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Grain trade between China and the United States shapes the spatial genetic pattern of common ragweed populations in East China cities

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Abstract

Common ragweed (*Ambrosia artemisiifolia* L.) is an invasive alien species (IAS) that can cause severe allergies among urban residents. Understanding its invasion pathways is critical for designing effective control programs. However, studies on the invasion of common ragweed normally skip urban areas. Results from a few studies based on analyzing occurrence records contain high uncertainties. We attempted to address this knowledge gap through a case study in East China cities by combining the population genetic method with the occurrence records. We first collected leaf samples of 37 common ragweed populations from 15 cities. We then quantified the spatial genetic pattern of common ragweed populations by analyzing genomic and chloroplast DNA extracted from the leaf samples. Combined with the analysis of occurrence data and trade data, we discovered that multiple introductions have impacted the spatial genetic pattern of common ragweed populations in East China Cities. We inferred that the modern-day grain trade between the United States and China could be the primary invasion source while the bridgehead introduction passage through Japan played a minor role. Among the studied cities, Nanjing and Shenyang dispersed more gene flows than other cities. The two cities' central roles in transportation and grain importation might explain the observed pattern. Based on our findings, we suggest that invasive species control programs should consider the potential role of cities as landing points and dispersal hubs of common ragweed in invaded countries.

Keywords: Invasion source, common ragweed, urban population, grain trade, genetic pattern

Introduction

Common ragweed (*Ambrosia artemisiifolia*) is native to North America but is now an important invasive alien species (IAS) species in all continents except Antarctica¹. Besides causing significant loss in agricultural production, common ragweed pollen is a primary allergen for seasonal allergic rhinitis and asthma, which result in substantial health costs and labor losses^{1,2}. The negative health impact of common ragweed pollens is worsened in urban areas because the production of pollens and allergenicity of pollens are both enhanced in urban environments^{3,4}. Therefore, control of the common ragweed has been given a high priority in many cities worldwide⁵.

Cities need information on the invasion pathway of common ragweed in order to control it more effectively. So far, this information was primarily inferred from occurrence records. For example, researchers found common ragweed populations in the urban area of Magdeburg, Germany and speculated that common ragweed was introduced through the seed trade⁶. Based on the occurrence data, a study found that communication lines played a vital role in the dispersion of common ragweed in urban areas of Croatia⁶. While those inferences are helpful, they also contain notable limitations. The study in Magdeburg could not further trace the source of common ragweed to countries exporting the contaminated seeds⁶. It is difficult to determine the real dispersion hub of common ragweed in urban areas of Croatia⁷.

Some typical features of occurrence records contributed to the limitations in the above studies. First, like many other IAS, data quality and availability of occurrence records of common ragweed are often not adequate^{8,9}. The quality and availability of occurrence data of IAS in cities is particularly uneven^{9,10}. Records with spatial and temporal errors may lead to incomplete or even wrong interpretation of the invasion pathway of an invasive plant species. Second, interpretation of the occurrence data is challenging even when the data quality is not an issue. The spatial distribution of a species is not always a good representation of its dispersal pathway. For instance, plant populations with distinct ancestors in a city may be incorrectly judged as close relatives due to their spatial proximity¹¹.

Population genetic methods provide a way to address the above limitations. The phylogenetic relationship among populations of IAS can be reconstructed using various genetic methods to

interpret the invasion pathway. For example, genetic diversity showed that the populations of wild sunflower (*Helianthus annuus* L.) in Argentina were first introduced to Buenos Aires and then spread to Mendoza ¹². The population structure of Slender false brome (*Brachypodium sylvaticum* (Huds.) P. Beauv.) in Corvallis, the United States, showed that the species was introduced from multiple locations in Europe ¹³. Population genetic methods have already been suggested for tracing the invasion pathways of common ragweed ¹⁴. Studies carried on common ragweed populations in rural areas proved this potential. For instance, the genetic structure of common ragweed populations in Europe, Asia, and South America revealed that multiple introductions formed these populations ^{15,16}. Different genetic clusters of common ragweed in North America served as origins of western and eastern European populations ^{16,17}. However, no study has specially applied the population genetic method to study the invasion pathway of common ragweed in urban areas over large regions as far as we know.

In this study, we intend to disclose the invasion pathways of common ragweed in urban areas by using a combination of the population genetic method and occurrence records. We selected cities in East China as the sites for this case study. China first recorded common ragweed in the 1930s. The common ragweed currently occur in more than 23 provinces, and most of the occurrences were in East China ^{18,19}. East China accounts for 43% of China's land area but nearly 94% of China's population ²⁰. The highly urbanized region contains key port cities for international trade and a well-developed transportation network ²¹. Existing studies have shown that ragweed seed is a common contaminant of seed trade, and international trade has accelerated the introduction of common ragweed ²². Therefore, the region is an ideal place for studying the invasion pathway of common ragweed in urban areas. Specifically, we have the following objectives: (1) to reveal in detail the genetic pattern of common ragweed in East China cities; (2) to identify the source of common ragweed in East China cities; (3) to examine the dispersal of common ragweed among East China cities. Also, we made recommendations on how to control the invasion of common ragweed based on our results.

Results

Genetic patterns of common ragweed populations in East China cities

Six nuclear microsatellite loci have been identified from the leaf samples. The results of exact tests for genotypic disequilibrium showed that none of the microsatellite loci presented significant linkage equilibrium. Also, the estimates of null alleles were highly variable (Supplementary Fig. 1). Therefore, these loci could be used for further analysis. Based on the nuclear microsatellite loci, deviation from Hardy-Weinberg proportions was detected in most common ragweed populations in East China cities (Table 1), which suggested heterozygote deficiency. Bottleneck effects caused by the population size reduction were found in six populations.

Ten cpDNA haplotypes were identified after considering indels and the seven polymorphisms observed within the 802-bp concatenated alignment in chloroplast intergenic spacers. The haplotype diversity (H_D) ranged from 0 to 0.68, and the nucleotide diversity (π) ranged from 0 to 0.00122 (Table 1). common haplotypes (e.g., Hap22 and Hap21) and rare haplotypes (e.g., Hap23, Hap 30, Hap 32 and Hap33) co-existed within populations in coastal cities such as Qingdao, Guangzhou, and Fuzhou (Fig. 1). Populations in inland cities such as Chongqing and Guiyang only had rare haplotypes like Hap 30 and Hap31. Three clades could be identified based on the haplotypes of common ragweed after considering both the rooted Neighbor-joining tree and the median-joining network (Supplementary Fig. 2).

The results from GENELAND and STRUCTURE jointly indicated that the common ragweed populations in East China cities could be classified into seven genetic clusters (Fig. 2). Posterior probability density calculated in GENELAND showed mixing around an apparent plateau at the value $k=7$ (Supplementary Fig. 3). The result from STRUCTURE showed that the highest Delta K value (Delta K= 31) was obtained at $K=5$, followed by $K= 2, 4$, and 3 (Supplementary Fig. 4). The membership of each population was shown in Supplementary Table 1.

The classification of the common ragweed populations into the seven clusters was supported by the moderate within-cluster pairwise F_{ST} values and significant or notable pairwise F_{ST} values among most genetic clusters (Supplementary Fig. 5). The pairwise F_{ST} values between Cluster D

and E were moderate. Nevertheless, the two clusters were separable based on the result of STRUCTURE.

The migration rates estimated by BayesAss, i.e., the fraction of individuals in a population that are migrants derived from another population per generation, indicated that the metapopulations from Nanjing and Shenyang exhibited more current gene flows than the metapopulations from other sampled cities (Fig. 3). The values of *strength* were also much higher at Nanjing and Shenyang than those of the remaining cities. Migration rates between paired cities can be found in Supplementary Table 2.

The similarity of common ragweed populations in East China cities to those in other countries

The common ragweed populations in East China cities were compared to those in North America and two European countries^{23,24}. The result of GENECLASS2 showed that around 80% of individual plants in East China cities were assigned to the modern North American cluster 2. The remaining individuals were assigned to the modern North American cluster 1 (around 10%) and the historical North American cluster (around 5%). No individual was assigned to the French and Italian cluster (Table 2).

The expected heterozygosity (H_E) of the populations in East China cities was not significantly different from these of the modern North American populations ($p=0.716$, $df=81$, $F=0.134$, Supplementary Fig. 6) and the French and Italian populations ($p=0.137$, $df=39$, $F=2.305$, Supplementary Fig. 6). The insignificant difference indicated no reduction of genetic diversity in the populations in East China cities. The inbreeding coefficients (F_{IS}) of the populations in East China cities were significantly lower than that of the modern North American populations ($p=0.027$, $df=81$, $F=5.11$, Supplementary Fig. 6). The low F_{IS} value might suggest that the populations in East China cities had lower levels of inbreeding than that of the modern North American populations.

Patterns inferred from the occurrence records of common ragweed

The occurrence records showed that common ragweed first appeared in the Yangtze River regions and then in other parts of China. About 157 prefecture-level regions in China have reported the

occurrences of common ragweed since 1930 (Fig. 4). Records from 1930 to 1949 were mainly along the Yangtze River. From 1970 to 1989, common ragweed appeared in regions further away from the Yangtze River, northeastern China, and the Taiwan Province.

Following the methods in literature ^{9,25}, Hangzhou (first recorded in 1935), Wuhan (1946), Jiujiang (1948), Nanjing (1958), Qingdao (1964), Mudanjiang (1973), Qinhuangdao (1978), Laibin (1985), and Fuzhou (1991) could be identified as regions that have a high dispersal potential.

Grain trade between the United States and China

The trade data showed that the states in the modern North American cluster 2 exported more grain products to China than those in the modern North American cluster 1 (Table 3). Importation of grains in the 15 cities showed that Nanjing and Qingdao received the most grain products from 2000 to 2006 (Fig. 5).

Discussion

A distinct spatial genetic pattern of common ragweed populations in East China cities

Based on the population genetic data, a distinct spatial genetic pattern of common ragweed populations in East China cities was observable. We identified seven genetic clusters from the urban populations. In a previous study using the microsatellite markers, four genetic clusters were found among rural populations of common ragweed in East China ²⁶. The unique features of cities may explain the different findings between the two studies. Cities are subjected to a longer time of introduction and higher propagule pressure of IAS than natural environments because they are traffic hubs ²⁷. As a result, the sources of IAS populations within cities are more diverse ²⁸. In turn, the spatial genetic pattern in populations between cities could be more complex.

The spatial genetic pattern of the common ragweed populations in East China cities is most likely formed by multiple introductions that occurred independently in different periods. High genetic variability, low mean F_{IS} , and rare bottleneck effects were observed in the populations in East China cities. Also, we found that populations from distant cities (e.g., Mudanjiang,

Qinhuangdao, and Wuhan) were grouped into the same cluster, but contemporary gene flows among them were low. The rare bottleneck effects, high genetic variability, and low mean F_{IS} were impossible to observe from a single introduction¹⁵. At least two independent introductions are required to form a genetic cluster that includes distinct populations with rare pairwise gene flows²⁹. The hypothesis of multiple introductions in different times was also supported by the fact that the source of the populations in East China cities could be traced to both the historical and modern North American clusters. Occurrence records also supported this hypothesis. The first landing points identified in different regions were far away from each other and appeared in different decades. Therefore, multiple introductions are a universal mechanism for common ragweed to reach the invaded natural environments^{14,17} and urban areas.

We also found that introductions occurred more frequently in coastal areas than in inland areas. The co-existence of the common and rare haplotypes from different clades in coastal cities indicated possible multiple introductions. The sole existence of the rare haplotype in inland cities suggested less frequent introductions. Most areas of East China are suitable habitats for common Ragweed^{30,31}. Higher international trade activities in coastal areas than inland areas might explain this pattern because the trade increases the propagules.

Invasion sources of common ragweed in East China cities

The results of assignment tests suggested that the modern North American cluster 2 was likely the primary source of common ragweed populations in East China cities. The states in modern North American cluster 2 exported far more grain products to China than other states. Studies showed that grain products in the United States retained a large proportion of common ragweed seeds^{32,33}. These findings jointly supported the possibility that grain exportation from the United States to China has introduced common ragweed to East China cities. While economic variables such as grain importation are not directly related to the establishment of IAS, they integrate the effect of variables that directly affect the outcome of invasion, such as propagule pressure and pathways of introduction^{34,35}. Exportation of grain from the United States to China could increase propagule pressure to facilitate invasion of common ragweed in East China cities.

The assignment test results also suggested that the historical North American clusters were minor sources of common ragweed populations in East China cities. Previous studies concluded that the invasion of common ragweed in China might be related to the transportation of grains by the Japanese army which invaded China in the 1930s^{36,37}. Japan first recorded common ragweed in 1877, and the plant became established in the 1930s³⁸. Therefore, combined with the genetic analysis result of our analysis, we could reasonably infer that grain transportation from Japan to China might facilitate the bridgehead introduction of common ragweed from North American to Japan, then to China. Researchers have already identified the bridgehead introduction passage between Europe and Australia¹⁴, and our finding pointed to the existence of another bridgehead introduction passage for common ragweed.

Dispersal of common ragweed populations in East China cities

Our results showed high gene flows from the metapopulations in Nanjing and Shenyang to other cities in East China, which might be partially attributed to the roles of Nanjing and Shenyang in grain importation. Nanjing was ranked the 1st in terms of the weight of imported grains among all studied cities. Shenyang imported more grains than other sampling cities within the genetic cluster. Shenyang is also close to Yingkou, which is a crucial grain importation port historically^{39,40}. Both Nanjing and Shenyang are transportation hubs in China^{41,42}, which might also contribute to their dominance in gene flows. Unlike in rural areas, where common ragweed was introduced by planting contaminated seeds or contaminated forage^{9,43}, common ragweed was primarily introduced into the urban areas through transportation. The bulk of grains imported by China are processed into food in factories⁴⁴. Many opportunities exist for common ragweed seeds to escape into the urban environment in this process. Also, the dispersal of common ragweed between cities is primarily dependent on transportation. While we could not entirely rule out natural dispersal, the chance that natural dispersal serves as the primary dispersal means among cities is low because the natural dispersal distance of common ragweed seed was less than 1 m/year in terrestrial habitats⁴⁵. The short distance of natural dispersal cannot explain the observed gene flows between cities that are hundreds of kilometers away from each other.

Based on the occurrence data collected in rural areas, previous studies listed Wuhan, Nanjing, and Shenyang as regions with a high dispersal potential of common ragweed¹⁹. Our result did not show that Wuhan had a high dispersal potential of common ragweed. Except for the difference in urban and rural environments, two potential reasons might cause the discrepancy. First, Wuhan's dispersal potential may have been significantly reduced due to effective biocontrol programs applied in recent years^{19,46}. Another possibility is the small sample size in Wuhan might reduce the influence of Wuhan's population among all urban populations because we could only locate one urban population from Wuhan. In addition to the cities mentioned above, we inferred that Hangzhou, Jiujiang, Qingdao, Mudanjiang, Qinhuangdao, Laibin, and Fuzhou had high dispersal potentials of common ragweed in China based on the temporal information of occurrence data. Among these cities, we analyzed samples collected from Fuzhou, Qingdao, Mudanjiang, and Qinhuangdao. The genetic analysis results did not corroborate with the inference based on the occurrence records. The discrepancy might due to the subjectivities and uncertainties of occurrence data.

Policy implications and limitations of the study

Findings from this study can contribute to the control of common ragweed in the following aspects: (1) Our results show that urban areas can serve as landing points and dispersal hubs of common ragweed. To control common ragweed requires controlling the dispersal among cities, and urban areas should not be left out of the overall control program. (2) There is plenty of room for improvement in quarantine work at Chinese port cities because the primary source of common ragweed might be from the modern North American clusters. Also, coastal cities have experienced more introduction events than inland cities. Strict inspection and quarantine of grains imported from regions as known sources of common ragweed seeds should be practiced in ports that handle grain importation. Reconnaissance programs should be set up in these cities to monitor the common ragweed populations too. Waste from factories which process imported grains must be treated before final disposal.

While our study contributes a new understanding of the invasion pathway of common ragweed in urban areas, several limitations should be addressed in future studies. First, although

our field campaign covered the East China cities well, more samples from more cities can further reduce the uncertainty in our results. Second, we could only obtain genetic data for North America and two European countries after searching through the major international genetic databases and contacting authors who published papers on common ragweed's genetics. Due to the lack of data, we could not explore the contribution of other potential sources to the genetic diversity of common ragweed populations in East China cities. For example, Australia is also a major exporter of grains to China in recent years ⁴⁷. It may provide a bridgehead introduction passage too.

Conclusion

Knowledge of the invasion pathway of common ragweed in urban areas is crucial for controlling this IAS. However, limited information is available so far because studies have not adequately addressed this topic. In this study, we examined the spatial genetic pattern of common ragweed plants in East China cities. We also explored the possible way played by the grain trade between China and the United States in shaping the genetic pattern. The results indicated that common ragweed in East China cities had experienced multiple introductions. We inferred that the modern-day grain trade between the United States and China could be the primary source of propagule. At the same time, the bridgehead introduction passage through Japan played a minor role. Finally, we identified cities that might serve as dispersal centers by examining the gene flows among the cities and the temporal information in occurrence records. Our findings contribute new knowledge on the invasion pathway of common ragweed in urban areas. Also, the information gained in this study is useful for controlling common ragweed in urban areas of China and other countries. Nevertheless, the entire study should be viewed only as a beginning of efforts to reveal invasion pathways of common ragweed and other IAS in urban areas. More studies combining the strength of observations and population genetic methods are needed to better understand the pathways and driving mechanisms.

Materials and methods

Study area

The study area includes cities in East China, an area east of the famous Hu-line (Supplementary Fig. 7). East China holds most of the Chinese population²⁰ and is the main suitable habitat for common ragweed³¹. To locate the current distribution of common ragweed populations in cities, we referred to the literature^{15,48,49} and consulted local experts. Also, we checked the geographic locations of occurrence records of common ragweed contained in the Chinese Virtual Herbarium (CVH)⁵⁰. Based on the compiled occurrence records, we selected 19 East China cities with reliable records of common ragweed to conduct field surveys and were able to find urban populations of common ragweed in 15 cities.

Data collection

Sampling common ragweed populations in East China Cities

We collected samples from 37 common ragweed populations in the 15 cities between 2017 and 2018 (Supplementary Table 1). Sampled populations were located in urban areas and were at least 3 km from each other. According to varied population size of urban populations, 6 to 19 plants were sampled at least 2 m from each other inside each population. We collected at least five fresh leaves from each sampled plant and stored leaves in sealed plastic bags filled with silica beads for desiccation. We recorded the longitudes and latitudes of sampling sites using a handheld GPS unit (AGM X2, with an accuracy of 10 m) during the field campaign.

DNA extraction, nuclear microsatellite and cpDNA amplifications, and fragment sizing

Genomic DNA was extracted from the leaf samples using the CTAB method^{51,52}. We also obtained genomic DNA of four French and Italian populations and one North American population from Ciappetta et al. (2016). Six microsatellite markers were used to mark genomic DNA of common ragweed populations mentioned above. To ensure compatibility of Chinese, French and Italian, and North American populations, the microsatellite markers used in this research were the same as those used by Martin et al. (2014). Microsatellite primer sequences

were Gen-Bank sequences FJ595149 (Ambart04), FJ5950 (Ambart06), FJ5952 (Ambart17), FJ5953 (Ambart18), FJ595155 (Ambart24) and FJ595156 (Ambart27) (Supplementary Table 3). In-house ROX-labeled size standards were used for genotyping⁵³. GENEMarker version 1.5 was utilized for microsatellite loci fragment analysis and allele calling. Microsatellite loci fragment data of modern and historical North American populations collected from Martin et al. (2014) were re-read for data consistency²³.

We sequenced chloroplast DNA (cpDNA) of the 37 East China populations. The two spacers (atpH–atpF, psbK–psbI) of chloroplast DNA spacer regions in common ragweed were chosen for analysis (Supplementary Table 4). Chloroplast DNA chromatograms of sequenced samples were aligned using MAFFT⁵⁴ and Geneious version 11.0.4 (Biomatters Ltd., Auckland, New Zealand).

To further trace the invasion sources of common ragweed populations in East China cities, we also obtained microsatellite loci fragment data of 45 North American populations and 426 historical herbarium individual plants (Supplementary Table 5) from Martin et al. (2014). The data was collected in the summer of 2009²³.

DNA extraction, amplification, and sequencing of nuclear microsatellite and cpDNA were completed by Bio-ulab company (Beijing, China) (Details of the procedure were included in the supplementary materials).

Data analysis

Genetic patterns of common ragweed populations in East China cities

Tests of genotypic linkage equilibrium and estimation of null allele frequency were performed in GENEPOP 4.7.0⁵⁵. Genetic diversity indices, including the number of different alleles (N_A) and expected heterozygosity (H_E), and inbreeding coefficients (F_{IS}) were estimated in GenAlEx 6.51 and GENEPOP 4.7.0^{55,56} to represent diversity at nuclear microsatellite locus, respectively. Deviations from Hardy-Weinberg equilibrium of sampled populations were assessed using F_{IS} ⁵⁷, and the significance was tested using GENEPOP 4.7.0⁵⁵. The potential bottleneck of sampled populations was detected using BOTTLENECK version 1.2.0.2⁵⁸.

We aligned *atpH*–*atpF*, *psbK*–*psbI* sequence of common ragweed from CBOL Plant working group⁵⁹ with our haplotypes to determine the correctness of our sequence. The number of haplotypes (*h*), haplotype diversity (H_D), and Nucleotide diversity (π) of sampled populations were computed using DnaSP 6⁶⁰. Except for software packages specifically noted, all statistical analyses were carried out using the basic R 4.0.2⁶¹.

The Bayesian clustering algorithms contained in STRUCTURE version 2.3.3⁶² and GENELAND version 4.0.3⁶³ were used to cluster the common ragweed populations based on the nuclear microsatellite and the cpDNA haplotype (details of the parameters were in the supplementary materials). Pairwise population-specific fixation indices (F_{ST}) between sampled populations were calculated based on nuclear microsatellite markers. Pairwise population F_{ST} were calculated in *diveRsity* package⁶⁴.

The geographical distribution of cpDNA haplotype was visualized using ArcGIS desktop version 10.2 (ESRI, Redlands, CA, USA). A rooted Neighbor-joining tree with *Ambrosia trifida* L. as an outgroup was constructed using Geneious version 11.0.4 (Biomatters Ltd., Auckland, New Zealand) with a Tamura-Nei genetic distance model using 1000 replicates. A median-joining network of haplotypes was generated by using NETWORK 10.1⁶⁵. The tree and the network were used to explore the relationships among cpDNA haplotypes.

The gene flows among sampled cities were estimated using BayesAss v3.0.4⁶⁶. A genetic graph was built using the gene flows among sampled cities. R package POPGRAPH⁶⁷ and IGRAPH⁶⁸ were used to construct the graph and calculated graph centrality measures. More details of the analyses can be found in supplementary materials.

Compare the similarity of common ragweed populations in East China cities to those in other countries

Assignment tests based on likelihood estimates were used to identify the source populations of common ragweed populations in East China cities. Each plant was assigned to French and Italian, modern North American, and historical North American populations. The North American samples were grouped by the genetic clusters identified by Martin et al. (2014). The assignment was performed in the GENECLASS2 software⁶⁹. Genetic diversity indices, including H_E and F_{IS} of

French and Italian, and modern North American populations were estimated in GenAlEx 6.51 and GENEPOP 4.7.0^{55,56}, respectively. Analysis of variance (ANOVA) implemented in the stats⁶¹ package were used to test differences among the geographic ranges in H_E and F_{IS} .

To explore the role of the grain trade in the introduction of common ragweed to East China cities, we collected exportation and importation data. Exports of grain products from states in the United States to China from 1999 to 2009 were looked up from Foreign Trade Division, the U. S. Census Bureau. The exports were adjusted by using the Consumer Price Index. Data of grain importation in studied cities were collected from EPS CHINA DATA (<http://microdata.sozdata.com/home.html>).

Collect and interpret occurrence records common ragweed populations in East China cities

We first extracted the list of prefecture-level cities in China from the China statistical yearbook 2017⁷⁰. According to the list, we searched occurrence data of common ragweed from databases such as Global biodiversity information facility, CVH, Plant photo bank of China (<http://ppbc.iplant.cn/>), and the Plant Specimen Database (<http://mnh.scu.edu.cn>) until June 07, 2021. The data was supplemented with survey data, anecdotal descriptions in literature, and images in literature. We removed occurrence records in rural areas. We then generated the temporal and spatial distribution map of common ragweed in mainland China using ArcGIS desktop version 10.2. We inferred a city as a regional first landing point when Common ragweed plants were observed in the city earlier than any other adjacent city. If adjacent cities are supposed to be suitable habitats for common ragweed^{30,31} and the occurrence records were continued in the city at a 20-year scale, we considered the city with a high dispersal potential of common ragweed following the method modified from literature^{9,25}.

Data availability

Microsatellite genotypes, chloroplast haplotype, input files and R codes used in analysis are accessible through Mendeley Data with the identifier DOI:10.17632/x4p8g7t47g.1. Chloroplast intergenic spacer locus sequences that support the findings of this study have been deposited in GenBank with the accession numbers from MZ826750 to MZ826763.

Reference

1. Montagnani, C., Gentili, R., Smith, M., Guarino, M. & Citterio, S. The worldwide spread, success, and impact of ragweed (*Ambrosia* spp.). *Critical Reviews in Plant Sciences* **36**, 139–178 (2017).
2. Zhou, Z. S., Wan, F. H. & Guo, J. Y. Common ragweed *Ambrosia artemisiifolia* L. in *Biological Invasions And Its Management In China* (eds. Wan, F. H., Jiang, M. X. & Zhan, A. B.) 99–109 (Springer Singapore, 2017).
3. Ziska, L. H. *et al.* Cities as harbingers of climate change: common ragweed, urbanization, and public health. *Journal of Allergy and Clinical Immunology* **111**, 290–295 (2003).
4. Ghiani, A., Aina, R., Asero, R., Bellotto, E. & Citterio, S. Ragweed pollen collected along high-traffic roads shows a higher allergenicity than pollen sampled in vegetated areas. *Allergy* **67**, 887–894 (2012).
5. Schaffner, U. *et al.* Biological weed control to relieve millions from *Ambrosia* allergies in Europe. *Nature Communications* **11**, 1745 (2020).
6. Brandes, D. & Nitzsche, J. Biology, introduction, dispersal, and distribution of common ragweed (*Ambrosia artemisiifolia* L.) with special regard to Germany. *Nachrichtenbl. Deut. Pflanzenschutz* **58**, 286–291 (2006).
7. Galzina, N., Barić, K., Ščepanović, M., Goršić, M. & Ostojić, Z. Distribution of invasive weed *Ambrosia artemisiifolia* L. in Croatia. *Agriculturae Conspectus Scientificus* **75**, 75–81 (2010).
8. Mang, T., Essl, F., Mosef, D. & Dullinger, S. Climate warming drives invasion history of *Ambrosia artemisiifolia* in central Europe. *Preslia* **90**, 59–81 (2018).
9. Bullock, J. *et al.* *Assessing and controlling the spread and the effects of common ragweed in Europe*(ENV.B2/ETU/2010/0037). 1–456 (2012).
10. Roy-Dufresne, E. *et al.* Modeling the distribution of a wide-ranging invasive species using the sampling efforts of expert and citizen scientists. *Ecol Evol* **9**, 11053–11063 (2019).
11. Yakub, M. & Tiffin, P. Living in the city: urban environments shape the evolution of a native annual plant. *Global Change Biology* **23**, 2082–2089 (2016).

- 428 12. Hernández, F., Presotto, A., Poverene, M. & Mandel, J. R. Genetic diversity and
429 population structure of wild sunflower (*Helianthus annuus* L.) in Argentina: reconstructing its
430 invasion history. *Journal of Heredity* **110**, 746–759 (2019).
- 431 13. Rosenthal, D. M., Ramakrishnan, A. P. & Cruzan, M. B. Evidence for multiple sources of
432 invasion and intraspecific hybridization in *Brachypodium sylvaticum* (Hudson) Beauv. in North
433 America. *Mol Ecol* **17**, 4657–4669 (2008).
- 434 14. van Boheemen, L. A. *et al.* Multiple introductions, admixture and bridgehead invasion
435 characterize the introduction history of *Ambrosia artemisiifolia* in Europe and Australia. *Mol Ecol*
436 **26**, 5421–5434 (2017).
- 437 15. Gaudeul, M., Giraud, T., Kiss, L. & Shykoff, J. A. Nuclear and chloroplast microsatellites
438 show multiple introductions in the worldwide invasion history of common ragweed, *Ambrosia*
439 *artemisiifolia*. *PLoS ONE* **6**, e17658 (2011).
- 440 16. Gladieux, P. *et al.* Distinct invasion sources of common ragweed (*Ambrosia*
441 *artemisiifolia*) in Eastern and Western Europe. *Biol Invasions* **13**, 933–944 (2011).
- 442 17. Genton, B. J., Shykoff, J. A. & Giraud, T. High genetic diversity in French invasive
443 populations of common ragweed, *Ambrosia artemisiifolia*, as a result of multiple sources of
444 introduction: genetic diversity in invasive common ragweed. *Molecular Ecology* **14**, 4275–4285
445 (2005).
- 446 18. Qin, Z., DiTommaso, A., Wu, R. S. & Huang, H. Y. Potential distribution of two
447 *Ambrosia* species in China under projected climate change. *Weed Res* **54**, 520–531 (2014).
- 448 19. Wang, F. H., Hou, H. M. & Jiang, M. X. *Invasion Biology*. (China Science Publishing &
449 Media Ltd., 2015).
- 450 20. Gao, X. D., Wang, X. X. & Zhu, B. Q. The distribution of Chinese minority populations
451 and its change based on the study of the Hu Huanyong line. *Int. J. Anthropol. Ethnol.* **1**, 2 (2017).
- 452 21. Hu, H. Y. The distribution, regionalization and prospect of China's population. *Acta*
453 *Geographica Sinica* **45**, 139–145 (1990).
- 454 22. Chapman, D. S. *et al.* Modelling the introduction and spread of non-native species:
455 international trade and climate change drive ragweed invasion. *Global Change Biology* **22**, 3067–
456 3079 (2016).

23. Martin, M. D. *et al.* Herbarium specimens reveal a historical shift in phylogeographic structure of common ragweed during native range disturbance. *Mol Ecol* **23**, 1701–1716 (2014).
24. Ciappetta, S. *et al.* Invasion of *Ambrosia artemisiifolia* in Italy: assessment via analysis of genetic variability and herbarium data. *Flora* **223**, 106–113 (2016).
25. Marchioro, C. A. & Krechmer, F. S. Potential global distribution of *Diabrotica* species and the risks for agricultural production: global distribution of *Diabrotica* species. *Pest. Manag. Sci* **74**, 2100–2109 (2018).
26. Li, F. F. *et al.* Patterns of genetic variation reflect multiple introductions and pre-admixture sources of common ragweed (*Ambrosia artemisiifolia*) in China. *Biol Invasions* **21**, 2191–2209 (2019).
27. von der Lippe, M., Bullock, J. M., Kowarik, I., Knopp, T. & Wichmann, M. Human-mediated dispersal of seeds by the airflow of vehicles. *PLoS ONE* **8**, e52733 (2013).
28. Reed, E. M. X., Serr, M. E., Maurer, A. S. & Burford Reiskind, M. O. Gridlock and beltways: the genetic context of urban invasions. *Oecologia* **192**, 615–628 (2020).
29. Hagenblad, J. *et al.* Low genetic diversity despite multiple introductions of the invasive plant species *Impatiens glandulifera* in Europe. *BMC Genet* **16**, 103 (2015).
30. Liu, X. L. *et al.* The current and future potential geographical distribution of common ragweed, *Ambrosia artemisiifolia* in China. *Pak.J.Bot.* **53**, 167–172 (2021).
31. Chen, H., Chen, L. J. & Albright, T. P. Developing habitat-suitability maps of invasive ragweed (*Ambrosia artemisiifolia*.L) in China using GIS and statistical methods. in *GIS for Health And The Environment* (eds. Lai, P. C. & Mak, A. S. H.) 106–121 (Springer Berlin Heidelberg, 2007).
32. Simard, M. J. & Benoit, D. L. Potential pollen and seed production from early- and late-emerging common ragweed in corn and soybean. *Weed Technol.* **26**, 510–516 (2012).
33. Schwartz-Lazaro, L. M. *et al.* Seed-shattering phenology at soybean harvest of economically important weeds in multiple regions of the United States. Part 1: broadleaf species. *Weed Sci* **69**, 95–103 (2021).
34. Lockwood, J. L., Cassey, P. & Blackburn, T. The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution* **20**, 223–228 (2005).

- 486 35. Pysek, P. *et al.* Disentangling the role of environmental and human pressures on
 487 biological invasions across Europe. *Proc Natl Acad Sci USA* **107**, 12157–12162 (2010).
- 488 36. Dong, W. D. Distribution and characteristics of common ragweed in Jiangxi. *Acta*
 489 *Agriculture Universitatis Jiangxiensis* **3**, 49–56 (1989).
- 490 37. Huang, B. H. Investigation on distribution and harm of common ragweed in China. *Plant*
 491 *Quarantine* **1**, 62–65 (1985).
- 492 38. National Institute for Environmental Studies. Invasive Species of Japan.
 493 <https://www.nies.go.jp/biodiversity/invasive/DB/detail/80400e.html> (2021).
- 494 39. Chi, Q. F. A study on the trade network of soybean in northeast China region in modern
 495 times(1861-1931). (Hebei University, 2013).
- 496 40. Zhang, X. Modern northeast grain trade. (Harbin Normal University, 2014).
- 497 41. Wu, L. Y. Shenyang's position and function in northeast Asia. *Northeast Asia Forum* **4**,
 498 68–69 (1994).
- 499 42. Yang, T. & Yang, S. F. Strengthen the status of Nanjing as a transport center, accelerate
 500 the growth of the metropolis of Nanjing. *Modern Urban Studies* **1**, 28–33 (2002).
- 501 43. Smith, M., Cecchi, L., Skjth, C. A., Karrer, G. & Šikoparija, B. Common ragweed: a
 502 threat to environmental health in Europe. *Environ Int* **61**, 115–126 (2013).
- 503 44. Xie, Z. Y., Wang, R. Y. & Sun, R. Industrial cluster development of grain and oil.
 504 *Cereals and Oils Processing* **7**, 14–21 (2015).
- 505 45. Lemke, A., Kowarik, I. & von der Lippe, M. How traffic facilitates population expansion
 506 of invasive species along roads: the case of common ragweed in Germany. *Journal of Applied*
 507 *Ecology* **56**, 413–422 (2018).
- 508 46. Zhou, Z. S., Guo, J. Y. & Wan, F. H. Review on management of *Ambrosia artemisiifolia*
 509 using natural enemy insects. *Chinese Journal of Biological Control* **31**, 657–665 (2015).
- 510 47. Li, L. & Mu, Y. Y. Research on China-Australia grain trade based on CMS model.
 511 *International Economics and Trade Research* **31**, 20–30 (2015).
- 512 48. Huang, J. X. *et al.* Genetic divergence of populations of *Ambrosia artemisiifolia* L. in
 513 Guangdong. *Guangdong Agricultural Science* **3**, 135–138 (2012).

- 514 49. Wang, F. H., Wang, R. & Qiu, S. B. Control method of severe invasive weed common
515 ragweed. *40 th Anniversary of Peking Insect Association* 155–156 (1990).
- 516 50. Institute of Botany, The Chinese Academy of Sciences. The Chinese Virtual Herbarium.
517 <https://www.cvh.ac.cn/index.php> (2017).
- 518 51. Lee, S. B., Milgroom, M. G. & Taylor, J. W. A rapid, high yield mini-prep method for
519 isolation of total genomic DNA from fungi. *Fungal Genetics Reports* **35**, 23 (1988).
- 520 52. Zhang, Y. J., Zhang, S., Liu, X. Z., Wen, H. A. & Wang, M. A simple method of genomic
521 DNA extraction suitable for analysis of bulk fungal strains: fungal DNA isolation by thermolysis.
522 *Letters in Applied Microbiology* **51**, 114–118 (2010).
- 523 53. DeWoody, J. A. *et al.* Universal method for producing ROX-labeled size standards
524 suitable for automated genotyping. *BioTechniques* **37**, 348–352 (2004).
- 525 54. Katoh, K. & Toh, H. Parallelization of the MAFFT multiple sequence alignment program.
526 *Bioinformatics* **26**, 1899–1900 (2010).
- 527 55. Rousset, F. GENEPOP'007: a complete re-implementation of the genepop software for
528 Windows and Linux. *Molecular Ecology Resources* **8**, 103–106 (2008).
- 529 56. Peakall, R. & Smouse, P. E. GenAlEx 6.5: genetic analysis in Excel. Population genetic
530 software for teaching and research-an update. *Bioinformatics* **28**, 2537–2539 (2012).
- 531 57. Weir, B. S. & Cockerham, C. C. Estimating F-statistics for the analysis of population
532 structure. *Evolution* **38**, 1358–1370 (1984).
- 533 58. Cornuet, J. M. & Luikart, G. Description and power analysis of two tests for detecting
534 recent population bottlenecks from allele frequency data. *Genetics* **144**, 2001–2014 (1996).
- 535 59. Hollingsworth, P. M. *et al.* A DNA barcode for land plants. *Proc Natl Acad Sci USA* **106**,
536 12794–12797 (2009).
- 537 60. Rozas, J. *et al.* DnaSP 6: DNA sequence polymorphism analysis of large data sets. *Mol*
538 *Biol Evol* **34**, 3299–3302 (2017).
- 539 61. R Core Team. *R: A Language and Environment for Statistical Computing*. (R Foundation
540 for Statistical Computing, 2018).
- 541 62. Pritchard, J. K., Stephens, M. & Donnelly, P. Inference of population structure using
542 multilocus genotype data. *Genetics* **155**, 945–959 (2000).

63. Guillot, G., Estoup, A., Mortier, F. & Cosson, J. F. A spatial statistical model for landscape genetics. *Genetics* **170**, 1261–1280 (2005).
64. Keenan, K., McGinnity, P., Cross, T. F., Crozier, W. W. & Prodöhl, P. A. diveRsity : an R package for the estimation and exploration of population genetics parameters and their associated errors. *Methods Ecol Evol* **4**, 782–788 (2013).
65. Bandelt, H., Forster, P. & Röhl, A. Median-joining networks for inferring intraspecific phylogenies. *Mol Biol Evol* **16**, 37–48 (1999).
66. Wilson, G. A. & Rannala, B. Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* **163**, 1177–1191 (2003).
67. Dyer, R. J. GeneticStudio: a suite of programs for spatial analysis of genetic-marker data. *Molecular Ecology Resources* **9**, 110–113 (2009).
68. Csardi, G. & Nepusz, T. The igraph software package for complex network research. (2006).
69. Piry, S. *et al.* GENECLASS2: a software for genetic assignment and first-generation migrant detection. *Journal of Heredity* **95**, 536–539 (2004).
70. National Bureau of Statistics. *China Statistical Yearbook*. (China Statistics Press, 2017).

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Author contributions

S.L conceived the research idea, designed and conducted field surveys, analyzed data and wrote the manuscript. X.L conducted field surveys, interpreted the results and designed figures. H.W interpreted the results, and revised the manuscript. R.G. and S.C. provided the DNA materials of

569 common ragweed in Europe and revised the manuscript. J.Y. and J.J. conducted field surveys,
570 analyzed data and interpreted the results. J.L. provided information about grain trade and
571 importation between China and USA. J.Y. concepted the research idea, secured the funding,
572 designed field surveys, interpreted the results, and revised the manuscript.

573 **Competing Interests statement**

574 The authors declare no competing interests.

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Fig. 1 Geographical patterns of cpDNA haplotypes in East China cities. **a** Study area. **b** Geographical patterns, color proportions of pie indicated the frequency of each cpDNA haplotype in the population. Abbreviations: Mudanjiang (MDJ), Changchun (CC), Shenyang (SY), Fushun (FS), Qinhuangdao (QHD), Beijing (BJ), Qingdao (QD), Shanghai (SH), Nanjing (NJ), Wuhan (WH), Changsha (CS), Fuzhou (FZ), Guangzhou (GZ), Chongqing (CQ), Guiyang (GY). Numbers are ids of the populations collected in the city.

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587 Fig. 2. Genetic clusters of the populations of common ragweed in East China cities inferred using relative probabilities of
 588 assignment to genetic clusters in STRUCTURE. Bar heights represent the relative probability of assignment of individual plants
 589 to varying numbers of genetic clusters. Genetic clusters identified by GENELAND were indicated by letters. Abbreviations are
 590 names of sampled cities and populations: Mudanjiang (MDJ), Changchun (CC), Shenyang (SY), Fushun (FS), Qinhuangdao
 591 (QHD), Beijing (BJ), Qingdao (QD), Shanghai (SH), Nanjing (NJ), Wuhan (WH), Changsha (CS), Fuzhou (FZ), Guangzhou
 592 (GZ), Chongqing (CQ), Guiyang (GY).

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Fig. 3. Directed weighted population genetic graph. **a** Study area. **b** Genetic graph, arrow indicates the direction of gene flow, and the width of the edge is weighted by the migration rate. The numbers underneath the city are values of strength, which measures the centrality of the genetic graph.

Fig. 4 The first observation time (20-year scale) of common ragweed in different regions in China.

Fig. 5 Annual importation of grain from overseas countries to customs at sampling cities in eastern China from 2000 to 2006. Abbreviations are names of sampled cities: Mudanjiang (MDJ), Changchun (CC), Shenyang (SY), Fushun (FS), Qinhuangdao (QHD), Beijing (BJ), Qingdao (QD), Shanghai (SH), Nanjing (NJ), Wuhan (WH), Changsha (CS), Fuzhou (FZ), Guangzhou (GZ), Chongqing (CQ), Guiyang (GY). (Sources: EPS CHINA DATA).

Table 1. Summary statistics of genetic diversity of the common ragweed populations in East China cities. Bold values of F_{IS} indicate significant ($P < 0.05$) deviations from Hardy-Weinberg equilibrium. Asterisk of population I.D. indicates experienced bottleneck effect. n1, number of individuals sampled. N_A , number of different alleles. H_E , expected heterozygosity. F_{IS} , inbreeding coefficient. n2, number of individuals used for cpDNA analysis. h , number of haplotypes. H_D , haplotype diversity. π , Nucleotide diversity.

Cities	Population I.D.	n1/n2	N_A	H_E	F_{IS}	h	H_D	π
Beijing	BJ1	13/12	4.50	0.650	0.074	1	0	0
Beijing	BJ2	15/13	5.33	0.644	0.341	1	0	0
Beijing	BJ3	16/13	6.17	0.726	0.494	1	0	0
Beijing	BJ4	16/13	6.67	0.728	0.351	2	0.52	0.0007
Changchun	CC1	10/10	7.00	0.732	0.303	1	0	0
Changchun	CC4	11/9	7.83	0.774	0.329	1	0	0
Changchun	CC6	10/10	7.83	0.709	0.301	1	0	0
Chongqing	CQ2	8/7	4.00	0.607	0.515	2	0.26	0.001
Changsha	CS1	6/1	5.00	0.694	0.324	1	0	0
Changsha	CS2	13/0	6.00	0.677	0.243	na	na	na
Fushun	FS1*	15/14	6.00	0.667	0.472	1	0	0
Fushun	FS2	14/14	9.00	0.751	0.399	3	0.46	0.0007
Fushun	FS3*	9/9	4.33	0.501	0.389	1	0	0
Fushun	FS4	15/12	8.33	0.730	0.384	2	0.16	0.0002
Fuzhou	FZ3	15/10	8.33	0.804	0.436	2	0.19	0
Fuzhou	FZ4	11/8	7.00	0.750	0.469	2	0.53	0.0007
Fuzhou	FZ5	8/8	6.83	0.777	0.369	1	0	0
Guiyang	GY1	15/12	4.83	0.613	0.511	1	0	0
Guangzhou	GZ1	10/9	6.50	0.753	0.162	2	0.47	0.0012
Mudanjiang	MDJ1	16/13	8.67	0.751	0.314	2	0.41	0.0005
Mudanjiang	MDJ2	16/14	9.17	0.811	0.387	3	0.37	0.0005
Mudanjiang	MDJ3	15/14	7.83	0.766	0.421	3	0.37	0.0005
Mudanjiang	MDJ4*	15/12	7.67	0.784	0.285	3	0.68	0.0011
Nanjing	NJ1	19/18	10.33	0.823	0.493	3	0.55	0.0008
Nanjing	NJ4	13/13	7.83	0.761	0.471	3	0.57	0.0008
Nanjing	NJ5	9/8	5.50	0.685	0.355	3	0.63	0.001
Qingdao	QD1	12/3	5.50	0.729	0.268	1	0	0
Qingdao	QD2*	11/7	7.17	0.782	0.365	1	0	0
Qingdao	QD4	14/6	7.17	0.771	0.327	1	0	0
Qinhuangdao	QHD1*	10/4	7.33	0.747	0.355	2	0.57	0.0007
Qinhuangdao	QHD2	11/11	8.00	0.766	0.356	2	0.17	0.0002
Qinhuangdao	QHD3	12/9	8.83	0.802	0.362	2	0.47	0.0006
Shanghai	SH1*	7/6	3.33	0.537	0.189	1	0	0

Shenyang	SY1	15/13	5.83	0.607	0.365	1	0	0
Shenyang	SY2	9/8	4.00	0.541	-0.198	1	0	0
Shenyang	SY3	15/15	6.83	0.646	0.207	1	0	0
Wuhan	WH2	17/16	9.83	0.791	0.449	2	0.39	0.0005

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Table 2. Assignment frequencies of individual plants in the seven clusters in East China cities to North American and French and Italian clusters. Modern North American cluster 1 included Connecticut, Maine, Massachusetts, New Hampshire, Pennsylvania, New Jersey, and Rhode Island. Modern North American cluster 2 included Arkansas, Florida, Georgia, Illinois, Iowa, Louisiana, Michigan, Minnesota, Missouri, Ohio, South Carolina, Tennessee, Wisconsin, Quebec, and Nova Scotia. Historical North American cluster 1 included Connecticut, Maine, Massachusetts, New Hampshire, Pennsylvania, New Jersey, Rhode Island, Illinois, Iowa, Minnesota, Ohio, South Carolina, Tennessee, and Wisconsin. Historical North American cluster 2 included Arkansas, Florida, Georgia, Michigan, Ontario, Louisiana, and Missouri (24).

Genetic clusters in other regions	Genetic clusters in East China cities							All
	A	B	C	D	E	F	G	
Modern North American cluster 1	0.205	0.086	0.000	0.120	0.078	0.050	0.077	0.110
Modern North American cluster 2	0.739	0.886	1.000	0.840	0.892	0.850	0.846	0.847
Historical North American cluster 1	0.023	0.029	0.000	0.000	0.012	0.000	0.000	0.014
Historical North American cluster 2	0.034	0.000	0.000	0.040	0.018	0.100	0.077	0.028
French and Italian cluster	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 3 Export of grain products from states included in the two modern North American genetic clusters to China from 1999 to 2009 after adjusted by Consumer Price Index (CPI, Year 2000=100). (Source: Foreign Trade Division, U. S. Census Bureau).

Year	Modern North American cluster 2		Modern North American cluster 1	
	Value (million dollars)	Percentage of total value (%)	Value (million dollars)	Percentage of total value (%)
1999	340.45	99.96	0.14	0.04
2000	820.34	99.89	0.90	0.11
2001	523.63	99.92	0.43	0.08
2002	638.35	99.95	0.30	0.05
2003	1882.65	99.99	0.21	0.01
2004	1971.19	99.98	0.48	0.02
2005	1732.08	99.93	1.28	0.07
2006	2026.50	99.99	0.19	0.01
2007	1526.42	99.98	0.34	0.02
2008	1767.33	97.41	46.95	2.59
2009	3168.65	94.40	187.84	5.60

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