Non-native plants homogenize global urban flora

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Abstract: Urban areas serve as hubs for non-native plant introductions, but the extent to which these introductions have homogenized city floras globally remains unexplored. We analyzed species inventories from 553 cities across six continents and show that non-native plants increase mean pairwise floristic similarity by ~50%, from a Jaccard index of 0.11 for native species alone to 0.16 when non-natives are included. Non-natives increase intracontinental similarity by 25%, but boost intercontinental similarity by 423%, due to intercontinental native floras sharing few species. City connectivity (indexed by air-travel frequency) amplifies non-native similarity more than native similarity, while geographic distance constrains native similarity more strongly, consistent with dispersal limitation. Contrary to our original hypothesis, climatic distance constrains non-native similarity as strongly as native similarity, confirming that climate is a hard environmental filter regardless of species' origin. Meanwhile, urban socio-economic and physical features also affect native and non-native floristic similarity comparably. Regional analyses reveal pronounced asymmetries, with non-native species strongly homogenizing cities in Europe, North America, and Oceania, whereas Asian cities show weak intercontinental convergence. Decomposing similarity into ecological components reveals distinct mechanisms: homogenization between city pairs that involve European cities is dominated by species transfers (taxa native in one region but naturalized in another), reflecting colonial and trade legacies, whereas North American-Oceanian convergence is driven by a shared pool of widespread non-native species. These findings demonstrate that human-mediated plant movement has become a dominant force reshaping global urban flora, with effects modulated by connectivity, environmental filtering, and region-specific historical legacies.

Significance statement: As global trade and travel expand, non-native plants also increasingly spread into cities worldwide. Analyzing plant species inventories from 553 cities, we show that

non-native species increase average city-to-city plant similarity by 50%, with effects far stronger across continents than within them. Cities with more flight connections share more non-native species, while native plants are more constrained by geographic boundaries. History also leaves clear signatures: European cities, shaped by centuries of colonial trade, have exported species to cities across the Americas and Oceania, whereas Asian cities remain more distinct. Global human movement is a major driver of urban floristic homogenization, progressively eroding the unique botanical identities of cities worldwide.

Introduction:

Cities have been hotspots for non-native plant introductions, functioning as sites of initial establishment and as source populations for onward spread (1, 2, 3). The same transport networks that drive urban economic integration move plant propagules across biogeographic boundaries. As a result, cities on dense trade and travel routes accumulate overlapping non-native species pools and converge floristically. Regional studies in Europe and North America confirm that non-native species drive cities toward compositional convergence, eroding the floristic distinctiveness of individual cities (4–9). However, whether such homogenization operates globally, whether its effect is stronger across than within continents, and the underlying environmental, socio-economic, and historical mechanisms remain unquantified.

Compositional similarity drivers are expected to differ between native and non-native assemblages. Native floras reflect dispersal limitation and environmental filtering over evolutionary timescales, making geographic distance and climate the dominant drivers of inter-city compositional similarity (4). For non-native species, human-mediated transport networks drive introduction and spread, strongly determining which cities share similar non-native assemblages while leaving native floras largely unaffected (2, 6, 10, 11). This intensive human-

mediated dispersal effectively bypasses geographic barriers, while the broad environmental tolerances of many introduced species (12) will reduce the constraint of urban climate and physical features relative to native groups (13, 14). City connectivity is therefore expected to amplify non-native floristic similarity more than native similarity (2, 6, 14). Socio-economic conditions add a further layer: for example, wealthier cities usually support larger non-native species pools (1, 15, 16), so pairs of wealthy cities are likely to share more similar non-native flora. Whether this socio-economic effect on floristic similarity differs between native and non-native floras globally remains untested.

Beyond assessing overall similarity changes, further decomposing floristic similarity into ecologically distinct components reveals the underlying processes (9, 14). Specifically, similarity between any two cities can be partitioned into contributions from shared native species, shared non-native species (i.e., taxa naturalized in both), and species transfers (i.e., taxa native to one city but non-native in the other, not necessarily direct transfer). Shared non-native species emerge when widespread invaders establish independently across cities (17); species transfers arise through directional plant movements usually tied to trade and /or colonialism (18). Regional variation in these components is expected. For example, similarity between North and South American and Oceanian cities likely reflects a shared non-native pool assembled during European colonization, whereas similarity involving European cities is expected to be dominated by species transfers, reflecting the asymmetric export of European natives to colonized regions and the reciprocal movement of colonial plants to Europe (17, 18). Disentangling these components globally reveals whether urban homogenization reflects the rise of a cosmopolitan weed flora or the legacy of historically contingent, directional plant movements.

Using plant species inventories from 553 cities worldwide (3), we provide the first global quantification of the contribution of non-native species to contemporary inter-city similarity, its environmental and socio-economic drivers, and its regional and mechanistic components (Fig. 1). We tested four hypotheses: First, non-native species substantially increase pairwise floristic similarity among cities, with the strongest effect for intercontinental city pairs, where native floras share very few species while widespread non-native species would be highly shared, and weaker within continents. Second, non-native floristic similarity is less constrained by geographic and climate distance than native similarity, consistent with dispersal limitation for native species and broader climatic tolerance for non-native species. Third, city connectivity increases non-native floristic similarity more than native similarity, and socio-economic similarity exerts a stronger positive effect on non-native than on native assemblage similarity. Fourth, similarity components vary regionally: for example, shared non-native species dominate similarity between North American and Oceanian cities — reflecting their shared introduction history from European colonization and similar temperate climate — whereas species transfers dominate intercontinental similarity involving European cities, reflecting asymmetric directional plant movements through European colonial and trade networks.

Results

Global contribution of non-native plants to urban floristic similarity

We quantified the overall contribution of non-native species to pairwise floristic similarity among 553 cities using the Jaccard similarity index. Across all city pairs, non-native plants substantially increased city-to-city floristic similarity (Fig. 2): Jaccard similarity based on native species alone averaged 0.109 ± 0.136 (mean ± SD) (Fig. 2B), whereas total similarity including both native and non-native species increased to 0.163 ± 0.145 (Fig. 2A; Fig. S1, Supporting information) — a mean increase of 49.5% attributable to non-native introductions

(paired Wilcoxon test at city level, $P < 0.001$, supporting Hypothesis 1). When considering non-native species alone, mean similarity was 0.120 ± 0.101 (Fig. 2C, note that Jaccard index is not simply additive).

Intra- and intercontinental comparisons revealed a striking spatial asymmetry. Within continents, native similarity averaged 0.220 ± 0.130 and increased to 0.275 ± 0.136 when non-native species were included - an average of 25% increase (paired Wilcoxon test at city level, $P < 0.001$). In contrast, among intercontinental city pairs, baseline native similarity was extremely low (0.013 ± 0.013) but rose to 0.068 ± 0.060 when non-native species were included, representing more than five-fold escalation (paired Wilcoxon test at city level, $P < 0.001$). Non-native species thus contribute significantly to urban floristic similarity globally, with a disproportionately strong homogenizing effect across continents where native floras share few species.

Drivers of pairwise floristic similarity between cities

We applied generalized linear mixed models to assess the effects of city connectivity (quantified by air-travel frequency), socio-economic distance (e.g., human population size, gross domestic product), climatic distance, physical property distance (e.g., built-up density, greenness), and geographic distance on the pairwise similarity of native, non-native, and total floras. Prior to modelling, we applied principal component analysis (PCA) to reduce the dimensionality of each multi-variable category (socio-economic, climatic, and physical variables): the first three PCA axes of each category were retained, and pairwise distances were then computed as Euclidean distances in these reduced PCA spaces.

Across all assemblages, socio-economic, physical, climatic, and geographic distances all exerted consistently negative effects on city-pair similarity (Fig. 3A), indicating strong environmental filtering and dispersal limitation in urban flora. Geographic distance had the

strongest negative effect overall, and its influence was markedly greater for native than non-native species (Fig. 3B), confirming that native floras are more strongly constrained by dispersal barriers (supporting Hypothesis 2). Contrary to our expectations (Hypotheses 2 and 3), city physical property and socio-economic distances reduced similarity with broadly comparable effects for native and non-native species, while climatic distance exhibited a slightly stronger negative effect on non-native floras. City connectivity increased similarity, with a more pronounced positive effect for non-native species (supporting Hypothesis 3), highlighting human-mediated transport's disproportionate role in shaping non-native urban floras.

Regional differences in the homogenization effects attributed to non-native species

Given strong spatial variation in environmental conditions, urban development, and connectivity, we expected regional differences in non-native homogenization effects. We thus analyzed six continents separately - Africa (AF), Europe (EU), Asia (AS), North America (NA), South America (SA), and Oceania (OC) - and quantified how non-native species altered both intra- and intercontinental city-pair similarity. For intracontinental city pairs, the largest increase attributable to non-native species occurred in Oceania, where total similarity rose by 59.2% compared to native-only similarity, whereas Asia showed the smallest increase (10.5%) (Fig. 4A). In contrast, the homogenizing effects of non-native species on mean intercontinental similarity were substantially stronger (Fig. 4B). With non-natives included, the increase in intercontinental similarity was also highest in Oceania (894%), but lowest in Asia (169%).

Examining individual continent pairs revealed that the strongest increases occurred among EU–NA, EU–OC, and NA–OC city pairs (Fig. 4C). In contrast, intercontinental city pairs involving Asia (EU–AS, SA–AS, AF–AS, and OC–AS, except AS-NA) showed markedly smaller increases. Non-native species thus disproportionately homogenize urban floras in

Europe, North America, and Oceania, while contributing far less to the similarity involving Asian cities.

Decomposition of floristic similarity

When decomposing similarity (across all intercontinental and intracontinental city pairs) into its specific component contributions (Fig. 5), we found that shared native species accounted for 35.6% ± 23.5% (mean ± SD; Fig. 5A) of city-to-city similarity, species transfers (taxa native to one region but naturalized in another) accounted for 35.4% ± 18.5% (Fig. 5B), and shared non-native species accounted for 29.0% ± 15.2% (Fig. 5C). This indicates that all three components play substantial and distinct roles in shaping overall city-wise similarity (Fig. 5D). When examining intercontinental similarity for each continental pair and focusing on the contributions of species transfers and shared non-natives (shared natives contributed negligibly across continents), some clear regional patterns emerged (Fig. 5E). Species transfers play more important roles in the similarity between Europe and other continents (Fig. 5B and E). In contrast, shared non-native species contributed most strongly to similarity between Oceania and North America (Fig. 5C and E), highlighting widespread, jointly shared non-native floras between these two regions, confirming Hypothesis 4.

Discussion:

Urban floras support key ecosystem functions but are strongly influenced by human activities, including land-use change, management, and species introductions. Analyzing 553 cities worldwide, we demonstrate that non-native plants markedly increase floristic similarity among cities, driving substantial intercontinental homogenization. This pattern reflects the joint influences of human-mediated connectivity, environmental filtering, and regional biogeographic history. Long-distance connectivity increased similarity among non-native

floras, and geographic distance constrained native floristic similarity far more strongly than non-native similarity. Unexpectedly, city climatic, socio-economic and physical factors exerted comparable effects on both groups. Moreover, similarity between Oceania and North America is driven largely by shared widespread non-native species, suggesting convergence toward a common pool of introduced plants. In contrast, similarity between Europe and other continents is more strongly shaped by species transfers, reflecting historical pathways of plant movement linked to colonial expansion and long-standing trade networks.

Across 553 cities, non-native plants increased mean city-to-city floristic similarity by nearly 50%, rising from an average Jaccard index of 0.11 for native species alone to 0.16 when non-natives were included. This increase was driven primarily by intercontinental city pairs, which share few native species but substantially more non-native species (Figs. 2, 4), a pattern consistent with recent findings for global urban tree species (19). This trend reflects the breaking down of strong biogeographic isolation that historically separated native floras, replaced by widespread human-mediated plant introductions through global trade and transport networks (14, 20, 21). Urban areas concentrate these introduction pathways, including the ornamental plant trade, botanical garden collections, private garden planting, and also international transport that facilitates accidental introductions (22–24). Consequently, non-native species frequently bypass biogeographical dispersal barriers, fostering long-distance convergence among cities. Our findings thus extend previous regional insights into urban homogenization (5–8) to a global scale.

Explicitly modelling multiple drivers of city-to-city similarity reveals that connectivity, environmental filtering, and dispersal limitation shape native and non-native floras in partially different ways. City connectivity accelerated similarity more strongly for non-native than for native species, underscoring the disproportionate role of human mobility and infrastructure in

facilitating the exchange of non-native plants among cities (2, 6, 10). Moreover, current air travel also partly reflects historic patterns of colonization (25). Because our connectivity metric relied solely on air-travel frequency and did not account for terrestrial or maritime transport networks, our estimates likely provide a conservative assessment of the full impact of human connectivity on urban floras. Consistently, non-native floras were less constrained by geographic distance than native floras, reflecting weakened dispersal limitation. This is attributable to human-facilitated long-distance transport as well as the inherently high dispersal and reproductive capacities of many successful non-native invaders (12).

In contrast, environmental filtering limited similarity across both native and non-native urban floras globally. Contrary to our initial hypothesis, climatic distance imposed an equally strong—or even slightly stronger—constraint on non-native than on native assemblages. This indicates that climate remains a strict ecological filter for urban plant establishment regardless of species origin (26). Interestingly, both city socio-economic and physical property distances affected native and non-native similarities to a comparable degree. Variations in city size, infrastructure, and urban configuration shape local habitat availability (e.g., the urban heat island effect, green space configuration) and management regimes, acting as shared environmental filters (e.g., convergence of microclimate, refs. 27–29). Consequently, structural and economic convergence in urban forms appears to reinforce global biological homogenization (30).

A process not explicitly captured by our similarity analyses is temporal changes in native species (extirpation and additions) driven by urbanization (31). Especially, urban expansion, habitat fragmentation, pollution, and intensive management disproportionately eliminate disturbance-sensitive or habitat-specialist native species, further eroding the local distinctiveness of urban floras (4, 9; but see refs. 32, 33). Utilizing historical species inventories

(e.g., ref. 34) or regional proxies for pre-urban baselines (e.g., adjacent natural or peri-urban floras) to quantify native species losses represents a vital direction for future research into the dynamics of urban floristic homogenization.

Our continental analyses revealed pronounced spatial asymmetries in the homogenizing effects of non-native plants. Cities in Europe, North America, and Oceania exhibited far stronger intercontinental homogenization than cities in Asia, Africa, or South America, with the most pronounced increases observed in Oceania but much less in Asia. These patterns likely reflect a combination of historical, biogeographic, climate, and economic factors (35). Centuries of European colonization, global trade networks, and long-standing plant exchanges have driven extensive, reciprocal plant introductions among European, North American, and Oceanian urban centers (18, 23, 36). Colonial-era data at the city level remains unavailable and warrants deeper exploration in future research. In contrast, many Asian cities have historically experienced fewer naturalized non-native introductions and retain highly diverse native species pools—particularly in subtropical and tropical zones—resulting in lower contemporary floristic convergence with other continents. However, ongoing globalization and rapid urban development are expected to alter these patterns, as expanding trade and horticultural demands accelerate non-native introductions into Asian cities (11).

Unlike Asia, Oceanian cities stand out as exceptionally susceptible to non-native-driven homogenization. This vulnerability is likely due to Oceania's evolutionarily distinct native flora, which shares very few species with other continents, combined with high susceptibility to biological invasions (37). These findings echo broader macroecological evidence that regions characterized by high endemism and long-term evolutionary isolation are uniquely sensitive to the impacts of non-native species (38). It should be noted that Oceania, Africa, and South America are underrepresented in our dataset (less than 20 cities), which could introduce

regional bias in the results. Greater sampling effort in these regions is needed to better characterize both regional and global patterns of urban biotic homogenization.

By decomposing floristic similarity into shared native species, shared non-native species, and species transfers, we uncovered the distinct mechanisms underlying global urban homogenization (Fig. 5). Globally, species transfers and shared native species contributed comparably to overall similarity, whereas shared non-natives accounted for a smaller proportion on average. This lower average contribution likely arises because widespread, highly successful invaders constitute only a small fraction of the total naturalized non-native flora (17). However, this balance shifted markedly in intercontinental comparisons. Floristic similarity between European cities and those in North America, Asia, or Oceania was heavily dominated by species transfers, capturing the enduring legacy of directional plant movements via colonial expansion, botanical exploration, and historical trade (18). In contrast, similarity between North American and Oceanian cities was driven primarily by shared non-native species, reflecting the establishment of a common global pool of introduced weeds and ornamental species originating largely from Europe and Asia (17, 36). These contrasting patterns demonstrate that urban homogenization is not a monolithic phenomenon, but rather a reflection of region-specific histories of plant introduction, exchange, and establishment (4, 9).

In summary, our study demonstrates that human-mediated introductions of non-native plants have become a dominant force shaping global patterns of urban floristic composition, particularly by homogenizing city floras across distinct continents. This process is jointly driven by human transport networks, environmental filtering, and historical legacies, operating through distinct mechanisms across different world regions. Our results highlight that tracking urban homogenization requires looking beyond simple changes in similarity metrics to uncover how that similarity arises—whether through the spread of a shared cosmopolitan weed flora or

through asymmetric exchanges between native and naturalized pools. As urban areas expand and global trade networks intensify, understanding the drivers and consequences of urban floristic homogenization will be essential for conserving urban biodiversity and guiding sustainable urban planning.

Materials and methods:

Species data: We used species occurrence data from Li et al. (3), who delineated urban centers using the Global Human Settlement Layer (39). Urban centers were defined as contiguous 1 km² grid cells with ≥1,500 inhabitants per km² or >50% built-up cover, forming clusters of at least 50,000 inhabitants with smoothed boundaries. For the 11,621 global urban centers identified, Li et al. (3) assembled plant records from three primary sources: (1) the Global Urban Biological Invasions Consortium (GUBIC), including contributed datasets, Dryad archives, and published literature; (2) the Urban Biodiversity Research Coordination Network (UrBioNet; ref. 27); and (3) the Global Biodiversity Information Facility. After data cleaning and quality control, our dataset comprised 66,362 plant species across 553 urban centers. Species names were standardized using the World Checklist of Vascular Plants via rWCVP package (40). We used GloNAF (Global Naturalized Alien Flora; ref. 41) to classify each species as native or non-native within the region of the urban center in which it was recorded.

City-to-city similarity and the role of non-native species: To quantify the contribution of non-native species to floristic homogenization, we calculated pairwise taxonomic similarity between cities *i* and *j* using the Jaccard index based on species occurrence:

$$S_{i,j} = \frac{|SP_i \cap SP_j|}{|SP_i \cup SP_j|}$$

where SP_i and SP_j represent species composition in city *i* and *j*, respectively, $SP_i \cap SP_j$ represents the number of shared species, and $SP_i \cup SP_j$ represents the total number of species present in either city. For each pair of cities, we computed $S_{i,j}$ for three assemblages: (1) native species

only, (2) non-native species only, and (3) the total species (natives + non-natives). Comparing similarity matrices obtained from (1) and (3) provides a direct assessment of how non-native species alter city-to-city floristic similarity.

For each city, we calculated its mean pairwise similarity to all other cities separately for the native-only and total species assemblages, yielding one city-level mean similarity value per city for each assemblage. Aggregating to the city level, rather than treating each pairwise comparison as an independent data point, avoids pseudoreplication, since similarity values involving the same city are not statistically independent. We then compared native-only versus total city-level mean similarity using a paired Wilcoxon signed-rank test. This procedure was repeated separately for three subsets of city pairs: (1) all pairs, (2) intracontinental pairs only, and (3) intercontinental pairs only.

Although Li et al. (3) filtered out cities with estimated richness completeness below 90%, variations in sampling effort across the remaining urban areas could still bias pairwise similarity metrics. To ensure robustness against unequal sampling intensity, we conducted a sensitivity resampling analysis. Specifically, we randomly selected 5,000 city pairs and standardized sampling effort within each pair by rarefying the occurrence records of the more heavily sampled city to match the less-sampled city (100 repetitions). We then recalculated pairwise floristic similarity based on these rarefied datasets. The resampled similarity values were highly correlated with those obtained from the full dataset (Pearson's $r = 0.98$), indicating that unequal sampling intensity had negligible effects on our global estimates of urban floristic similarity (Appendix S1).

Drivers of floristic similarity: We used regression models to identify drivers of city-pairwise floristic similarity. Following Potgieter et al. (1), we quantified city-pairwise distance across

four variable groups (biogeography and climate, physical properties, socio-economic conditions, and city connectivity) to identify drivers of urban floristic similarity.

Biogeography and climate: We calculated geographic distance (GD) as the Great-Circle distance (km) between city centers (geometric centroids) for each city pair. For climate, we extracted five variables for each city from WorldClim (42) and Copernicus Digital Elevation Model (DEM) (43): mean annual temperature, temperature seasonality, mean annual precipitation, precipitation seasonality, and mean elevation. To reduce dimensionality and collinearity, we standardized all variables (mean = 0, SD = 1) and performed a principal component analysis (PCA) and retained the first three axes, which explained 83% of the total variance. Climate distance (CD) was then calculated as the Euclidean distance within this reduced climate PCA space.

City physical properties: We quantified a series of urban physical environment variables extracted from the GHS Urban Center Database (43, 44): city total area (km^2), road length (m), road density (m/m^2), built-up surface area (m^2), built-up volume (m^3), built-up area per capita (m^2/person), built-up mean height (m), greenness, and proportion of built-up area (%), proportion of vegetation (%, including forests, shrubland and grassland). We also performed a PCA on these physical attributes and retained the first three axes, which explained 73% of the total variance. Physical property distance (PD) was calculated as the Euclidean distance in this reduced PCA space.

Socio-economic distance (SD): We compiled six socio-economic attributes for each city: total gross domestic product (GDP, purchasing power parity), GDP per capita, human development index (HDI), human population size, population compound growth rate, and population growth rate (43). To reduce collinearity, we performed a PCA and retained the first

three axes, which explained 68% of the total variance. Socio-economic distance between city pairs was then quantified as the Euclidean distance in this reduced socio-economic PCA space.

City connectivity (CC): We quantified connectivity between cities using global air-transport data obtained from FlightConnections (45), which reports the number of scheduled flights between airports. We used flight frequency because air travel is the only transport mode providing consistent, worldwide coverage, whereas road, railway, and shipping networks lack comparable global resolution. We created a 100 km buffer around each city centroid and assigned any airports whose location falls within that buffer, so that a city's flight pairs were based on all nearby airports. Then we built a city-level flight network by summing the number of flights across all airport pairs connecting the same pair of cities. In this network, cities represent nodes and flight connections represent links. To account for both direct flights and routes involving transfers, we calculated the shortest travel path between all pairs of cities. Shortest-path calculations require a measure of travel "cost", where smaller values indicate easier movement. Specifically, for each city pair i and j, we defined travel cost as

$$\text{Cost}_{ij} = \frac{1}{log(1+f_{ij})}$$

where f_{ij} is the number of flights per month between cities i and j. This formulation assigns lower costs to city pairs connected by more frequent flights, while the log transformation reduces the influence of extremely high-traffic routes. The shortest-path distance (d_{ij}) between two cities thus represents the minimum cumulative travel cost required to move between them through the global flight network, accounting for both direct flights and routes involving transfers (using the distance function in the igraph R package; ref. 46). We then converted this distance into a measure of city connectivity by taking its inverse: $CC_{ij} = 1/d_{ij}$ (Appendix S2, Supporting information).

All variables for city physical and socio-economic attributes were extracted from the GHS Urban Center Database 2024A (43). Physical property distance, socio-economic distance, and climate distance were all quantified as Euclidean distances in the reduced PCA space (the first three axes kept for each group). After matching across datasets, 537 cities with complete data remained for the regression analyses. All continuous predictors were standardized to a mean of 0 and a standard deviation of 1 to ensure the comparability of effect sizes.

Statistical analysis: We modelled city-to-city floristic similarity using generalized linear mixed models with a beta distribution (since Jaccard similarity ranges from 0 to 1). As beta distribution does not allow zero values, we added 0.001 to all similarity values to accommodate exact zeros. For each similarity group — native species (S_{native}), non-native species ($S_{non\text{-}native}$), and total species (S_{total}), we fitted separate models including geographical distance (GD), physical property distance (PD), socio-economic distance (SD), climate distance (CD), and city connectivity (CC) as fixed effects. The predictors show low inter-correlation (Pearson's $r < 0.5$), minimizing concerns about multicollinearity. To account for non-independence arising from the repeated use of the same cities across multiple city pairs, we included random intercepts for both cities involved in each pair:

$$S_{ij} \sim \text{Beta}\ (\mu_{ij}, \phi)$$

$$\text{logit}(\mu_{ij}) = \beta_0 + \beta_1 GD_{ij} + \beta_2 PD_{ij} + \beta_3 SD_{ij} + \beta_4 CD_{ij} + \beta_5 CC_{ij} + u_i + v_j$$

$$u_i \sim \text{N}\ (0, \sigma^2),\ v_j \sim \text{N}\ (0,\sigma^2)$$

where S_{ij} is the Jaccard similarity between cities i and j; μ_{ij} is the expected similarity; ϕ is the precision parameter of the beta distribution; β_0 is the intercept; u_i and v_j are random intercepts for city i and city j, respectively. By including u_i and v_j, we control for the non-independence among city pairs that share a common city. Models were fitted by the '*glmmTMB*' *package* in R (47).

Continental asymmetry: To characterize spatial variations in urban floristic homogenization, we examined how similarity varied across six continents: Europe (EU; 360 cities in our analyses), North America (NA; 84), Asia (AS; 57), Oceania (OC; 19), South America (SA; 18) and Africa (AF; 15). For each continent, we quantified intra-continental similarity, defined as the pairwise Jaccard similarity between all city pairs within the same continent. We then calculated inter-continental similarity, defined as the similarity between city pairs belonging to different continents, considering all pairwise combinations of the six continents. For each intra- and inter-continental combination, we computed similarity for both native species (S_{native}) and total species (S_{total}). Comparing these two metrics revealed how much of the observed continental pattern was driven by non-native species establishment versus shared native biogeographic history.

Disentangling the different components of similarity: To better understand the mechanisms driving pairwise floristic similarity, we decomposed the Jaccard similarity index into distinct ecological components. Let:

- A_{ij}: the number of shared non-native species between the two cities ("shared non-natives");
- E_{ij}: the number of species that are non-native to one city but native to the other ("species transfer");
- N_{ij}: the number of shared native species ("shared natives");
- U_i and U_j: the number of unique species (native or non-native) occurring exclusively in city *i* or *j*, respectively.

Thus, the overall Jaccard similarity can be expressed as:

$$S_{ij} = \frac{A_{ij} + E_{ij} + N_{ij}}{A_{ij} + E_{ij} + N_{ij} + U_i + U_j}$$

This formulation quantifies each component's relative contribution to the shared-species pool. For the shared species of any city pair (*i, j*), we calculated (1) the contribution (%) of shared non-natives ($A_{ij} / A_{ij} + E_{ij} + N_{ij}$), (2) the contribution (%) of species transfers ($E_{ij} / A_{ij} + E_{ij} + N_{ij}$), and (3) the contribution (%) of shared native species ($N_{ij} / A_{ij} + E_{ij} + N_{ij}$). These partitions quantify each component's contribution to overall floristic similarity for each city pair.

Because inter-continental floristic similarity is driven primarily by non-native species, we further examined the relative contributions of shared non-natives and species transfers to inter-continental similarity for each continental pair. For each inter-continental pair, we calculated the mean contributions of A_{ij} (shared non-natives) and E_{ij} (species transfers) across all city pairs. This determines whether inter-continental homogenization is driven by widely shared non-native species or by asymmetric species transfers between cities.

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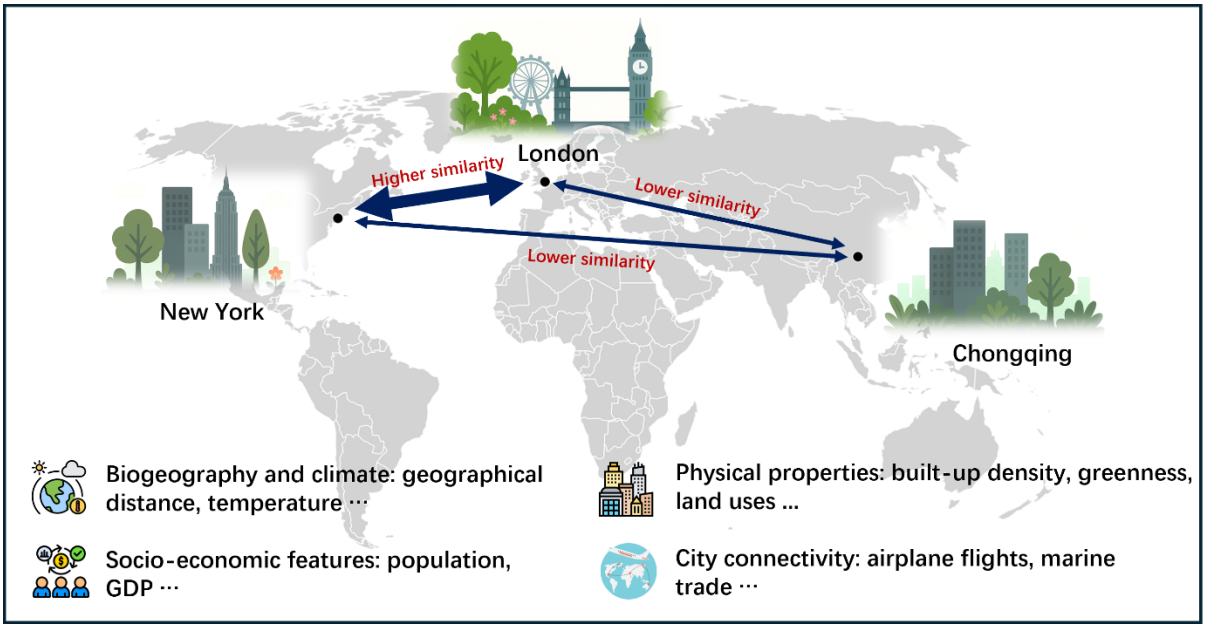

Figure 1. Conceptual illustration of the factors influencing similarity among urban floras contributed by non-native species. London (UK) and New York (USA) are expected to show higher floristic similarity through both species transfers and shared non-native species because they overlap across multiple drivers: similar economic status that promotes comparable species introductions, strong global connectivity (frequent air and trade routes), broadly similar temperate climates, comparable built-up structure (city physical feature) providing similar habitat patches, and a historical colonial connection. In contrast, Chongqing (China) shares few of these features, lacks colonial ties, possesses a different socio-economic status and built-up structure, has received fewer non-native introductions, and experiences a distinct subtropical climate. As a result, the floristic similarity of Chongqing with London or New York is expected to be substantially lower. That said, city climate, connectivity, socio-economic status, physical features, geographical distance and colonial history all could influence floristic similarity.

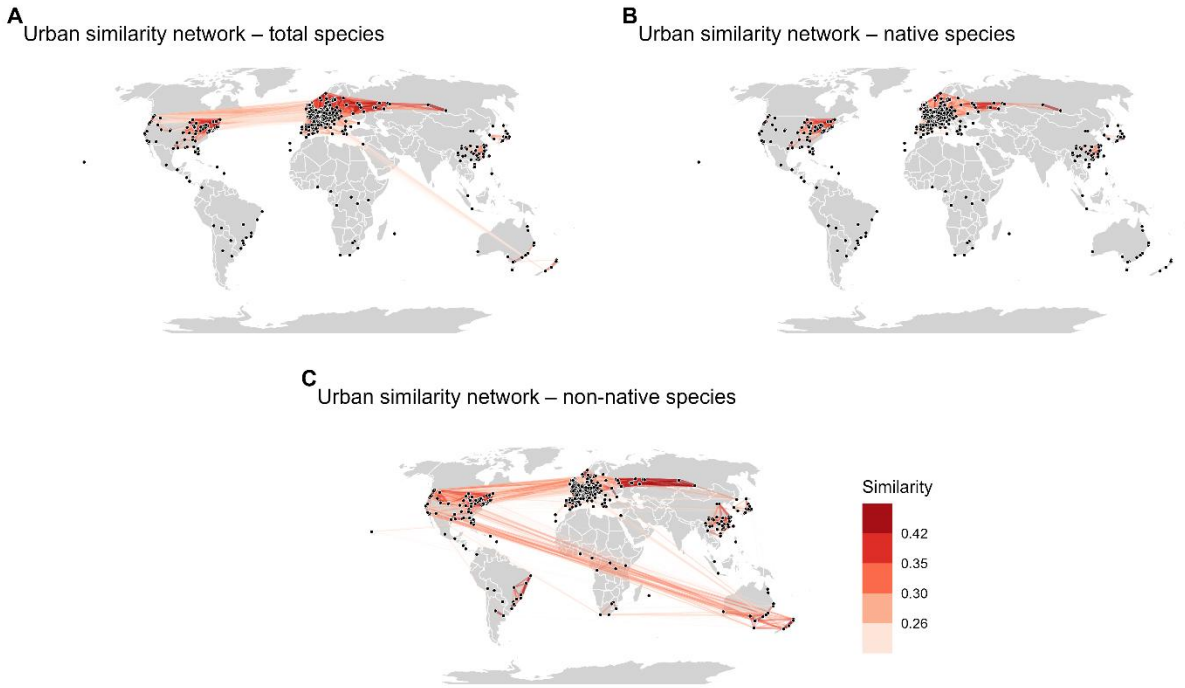

Figure 2. Pairwise Jaccard similarity among global cities for total species (natives and non-natives combined, A), native species only (B) and, non-native species only (C). In the maps, link color indicates the strength of floristic similarity; for visual clarity, only links exceeding the 70th percentile of total-species similarity (≥ 0.22) are shown. Color is binned into five quantile classes (20th, 40th, 60th and 80th percentiles of similarity), pooled across all three panels.

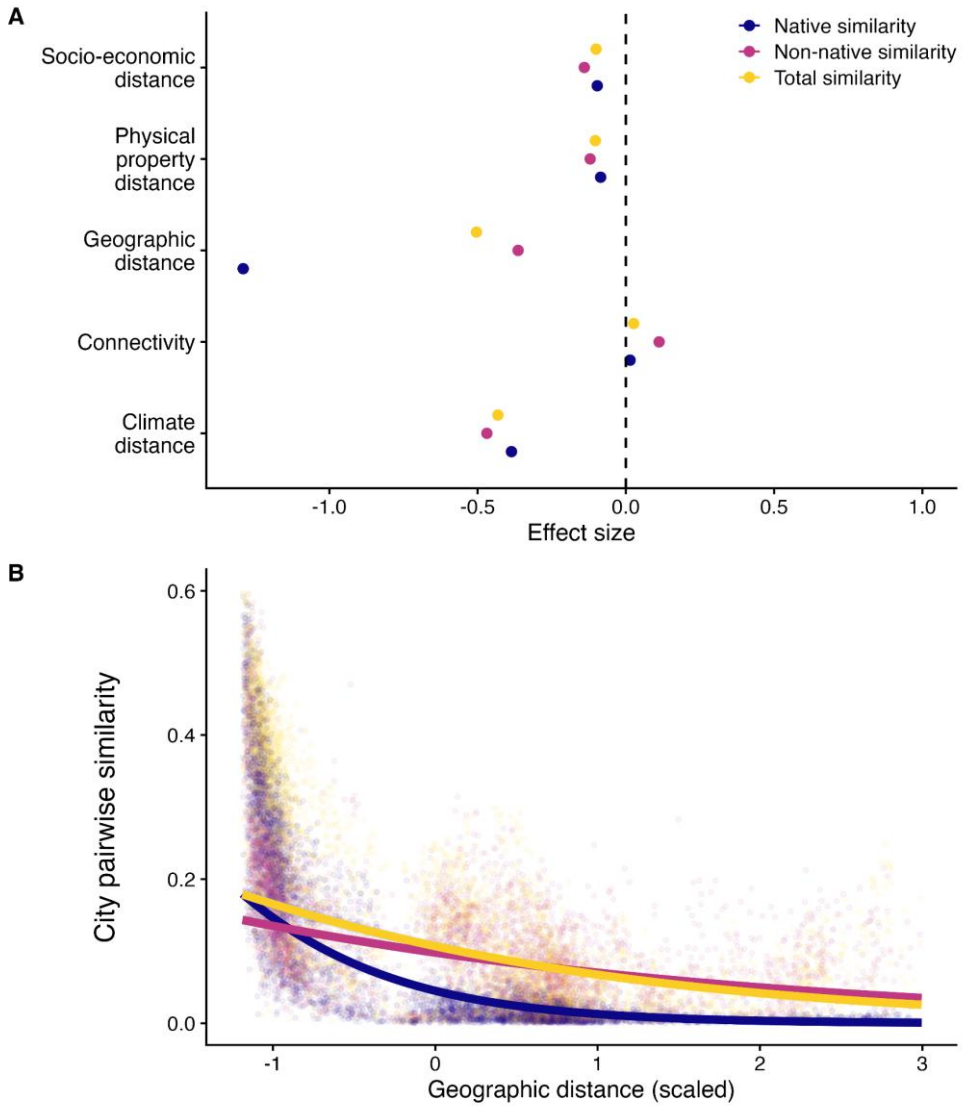

Figure 3. Effect sizes (slope ± 95% confidence intervals, small intervals because of the large sample size) from generalized linear mixed models examining predictors of floristic similarity among global cities (A). Models were fitted separately for total similarity, native-only similarity, and non-native-only similarity. Panel (B) presents the corresponding response curves illustrating the relationships between geographic distance (scaled) and predicted floristic similarity (distance decay).

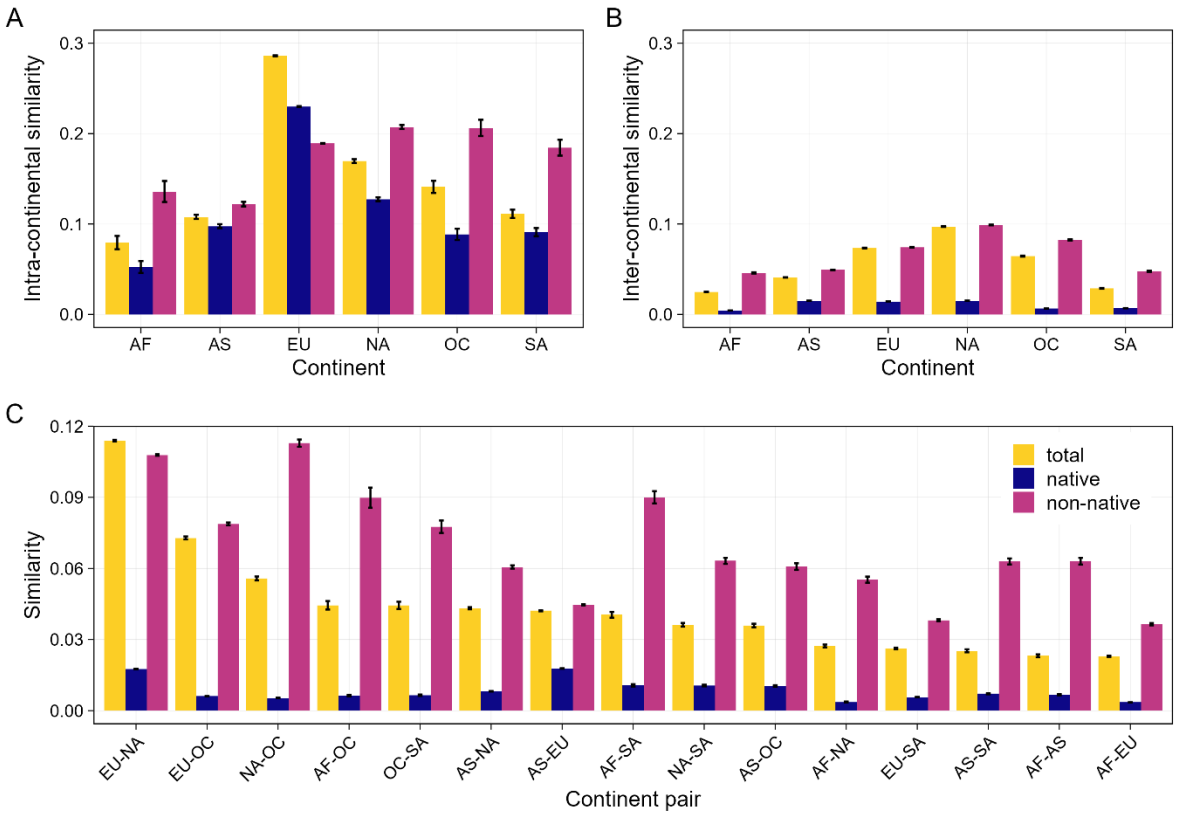

Figure 4. Changes in city–city floristic similarity attributable to non-native plants. Panels (A) and (B) show mean intra-continental and inter-continental pairwise (city-city) similarity, while panel (C) presents similarity for specific continent pairs. "Native" refers to similarity based solely on native species, "non-native" refers to similarity based solely on non-native species, and "total" refers to similarity including both native and non-native species. Error bars represent standard errors. Continent abbreviations: AF = Africa, AS = Asia, EU = Europe, NA = North America, OC = Oceania, SA = South America.

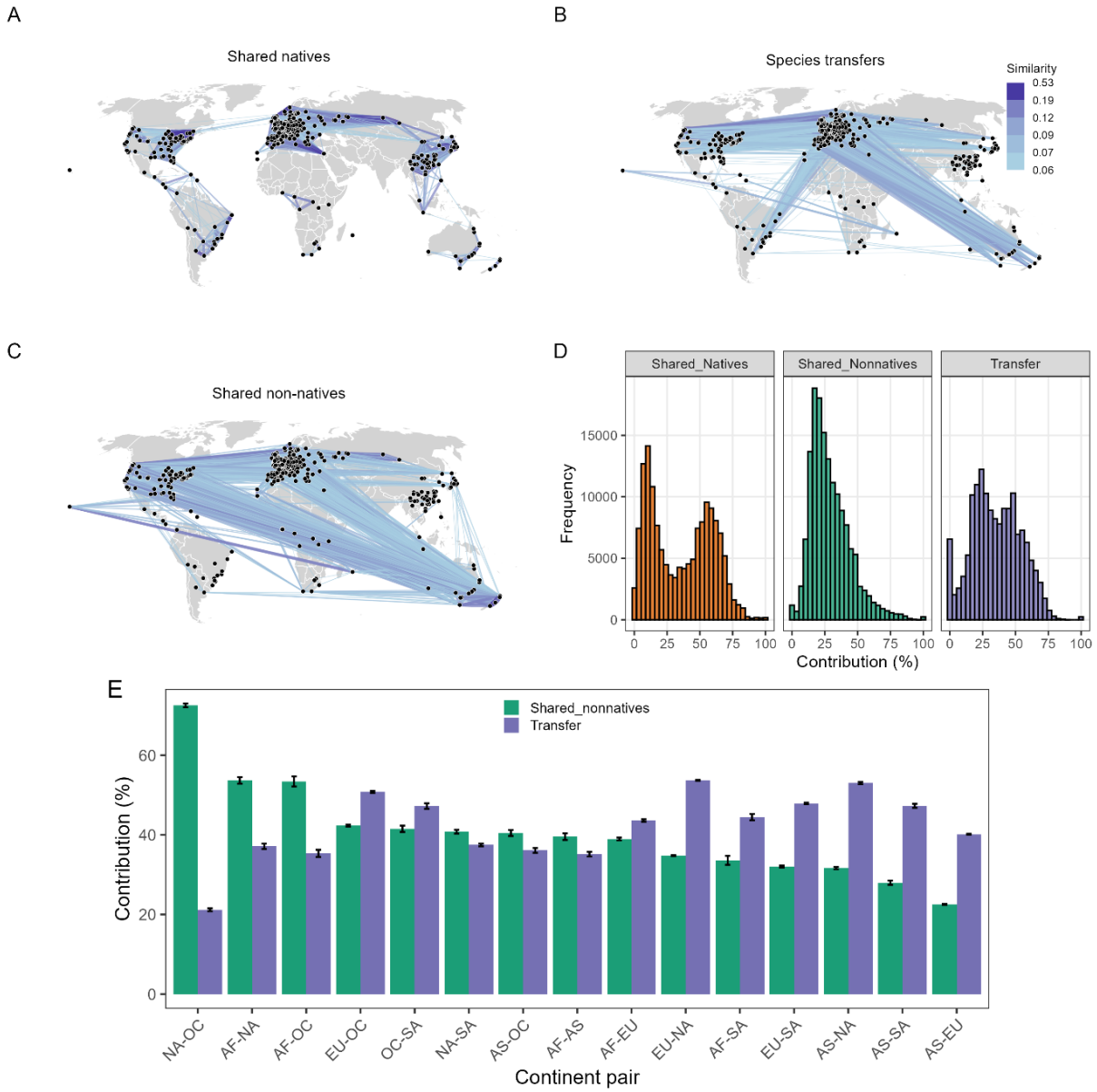

Figure 5. City-level decomposition of floristic similarity into (A) shared native species, (B) species transfers (species native in one city but non-native in another), and (C) shared non-native species. (D) Frequency distributions of the percentage contribution of each component to total similarity. (E) The contributions of species transfers and shared non-natives to inter-continental similarity. For visual clarity in the similarity networks, we applied a threshold corresponding to the 70th percentile of all similarity values (0.062) and retained only links above this value. Color is binned into five quantile classes (20th, 40th, 60th and 80th percentiles of similarity), pooled across all three panels. Error bars indicate standard errors. Continent abbreviations: AS = Asia, AF = Africa, EU = Europe, NA = North America, OC = Oceania, SA = South America.

Supplementary Material

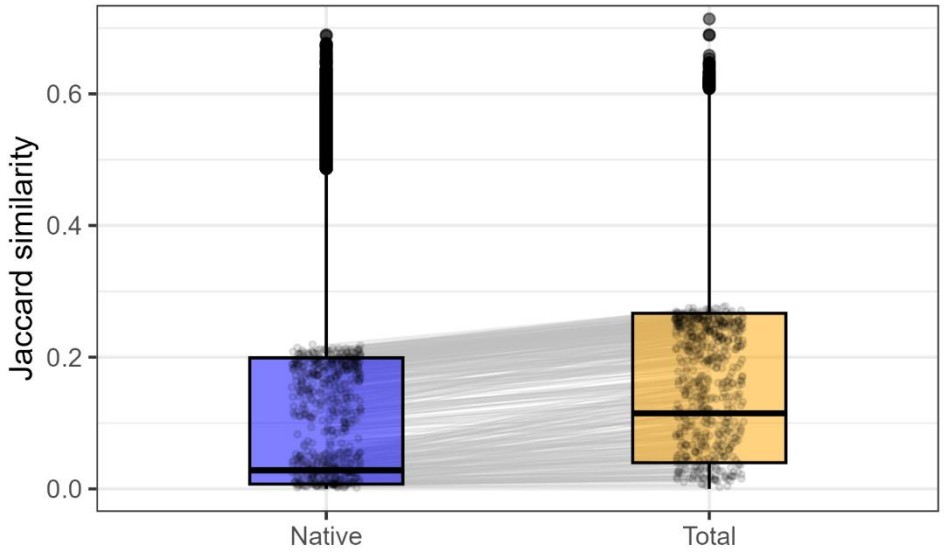

Figure S1. Effect of non-native species on inter-city floristic similarity. Boxplots show the distribution of pairwise Jaccard similarity in species composition between cities, calculated separately from native-only and total species assemblages. Grey lines connect each city's mean similarity (averaged across all its pairwise comparisons) between the two assemblage types; grey points show these city-level means, jittered horizontally to reduce overplotting.

Appendix S1 Sampling effects on measuring pairwise urban similarity

To assess whether unequal sampling intensity among cities biased estimates of floristic similarity, we conducted a rarefaction-based resampling analysis. We randomly selected 5,000 city pairs and standardized sampling effort within each pair by rarefying the city with more occurrence records to the same number of records as the less-sampled city. For each pair, species records were randomly resampled 100 times without replacement, converted to presence–absence data, and Jaccard similarity was recalculated. We then compared these rarefied similarity estimates with the original values calculated from the full dataset. The rarefied and original similarities were highly consistent and strongly correlated (Pearson's Correlation = 0.98; Figure S2), indicating that unequal sampling intensity among cities had little influence on our estimates of floristic similarity.

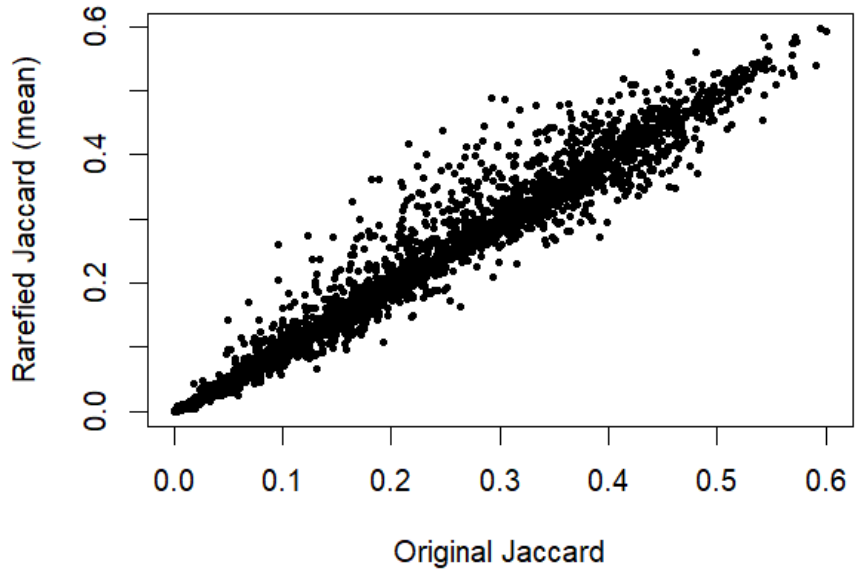

Figure S2. Comparison between original Jaccard similarity values and rarefied Jaccard similarity values from the resampling analysis. For 5,000 randomly selected city pairs, sampling effort was standardized by rarefying the city with more occurrence records to match the number of records in the less-sampled city. Rarefied similarity values represent the mean of 100 resampling iterations per city pair.

Appendix S2 City pairwise connectivity quantified by flight frequency

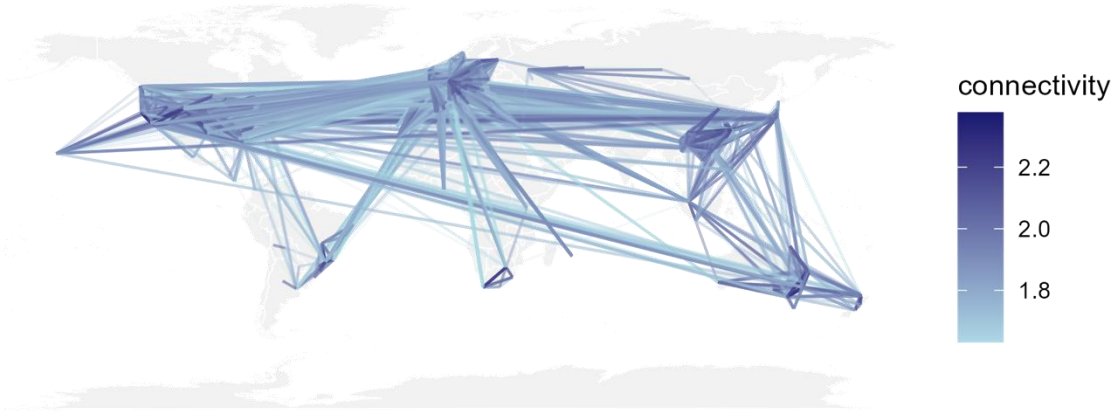

Figure S3. Global connectivity among cities inferred from the air-transport network. Lines represent the strength of city-to-city connectivity derived from weighted shortest-path analyses of the global flight network. Only the strongest connectivity (top 20%) is shown for visualization clarity.