or frequently visited places (for example, rental apartments, schools, and senior housing. A detailed literature review is included in Supplementary Table 3 (refs. 19,22,23)). Such home-neighborhood- or visit-based strategies of socioeconomic proxies are approximate and much less applicable in compact cities such as Hong Kong and Singapore, where people with different income levels and/or ethnicities often live in close proximity^{20,24,25}. Moreover, the high density and diversity of land use also makes using mobile phone traces to identify school visits (often used to infer age and/or child caring responsibilities) or type of housing (for example, affordable housing to infer income) challenging beyond broad categories of home, work and other activity locations²⁶.

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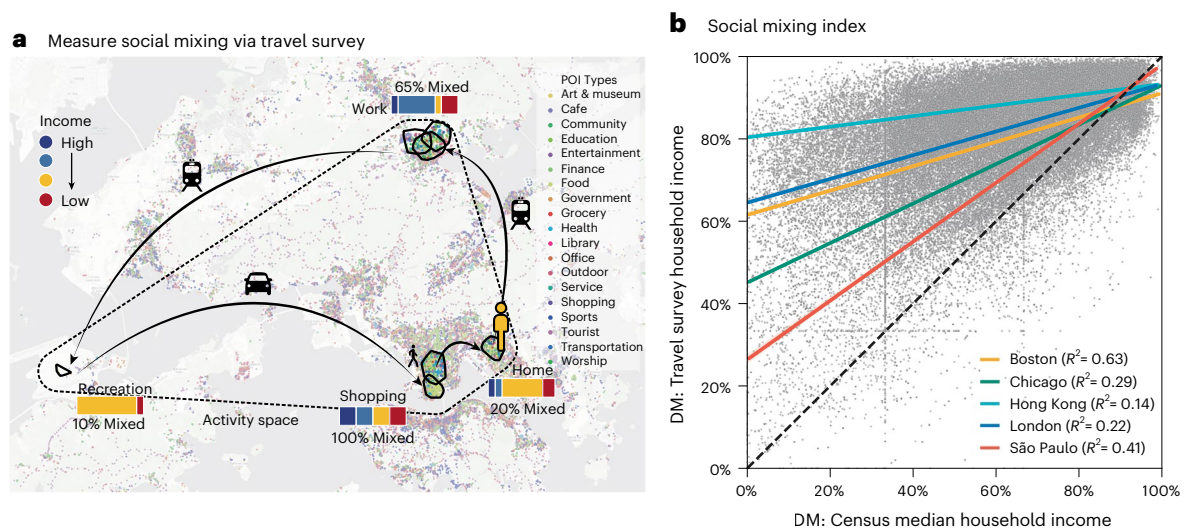


Fig. 1 | Measures of the daytime and nighttime social mixing for five cities.

a, Measure the daytime social mixing. An individual visits different places and encounters others from a different income group, thus experiencing different level of social mixing. **b**, Compare the daytime social mixing (DM) measured using census survey median household income and reported income level in the travel survey. The dashed line indicates $y = x$. For each city, we fit an ordinary

least square regression line to show the relationship between y and x . The scatter plot includes only participants over age 11 and who traveled at least once on the survey day (Boston $n = 7,626$, $P \leq 0.001$; Chicago $n = 18,258$, $P \leq 0.001$; Hong Kong $n = 33,289$, $P \leq 0.001$; London $n = 30,381$, $P \leq 0.001$; São Paulo $n = 46,957$, $P \leq 0.001$). Map data in **a** © OpenStreetMap.

This study takes a different approach by leveraging large-scale travel surveys that include detailed individual-level socioeconomic information. It is recognized that official territory-wide travel surveys also suffer from issues such as nonresponse and underreporting^{27–30}. Yet, the rich and detailed socioeconomic and trip data allow researchers to identify latent patterns in social mixing that can only be revealed by disaggregated individual-level data. Hence, rather than maximizing spatial and temporal detail from mobility traces, we draw on the granular socioeconomic and trip data provided by travel surveys, which capture rich demographic and behavioral information consistently across cities. By analyzing more than 200,000 travel diary entries, we provide a cross-continental study of how daily mobility shapes social mixing across five contrasting global cities—Boston, Chicago, Hong Kong, London and São Paulo.

Results

The five travel survey data included are the Massachusetts Travel Survey (Boston), My Daily Travel (Chicago), Travel Characteristics Survey (Hong Kong), London Travel Diary (LTD) and São Paulo Travel Diary. These surveys were published between 2011 and 2018. The coverage, resolution and survey time period are shown under Methods. The number of participants interviewed for each survey ranges from 26,770 to 101,385. When compared with the size of the local population as of the year of each survey, the coverage ranged from 0.29% to 0.53%. As they were official surveys conducted by professional survey teams, expansion factors have been provided to correct sampling bias and for data expansion.

Measure social mixing using travel survey data

The first goal of the research is to reveal the impact on levels of social mixing using the individual self-reported household income in travel surveys in comparison with home-location-inferred income. Our primary measure, the daytime mixing (DM_i), is adapted from Moro et al.³ and quantifies how evenly an individual encounters people from different income groups during the day (excluding trips back home) (Fig. 1a). To calculate DM_i , we first rank participants within each city by their reported household income and then assign them to one of four groups: low, medium-low, medium-high or high. The four income groups within each city have relatively similar proportions after

applying the expansion factors to all participants (see the Supplementary Information for details). Next, using the recorded stops from travel surveys, we identify when participants might have encountered others during the day. Because each city defined travel stops differently (for example, by street blocks, coordinates or census blocks), we standardize the location unit by using the H3 hexagon index³¹ as our primary definition of place. With an individual's income group i and a series of places that they visited, we can compute DM_i using equation (1):

$$DM_i = \frac{2}{3} \sum_q \left| \tau_{iq} - \frac{1}{4} \right|, \quad (1)$$

where τ_{iq} is individual i 's relative exposure to income group q . Here, τ_{iq} is defined as equation (2):

$$\tau_{iq} = \sum_\alpha \tau_{i\alpha} \tau_{aq}, \quad (2)$$

where $\tau_{i\alpha}$ is individual i 's proportion of visits at a place α among all places that i visited. τ_{aq} is all people from the income group q 's proportion of total visits at place α . A $DM_i = 1$ means that an individual meets other income groups evenly throughout the day, whereas a $DM_i = 0$ indicates that an individual only meets people of the same income group in places the individual visited in a day. We demonstrate the robustness of our primary measure of DM against the definitions of trip stops, income groups and weighting factors in Supplementary Section 2. Furthermore, we show that the main findings in this study are not sensitive to the definition of collocation, including taking into consideration of the estimated time that people will meet each other, and the spatial unit of place (see 22 variations of social mixing measure for robustness test in Supplementary Table 2). It is worth noting that people together at a place does not necessarily imply social interaction, although physical collocation is a prerequisite for any in-person interaction to take place. Previous studies suggest that people staying in the same place, especially for a longer duration, are more likely to interact (for example, having conversations) and engage in group activities^{16,32,33}. In this Article, we describe the collocation as social mixing and recognize that social interaction is only a potential outcome.

Next, as a comparison, we extract the median household income (from local census surveys) based on each participant's home location.

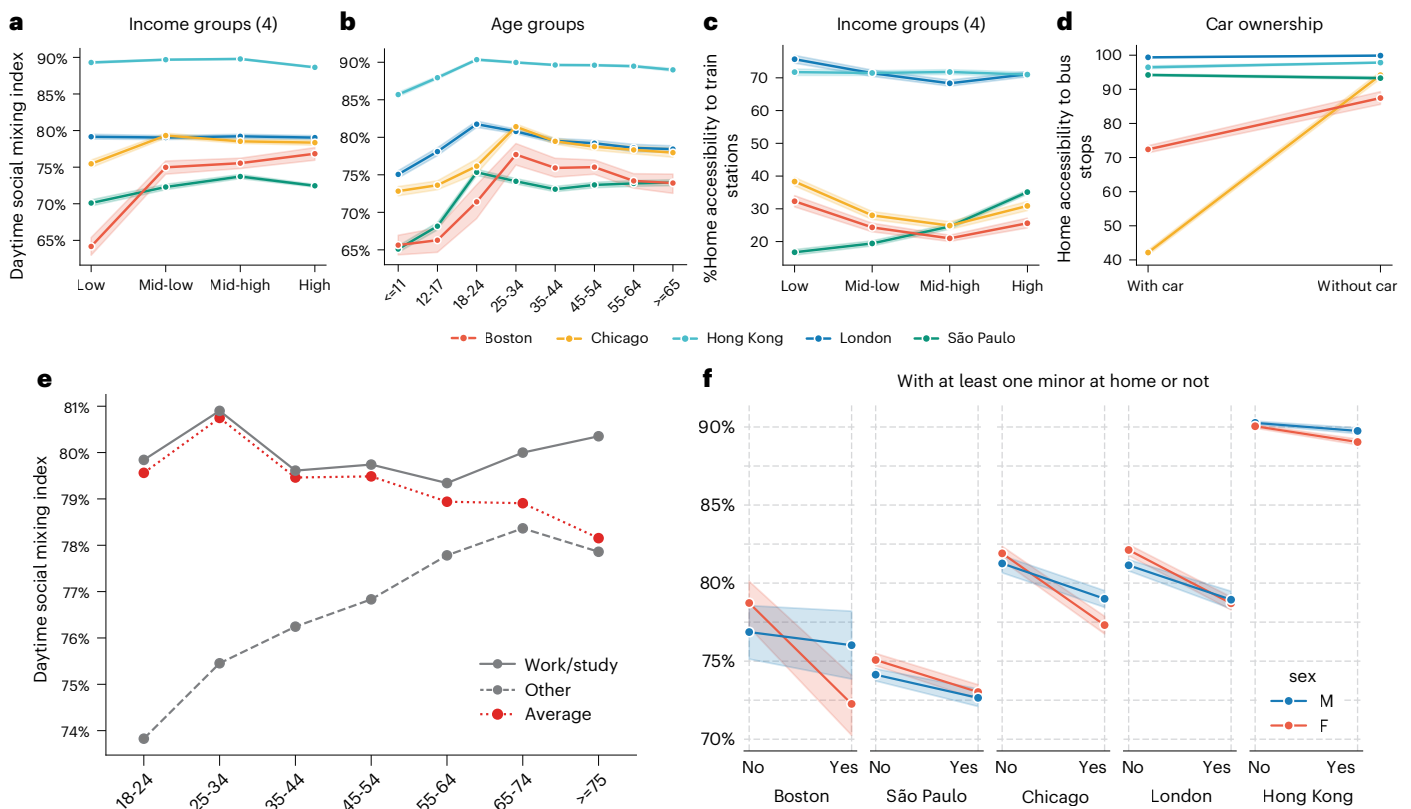


Fig. 2 | Explain daytime social mixing. **a**, DM is lower for low-income groups than for mid-income groups in Boston ($n = 5,894$), Chicago ($n = 15,738$) and São Paulo ($n = 40,896$), while gaps are less pronounced in Hong Kong ($n = 51,619$) and London ($n = 30,277$). Only people with age >17 are included. **b**, DM distribution by age and city. **c**, Home accessibility to train stations by income group in each city. **d**, Home accessibility to bus stops by household car ownership. **e**, Average DM across all cities by age group and work status. DM declines gradually with age (dashed line), but rises again after retirement (65–74). Working individuals report higher DM than nonworking peers,

especially at younger ages. **f**, DM distribution by gender and care-taking responsibilities at early career age. Only individuals between age 21 and 45 are included (Boston $n = 2,064$, Chicago $n = 8,365$, Hong Kong $n = 25,594$, London $n = 15,394$, São Paulo $n = 20,227$). In **a–d** and **f**, the solid dot marker shows the mean value of the sample by each group. The error bar area represents the 95% confidence interval. Overall income distributions with different definitions are shown in Supplementary Figs. 3 and 4. Details of work status standardization across different surveys are included in Supplementary Table 9.

With the approximated household income, we re-estimate the associated DM index by replacing the participant's income group with the home-location-inferred income group (see the Methods for details on the census data source and city-specific resolution). Figure 1b shows that when we replaced the survey income with median household income from respondents' neighborhoods, DM fell by an average of 16%. In Chicago—a city known for its residential segregation (with its nighttime social mixing (NM) level around 58%)—the survey-based DM is 12% higher than the census tract-based estimate. This result shows that, using the same set of survey data, home neighborhood proxies tend to estimate lower social mixing levels than using self-reported data.

Patterns of social mixing based on age, gender and caregiving responsibilities

Besides income, travel surveys also provide other rich socioeconomic attributes. Previous literature has shown that vulnerable population, such as teenagers and low-income groups, tend to be more socially segregated^{19–21,23}. As age is generally missing from the mobile-phone based records, these studies have used proxies such as school visits to estimate people's age²³. Focusing on the vulnerable population, we check the DM distribution across income groups, age groups and caregiving responsibilities (by gender) leveraging the self-reported income, age and gender information in travel surveys. Figure 2a shows that people in the low-income group are likely to be less socially mixed than mid-income groups in Boston, Chicago and São Paulo, while such gaps

among income groups are less pronounced in Hong Kong and London. Figure 2b shows that teenagers (aged 12–17) exhibit much lower social mixing levels than young adults (aged 18–24). In Chicago and Boston, the highest social mixing occurs among individuals aged 25–34, whereas it peaks earlier among those aged 18–24 in the other cities.

Moreover, we found data support for the 'second youth' or 'third age' effect when combining the working status and age information. Even though DM tends to decline gradually across all cities with age (Fig. 2e, dashed red line), separating the actively working or studying population (full-time, part-time, student or home making) from their counterparts reveals a reversal. Both groups show higher DM immediately after the retirement age (group 65–74) compared with the late working age (55–64) (0.75% and 0.83% increase post-retirement age, respectively). While working/studying individuals on average experience more social mixing than their counterparts, such gap is much larger at younger age. We repeat the analysis by testing each city separately and using an alternative measure of social mixing. The results are robust that DM largely remains similarly high or increases immediately after the retirement age (group 65–74) in all five cities (Supplementary Fig. 8).

Another advantage of travel survey data is that we can combine information of age, household composition and gender to identify people who are likely to be caretakers (often parents) and have caregiving responsibilities (Methods). While men and women (per reported gender) are equally socially mixed in our selected cities, Fig. 2f implies that women with caregiving responsibilities experience a higher reduction

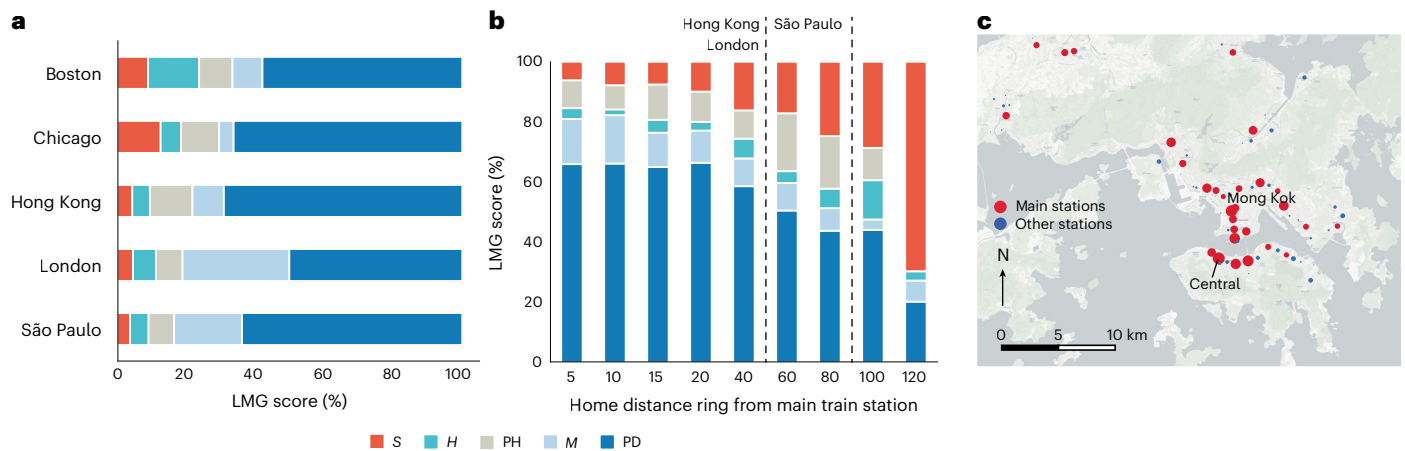


Fig. 3 | Explain DM. a, LMG score of equation (3). Full regression results are included in Supplementary Table 6 and Supplementary Figs. 16 and 17. We show a variation of this figure by limiting the samples only to people who live within 30 km of the downtown area in Supplementary Fig. 15. In addition, Supplementary Fig. 18 shows the results when normalizing the PD vector by average total POIs an individual visited. **b**, Average LMG score of the five cities

when grouping people based on their home distance from their closest main transit stations. Dashed lines indicate the total size of the specific city. Results by each city are shown in Supplementary Fig. 15. **c**, Distribution of main train stations and other stations in Hong Kong. The size of the circle shows the weighted inflow of each station in the morning between 6:00 and 11:00. Map data in c © OpenStreetMap.

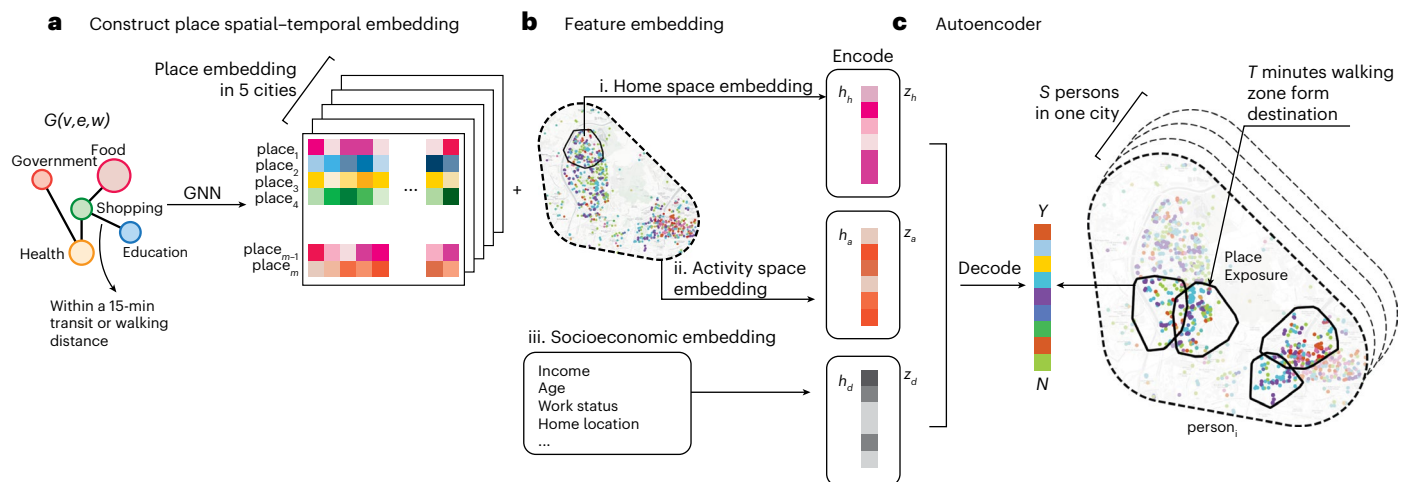


Fig. 4 | Conceptual diagram of an encoder-decoder architecture that predicts individual place exposure. a, Construct a POI place spatial network using distance and travel-time-based method (Methods). Then, use a GNN model to encode all POI places in each city into an embedding vector. The embedding dimension is 32. **b**, Create the feature embedding. The home-space embedding (h_h) is the mean embedding of all POI places associated with their home location 15-min walking isochrone. Similarly, the activity-space embedding (h_a) is the

mean embedding of all POI places within the person's activity space. Sociodemographic embedding includes all personal attributes such as age, gender and work status (h_d). **c**, The autoencoder model takes the three embeddings in a permutation fashion and compresses them into a latent code z , and then decodes to an output layer, which is the N -dimensional POI place exposure vector (N is the total POI types). Map data in b and c © OpenStreetMap.

in social mixing (ranging from 1.0% to 6.5% reduction) than their male counterparts (ranging from 0.5% to 2.3% reduction) (see a full statistical comparison in Supplementary Table 5). Given that women with caregiving responsibilities are likely to be at an early career stage, this pattern suggests that unequal mobility constraints may be a contributing factor to broader gender disparities in career advancements (often described as the 'leaky pipeline'), although further research is needed to disentangle this relationship from other structural barriers.

Explaining social mixing: demographics versus place exposure

Moving beyond describing patterns, we look at how individuals' social background, mobility pattern and the associated urban structure influence their social mixing levels across the five cities using travel survey and other location data. We build a series of regression models that estimate social mixing based on five groups of variables (Methods):

- Sociodemographic background (S): income, age, gender, caregiving responsibilities, employment status, vehicle ownership, and home public transit accessibility.
- Home-transit hub distance (H): the network distance of an individual's home zone to the nearest transit hubs with the highest inflow during morning peak hours. To avoid biases due to urban size, we allow for both monocentric and polycentric city concepts for transit hub identification following methods developed by Roth et al.³⁴
- Place exposure at all destinations (PD): the aggregated number of points of interest (POIs) within a t -minute walk of all destinations of a person's daily trip, categorized into N place categories (for example, restaurants, schools, retail and hospitals).
- Place exposure at the home zone (PH): mirroring PD, it measures the number of POIs grouped by categories within a t -minute walking time of an individual's home zone.

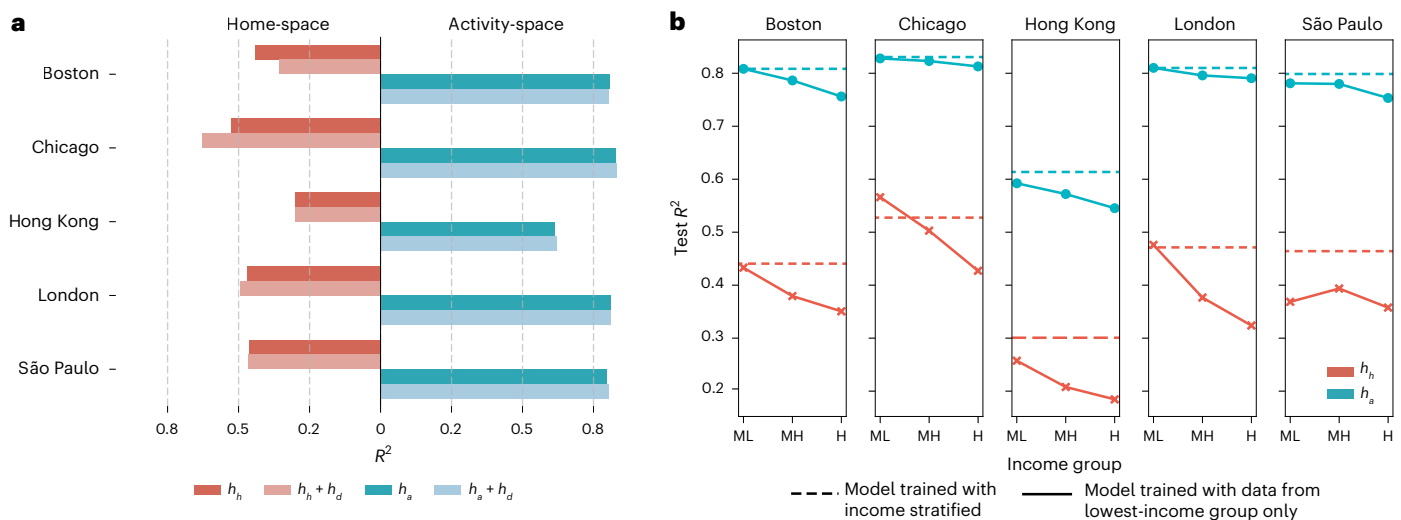


Fig. 5 | Predicting individual-level place exposure. a, The mean R^2 of models that include h_h , $h_h || h_d$, h_a , $h_a || h_d$. $||$ indicates that two embeddings are further concatenated to create a latent code for the decoder to reconstruct the place exposure. **b**, We use the low-income group as the training data, train the autoencoder model and then apply the model to predict the place exposure of all other income groups. ML stands for medium low; MH stands for medium high;

H stands for high. The dashed line indicates the average model performance using random split stratified on income (75% data used for training and 25% used for testing, repeated with ten different seeds). Full results that use other income groups as the training data and other evaluation metrics are shown in Supplementary Figs. 23 and 24.

- Mobility pattern (M): percentage of trips taken by different transportation modes (public transit or private cars).

The full regression model is specified as equation (3):

$$DM = \{S\} + \{H\} + \{PD\} + \{PH\} + \{M\}. \quad (3)$$

The unit of measurement is at individual level. Using the Lindeman, Merenda and Gold (LMG) method³⁵ (see Supplementary Section 4 for details), we compute the relative importance of each variable group in equation (3). Figure 3a illustrates that place exposure at destinations explains 50–69% of the model predictive power across all five cities. Sociodemographic factors, place exposure at home locations, and distance from transit hubs generally have lower explanatory power for social mixing levels. Overall, individual sociodemographic factors contribute more in Chicago (12.5%) and Boston (8.9%) than the three other cities (<5%). Full variable coefficients are included in Supplementary Figs. 15 and 16.

As the five cities in our study have different urban forms, we repeat the analysis by stratifying residents by distance to the nearest transit hub. Figure 3b unveils an underlying pattern: for those living farther from major transportation hubs, sociodemographic factors are more important and can explain up to 76% of social mixing. For people living within 20 km of a major transit hub, their social mixing level is largely determined by place exposure at destinations (50–79%).

Transportation modes

When summarizing the modal distribution of trips, we recognize that transit accessibility varies within the five cities across different income groups. Figure 2c shows that accessibility to train stations is rather uniform across all income groups in Hong Kong and London. On the contrary, both the lowest and highest income groups in Chicago and Boston have higher access to train stations. In São Paulo, people with higher income have better access to train stations. Figure 2d further describes the connection between vehicle ownership and access to bus stations. In Chicago and Boston, people who have at least one car at home are less likely to live closer to bus stations, while for Hong Kong, São Paulo and London, home accessibility to bus stations is rather independent from household car ownership.

After controlling for related variables, we see that the percentage of trips taken by public transit is positively correlated with DM in all five cities. Specifically, a 1% increase of public transit trips is associated with 0.1–0.3% increase of DM (Table 1). By contrast, private car usage shows smaller or even negative associations with DM, indicating that private cars contribute less to fostering social mixing. Comparing model 1 and model 2 reveals that the positive effect of public transit weakens after accounting for place exposure variables (PD and PH). This suggests that the positive relationship between public transit and mixing in most cities can be partially explained by the types of places that transit users access—namely, places with higher levels of POI density and diversity. In London and Hong Kong, the weaker decline in coefficients implies that the link between public transit and DM operates more independently of home and destination characteristics, reflecting these cities' relatively high POI density across the broader urban fabric.

Stratified activity spaces across income groups

Although our earlier results show that place exposure at destinations (PD) is the strongest predictor of individual-level social mixing, a remaining issue is that exposure itself is a result of the complex interplay of a city's underlying built environment, notably the distribution of POIs and transport network, and people's characteristics and mobility patterns. To tease out the different effects, we develop a machine learning framework to predict individual daily place exposure—represented as an N -dimensional vector of potential visits to urban amenities—using urban (transport) structure, home and activity spaces, and socioeconomic attributes.

Specifically, we construct spatiotemporal place networks for each city (over 100,000 POIs and 12.7 million edges) and embed them using a graph neural network (GNN) to capture the full spatial context that a person may experience. Compared with using raw POI categories within the same space, GNN embeddings capture latent spatial context (for example, street network and POI relationships into a dense vector). These embeddings, combined with demographics and travel features, are then fed into a supervised autoencoder designed to predict individual exposure vectors (Fig. 4a–c). Using this model, we evaluate three inputs systematically: home-space features (h_h), activity-space features (h_a) and demographic attributes (h_d). Home-space features represent the POIs accessible within

Table 1 | Estimate daytime social mixing with transit modes

Variable	Daytime social mixing (DM)								São Paulo	
	Boston		Chicago		Hong Kong		London			
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
% public transit	0.337*** (0.016)	0.091*** (0.013)	0.142*** (0.012)	0.044*** (0.011)	0.140*** (0.005)	0.127*** (0.005)	0.167*** (0.004)	0.128*** (0.004)	0.107*** (0.002)	0.060*** (0.002)
% private transit	-0.022*** (0.007)	0.027*** (0.006)	0.031*** (0.000)	0.064*** (0.000)	0.076*** (0.000)	0.075*** (0.000)	-0.066*** (0.000)	-0.049*** (0.000)	0.008*** (0.000)	-0.003*** (0.000)
Observations	7,623	7,623	18,257	18,257	42,736	42,736	30,382	30,382	46,957	46,957
R ²	0.3448	0.5677	0.1077	0.3001	0.0724	0.2877	0.1428	0.2208	0.1122	0.2899
Control S+H	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Control PD+PH	No	Yes	No	Yes	No	Yes	No	Yes	No	Yes

This table reports results of two variations of equation (3). Model 1 estimates daytime social mixing with S+H+M. Model 2 estimates daytime mixing with S+H+M+PD+HD. Robust standard error in parentheses. *** $P < 0.001$.

a 15-min walking distance from an individual's home. Activity-space features represent amenities within the convex hull encompassing all visited locations in a day. Both features were constructed using the representation of each POI aggregated from the GNN embeddings (see the Methods for identifying the adjacent POIs, definition of activity space, embedding aggregation and model details). Demographic features capture socioeconomic information such as age, gender and employment status. These inputs are processed separately through corresponding encoders, producing three embeddings that are concatenated into the comprehensive latent vector $\mathbf{z}$ in a permutation fashion, summarizing essential demographic, home and activity-space details.

To predict place exposure vector $\mathbf{Y}$, we have the decoder as equation (4):

$$\hat{Y}^{(i)} = W_d \mathbf{z}^{(i)} + b_d \in \mathbb{R}^N, \quad (4)$$

where b_d is the bias term and W_d is the weight matrix. To analyze the contribution of the three approaches of embedding, we conduct an ablation study by setting one of the $\mathbf{h}_h$, $\mathbf{h}_h$ or $\mathbf{h}_a$ from the equation (4) to zero and evaluate the change in reconstruction loss. We repeat the analysis by randomly reconstructing the train/test datasets ten times and report the average results here (each time we use 75% data as training and 25% data as test). All train and test data have equal distribution of people from different income groups.

Figure 5a visualizes the change of test data mean – R^2 for the three models in the five global cities. Here the mean – R^2 represents the average R^2 of each POI category in the place exposure vector (see Supplementary Fig. 22 for model performance results measured by the mean absolute error and mean squared error). Results show that activity-space embeddings or mobility patterns are far more predictive than home-space or demographic features. Across cities, $\mathbf{h}_a$ predicts about 60–80% (average of 59%) variance of the place exposure, compared with 25–45% for $\mathbf{h}_h$ and <10% for $\mathbf{h}_h$. Adding demographics provides marginal improvements. Robustness tests in Supplementary Section 3 using alternative POI datasets and feature construction methods show consistent results.

Lastly, we retrain the model using only one income group and then test the performance on all other income groups. If people's mobility pattern is independent from their socioeconomic background, we should see the model trained with one income group transferable to other income groups. On the contrary, if the structure of people's mobility pattern differs by their socioeconomic background, the model trained with one income group will not be as accurate when transferred to other income groups. Figure 5b shows a pattern of model accuracy loss, indicating stratified visitation patterns across different income groups within the same city (Fig. 5b). Using single-income-group

activity space embeddings shows 2–7% loss in accuracy, while using single-income-group home-space models leads to a drop of accuracy by 12–19%. Performance declines systematically as the income gap between the training and test groups widens (for example, when the single-income group for training is at the highest or lowest). Even in London and Hong Kong—where overall mixing levels appear relatively equal—we still observe performance loss when transferring visitations across groups. This indicates that, while sociodemographic attributes contribute little directly to predicting mixing at the individual level, differences in where income groups travel create distinctive patterns of urban exposure, and thus unequal opportunities for social mixing (see Supplementary Fig. 27 for model performance using other income groups as training data). Such results further emphasize the value of embedding rich socioeconomic data of mobility patterns into urban mixing or segregation studies.

Discussion

By combining the socioeconomic depth of travel surveys with a cross-continent comparative analysis across five global cities (covering more than 200,000 travel diaries), our study offers several contributions. First, we validate the use of travel survey data for capturing experienced social mixing. Comparing our travel-survey-based index with one derived from home-census median household income, we find that the survey-based measure is on average 16% higher for the former. This suggests that previous reliance on combining mobility traces from mobile phones and home-location proxies could yield systematic lower estimates of mixing people experience throughout daily travel.

Second, the rich socioeconomic information of travel surveys allows us to uncover life-course and gendered dynamics often invisible in mobility-only studies. We find support for the 'second youth' or 'third age' hypothesis: individuals in post-working life are as socially mixed as—or more so than—those in late working life, especially after employment status is accounted for. Regarding gender, we find that, while gender alone is not predictive of social mixing, individuals identified as likely caregivers (based on household composition) exhibit reduced social mixing compared with noncaregivers. This trend is particularly pronounced for women, suggesting a potential intersection of mobility constraints, household responsibilities and career development, although future work using direct caregiving data is required to confirm any causal link.

Third, leveraging travel survey data, we identify the central role of mobility patterns and destination diversity. Place exposure at destinations explains most of the variations in social mixing, overshadowing sociodemographics, home environment and transit proximity. Public transit use is consistently associated with higher social mixing, but this effect weakens once place exposure is controlled for, especially in

Table 2 | Travel survey summary

Study region	Boston, MA, USA	Chicago, IL, USA	Hong Kong, SAR	London, UK	São Paulo, Brazil
Site description	Boston Metropolitan Area within MA	Chicago Metropolitan Area within IL	Hong Kong Special Administrative Region (HKSAR)	Greater London area/32 London boroughs and the City of London	Metropolitan Area of São Paulo
Years of survey	2009–2011	2017–2018	2010–2011	2012–2014	2017
Survey duration	17 months	4 months	4.5 months	continuous rolling survey	16 months
Travel survey name	Massachusetts Travel Survey	My Daily Travel	Travel Characteristics Survey	London Travel Diary (LTD)	São Paulo Travel Diary
Original survey trip reported resolution	Census block	Census tract	Small street block	Northing, Easting	Coordinates
Travel survey methods	- Computer-assisted telephone interviewing (CATI) for recruitment and retrieval - Mail-back diaries option (52.5% mailed back, 47.5% phone retrieval) - Advance letter followed by telephone contact	- Primarily web-based recruitment surveys - Smartphone app option (Daily Travel App) for recording travel - Mail invitations with online completion	- Self-administered questionnaire with option for face-to-face interview upon request - Hotline available for assistance	- Face-to-face household interviews - Three questionnaires used: household questionnaire, individual questionnaires and trip sheets/travel diaries - All completed in-person	- Two-part survey: Household Survey (domestic) + Boundary Line Survey (external trips) - Tablet-based application for interviews - Multiple interview locations (roadways, bus terminals, airports and metro stations)
Survey resolution	Trip	Stop	Trip leg	Stage	Stop
Population of the year (million)	4.24	5.17	6.88	8.6	21
Total households included	10,785	12,391	35,401	24,248	31,847
Total participants interviewed	26,770	30,683	101,385	57,640	86,318
Total weighted participants (million)	4.03	6.67	6.31	8.95	16.7

This table reports the detail of each travel survey data. London and São Paulo's survey data contain coordinate-level information for each trip; thus, we do not provide the original resolution size here. An expanded table including details in data administration from each original survey is shown in Supplementary Table 1.

Boston, Chicago and São Paulo—implying that transit contributes to mixing primarily by connecting people to POI-rich areas. By contrast, this mediating effect is less pronounced in Hong Kong and London, where diverse amenities are more evenly distributed. Moreover, proximity to major transit stations reduces the influence of individual socioeconomic status on social mixing. However, we interpret these findings with caution, as individuals living near transit may differ systematically from those who do not, leading to a phenomenon called self-selection³⁶. Nevertheless, these patterns clearly highlight the importance of urban accessibility and destination diversity in shaping opportunities for social exposure.

Furthermore, our single-income-group transferability tests via the autoencoder model reveal a critical nuance. Even though sociodemographic attributes contribute little directly to predicting individual mixing, the visitation patterns of different income groups remain stratified. These structural differences in travel patterns across income groups remain evident even in cities like London and Hong Kong, where the overall mixing levels appear rather balanced across social groups. In short, people from different income groups may share a similar level of social mixing. Yet, they experience parallel rather than shared urban experiences as people of different income groups systematically visit different places. Recent studies show that embedding activities directly into mobility models can boost both interpretability and out-of-distribution performance^{37,38}. Our study joins this group of research and attempts to lay the ground for an ‘urban AI’ approach where theories of human behavior and mobility inform algorithmic models, improving their generality and fairness.

Finally, our cross-city comparison underscores the relationship between transit systems and social segregation. By pulling five distinctly different cities in this study, we observe that the gap in social

mixing between low and high income is smaller in Hong Kong and London than in the other three cities. This is probably due to the rather tightly connected amenities and more homogeneous public transit usage and accessibility in these two cities so that people of different income groups have higher chances to collocate in transit hubs and public spaces. In the case of Boston and Chicago, public transit stations are located closer to lower-income groups who also have lower car ownership, while in São Paulo, the highest-income group has both higher access to train stations and higher car ownership, exacerbating the unequal distribution of transportation opportunities.

It is important to acknowledge the limitations of this study. First, while survey weights ensure resident-level representativeness, they may not strictly capture trip-level exposure precision. We address this via robustness checks (Supplementary Table 2), confirming that our core findings hold across time-weighted and unweighted specifications. In addition, we acknowledge that travel survey data, like mobile phone or other data, are not error-free. In particular, nonresponse and underreporting, although partially overcome by professional data weighing and expansion statistically, should be recognized^{26–30}. Combining travel surveys with other big data (notably mobile phone traces) (for example, through simulated or synthetic datasets) is a promising direction²⁶. Second, this study focuses on social mixing only as social interaction is difficult, if not impossible, to capture without detailed observations or recordings (for example, that a conversation has taken place or people were shaking hands)^{32,33}. Future research that distinguishes trip purposes may be a step closer toward estimating potential interaction. Third, travel surveys, by their nature, are cross-sectional snapshots collected at intervals (typically every decade) and often restricted to weekday activities. Thus, the social mixing patterns we capture may not reflect weekend or seasonal dynamics, not to mention

dynamic changes in behavior (for example, shifts due to the COVID-19 pandemic or emerging mobility services such as ride-hailing and bike-sharing). Given that the survey collection years of this study vary from 2011 to 2018 (encompassing different economic cycles and phases of transit infrastructure development), observed disparities may involve temporal context impacts that are worth further studies to confirm. Lastly, while our five-city comparison spans a diversity of global contexts, it by no means covers the full spectrum of urban environment. Replicating our analysis in other cities, especially in the developing world, would further test the generalizability of our conclusions.

Methods

Datasets

Five study area. The definition of city in this study is intended to be devoid of additional administrative boundaries, including urban cores or other subdivisions. For Boston, MA, and Chicago, IL, the definition corresponds to the metropolitan statistical areas within the respective states (Massachusetts and Illinois, respectively); for London, this refers to the Greater London area; for São Paulo, we use the metropolitan area of São Paulo; for Hong Kong, given its peninsula nature, we use the entire administrative region. Maps of all cities are shown in Supplementary Figs. 1 and 2.

Travel surveys from five cities. Travel surveys in the selected cities, although in different formats, contain common information including person unique identifier, household unique identifier, home location (at survey zone level), household income (in local currency), age, sex, employment status, trip purpose, trip starting time and end time, distance, trip mode (and trip leg mode), participants home location (at a street block, zone or census block level) and expanded trip factors (see Supplementary Section 1 for manual standardization of the employment status, trip purpose and so on). Each participant reported multiple origins and destinations on a weekday. Each metropolitan area has different trip measures. The details of each travel survey are explained in Table 2. The finest details of travel diary are reported using different terms. To illustrate, London's survey uses 'stage' to document each stop within one trip. Hong Kong's survey is leg-based—each trip can contain multiple legs. To standardize the calculation, we use trip legs as the finest unit. Supplementary Table 1 includes details in original survey methods from each city.

Because the participants in these travel surveys were primarily random samples of the total population, each survey team provides an expansion factor that allow us to correct sampling bias. Previous research has demonstrated that the five surveys used in this study is well-balanced among income groups, gender and geography. We repeat our core analysis by using weighted and unweighted trips to test for the results' robustness (Supplementary Table 1).

From all cities, the raw survey data contain a total of 302,796 participants, among which 209,817 reported at least one trip. We applied filters to improve the reliability of the data. We removed the people who did not have complete data regarding the home zone, income level, age and gender reported. People who did not report any travel were also excluded from the main analysis. All travel surveys used in this study have been used for research in the transport literature^{12,39–42}. See how we standardize work status, trip purpose and trip mode in Supplementary Section 1.

To validate the travel-survey samples, we paired each study area with the smallest readily available census-style geography that reports population and income: US census tracts, UK Middle Super Output Areas (MSOAs), Hong Kong Tertiary Planning Units (TPUs) and São Paulo research zones. This process yields 1,471 tracts in Boston, 2,014 in Chicago, 1,141 MSOAs in London, 289 TPUs in Hong Kong and 517 research zones in São Paulo, with median unit areas ranging from 2.1 km² (Hong Kong) to 7 km² (Boston) (see Supplementary Section 2.1 for details of census survey geometry from each study city).

Train and bus stations from OpenStreetMap. We obtain train and bus stations data from OpenStreetMap using the osmnx Python package⁴³ by specifying the tags including bus stops, stations, and railways. A total of 82,362 bus stations and a total of 1,624 train stations are downloaded. The data were accessed in March 2024. To make sure that the station data are aligned with the travel survey data, we obtain the train stations' open date by looking up the train station names through local transportation department websites, Wikipedia and online newspapers via ChatGPT API (model 4o). Among the 1,624 train stations, we found 63 train stations that were built during or after the travel surveys were conducted. These train stations have been removed from the household transportation opportunities measure. We cannot further identify the exact open year of the bus stops, so all bus stops are kept for this study. We acknowledge that this is a limitation of the data.

Other POI amenities. We use POI data in each city to analyze people's exposure to different places. The primary analysis uses the POI data downloaded from OpenStreetMap. We need to standardize the raw POI tags (2,688 unique tags in total) into standard POI categories. To do so, we first use ChatGPT's 4o API to read all the POI tags and prompt to label them as one of the categories we specified: accommodation, agriculture, art and museum, café, community, education, construction, entertainment, finance, food, government, grocery, health, industry, library, office, outdoor, service, shopping, sports, tourism, transportation, utilities, worship and other. Then, we manually review the categories generated from the API call. The category selection follows the previous literature⁴⁴. For the analysis, we include only 18 categories that are relevant in our studies. Accommodation, agriculture, construction, industry, others and utilities categories are removed. We tested that our results are robust by adding or removing one or more categories. For the robustness of the study, we also collect and analyze POI data from Safegraph (Boston and Chicago), Geo Data Store (Hong Kong), Digimap (London) and Google Place API (São Paulo) to repeat the major portion of the study. See the details of the POI data verification in Supplementary Section 3.4.

Data processing

Identify gender, age and caregiving responsibilities from travel surveys. The overall data processing pipeline are visualized in Extended Data Fig. 1. With each participant's household member surveyed, we can identify participants that are likely to be parents or caretakers by looking at the age distribution of household members. For participants older than 21 and with at least one minor (age below 18) who are at least 18 years younger than the participants, we label them as caretakers (parents). Among all participants that are between 21 and 65 years old (195,710), 35.6% of participants are likely to be parents (38.1% after weighting by the expansion factor). Specifically, after counting the number of adults in each household, we identify 5.9% participants (9.6% after weighting) as single parents. Sixty-six percent of parents (67.8% after weighting) reported traveling at least once on the survey day.

Standardize the study unit. Travel survey data provide the origins and destinations of each trip leg. These locations are coded with local spatial units (census blocks, street blocks, latitude and longitude). To standardize the calculation, we use the H3 hexagons to code all origins and destinations for the analysis. The primary measure uses the level 8 (average edge length of 0.53 km) H3 hexagons for analysis. We use level 8 considering its size is comparable to census tract in the USA. We also repeat the social mixing measure by change the H3 unit to 4, 5, 6, 7, 9 and 10 for understanding the impact of the unit resolution. We repeat the social mixing measure estimations using the census geometry from each survey area. When the hexagon size increase, overall social mixing level increases for each person given they are defined to be exposed to more people within the same hexagon (see Supplementary Figs. 6 and 7 for systematic comparisons of social mixing by changing the

destination resolution). Supplementary Fig. 18 shows that our results are robust against the choice of destination definition.

Residential zones. The original travel surveys already provided a high-resolution residential location for each survey respondent. Their original residential zones are listed as following. Boston: census block; Chicago: census tract; Hong Kong: small street block; London: Northing and Easting imputed from the Travel Survey Unit; São Paulo: research zone. Similar to the activity locations, we transform the residential zone to H3 hexagons (level 8) and census zones with similar sizes across the cities. The transformed census zones used are the same as specified in Supplementary Section 2.1.

Income categories. To calculate the social mixing index, we first need to label the participants with different income categories based on the rank of their household income within the selected study area (see Supplementary Figs. 3 and 4 for the distribution of income groups across five region). Altogether, 299,955 participants (99.06%) have available household income provided in the original travel surveys. Then, after applying expansion factors, we divide the participants into four income groups: low, mid-low, mid-high and high income. The distribution of income groups within each study area is relatively equal. To test the impact of income group definition on the social mixing index measure, we also repeat the analysis by putting participants into five income groups. In addition, to compare with the method of using home zone census income directly, we also extract each participants' home census area's median household income and repeat the analysis.

Household transport opportunities. We calculate the walking distance of each household's home location's zone centroid to their nearest train station and bus station (see 'Train and bus stations from OpenStreet-Map' section for data sources). Households within 1 km of train stations or 800 m of bus stations are considered accessible to public transit. The walking distance used here is the network distance computed using Open Source Routing Machine⁴⁴ (OSRM)'s routing API service. For each household, we also obtain self-reported information about vehicle ownership from the travel surveys.

Major transit hubs. Our method of transit hubs identification follows the model by Roth et al.³⁴. We first compute the total weighted arrivals and departures of all train stations located hexagons during morning hours (6:00 to 11:00). Then, we gather these spatial units by the descending order of morning arrivals. By using the hexagon unit directly, we aggregate the total arrivals that could be generated from more than one very close stations. For the monocentric model, we pick only a single hexagon that has the highest number of arrivals as the main transit hub. For the polycentric model, we select the top N stations that accumulate at least 60% of the total arrivals (see Supplementary Section 3.1 and Supplementary Fig. 13 for more details).

Place exposure

The POI data contain place types, latitude, longitude, place names and place unique identifier. To analyze people's exposure to different places, we create two vector representations P_{di} and P_{hi} , to represent the list of places' counts by POI categories ($N = 18$ categories included in our study) that are within T -minute walking distance of an individual i 's destination and home. To get all places within any location's T -minute walking distance, we use the Python omnx package⁴⁵, which leverages OpenStreetMap's road network to calculate the walking isochrone from each trip leg destination, and then query all places within the isochrone. For a person i , visiting a list of destination $D_i = \{d_1, d_2, d_3, \dots, d_j\}$, the P_{di} reflects the average place counts by POI categories: $P_{di} = \frac{1}{D} \sum_{d_j \in D_i} P_{di,j}$, $POI_j \in R^N$. Here, POI_j is a vector of integers that count the number of POI by category in destination j within walking distance T . The main analysis uses $T = 15$ min to report the results. A visualization

of the POI query can be found in Supplementary Fig. 12. We also test $T = 5$ or 10, and the results are included in Supplementary Fig. 20b,c. In addition, we also repeat the analysis by completely replacing the POI sources with POI data source from each local POI provider (Supplementary Fig. 18).

Predicting place exposure

Model details. The aim of this analysis is to predict individual daily exposure to different categories of urban places, represented as an N -dimensional vector where each dimension corresponds to the count of potential visits to a specific place category (N being the total number of place categories included in this study). We do not know exactly which POI (for example, the name of the shop or a facility) the person visits at destinations. Therefore, we query all POIs within 15-min walking distance of each trip destination to represent the places that they are exposed to. We also tested 5-min and 10-min walking distance for robustness.

To predict the daily exposure, we integrate the information about individuals' socioeconomic factors, home locations, daily travel activity areas and the spatial and transit characteristics of each city. Our model leverages three key insights about urban networks and human mobility: (1) places that are geographically closer influence each other more strongly^{46,47}; (2) places can also have important long-distance connections facilitated by human mobility⁴⁴; and (3) public transit accessibility impacts people's place exposure²⁰. To represent these relationships, we first construct a spatiotemporal place network for each city, incorporating both physical proximity based on road networks and travel time derived from public transit schedules (the General Transit Feed Specification data). We embed the detailed network information into each place using a GNN⁴⁸ (Fig. 4a). A total of 107,750 POIs with 12.7 million edges are created. Next, we employ a supervised autoencoder⁴⁹ neural network designed in an encoder-decoder structure (Fig. 4b,c). Unlike traditional autoencoders, which compress and reconstruct their input exactly, our autoencoder aims to learn a concise, meaningful representation of input features to predict the individual place exposure vector. Specifically, the encoder processes individuals' sociodemographic attributes and their associated place network features (either around home or throughout their daily activity space), as mapped from their travel trajectories to create a compact latent embedding. The decoder then uses this embedding to output the predicted place exposure vector, quantifying the expected number of urban amenities a person is exposed to (Fig. 4).

Construct POI place embeddings with GNN. To represent each city's spatial network information with POI places, we first build a POI graph $G(v, e, w)$ for each city that uses each POI as the node v ; the edge w_{ij} measures the connectivity between two nodes v_i and v_j . For robustness of the study, we build four different graph G using road network attributes and transit availability (using public GTFS data). The primary measure uses the transit-time-aware network that finds v_j within 15-min walking or transit time of v_i . We assign $w_{ij} = 1$ if within the 15-min travel time, 0 otherwise. On average, this network contains 8.7 million to 39.7 million edges in all cities. The average edge per node ranges from 33.6 (Boston) to 230.9 (London). The second method creates network edges that are time-weighted ($w_{ij} = e^{-t_{ij}/\alpha}$), where t_{ij} is the travel time between nodes v_i and v_j . In addition, we also construct two more distance-based measures. The third one uses $w_{ij} = 1$ to indicate that within 1.26 km (approximately 15-min walking distance) of node v_i , we can find v_j . The fourth measure constructs the $w_{ij} = e^{-d_{ij}/\alpha}$ to further indicate the strength of spatial proximity, where d_{ij} is the distance between the two POI places, and α here is a scale factor. The GNN model performance by four edge types is presented in Supplementary Table 7. Our results are robust against variations on spatial graph construction (see Supplementary Section 5.1 for a detailed construction of the model). With the network established, we train a two-layer graph coevolutionary

neural network model (one type of GNN model) to predict the category of each POI place (Supplementary Section 6.1). The contribution of GNN embedding is presented in Supplementary Table 11.

It is important to clarify that the target variable of daily exposure and the input variable of place embedding in the GNN model capture fundamentally different geometric and statistical dimensions of the spatial data. The target variable is an aggregate categorical frequency distribution representing the density and diversity of potential encounters with people of the same and other income groups specifically at discrete destination points where an individual stopped. By contrast, the activity-space embedding ($\mathbf{h}_a$) generated by the GNN encodes the latent spatial topology of the wider geographical contexts within all potentially accessible areas of an individual. Because $\mathbf{h}_a$ is constructed from all POIs within the spatial convex hull encompassing people's full daily trajectories, it represents the broader geographic boundaries of their movements, rather than just their chosen stops. Consequently, the autoencoder does not perform a mechanical aggregation. Rather, it offers an interpretable test on a structural hypothesis: whether the topological shape and total area of a person's movement network intrinsically determine their specific categorical exposure profile. The nontrivial nature of this distinction is indicated by our transferability tests, which show that the relationship between place exposure and spatial territory is highly complex and stratified by income.

Reporting summary

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

Data availability

The aggregated data for repeating the analysis are available via GitHub at <https://github.com/brookefzy/social-mixing-5-city>. The raw travel survey data cannot be directly shared given the signed nondisclosure agreement.

Code availability

The full analysis is available via the same repository above.

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Author contributions

Z.F. contributed to the datasets, formal analysis, validation, visualization and writing – original draft, and editing and reviewing; B.P.Y.L. contributed to the conceptualization, datasets, supervision and writing – original draft, and editing and reviewing; F.D. and C.R. contributed to the datasets, supervision and writing – editing and reviewing; E.M. contributed to the methodology, supervision and writing – editing and reviewing.

Competing interests

The authors declare no competing interests.

Additional information

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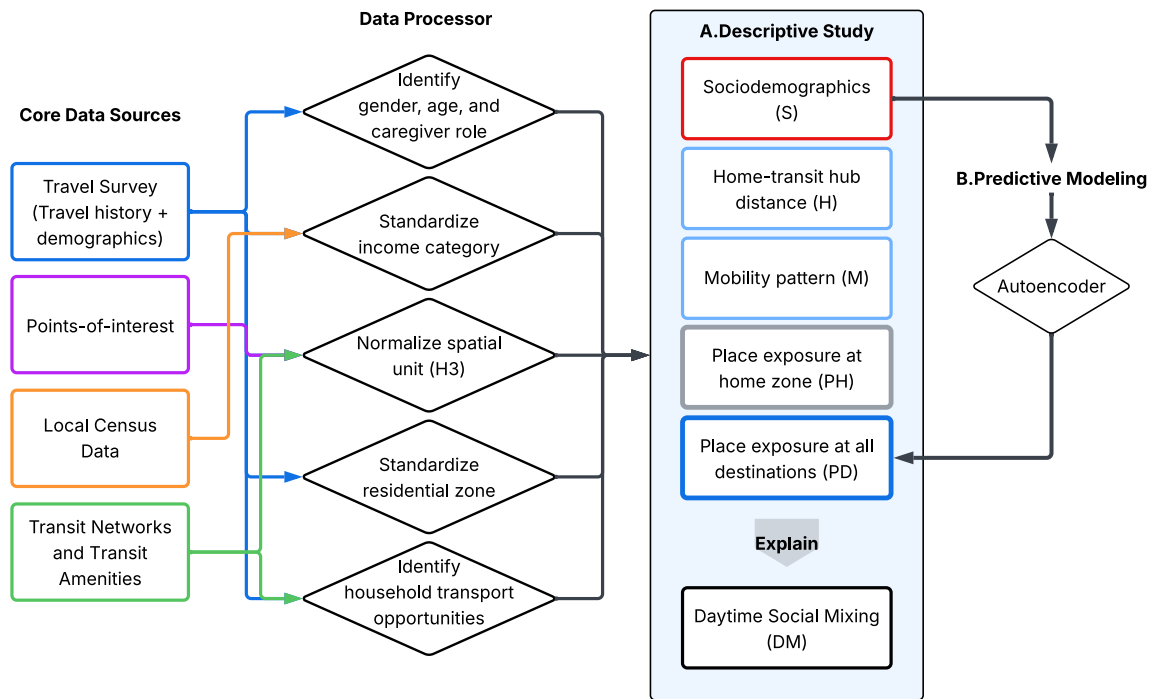
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Extended Data Fig. 1 | Schematic data processing pipeline. Details in how the transportation modes, work status, and trip purposes are standardized are included in SI Table S8-10.

Reporting Summary

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Software and code

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

Data collection Our main sources of data are travel survey data from Boston, MA, Chicago, IL, Hong Kong, London, Sao Paulo. The full data description is provided in Appendix Table S1.

Data analysis All data analysis was conducted in Python 3.12

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

Data

Policy information about [availability of data](#)

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

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

All travel survey data used in this study has a non-disclosure agreement signed with the related party. We cannot share raw travel survey data with the public. But we will provide aggregated data for repeating the analysis through public repository (<https://github.com/brookefzy/social-mixing-5-city>)

Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

Reporting on sex and gender	In the survey data, the gender were self-reported by each participants.
Reporting on race, ethnicity, or other socially relevant groupings	This study groups participants by their reported income level, age, gender, car ownership so that we can understand the effect of these demographic information on their social mixing level.
Population characteristics	See details in the Behavioural & social sciences study design section below
Recruitment	We didn't directly recruit the participants. They were recruited by each travel survey agency from the five cities involved.
Ethics oversight	University of Hong Kong approved the study

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

Field-specific reporting

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

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

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

Behavioural & social sciences study design

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

Study description	The study is cross-sectional quantitative. We use travel survey data from five cities to analyze the effect of public transit, places visited, home locations, and demographics on their experienced social mixing level.
Research sample	The research samples were collected by each travel survey agency from the five cities. Survey participants are residents in each city. The gender, population, and age distribution are shown in the SI Table S1.
Sampling strategy	The total participants represents about 0.3-0.9% of the local population of the survey year for the cities included in the study. For each city, a weighting mechanism was conducted to make sure the analysis was not biased by the sampled population. We compared impacts of different sample methodology on our study results in SI. Table S2 provided full overview of the entire robustness test on different sample methods.
Data collection	We didn't directly collect the data. The data was provided by each transportation department of the city we studied.
Timing	Boston: 2009-2011 Chicago: 2017-2018 Hong Kong: 2010-2011 London: 2012-2014 Sao Paulo: 2017
Data exclusions	Participants who didn't report any effective trips were not included in the study. We show the full results of dropping different types of samples in the study in SI Table S2.
Non-participation	See Table S2 for full description of the impact of dropping different participants. We sequentially dropped participants who took too few trips and summarizes the impact on our results.
Randomization	The gender distribution, income distribution, and age distribution of participants from each city matches their local census survey data.

Reporting for specific materials, systems and methods

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

Materials & experimental systems

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

Methods

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

Antibodies

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

Eukaryotic cell lines

Policy information about [cell lines and Sex and Gender in Research](#)

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

Palaeontology and Archaeology

Specimen provenance	Provide provenance information for specimens and describe permits that were obtained for the work (including the name of the issuing authority, the date of issue, and any identifying information). Permits should encompass collection and, where applicable, export.
Specimen deposition	Indicate where the specimens have been deposited to permit free access by other researchers.
Dating methods	If new dates are provided, describe how they were obtained (e.g. collection, storage, sample pretreatment and measurement), where they were obtained (i.e. lab name), the calibration program and the protocol for quality assurance OR state that no new dates are provided.
☐ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.	
Ethics oversight	Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.

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

Animals and other research organisms

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

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

numbers in this Reporting Summary. Please state if this information has not been collected. Report sex-based analyses where performed, justify reasons for lack of sex-based analysis.

Field-collected samples

For laboratory work with field-collected samples, describe all relevant parameters such as housing, maintenance, temperature, photoperiod and end-of-experiment protocol OR state that the study did not involve samples collected from the field.

Ethics oversight

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

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

Clinical data

Policy information about [clinical studies](#)

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

Clinical trial registration

Provide the trial registration number from ClinicalTrials.gov or an equivalent agency.

Study protocol

Note where the full trial protocol can be accessed OR if not available, explain why.

Data collection

Describe the settings and locales of data collection, noting the time periods of recruitment and data collection.

Outcomes

Describe how you pre-defined primary and secondary outcome measures and how you assessed these measures.

Dual use research of concern

Policy information about [dual use research of concern](#)

Hazards

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

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

Experiments of concern

Does the work involve any of these experiments of concern:

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

Plants

Seed stocks	Report on the source of all seed stocks or other plant material used. If applicable, state the seed stock centre and catalogue number. If plant specimens were collected from the field, describe the collection location, date and sampling procedures.
Novel plant genotypes	Describe the methods by which all novel plant genotypes were produced. This includes those generated by transgenic approaches, gene editing, chemical/radiation-based mutagenesis and hybridization. For transgenic lines, describe the transformation method, the number of independent lines analyzed and the generation upon which experiments were performed. For gene-edited lines, describe the editor used, the endogenous sequence targeted for editing, the targeting guide RNA sequence (if applicable) and how the editor was applied.
Authentication	Describe any authentication procedures for each seed stock used or novel genotype generated. Describe any experiments used to assess the effect of a mutation and, where applicable, how potential secondary effects (e.g. second site T-DNA insertions, mosaicism, off-target gene editing) were examined.

ChIP-seq

Data deposition

- ☐ Confirm that both raw and final processed data have been deposited in a public database such as [GEO](#).
- ☐ Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

Data access links May remain private before publication.	For "Initial submission" or "Revised version" documents, provide reviewer access links. For your "Final submission" document, provide a link to the deposited data.
Files in database submission	Provide a list of all files available in the database submission.
Genome browser session (e.g. UCSC)	Provide a link to an anonymized genome browser session for "Initial submission" and "Revised version" documents only, to enable peer review. Write "no longer applicable" for "Final submission" documents.

Methodology

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

Flow Cytometry

Plots

Confirm that:

- ☐ The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).
- ☐ The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).
- ☐ All plots are contour plots with outliers or pseudocolor plots.
- ☐ A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparation	Describe the sample preparation, detailing the biological source of the cells and any tissue processing steps used.
Instrument	Identify the instrument used for data collection, specifying make and model number.
Software	Describe the software used to collect and analyze the flow cytometry data. For custom code that has been deposited into a community repository, provide accession details.

Cell population abundance

Describe the abundance of the relevant cell populations within post-sort fractions, providing details on the purity of the samples and how it was determined.

Gating strategy

Describe the gating strategy used for all relevant experiments, specifying the preliminary FSC/SSC gates of the starting cell population, indicating where boundaries between "positive" and "negative" staining cell populations are defined.

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

Magnetic resonance imaging

Experimental design

Design type

Indicate task or resting state; event-related or block design.

Design specifications

Specify the number of blocks, trials or experimental units per session and/or subject, and specify the length of each trial or block (if trials are blocked) and interval between trials.

Behavioral performance measures

State number and/or type of variables recorded (e.g. correct button press, response time) and what statistics were used to establish that the subjects were performing the task as expected (e.g. mean, range, and/or standard deviation across subjects).

Acquisition

Imaging type(s)

Specify: functional, structural, diffusion, perfusion.

Field strength

Specify in Tesla

Sequence & imaging parameters

Specify the pulse sequence type (gradient echo, spin echo, etc.), imaging type (EPI, spiral, etc.), field of view, matrix size, slice thickness, orientation and TE/TR/flip angle.

Area of acquisition

State whether a whole brain scan was used OR define the area of acquisition, describing how the region was determined.

Diffusion MRI

☐

Used

☐

Not used

Preprocessing

Preprocessing software

Provide detail on software version and revision number and on specific parameters (model/functions, brain extraction, segmentation, smoothing kernel size, etc.).

Normalization

If data were normalized/standardized, describe the approach(es): specify linear or non-linear and define image types used for transformation OR indicate that data were not normalized and explain rationale for lack of normalization.

Normalization template

Describe the template used for normalization/transformation, specifying subject space or group standardized space (e.g. original Talairach, MNI305, ICBM152) OR indicate that the data were not normalized.

Noise and artifact removal

Describe your procedure(s) for artifact and structured noise removal, specifying motion parameters, tissue signals and physiological signals (heart rate, respiration).

Volume censoring

Define your software and/or method and criteria for volume censoring, and state the extent of such censoring.

Statistical modeling & inference

Model type and settings

Specify type (mass univariate, multivariate, RSA, predictive, etc.) and describe essential details of the model at the first and second levels (e.g. fixed, random or mixed effects; drift or auto-correlation).

Effect(s) tested

Define precise effect in terms of the task or stimulus conditions instead of psychological concepts and indicate whether ANOVA or factorial designs were used.

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

Statistic type for inference

Specify voxel-wise or cluster-wise and report all relevant parameters for cluster-wise methods.

(See [Eklund et al. 2016](#))

Correction

Describe the type of correction and how it is obtained for multiple comparisons (e.g. FWE, FDR, permutation or Monte Carlo).

Models & analysis

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

Functional and/or effective connectivity

Report the measures of dependence used and the model details (e.g. Pearson correlation, partial correlation, mutual information).

Graph analysis

Report the dependent variable and connectivity measure, specifying weighted graph or binarized graph, subject- or group-level, and the global and/or node summaries used (e.g. clustering coefficient, efficiency, etc.).

Multivariate modeling and predictive analysis

Specify independent variables, features extraction and dimension reduction, model, training and evaluation metrics.