Comparative Genetic Diversity and Structure of the Rhus Gall Aphid Schlechtendalia Chinensis and Its Host-Plant Rhus Chinensis

Zhu Ren
Shanxi University
Hong He
Shanxi University
Yang Zhang
Branch of Shanghai Science & Technology Museum
Xu Su (xusu8527972@126.com)
Qinghai Normal University

Research Article

Keywords: Population genetic structure, AFLP marker, Schlechtendalia chinensis, Host-plant, Coevolution

Posted Date: January 6th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-134141/v1

Comparative genetic diversity and structure of the *Rhus* gall aphid *Schlechtendalia chinensis* and its host-plant *Rhus chinensis*

Zhu Mei Ren[1], Hong Li He[1], Yang Zhang[2,3] & Xu Su[4,5,6]

[1]School of Life Science, Shanxi University, Taiyuan, Shanxi, 030006, China. [2]Natural History Research Center, Shanghai Natural History Museum, Branch of Shanghai Science & Technology Museum, Shanghai, 200127, China. [3]Jing'an Association for Science & Technology, Shanghai, 200127, China. [4]Key Laboratory of Medicinal Plant and Animal Resources of the Qinghai-Tibet Plateau in Qinghai Province, School of Life Science, Qinghai Normal University, Xining, Qinghai, 810008, China. [5]Key Laboratory of Education Ministry of Earth Surface Processes and Ecological Conservation of the Qinghai-Tibet Plateau, Qinghai Normal University, Xining, Qinghai, 810008, China. [6]Academy of Plateau Science and Sustainability, Xining, Qinghai, 810016, China. Correspondence and requests for materials should be addressed to X. S. (email: xusu8527972@126.com) or Z.M.R. (email: zmren@sxu.edu.cn)

Abstract

Studying the population genetic structure of both parasites and their host-plants is expected to yield new valuable insights into their coevolution. In this study, we examined and compared the population genetic diversity and structure of 12 populations of the *Rhus* gall aphid, *Schlechtendalia chinensis*, and its host-plant, *Rhus chinensis*, using amplified fragment length polymorphism (AFLP) markers. AMOVA analysis showed that the genetic variance of the aphid and its host-plant were both higher within populations compared to that among them, suggesting that a co-evolutionary history has yielded similar patterns of population genetic structure. We did not detect significant correlation between genetic and geographic distance for either the aphid or host-plant populations, therefore rejecting an isolation by distance model for the demographic histories of the two species. However, our results appeared to suggest that genetically diverse host -plant *Rhus* populations correlated to similarly genetically diverse populations of gall aphid parasites.

Keywords Population genetic structure; AFLP marker; *Schlechtendalia chinensis*; Host-plant; Coevolution

The *Rhus* gall aphids (Hemiptera: Aphididae: Eriosomatinae) have complex life cycles with alternating sexual and parthenogenetic generations, and they are unique in alternating between *Rhus* (Anacardiaceae) as their primary host in summer and mosses (Bryophyta) as their secondary hosts in winter to complete their life cycle[1]. *Rhus* gall aphids include six genera and 12 species, which live on primary host *Rhus* species to form galls with rich tannins to be applied as a raw material in different fields, e.g., medicine, food, dye, chemical and military industry[2]. Among these aphids, *Schlechtendalia chinensis* is widely distributed in East Asia, and *Rhus chinensis* is its unique primary host-plant[2].

Diversification in parasitic species is known to be tightly linked to diversification in their hosts, so that even small evolutionary or demographic changes in the host may profoundly impact population structures or adaptive change in the parasite[3]. These linked, or co-evolutionary relationships have been studied in numerous parasitic species and their plant or animal hosts[4,5]. For example, Jobet et al. examined the population genetic diversity and structure of the urban cockroach and its haplodiploid parasite, an oxyuroid nematode, using RAPD markers and found that the genetic diversity within populations was higher than that between populations for both the oxyuroid nematode and the host-plant[4]. Similarly, Jerome & Ford revealed that the gene flow among populations of the dwarf mistletoe, *Arceuthobium americanum* Nutt. ex Engelm. (Viscaceae) was similar to its host-plant comprising of *Pinus* species, and they considered that the population structures were influenced by geographic isolation among populations of *Pinus* and different environmental conditions[5].

In a previous study of *Schlechtendalia chinensis* from China, random amplified polymorphic DNA (RAPD) revealed high genetic variation that the authors attributed to geographic isolation among populations[6]. Subsequently, Ren et al. compared the population structures of *S. chinensis* and *Rhus chinensis* in eight populations from Guizhou Province in southwestern China using inter-simple sequence repeat (ISSR) markers[7]. Their results showed

that the population genetic structure of *S. chinensis* was similar to its host-plant, but there was no significant correlation between geographic and genetic distances for either the aphid or its host-plant. A more recent study discussed the origin and genetic divergence of Melaphidina aphids between East Asia and North America to suggest that the distribution of the aphids was influenced by the both the host-plant and the environment, with evidence for the latter being that the aphids do not occur throughout the full range of the hosts[8].

By comparison to parasites, the demography of the host plants might be influenced by many factors such as rates of seed and pollen transmission and, consequently, gene flow among populations and species as well as historical factors of climate, geology and regional biota[9,10]. The genus *Rhus* (family Anacardiaceae) contains a number of wide spread species, which migrated from North America into Asia during the late Eocene (33.8 ± 3.1 million years ago) by the Bering land bridge[11]. The species of *R. chinensis* exhibited a demographic structure in the temperate and subtropical zones in China, which has been impacted by the uplift of the Qinghai-Tibet Plateau (QTP)[12].

In this study, we investigated the population genetic structures of *Schlechtendalia chinensis* and its unique host-plant *Rhus chinensis* from 12 corresponding populations from six provinces, and tested the correlations between their population structure, genetic diversity, and gene flow using AFLP markers. We expect that our results will provide a framework for coevolution between insects and host plants, and also for the further genetic studies and conservative action.

Results

We found that eight of 64 pairs of AFLP primers tested had high levels of polymorphism and were, therefore, useful for investigating the genetic structure of *Schlechtendalia chinensis* and *Rhus chinensis* (Table 1). These primers produced 269 polymorphic bands for the 12 aphid populations, and the rate of polymorphism was 75.6%. For the host-plant, 333 specific bands were produced, and the rate of polymorphism was 81.5% (Table 2).

Table 1 Primer combinations in the selective amplification of the aphid and its host plant

Aphid Primer	Sequence	Host Primer	Sequence
E-AAG/M-CAG	5'-GACTGCGTACCAATTCAAG-3' 5'-GATGAGTCCTGAGTAACAG-3'	M-CAA/E-AAG	5'-GATGAGTCCTGAGTAACAA-3' 5'-GACTGCGTACCAATTCAAG-3'
E-AAG/M-CAT	5'-GACTGCGTACCAATTCAAG-3' 5'-GATGAGTCCTGAGTAACAT-3'	M-CAC/E-AAG	5'-GATGAGTCCTGAGTAACAC-3' 5'-GACTGCGTACCAATTCAAG-3'
E-ACG/M-CAA	5'-GACTGCGTACCAATTCACG-3' 5'-GATGAGTCCTGAGTAACAA-3'	M-CAA/E-ACA	5'-GATGAGTCCTGAGTAACAA-3' 5'-GACTGCGTACCAATTCACA-3'
E-ACT/M-CAG	5'-GACTGCGTACCAATTCACT-3' 5'-GATGAGTCCTGAGTAACAG-3'	M-CAA/E-AT	5'-GATGAGTCCTGAGTAACAA-3' 5'-GACTGCGTACCAATTCAT-3'
E-ACA/M-CAT	5'-GACTGCGTACCAATTCACA-3' 5'-GATGAGTCCTGAGTAACAT-3'	M-CAT/E-AT	5'-GATGAGTCCTGAGTAACAT-3' 5'-GACTGCGTACCAATTCAT-3'
E-ACT/M-CTG	5'-GACTGCGTACCAATTCACT-3' 5'-GATGAGTCCTGAGTAACTG-3'	M-CAC/E-AT	5'-GATGAGTCCTGAGTAACAC-3' 5'-GACTGCGTACCAATTCAT-3'
E-AGC/M-CAA	5'-GACTGCGTACCAATTCAGC-3' 5'-GATGAGTCCTGAGTAACAA-3'	M-CTC/E-AT	5'-GATGAGTCCTGAGTAACTC-3' 5'-GACTGCGTACCAATTCAT-3'
E-AGC/M-CAT	5'-GACTGCGTACCAATTCAGC-3' 5'-GATGAGTCCTGAGTAACAT-3'	M-CTT/E-AT	5'-GATGAGTCCTGAGTAACTT-3' 5'-GACTGCGTACCAATTCAT-3'

For the aphid populations, Nei's genetic diversity index (H) and Shannon's information index (I) were 1.0573 and 0.3231, respectively. The mantel test showed that the correlation between genetic and geographic distances (log) was not significant [$r = 0.0153$, $P = 0.5628$ (> 0.05)]. AMOVA showed that 62.3% of the genetic variance was found within the populations and 37.7% among the populations ($P < 0.001$). The genetic differentiation within aphid populations was slightly higher than that among them ($F_{ST} = 0.4566$).

For the host-plant *Rhus chinensis*, the values of H and I values were 1.2075 and 0.4168, respectively. AMOVA analyses revealed similar results to those of the aphid, with 77.1% of the genetic variance within the populations and 22.9% among the populations ($P < 0.001$). The genetic differentiation among populations ($F_{ST} = 0.5167$) was slightly greater than that within them. The mantel test showed that the correlation between genetic and geographic distances (log) for the host-plant was insignificant [$r = 0.25280$, $P = 0.9940$ (> 0.05)]. The relative genetic distances (F_{ST}/1-F_{ST}) between the aphid and its host-plant populations indicated that there was no significant correlation between the two species ($P > 0.05$) (Fig. 1A). There was also no

significant correlation between the genetic and geographic distances for either the aphid or its host-plant populations ($P > 0.05$) (Fig. 1B and Fig. 1C).

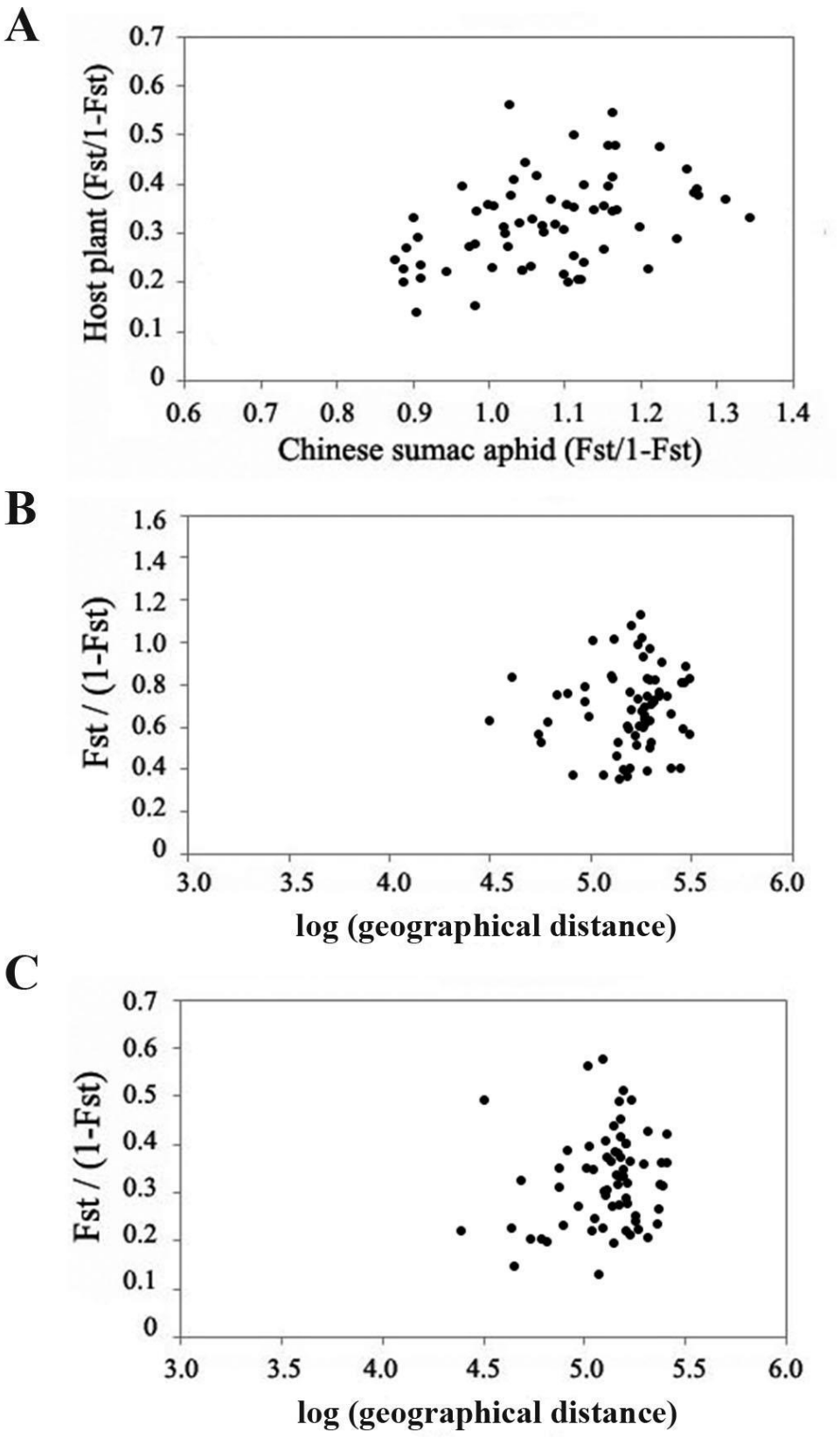

Fig. 1 Scatterplots of pairwise distances for 12 populations in the aphid (*Schlechtendalia chinensis*) and its host plant (*Rhus chinensis*) system: A. the aphid genetic distance [F_{ST}/(1-F_{ST})] versus host-plant genetic distance [F_{ST}/(1-F_{ST})], B. the aphid genetic distance [F_{ST}/(1-F_{ST})] versus geographical distance [log(km)], C. the host-plant genetic distance [F_{ST}/(1-F_{ST})] versus geographical distance [log (km)].

Aphid populations were clustered into four groups in the program STRUCTURE (K = 4), that was as followings: 1) Anxian and Zhushan, 2) Emei, Hanzhong and Chenggu, 3) Danzhai, Taijiang, Wufeng and Shuifu, and 4) the remaining populations, i.e., Longsheng, Jingping and Malipo (Fig. 2). Similarly to the aphid, the most highly supported number of clusters among the plant populations was K = 4, and the 12 populations were divided into the following four groups: 1) Anxian, 2) Chenggu, Emei and Hanzhong, 3) Danzhai, Longsheng, Shuifu, Wufeng, Taijiang and Zhushan, and 4) Jinping and Malipo (Fig. 2).

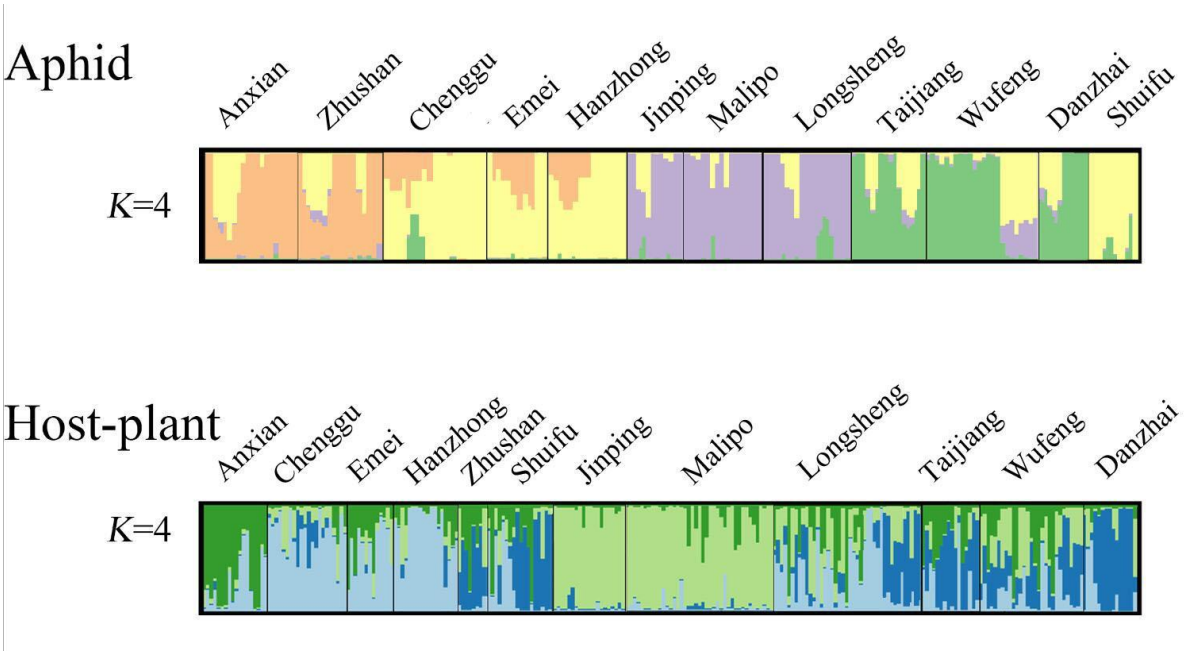

Fig. 2 The genetic structure analysis of aphid and its host-plant based on STRUCTURE (K = 4).

Based on the genetic distances, the NJ tree of the host-plant showed that the populations were clustered into three groups (I, II and III), which were shown in Fig. 3B (left). There were

six populations in group I, i.e., Anxian, Chenggu, Emei, Hanzhong, Shuifu and Zhushan, that were all located in Daba Mountains and Sichuan Basin. Group II contained two populations, Jinping and Malipo, which occurred in Yunnan Province near the China-Vietnam border, where they experienced a tropical climate. Group III was comprised of Wufeng, Longsheng, Danzhai, and Taijiang, which occurred in the Yunnan-Kweichow Plateau and adjacent areas, and thus, sharing the same environment. These are comparable to the groups revealed in STRUCTURE except that Shuifu and Zhushan were separated from Wufeng, Longsheng, Danzhai, and Taijiang.

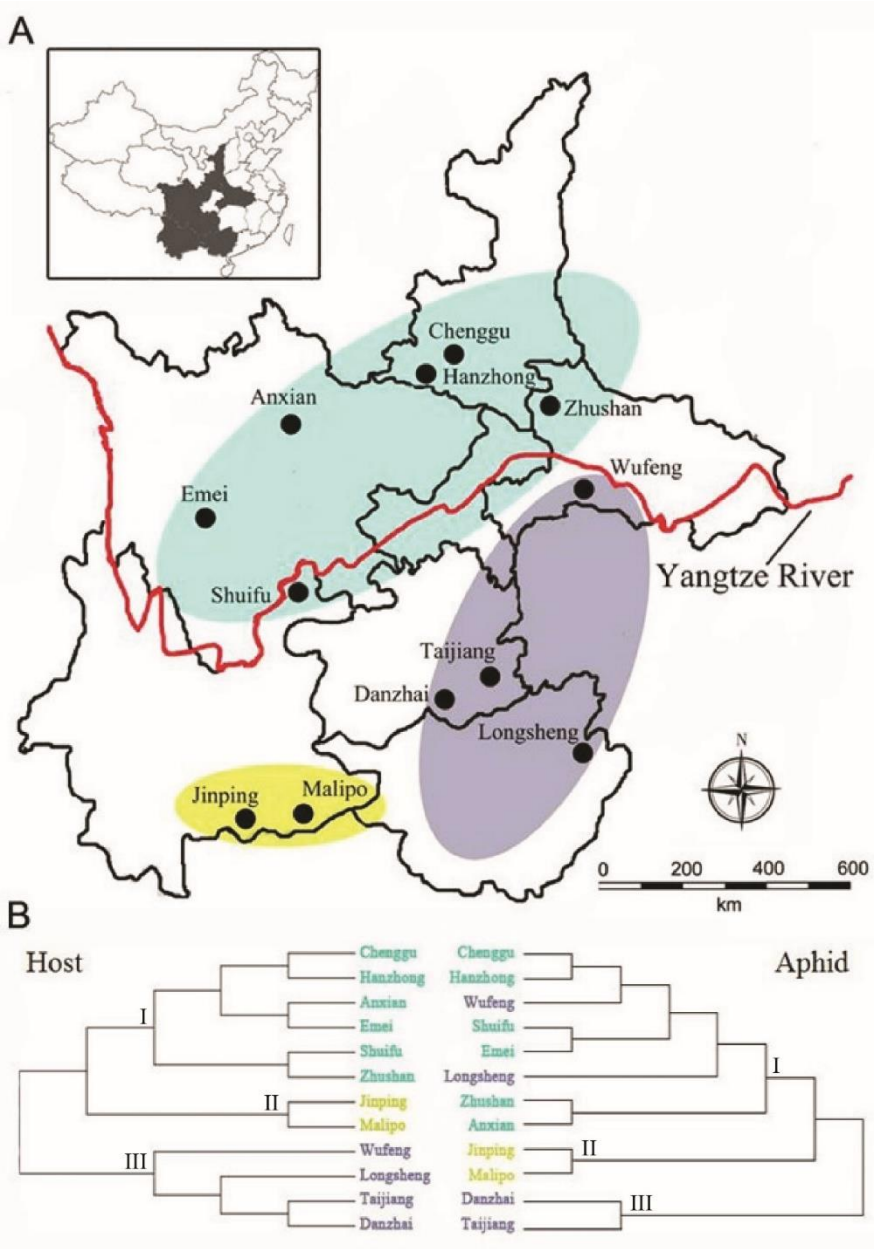

Fig. 3 The population distribution of the collected samples (A) and the NJ tree (B) obtained from the analysis of AFLP data for the aphid *Schlechtendalia chinensis* and its host-plant *Rhus chinensis*.

Based on the groupings from the NJ tree of *Schlechtendalia chinensis*, the Yangtze River appeared to be an important geographic isolation factor and separated group III from groups I and II, seeing Fig. 3B (right). The Shuifu population may represent a connection across the Yangtze River, as the population occurred on both the northern and southern banks. The results for the aphids were similar to those of the host plants in showing three major groups. However, the groups greatly differed in Wufeng and Longsheng populations, which comprised a clade within group III for the plants, whereas, in distant positions within group I for the aphids (Fig. 3B). Based on the topology of the NJ trees of the aphid *Schlechtendalia chinensis* and its host plant *Rhus chinensis*, we calculated their similarity and correlation using TOPD/FMTS[13] to get the split distance with the value 0.667 (12/18).

Discussion

In the present study, we found that the genetic structure of the aphid, *Schlechtendalia chinensis*, was partially similar to that of the host plant; or, stated another way, similar by some measures. The diversity levels within population of the aphids and their host plants are more similar for Anxian, Zhushan, Emei, Jingping and Malipo by comparing to the others, such as Wufeng, Shuifu and Longsheng. We thought that this population genetic structure and diversity were the result of geographic isolation and coevolution[6, 8-9]. However, the levels of inter-populational introgression were similar for plants and aphids within each population according to STRUCTURE (Fig. 2). For example, both the plants and aphids from Jinping and Malipo populations showed relatively small amounts of introgression from other populations, while Taijiang and Wufeng showed considerably more for both species. In addition, the previous studies showed that both aphids and their host-plants had the same patterns of gene flow[7, 14], so

there should also be relatively high gene flow among *S. chinensis* populations based on high gene flow among *R. chinensis*, which was well supported by our current study.

The similar population structures between the aphids and their host plants suggested a coevolutionary history[8]. This was also supported by the similar divergence times of *Rhus* gall aphids and *Rhus* plants (Eocene-Oligocene boundary, 33 - 35 million years ago)[8, 11, 15] as well as the NJ trees, which resolved similar major groups of aphid and plant populations, which were consistent with the largely co-evolving of aphids and their host plants. Nevertheless, some discrepancies existed between the two trees. Most notably, aphids from Wufeng population, lying in the south of the Yangtze River, likely came from populations in the Chenggu and Hanzhong areas, which were to the north of the river. Similarly, aphids from Longsheng population, which is located in the south of the Yangtze River, were also likely originated from the north of the river. All of them suggested that the river was a much greater barrier for the gene flow of either the aphid or its host-plant.

The population history of the host plants has undoubtedly had a profound impact on the aphid population structures, while aphids also responded to the abiotic environment and/or the availability of their host plants. For example, the survival rates of the aphid *Schlechtendalia chinensis* were known to be seriously impacted by the average temperature and precipitation in March along with the distribution of its secondary host plant[14]. Thus, the aphids were not present throughout the entire range of its host-plant *Rhus chinensis*[7].

The level of genetic diversity of the host-plant was higher than other woody plants in the region, such as *Phellodendron amurense* Rupr.[16-18]. High levels of genetic diversity were often observed in plants with long life spans, such as trees, wide geographic distributions, wind pollination, and an abundant fruit yield[19]. *Rhus chinensis* is a widespread species, which is a perennial small tree or shrub, with long generation cycle, with pollen dissemination by wind[19-20]. Therefore, these functional traits of the plant likely interacted with the environment to

strongly influence the genetic diversity of the species[9, 20-21].

The genetic diversity within the Longsheng and Wufeng populations of *Rhus chinensis* were the highest among all the populations, which might result from their greater isolation from other populations by wide rivers and mountains. The two populations both occur in the eastern part of the Yunnan-Kweichow Plateau within the subtropical zone, which receives abundant annual rainfall and heat. Moreover, this region is biotically diverse because floristic elements from the south, southeast, and central China meet overlapping ranges. High levels of biodiversity were often correlated with scattered, genetically isolated individuals or populations[22]. Besides, the pollen could occasionally be carried across the water and over mountain barriers by birds[23], which might make the genetic diversity of *R. chinensis* become higher.

We found that the genetic diversity in Wufeng, Anxian, and Zhushan populations of both the aphid and host-plant was higher than other populations. The higher genetic diversity might correspond to an equitable environment and extensive gene flow[24]. Based on the results from STRUCTURE analysis of *Schlechtendalia chinensis* population, Wufeng, Anxian, and Zhushan populations contained relatively high frequencies of all observed genotypes and might, therefore, be the sources for all other sampled populations. Within the three populations, the genetic diversity of the host-plant was also higher than other populations and might help to facilitate higher diversity among the aphids through co-evolutionary processes[25-27].

The migratory flight of the aphid was strong, reaching a maximum distance of 22 - 26 km and having a maximum flight time of 118 min[28]. High gene flow usually leaded to high genetic diversity of species[29]. Therefore, the gene flow was strong, especially for aphids in the same geographic environment, and the genetic diversity of these populations, such as Wufeng and Zhushan, was high. These factors led to more genetic differentiation among populations, while the genetic variance was within populations. These results were similar to those of previous researches[5,7].

Materials and Methods

Sample collection. We collected aphid galls and host-plant leaf samples from 12 locations in China (Fig. 3A). When the galls were mature, we cut them open and collected the aphids in absolute ethanol. We stored leaves in plastic zipper bags with silica gel prior to DNA isolation. We deposited all the voucher specimens at the School of Life Science in Shanxi University, China.

DNA extraction and AFLP analysis. We immersed the aphid samples in sterile water for 24 hours with the water being changed every eight hours. Thereafter, we extracted genomic DNA of aphid individuals using the conventional phenol/chloroform method[30]. For the host-plant, we extracted genomic DNA using a modified CTAB method[31].

We performed restriction enzyme digestion of template DNA using *EcoR*I and *Mse*I in a 25 μL reaction mixture that contained 4 μL 10 × Tango buffer, 10 u *EcoR*I, 4 u *Mse*I and about 200 ng template DNA. The product of the enzyme reaction was ligated into the vector, and immediately pre-amplified. The selective amplification occurred in a total volume of 25 μL, including 2 μL pre-amplification reaction mixture, 2 μL 10 × Taq buffer (with Mg^{2+}), 0.25 mM dNTPs, 0.4 μM *Mse*I primer, 0.4 μM *EcoR*I primer, 1.5-unit Taq DNA polymerase. The PCR amplification protocol for the aphid and host-plant was as follows: initial denaturation for 2 min at 94°C, followed by 1 cycle of 30 s at 94°C, 30 s at 65°C and 1 min at 72°C. Thereafter, we reduced the annealing temperature by 0.7°C for each of 12 subsequent cycles, followed by 25 cycles of 30 s at 94°C, 30 s at 56°C and 1 min at 72°C. We visualized the resulting products on 6% denaturing polyacrylamide gels and scored bands as binary data (presence = 1; absence = 0) for downstream statistical analyses.

Data analyses. We used POPGENE 3.2 to calculate the percentage of polymorphic loci (*P*), Nei's genetic diversity index (*H*) and Shannon's information index (*I*)[32], and performed a mantel test using NTSYSpc 0/1-version 2.11 software based on the binary matrix to analyze

the relationships among genetic and geographic distances between the 12 populations[33-34]. AMOVA was conducted using ARLEQUIN 3.01[35]. We constructed neighbor-joining (NJ) trees of both aphid and its host-plant based on genetic distances using Mega 4.0 software[36]. To compare the most likely number of population genetic clusters (*K*) in the AFLP datasets for the aphid and host plants (independently), we compared values of *K* value from two to nine, with ten replicates performed for each *K*, a burn-in of 1×10^5 iterations, and 1×10^5 Monte Carlo and Markov Chain (MCMC) steps. We determined the best-fit of clusters using Δ*K*in STRUCTURE HARVESTER[37].

References

1. Eastop, V. F. and Hille Ris Lambers, D. Survey of the World's Aphids. Dr. W. Junk b. v., Publishers, The Hague, Netherlands (1976).
2. Zhang, G. X., Qiao. G. X., Zhong. T. S. and Zhang, W. Y. Homoptera: Mindaridae and Pemphigidae (Science Press, Beijing, 1999).
3. van Schaik, J., Kerth, G., Bruyndonckx, N. and Christe, P. The effect of host social system on parasite population genetic structure: comparative population genetics of two ectoparasitic mites and their bat hosts. *BMC Evolutionary Biology* 14, 18, https://doi.org/10.1186/1471-2148-14-18 (2014).
4. Jobet, E., Durand, P., Langand, J., Müller, C. D., Hugot, J. P., Bougnoux, M. E., Rivault, C., Cloarec, A. and Morand, S. Comparative genetic diversity of parasites and their hosts: population structure of an urban cockroach and its haplo-diploid parasite (Oxyuroid nematode). *Molecular Ecology* 9(4), 481-486, https://doi.org/10.1046/j.1365-294x.2000.00880.x (2000).
5. Jerome, C. A. and Ford, B. A. Comparative population structure and genetic diversity of *Arceuthobium americanum* (Viscaceae) and its *Pinus* host species: insight into host-parasite evolution in parasitic angiosperms. *Molecular Ecology* 11(3), 407-420,

https://doi.org/10.1046/j.0962-1083.2002.01462.x (2002).

6. Yang, Z. X., Chen, X. M., Feng, Y. and Zhang, Y. P. RAPD Analysis of phylogenetic relationships in Chinese gallnut aphids (Homoptera: Pemphigidae) and genetic differentiation in four populations of *Schlechtendalia chinensis*. *Scientia Silvae Sinicae* 43(7), 43-50, https://dx.doi.org/10.11707/j.1001-7488.20070708 (2007).
7. Ren, Z. M., Zhu, B., Wang, D. J., Ma, E. B., Su, D. M. and Zhong, Y. Comparative population structure of Chinese sumac aphid *Schlechtendalia chinensis* and its primary host-plant *Rhus chinensis*. *Genetica* 132(1), 103-112, https://doi.org/10.1007/s10709-007-9153-6 (2008).
8. Ren, Z. M., Zhong, Y., Kurosu, U., Aoki, S., Ma, E. B., von Dohlen, C. D. and Wen, J. Historical biogeography of eastern Asian-eastern North American disjunct Melaphidina aphids (Hemiptera: Aphididae: Eriosomatinae) on *Rhus* hosts (Anacardiaceae). *Molecular Phylogenetics and Evolution* 69, 1146-1158, http://dx.doi.org/10.1016/j.ympev.2013.08.003 (2013).
9. Hou, Y. and Lou, A. Population genetic diversity and structure of a naturally isolated plant species, *Rhodiola dumulosa* (Crassulaceae). *PLoS One* 6(9), e24497, http://dx.doi.org/10.1371/journal.pone.0024497 (2011).
10. McCoy, K. D., Boulinier, T. and Tirard, C. Comparative host-parasite population structures: disentangling prospecting and dispersal in the black-legged kittiwake *Rissa tridactyla*. *Molecular Ecology* 14(9), 2825-2838, http://dx.doi.org/10.1111/j.1365-294X.2005.02631.x (2005).
11. Yi, T. S., Miller, A. J. and Wen, J. Phylogenetic and biogeographic diversification of *Rhus* (Anacardiaceae) in the Northern Hemisphere. *Molecular Phylogenetics and Evolution* 33(3), 861-879, http://dx.doi.org/10.1016/j.ympev.2004.07.006 (2004).
12. Liang, Y. K., Zhang, Y., Wen, J., Su, X, and Ren, Z. M. Evolutionary history of *Rhus chinensis* (Anacardiaceae) from the temperate and subtropical zones of China based on

cpDNA and nuclear DNA sequences and ecological niche model. *Frontiers in Genetics* 10, 171, http://doi. 10.3389/fgene.2019.00171 (2019).

13. Puigbò, P., Garcia-Vallvé, S. and McInerney, J. O. TOPD/FMTS: a new software to compare phylogenetic trees. *Bioinformatics* 23(12), 1556-1558, https://doi.org/10.1093/bioinformatics/btm135 (2007).
14. Wang, D. J., Yang, H. Y., Zhong, Y. and Ren, Z. M. Genetic diversity of eight *Schlechtendalia chinensis* populations from Guizhou Province: a study with inter-simple sequence repeats markers. *Chinese Journal of Ecology* 27(10), 1729-1733 (2008).
15. Brouat, C., Tatard, C., Machin, A., Kane, M. Diouf, M., Bã, K. and Duplantier, J. M. Comparative population genetics of a parasitic nematode and its host community: The trichostrongylid *Neoheligmonella granjoni* and *Mastomys* rodents in southeastern Senegal. *International Journal of Parasitology* 41(12), 1301-1309, https://doi.org/10.1016/j.ijpara.2011.07.014 (2011).
16. Heider, B., Andersson, M. S. and Schultze-Kraft, R. RAPD variation among North Vietnamese *Flemingia macrophylla* (Willd.) Kuntze ex Merr. *Plant Conservation and Biodiversity* 16, 1617-1631, https://doi.org/10.1007/s10531-006-9024-y (2007).
17. Vashishtha, A., Jehan, T. and Lakhanpaul, S. Genetic diversity and population structure of *Butea monosperma* (Lam.) Taub. - a potential medicinal legume tree. *Physiology and Molecular Biology Plants* 19(3): 389-397, https://doi.org/10.1007/s12298-013-0170-x (2013).
18. Yan, Z. F., Zhang, B. G., Zhang, Z. and Yu, J. L. Genetic diversity in wild populations of *Phellodendron amurense*, a rare and endangered medicinal plant, detected by AFLP. *Biodiversity Science* 14(6): 488-497, https://doi.org/10.1360/biodiv.060041 (2006).
19. Hamrick, J. L., Minon, J. B. and Linhart, Y. B. Levels of genetic variation in tree influence of life history characteristics//Isozymes of north American forest trees and forest insects.

USDA. Berkeley Geotechnology Report 3511-3534 (1981).

20. Li, J. B., Ren, Z. M. and Ma, E. B. Comparative genetic diversity of *Schlechtendalia chinensis* and their hosts *Rhus chinensis population*. *Journal of Shanxi University (Nat. Sci. Ed.)* 32(2): 298-302, https://doi.org/10.13451/j.cnki.shanxi.univ (nat. sci.) (2009).
21. Theim, T. J., Shirk, R. Y. and Givnish, T. J. Spatial genetic structure in four understory *Psychotria species* (Rubiaceae) and implications for tropical forest diversity. *American Journal of Botany* 101(7), 1189-1199, https://doi.org/10.3732/ajb.1300460 (2014).
22. Janzen, D. H. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104(940), 501-528, https://doi.org/10.1086/282687 (1970).
23. Moore, R. P., Robinson, W. D., Lovette, I. J. and Robinson, T. R. Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters* 11(9), 960-968, https://doi.org/10.1111/j.1461-0248.2008.01196.x (2008).
24. Bao, F. and Wells, J. D. Population genetic structure of an invasive forensically important insect. *Electrophoresis* 35(21-22): 3193-3120, https://doi.org/10.1002/elps.201400108 (2014).
25. Wilfert, L. and Jiggins, F. M. Host-parasite coevolution: genetic variation in a virus population and the interaction with a host gene. *Journal of Evolutionary Biology* 23(7), 1447-1455, https://doi.org/10.1111/j.1420-9101.2010.02002.x (2010).
26. Wilkinson, T. J., Rock, J., Whiteley, N. M., Ovcharenko, M. O. and Ironside, J. E. Genetic diversity of the feminising microsporidian parasite *Dictyocoela*: new insights into host-specificity, sex and phylogeography. *International Journal for Parasitology* 41, 959-966, https://doi.org/10.1016/j.ijpara.2011.04.002(2011).
27. Fisher, R. M., Henry, L. M., Cornwallis, C. K., Kiers, E. T. and West, S. A. The evolution of host-symbiont dependence. *Nature Communications* 8, 15973, https://doi.org/10.1038/ncomms15973 (2017).

28. Smith, M. A. H. and Machay, P. A. Seasonal variation in the photoperiodic responses of a pea aphid population: evidence for long-distance movements between populations. *Oecologia* 81(2), 160-165, https://doi.org/10.2307/4219122(1989).

29.Johnson, K. S., Plant, J. N., Coletti, L., Jannasch, H., Sakamoto, C. M., Riser, S., Swift, D. D., Williams, N. L., Boss, E. S., Haëntjens, N., Talley, L. D. and Sarmiento, J. L. Biogeochemical sensor performance in the SOCCOM profiling float array. *Journal of Geophysical Research Oceans* 122, 6416-6436, https://doi.org/10.1002/2017JC012838 (2017).

30. Ren, Z. M., Ma, E. B. and Guo, Y. P. Genetic relationships among *Oxya agavisa* and other relative species revealed by Cytb sequences. *Acta Genetica Sinica* 29(6), 507-513, https://doi.org/10.1006/jfls.2001.0409(2002).

31. Doyle, J. J. and Doyle, J. L. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemistry Bulletin* 19(1), 11-15 (1987).

32. Yeh, F. C., Yang, R. C., Boyle, T. B. J., Ye, Z. H., Mao, J. X., Yeh, C., Timothy, B. and Mao, X. PopGene, the user-friendly shareware for population genetic analysis. Molecular Biology and Biotechnology Center, University of Albert, Edmonton (1997).

33. Mantel, N. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27(2), 175-178, https://doi.org/10.1007/s00253-002-1013-9(1967).

34. Rohlf, F. J. NTSYS pc: numerical taxonomy and multivariate analysis system, version 2.02. Exeter Software, Setauket, New York, USA, http://www.exetersoftware.com/cat/ntsyspc/ntsyspc.html. (1998).

35. Schneider, S., Roessli, D., Excoffier, L. and Roeslli, D. Arlequin: a software for population genetics data analysis, version 2.000. Genetics and Biometry Laboratory, University of Geneva, Switzerland, (2000).

36. Tamura, K., Dudley, J., Nei, M. and Kumar, S. MEGA4: molecular evolutionary genetics

analysis (MEGA) software version 4.0. *Molecular Biology and Evolution* 24(8), 1596-1599, https://doi.org/10.1093/molbev/msm092(2007).

37. Earl, D. A. and von Holdt, B. M. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources* 4(2), 359-361, https://doi.org/10.1007/s12686-011-9548-7 (2012).

Acknowledgments

This research was financially supported by the National Natural Science Foundation of China (31870366, 31800310), Shanxi International Science and Technology Cooperation Project (201803D421051), Research Project Supported by Shanxi Scholarship Council of China (2020-018), the National High Technology Research and Development "863" Program (2014AA021802), the Key Laboratory of Medicinal Animal and Plant Resources of the Qinghai-Tibet Plateau in Qinghai Province (2020-ZJ-Y40), the Natural Science Foundation of Shanxi Province (2007011078), and the Specimen Platform of China (Teaching Specimens Sub-platform).

Author Contributions

Z.-M.R and Y.Z. collected the samples; H.-L.H and Y.Z. conducted molecular laboratory work and analyzed the data; Z.-M.R and X.S. conceived the experiments; Z.-M.R, H.-L.H, Y.Z. and X.S. wrote the paper.

Additional Information

Competing Interests: The authors declare no competing interests.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Table 2 Sampling information and genetic polymorphism of AFLP analysis for the aphid and its host-plant populations

Population	Provinces	Samples No.		Altitude (m)	Latitude	Longitude	Voucher specimens		P. L		P (%)	
		Aphid	Host				Aphid	Host	Aphid	Host	Aphid	Host
Taijiang	Guizhou	16	16	721	26°39’	108°19’	SC-TJ17	RC-TJ17	111	234	41.1	62.9
Danzhai	Guizhou	11	15	1005	26°11’	107°47’	SC-DZ13	RC-DZ16	115	197	42.6	52.9
Wufeng	Hubei	24	29	614	30°12’	110°40’	SC-WF25	RC-WF33	144	241	53.3	64.8
Zhushan	Hubei	18	8	717	32°13’	110°14’	SC-ZS20	RC-ZS9	129	186	47.8	50.0
Chenggu	Shaanxi	22	22	605	33°09’	107°99’	SC-CG23	RC-CG23	70	183	25.7	49.2
Hanzhong	Shaanxi	17	18	1453	33°05’	107°02’	SC-HZ18	RC-HZ20	61	190	22.7	51.2
Longsheng	Guangxi	19	41	702	25°47’	110°01’	SC-LS20	RC-LS43	76	248	28.2	66.7
Anxian	Sichuan	20	18	557	31°31’	104°33’	SC-AX15	RC-AX15	127	207	47.0	55.7
Emei	Sichuan	17	13	899	29°36’	103°29’	SC-EM18	RC-EM14	91	163	33.7	43.3
Shuifu	Yunnan	11	18	1644	28°37’	110°14’	SC-SF12	RC-SF19	75	180	27.8	48.4
Jinping	Yunnan	12	20	1248	22°46’	103°13’	SC-JP15	RC-JP16	81	175	30.0	47.0
Malipo	Yunnan	11	41	1619	23°07’	104°42’	SC-MLP1	RC-MLP1	94	204	34.8	54.8
Total		198	259						269	333	75.6	81.5

Notes: P.L - Polymorphic bands. P - Polymorphism rate.

Figures

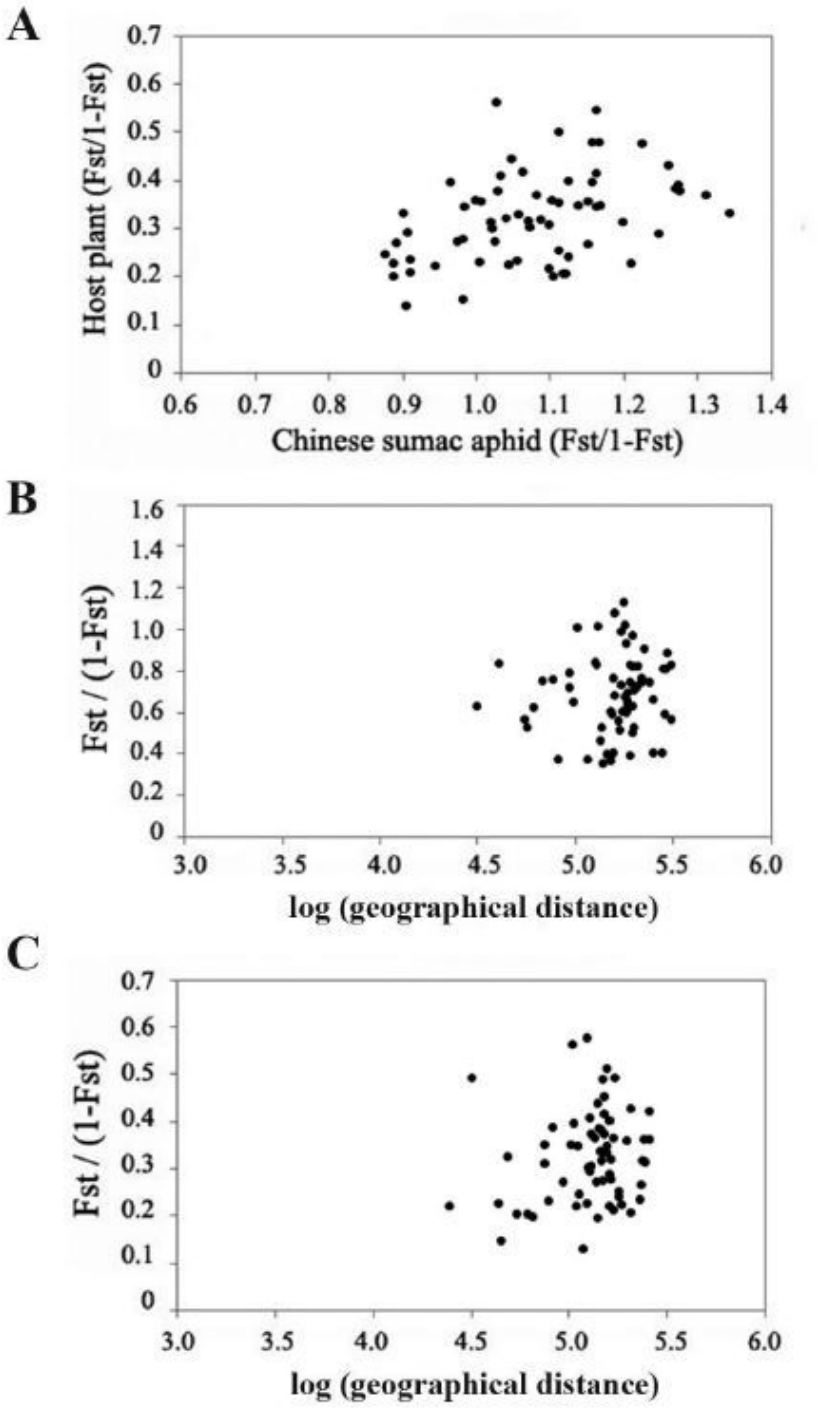

Fig. 1

Figure 1

Scatterplots of pairwise distances for 12 populations in the aphid (Schlechtendalia chinensis) and its host plant (Rhus chinensis) system: A. the aphid genetic distance [FST/(1-FST)] versus host-plant genetic

distance [FST/(1-FST)], B. the aphid genetic distance [FST/(1-FST)] versus geographical distance [log(km)], C. the host-plant genetic distance [FST/(1-FST)] versus geographical distance [log (km)].

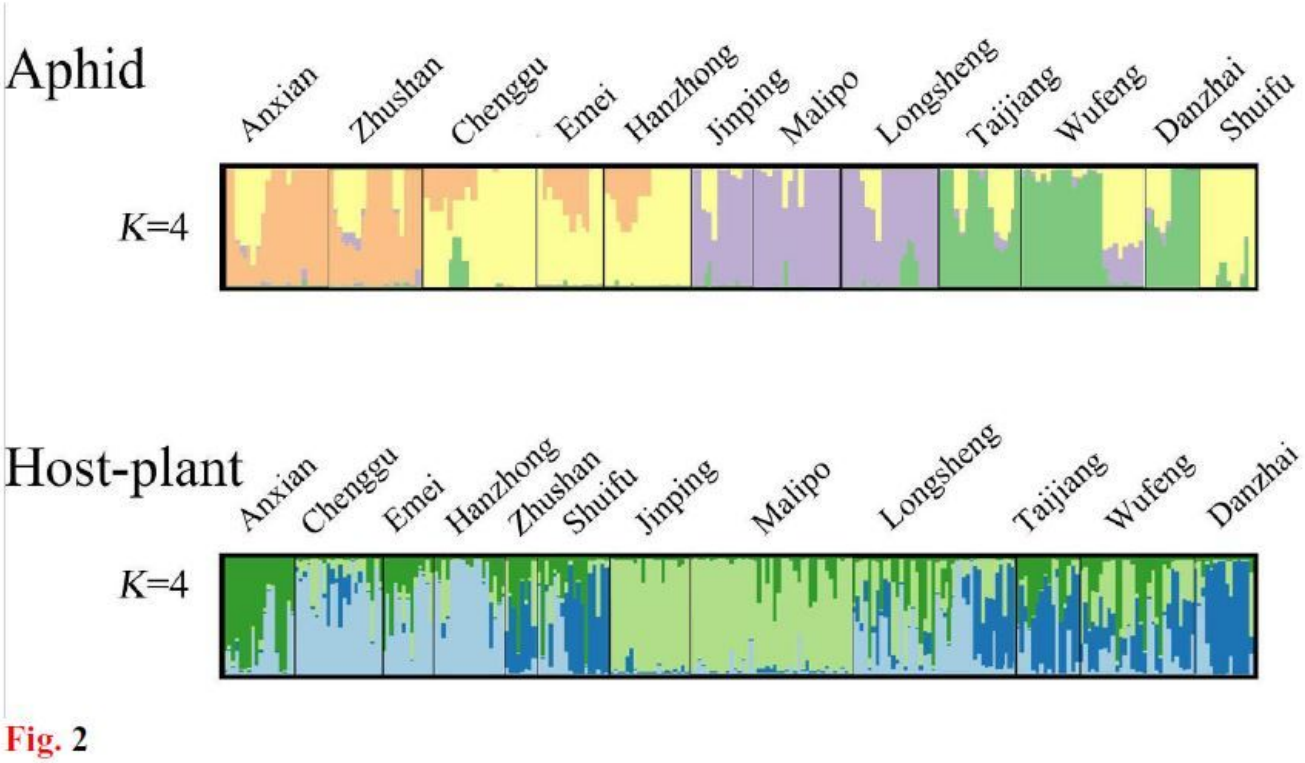

Fig. 2

Figure 2

The genetic structure analysis of aphid and its host-plant based on STRUCTURE (K = 4).

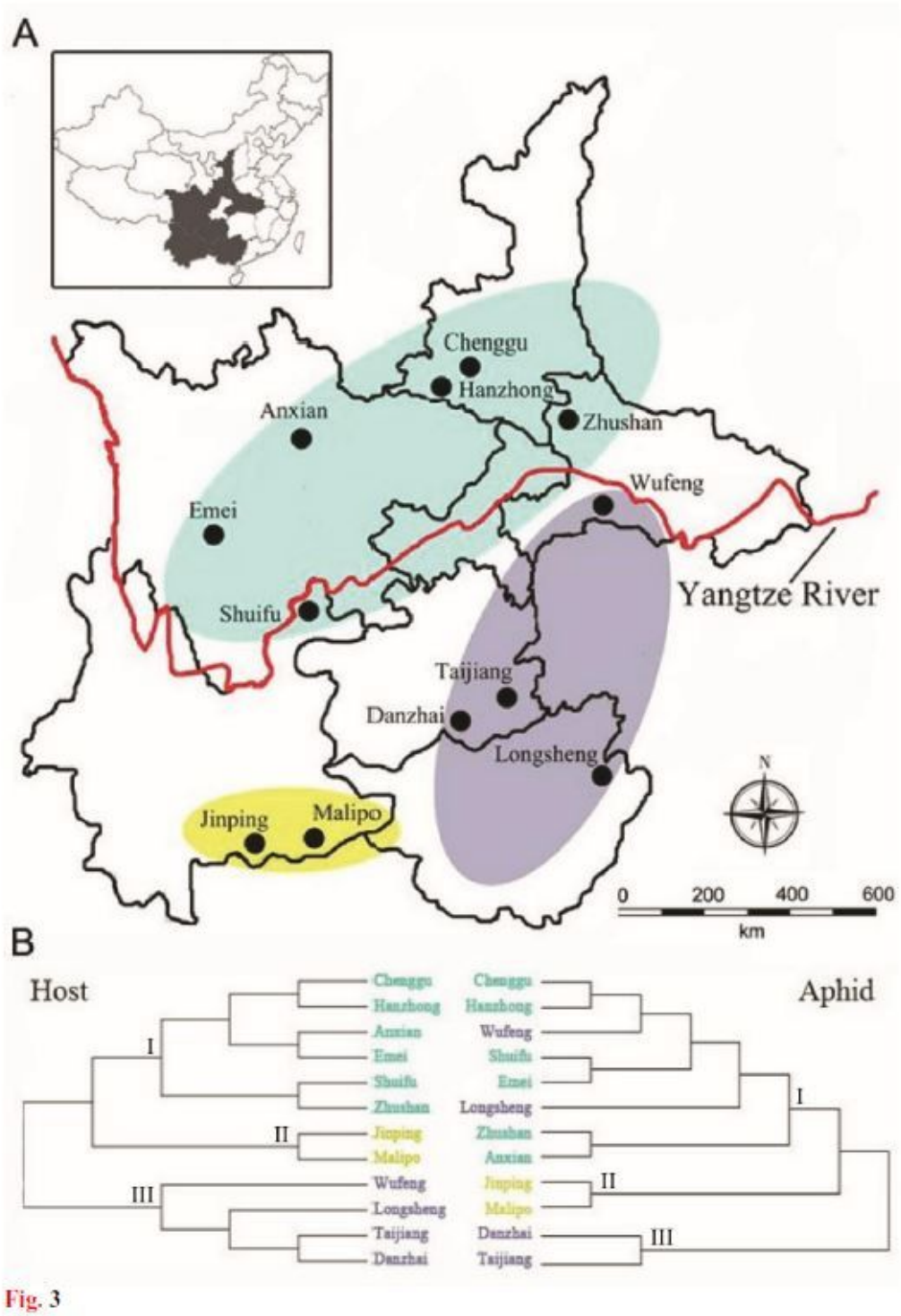

Fig. 3

Figure 3

The population distribution of the collected samples (A) and the NJ tree (B) obtained from the analysis of AFLP data for the aphid Schlechtendalia chinensis and its host-plant Rhus chinensis. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country,

territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.