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Population genetic analyses highlight an eastward dispersal of *Puccinia striiformis* f. sp. *tritici* from the Shaanxi province to the North China Plain

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Abstract

Wheat stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is a common airborne wheat disease. The frequent occurrence at a large scale in China has caused significant yield losses and poses a considerable threat to food security. To effectively manage and forecast the disease, a comprehensive understanding of the long-distance migration patterns of *Pst* is essential. Shaanxi province, situated in close proximity to the northwestern epidemic areas in China, plays a crucial role as a key overwintering region for *Pst*. However, it remains uncertain whether *Pst*, after winter reproduction in Shaanxi province, can extend its spread to the primary wheat regions in the North China Plain. In this study, during February and June 2022, a total of 302 *Pst* samples were collected from Shaanxi province and the North China Plain. Thirteen pairs of simple sequence repeat (SSR) markers were adopted to analyze the population genetic structure. It was observed that both genetic and genotypic diversities exhibited a discernible decline from the Shaanxi to the North China Plain. Moreover, Shaanxi displayed a close genetic relationship with Henan and Shandong, whereas Henan exhibited the most substantial population exchange with Shaanxi. Further analysis revealed that Shaanxi served as the primary inoculum of *Pst* in the investigated region, and the spread of *Pst* to Henan and Shandong originated from Shaanxi. As a result, the epidemics in Shandong further led to the prevailing of the disease in Hebei. Our study enhances the understanding of the epidemiological patterns of wheat stripe rust in the springtime prevalent regions of China, and it provides insights for future disease management.

Keywords *Puccinia striiformis* f. sp. *tritici*, Molecular marker, Population genetics, Plant disease epidemiology

Background

Wheat stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is a globally distributed fungal disease, posing a severe threat to the global food supply (Wellings 2011; Chen and Kang 2017). China, as one of the major wheat producers, has frequently suffered from the most severe wheat stripe rust (Chen et al. 2014; Chen 2020). Several recent epidemics in China have led to substantial economic losses in wheat production region (Wan et al. 2007; Chen et al. 2009a, 2014), damaging over 20 million hectares of wheat (Awais et al. 2022). Medium- and

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long-distance dispersal of the spores is the spreading strategies employed by *Pst*, which enables its urediniospore to distribute to diverse ecological conditions and leads to disease epidemics in large areas (Hovmøller et al. 2011; de Vallavieille-Pope et al. 2012; Chen et al. 2014; Chen 2020).

The unique endemic flora, terrain, farming system, and climatic conditions in China contribute to distinctive characteristics of wheat stripe rust epidemics in comparison to other countries worldwide (Zeng and Luo 2006). Extensive researches have indicated that *Pst* can oversummer in Northwest China, such as eastern and southern area of Gansu province, two places that were recognized as the advantaged region for stripe rust epidemics in China. *Pst* can survive all seasons in the region and provide primary inoculum to the neighboring provinces (Hu et al. 2017; Liang et al. 2021; Wang et al. 2022; Zeng et al. 2022). During autumn, *Pst* disseminates from the oversummering region to the winter reproduction regions, such as Shaanxi, Hubei, and Sichuan provinces, where it continues to reproduce and accumulate inoculum sources for the next epidemic in the spring season (Chen et al. 2014). Notably, Hubei province functions as a crucial bridge or stopover for inoculum sources. Wang et al. (2020) observed a significant reduction in genetic diversity revealed the migration of *Pst* from Hubei to North China. Yan et al. (2023) further identified southern Hubei as a crucial stopover for the primary inoculum source originating from Yunnan spreading towards Zhejiang through genetic structure analysis and high-altitude air current trajectory analysis. When climatic conditions are favorable, a large number of urediniospores disperse from overwintering regions like Hubei province, leading to outbreaks on susceptible wheat in the spring epidemic region (Chen et al. 2014). The spring epidemic region primarily refers to the North China Plain winter wheat region, where the planted wheat varieties are very limited (Chen et al. 2014). Unlike those in the oversummering and winter reproduction regions, *Pst* cannot survive the winter or summer seasons in most spring epidemic regions. The disease outbreak in these regions heavily relies on external inputs of *Pst* (Zeng and Luo 2006).

Shaanxi province is a key area locating between the *Pst* origin regions of the southern and eastern areas of Gansu province and the North China Plain winter wheat region (Xue 2016). If Shaanxi province fails to implement timely and effective measures to prevent and control wheat stripe rust, it may bring considerable pressure to the North China Plain. Nevertheless, it remains uncertain whether *Pst* has completed its reproductive cycle in Shaanxi province throughout winter, and can spread to regions such as Henan, Hebei, and Shandong provinces in the North China Plain. The dispersal route and the associated inoculum within Shaanxi province and the North China Plain require an urgent investigation.

However, investigating the spread of *Pst* encounters many challenges due to the difficulty in tracking the movement of *Pst* urediniospores via air. Population genetics and molecular biology tools provide valuable theoretical and technical approaches to overcome these challenges (Grünwald et al. 2003; Milgroom and Peever 2003). In this study, SSR markers were used to characterize the *Pst* populations in diverse wheat ecological regions of Shaanxi, Henan, Hebei, and Shandong provinces. The goal is to clarify the dispersal routes of early spring *Pst* populations in these regions. The objectives of the study are as follows: (i) to assess the genetic diversity, genotypic diversity, population differentiation, population structure, and potential reproductive mode of *Pst* populations in Shaanxi province and the North China Plain at different regional scales; (ii) to identify the sources of *Pst* inoculum in the investigated regions; and (iii) to investigate the routes of the dispersal of *Pst* within the studied regions.

Results

Genetic diversity

The genetic diversity analysis revealed distinct patterns within the investigated regions. All subpopulation abbreviations are detailed in Additional file 1: Table S1. In general, subpopulations in Shaanxi had high genetic diversity than those in Henan, Shandong, and Hebei, although a few subpopulations had some exception. Specifically, in the group of provinces (Table 1), Shaanxi (SX) displayed the highest genetic diversity, with maximum values of number of polymorphic alleles (*Na*) (3.538), number of effective alleles (*Ne*) (1.986), Shannon's information index (*I*) (0.735), and expected heterozygosity (*He*) (0.424). However, Hebei (HB) demonstrated the lowest values for *Na* (1.538), *Ne* (1.476), *I* (0.342), and *He* (0.243). In summary, subpopulations in Shaanxi exhibited the highest levels of genetic diversity, while subpopulations in Hebei displayed the lowest levels.

Genotypic diversity

Overall, the genotypic diversity analysis suggested that subpopulations in Shaanxi maintained at higher levels of genotypic diversity over other subpopulations, which was consistent with the result for genetic diversity. In the group of provinces (Table 2), HB demonstrated the lowest diversity, with a ratio of multi-locus genotype to total individual numbers (MLG ratio), effective multilocus genotype (eMLG), Shannon-wiener index (*H*), Stoddart and Taylor's index (*G*), Simpson's index (λ) of 0.128, 5.362, 1.067, 2.106, and 0.525, respectively, which indicated that subpopulations in Hebei had an overall

Table 1 Genetic diversity of *Puccinia striiformis* f. sp. *tritici* populations analyzed with 13 simple sequence repeat (SSR) markers

Groups	Population	*N*	*Na*	*Ne*	*I*	*Ho*	*He*
County	HBA1	24	1.538	1.491	0.355	0.487	0.252
	HBB1	23	1.462	1.462	0.320	0.462	0.231
	HNA1	13	1.692	1.416	0.338	0.382	0.228
	HNA2	12	1.692	1.347	0.305	0.314	0.200
	HNB1	12	1.538	1.538	0.373	0.538	0.269
	SDA1	19	1.846	1.501	0.366	0.470	0.246
	SDB1	47	2.385	1.499	0.429	0.397	0.263
	SXA1	23	2.154	1.504	0.447	0.395	0.283
	SXA2	26	1.923	1.516	0.444	0.376	0.288
	SXA3	5	1.462	1.320	0.262	0.308	0.178
	SXA4	9	1.846	1.490	0.400	0.393	0.264
	SXA5	33	2.462	1.623	0.505	0.562	0.325
	SXA6	12	1.846	1.515	0.400	0.455	0.267
	SXA7	19	1.462	1.334	0.256	0.324	0.176
	SXB1	18	2.154	1.534	0.429	0.355	0.253
	SXB2	3	1.846	1.563	0.480	0.410	0.325
	SXC1	4	1.538	1.538	0.373	0.538	0.269
Prefecture	HBA	24	1.538	1.491	0.355	0.487	0.252
	HBB	23	1.462	1.462	0.320	0.462	0.231
	HNA	25	2.000	1.463	0.417	0.348	0.271
	HNB	12	1.538	1.538	0.373	0.538	0.269
	SDA	19	1.846	1.501	0.366	0.470	0.246
	SDB	47	2.385	1.499	0.429	0.397	0.263
	SXA	127	2.923	1.900	0.671	0.426	0.407
	SXB	21	2.615	1.695	0.555	0.363	0.319
	SXC	4	1.538	1.538	0.373	0.538	0.269
Province	HB	47	1.538	1.476	0.342	0.475	0.243
	HN	37	2.385	1.644	0.569	0.414	0.348
	SD	66	2.615	1.575	0.463	0.417	0.278
	SX	152	3.538	1.986	0.735	0.420	0.424

N, number of individuals; *Na,* number of polymorphic alleles; *Ne,* number of effective alleles; *I,* Shannon's information index*; Ho,* observed heterozygosity; *He,* expected heterozygosity

high clonality. The overall genotypic diversity of *Pst* subpopulations showed a decreasing trend from Shaanxi to the North China Plain regions (Henan, Shandong, and Hebei).

Population differentiation

The results of the analysis of molecular variance (AMOVA) suggested that most genetic variance existed within individuals (Table 3). The highest percentage of variation was observed within the individuals for province at 88%, followed by individuals for prefecture at 83%, and the lowest was within individuals for county at 75%, which reflected that following the population division scale became smaller, the degree of variation within individuals decreased.

The pairwise comparisons of F_{ST} values revealed genetic differentiation among different subpopulations (Additional file 1: Tables S2–S4). The result showed that the highest genetic differentiation was observed between Henan and Hebei subpopulations, while the lowest genetic differentiation was observed between Shandong and Hebei subpopulations, suggesting that Henan and Hebei may be influenced by distinct sources of *Pst* or have limited *Pst* exchange, whereas Shandong and Hebei may share a common source of *Pst* or experience frequent exchange.

The possible migration among different subpopulations was further confirmed by measuring the number of migrants (*Nm*) which is a parameter used to quantify gene flow or migration (Additional file 1: Tables S2–S4). Overall, a higher migration rate was observed between

Table 2 Genotypic diversity of *Puccinia striiformis* f. sp. *tritici* populations analyzed with 13 simple sequence repeat (SSR) markers

Groups	Population	*N*	MLG	MLG ratio	eMLG	*H*	*G*	*λ*
County	HBA1	24	5	0.208	3.644	1.231	2.824	0.646
	HBB1	23	3	0.130	2.273	0.560	1.426	0.299
	HNA1	13	9	0.692	7.378	2.058	6.760	0.852
	HNA2	12	6	0.500	5.167	1.350	2.667	0.625
	HNB1	12	3	0.250	2.667	0.566	1.412	0.292
	SDA1	19	5	0.263	3.546	1.083	2.215	0.548
	SDB1	47	25	0.532	8.065	2.911	13.071	0.923
	SXA1	23	9	0.391	5.220	1.687	3.599	0.722
	SXA2	26	4	0.154	2.800	0.774	1.633	0.388
	SXA3	5	3	0.600	3.000	1.055	2.778	0.640
	SXA4	9	5	0.556	5.000	1.465	3.857	0.741
	SXA5	33	9	0.273	4.197	1.395	2.503	0.601
	SXA6	12	3	0.250	2.833	0.888	2.182	0.542
	SXA7	19	4	0.211	2.579	0.610	1.394	0.283
	SXB1	18	5	0.278	3.745	1.080	2.104	0.525
	SXB2	3	3	1.000	3.000	1.099	3.000	0.667
	SXC1	4	1	0.250	1.000	0.000	1.000	0.000
Prefecture	HBA	24	5	0.208	3.644	1.231	2.824	0.646
	HBB	23	3	0.130	2.273	0.560	1.426	0.299
	HNA	25	15	0.600	7.391	2.410	7.911	0.874
	HNB	12	3	0.250	2.667	0.566	1.412	0.292
	SDA	19	5	0.263	3.546	1.083	2.215	0.548
	SDB	47	25	0.532	8.065	2.911	13.071	0.923
	SXA	127	36	0.283	7.435	2.936	11.886	0.916
	SXB	21	8	0.381	4.857	1.493	2.809	0.644
	SXC	4	1	0.250	1.000	0.000	1.000	0.000
Province	HB	47	6	0.128	5.362	1.067	2.106	0.525
	HN	37	18	0.486	18.000	2.442	7.564	0.868
	SD	66	28	0.424	19.304	2.894	11.967	0.916
	SX	152	44	0.289	19.183	3.153	14.944	0.933

N, number of individuals; MLG, multi-locus genotype; MLG ratio, ratio of multi-locus genotype to total individual numbers; eMLG, effective multi-locus genotype; *H,* Shannon-Wiener index; *G,* Stoddart and Taylor's index; *λ,* Simpson's index

Table 3 Analysis of molecular variance (AMOVA) of *Puccinia striiformis* f. sp. *tritici* populations

Groups	Source of variance	Degree of freedom	Sum of squares	Mean squares	Estimated variance	Percentage of variation (%)	*P* value
County	Among populations	16	524.116	32.757	0.922	25	0.001
	Among individuals	285	218.899	0.768	0.000	0	0.001
	Within individuals	302	827.500	2.740	2.740	75	0.001
Prefecture	Among populations	8	269.489	33.686	0.552	17	0.001
	Among individuals	293	473.526	1.616	0.000	0	0.001
	Within individuals	302	827.500	2.740	2.740	83	0.001
Province	Among populations	3	151.629	50.543	0.366	12	0.001
	Among individuals	298	591.386	1.985	0.000	0	0.001
	Within individuals	302	827.500	2.740	2.740	88	0.001

Shandong and Hebei subpopulations, contrasting with a lower migration rate between Henan and Hebei subpopulations. The above results might reflect that varying levels of gene flow and migration happened among the studied regions.

The level of migration could also be determined by assessing the multi-locus genotypes (MLGs) shared between subpopulations. A total of 93 MLGs were detected in 302 individuals (Additional file 1: Table S5), of which six MLGs (MLG-10, MLG-63, MLG-69, MLG-70, MLG-71, and MLG-75) were shared within county, five MLGs (MLG-63, MLG-69, MLG-70, MLG-71, and MLG-75) were shared within prefecture and three MLGs (MLG-63, MLG-69, and MLG-70) were shared within province (Fig. 1). Shared MLGs distribution reflected that Hebei subpopulations had a large number of shared MLGs only with Shandong subpopulations, and there was no shared MLG with Henan subpopulations. However, Shaanxi subpopulations shared MLGs with Shandong and Henan subpopulations, suggesting that there was a close genotype exchange between the subpopulations of Shaanxi and Henan as well as between Shaanxi and Shandong. These results imply that the *Pst* inoculum sources from Shaanxi converged in Shandong and Henan, and then *Pst* inoculum sources continued to spread northward to Hebei through Shandong.

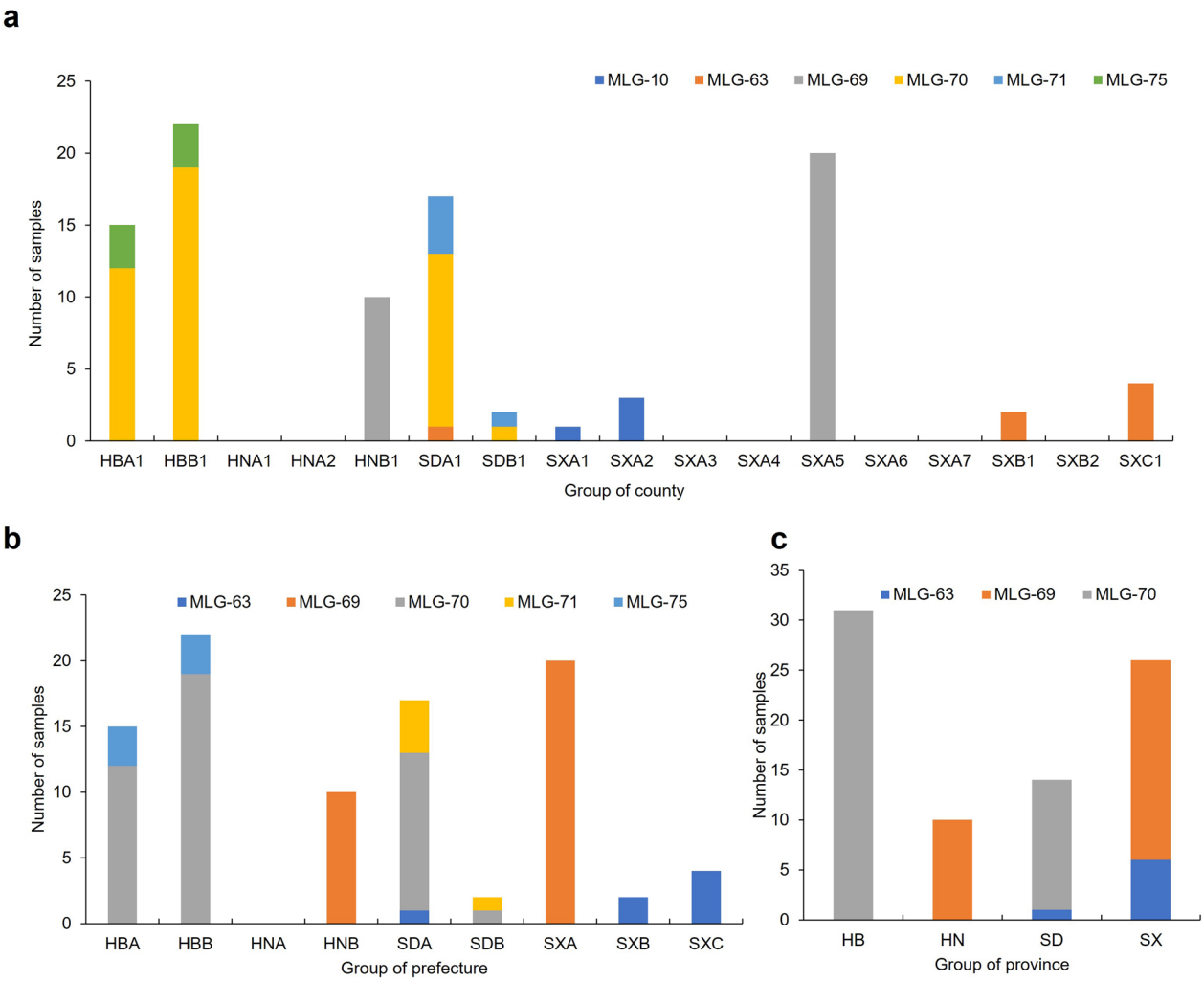

Fig. 1 Distribution of shared multi-locus genotypes (MLGs) of *Puccinia striiformis* f. sp. *tritici* populations under three levels of group divisions. **a** Populations based on group of counties from Ningjin (HBA1), Daming (HBB1), Dancheng (HNA1), Xihua (HNA2), Lankao (HNB1), Fushan (SDA1), Yuncheng (SDB1), Mei (SXA1), Qishan (SXA2), Fengxiang (SXA3), Fufeng (SXA4), Long (SXA5), Qianyang (SXA6), Feng (SXA7), Xiyi (SXB1), Zhouzhi (SXB2), and Chenggu (SXC1). **b** Populations based on group of prefecture from Xingtai (HBA), Handan (HBB), Zhoukou (HNA), Kaifeng (HNB), Yantai (SDA), Heze (SDB), Baoji (SXA), Xi'an (SXB), and Hanzhong (SXC). **c** Populations based on group of provinces from Hebei (HB), Henan (HN), Shandong (SD), and Shaanxi (SX)

Phylogenetic tree

A circular phylogenetic tree based on Nei's genetic distance by unweighted pair group method with arithmetic mean (UPGMA) method (Fig. 2) revealed three molecular groups (MGs) at the county level. The MG in blue, with 11 subpopulations across four provinces, was dominated by subpopulations from Shaanxi (54.55%), followed by subpopulations from Shandong (18.18%) and Hebei (18.18%). The MG in green comprised subpopulations from Shaanxi (60.00%) and Henan (40.00%). The MG in red consisted of subpopulations that were solely from Shaanxi. Notably, Shaanxi subpopulations were distributed across three MGs, indicating genetic connectivity between Shaanxi and the North China Plain regions.

Population structure

In this study, three analytical approaches were employed to assess the spatial distribution of the *Pst* populations: the nonparametric model-based principal coordinate analysis (PCoA), nonparametric model-based discriminant analysis of principal components (DAPC), and the parametric model-based Bayesian analysis.

In the PCoA analysis, 22.13% of the variation was along the horizontal principal coordinate 1, and 17.25% of the variation was along the vertical principal coordinate 2 (Fig. 3). Moreover, the subpopulations from Shaanxi showed the most dispersal pattern and were mostly located in every quartiles, which had clearly and relatively extensive population exchanges with subpopulations from Henan and Shandong. In contrast, the

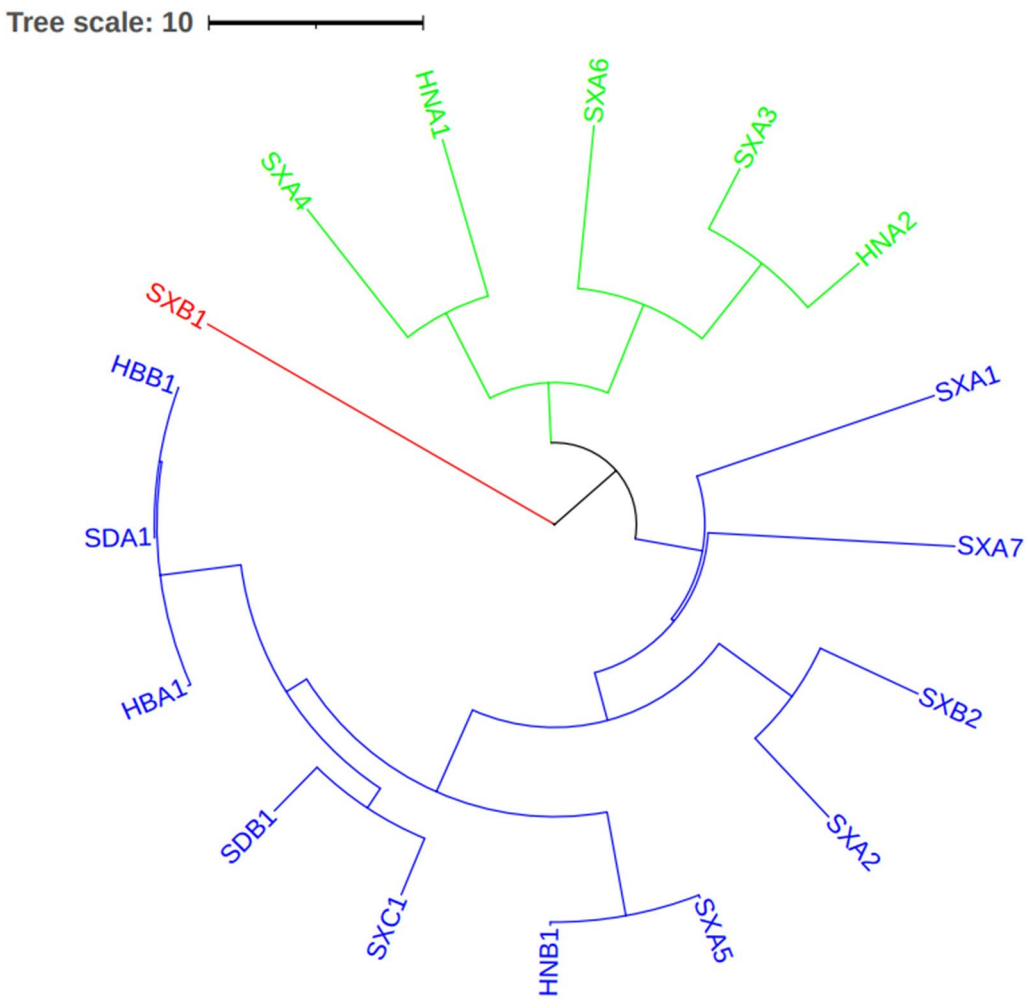

Fig. 2 Phylogenetic tree based on Nei's genetic distance constructed using the unweighted pair group method with arithmetic mean (UPGMA) method at county level populations from Ningjin (HBA1), Daming (HBB1), Dancheng (HNA1), Xihua (HNA2), Lankao (HNB1), Fushan (SDA1), Yuncheng (SDB1), Mei (SXA1), Qishan (SXA2), Fengxiang (SXA3), Fufeng (SXA4), Long (SXA5), Qianyang (SXA6), Feng (SXA7), Xiyi (SXB1), Zhouzhi (SXB2), and Chenggu (SXC1)

subpopulations from Hebei only overlapped with the subpopulations from Shandong, suggesting a stronger *Pst* exchange between Hebei and Shandong.

DAPC method was employed, which also does not rely on any underlying assumptions or premises. Optimal population separation was achieved when assuming a grouping of 2 (Fig. 4). However, when assuming a grouping of 3, a slight overlap between the red and blue components hindered complete separation of the groups. The geographical distribution of the population structure was visualized for the assumed groupings of 2 and 3 in Fig. 5. When K was set as 2, the overall trend across county, prefecture, and province revealed that the content of green groups gradually decreased from the southern to the northern regions, while the content of red groups increased in the opposite direction (Fig. 5a–c). Notably, the Hebei subpopulations primarily consisted of a single red group, whereas the other populations exhibited various degrees of mixture. When K was set as 3, the composition of Shaanxi subpopulations was the most complex (Fig. 5d–f). In contrast, the composition in Hebei subpopulations was more uniform. It was suggested that genetic differentiation occurred from south to north and from west to east, with the inferred route from Shaanxi to Henan, Shandong, and finally Hebei.

Population structure was also performed based on the parametric model-based Bayesian analysis. The results showed that when the assumption of grouping was set as K = 3, the population showed the best grouping value (Additional file 2: Figure S1). When K = 2 or K = 3, it has the same result as the DAPC grouping (Additional file 2: Figure S2).

Based on the above three methods, the findings revealed distinctive patterns of the genetic structure among the populations. It suggested that the genetic composition of Hebei subpopulations was more similar to Shandong subpopulations, followed by Shaanxi subpopulations, and less similar to Henan subpopulations. Moreover, a certain similarity was observed between the Shandong and Shaanxi subpopulations, suggesting that *Pst* dispersal likely occurred through gradual dissemination, where it spread to Henan and Shandong province occurred via Shaanxi originally and then subsequent from Shandong to Hebei. Overall, the role of the inoculum from Henan in the dispersal process toward Hebei was considered insignificant.

Reproductive mode

The linkage disequilibrium analysis of the *Pst* populations showed that Dancheng (HNA1), Fengxiang (SXA3), and Zhouzhi (SXB2) accepted the null hypothesis with random recombination (Additional file 2: Figure S3). It indicated that the populations likely had sexual recombination in Henan and Shaanxi.

Discussion

Population genetics plays a crucial role in dissecting the interrelation between different regions and understanding population dynamics, providing a theoretical framework for investigating the dispersal of wheat stripe rust and developing integrative management strategies (Linde 2010). In this study, SSR markers were employed to characterize *Pst* populations from multiple wheat ecological zones in Shaanxi, Henan, Hebei, and Shandong provinces, including the spring epidemic hotspots in major wheat growing regions. Our study suggested the potential migration of *Pst* from Shaanxi province to the North China Plain, providing insights into its most likely dispersal route. Our study advances the understanding of wheat stripe rust epidemics in the spring epidemic regions of China.

According to empirical investigations, when a population migrates from the center of a range to the periphery, the genetic diversity tends to decline and the genetic differentiation tends to increase (Duncan et al. 2015; Pironon et al. 2017). The Shaanxi subpopulations in our study had the highest genetic diversity, whereas the Hebei subpopulations had the lowest, which may be attributed to the presence of sexual recombination of *Pst* in this region (Duan et al. 2010). Another possible reason is that Shaanxi belongs to the northwest wintering region, and the pathogen population structure has been reconfigured due to the diversity of host resistance background, resulting in the high genetic diversity of the population (Chu et al. 2021). The most homogeneous population composition and lowest genetic diversity were found in Hebei, suggesting that external *Pst* inoculum initiated the

(See figure on next page.)

Fig. 3 Principle coordinate analysis (PCoA) of *Puccinia striiformis* f. sp. *tritici* populations analyzed using GenAlEx 6.5. Each color represents a population. **a** Populations based on group of counties from Ningjin (HBA1), Daming (HBB1), Dancheng (HNA1), Xihua (HNA2), Lankao (HNB1), Fushan (SDA1), Yuncheng (SDB1), Mei (SXA1), Qishan (SXA2), Fengxiang (SXA3), Fufeng (SXA4), Long (SXA5), Qianyang (SXA6), Feng (SXA7), Xiyi (SXB1), Zhouzhi (SXB2), and Chenggu (SXC1). **b** Populations based on group of prefecture from Xingtai (HBA), Handan (HBB), Zhoukou (HNA), Kaifeng (HNB), Yantai (SDA), Heze (SDB), Baoji (SXA), Xi'an (SXB), and Hanzhong (SXC). **c** Populations based on group of provinces from Hebei (HB), Henan (HN), Shandong (SD), and Shaanxi (SX)

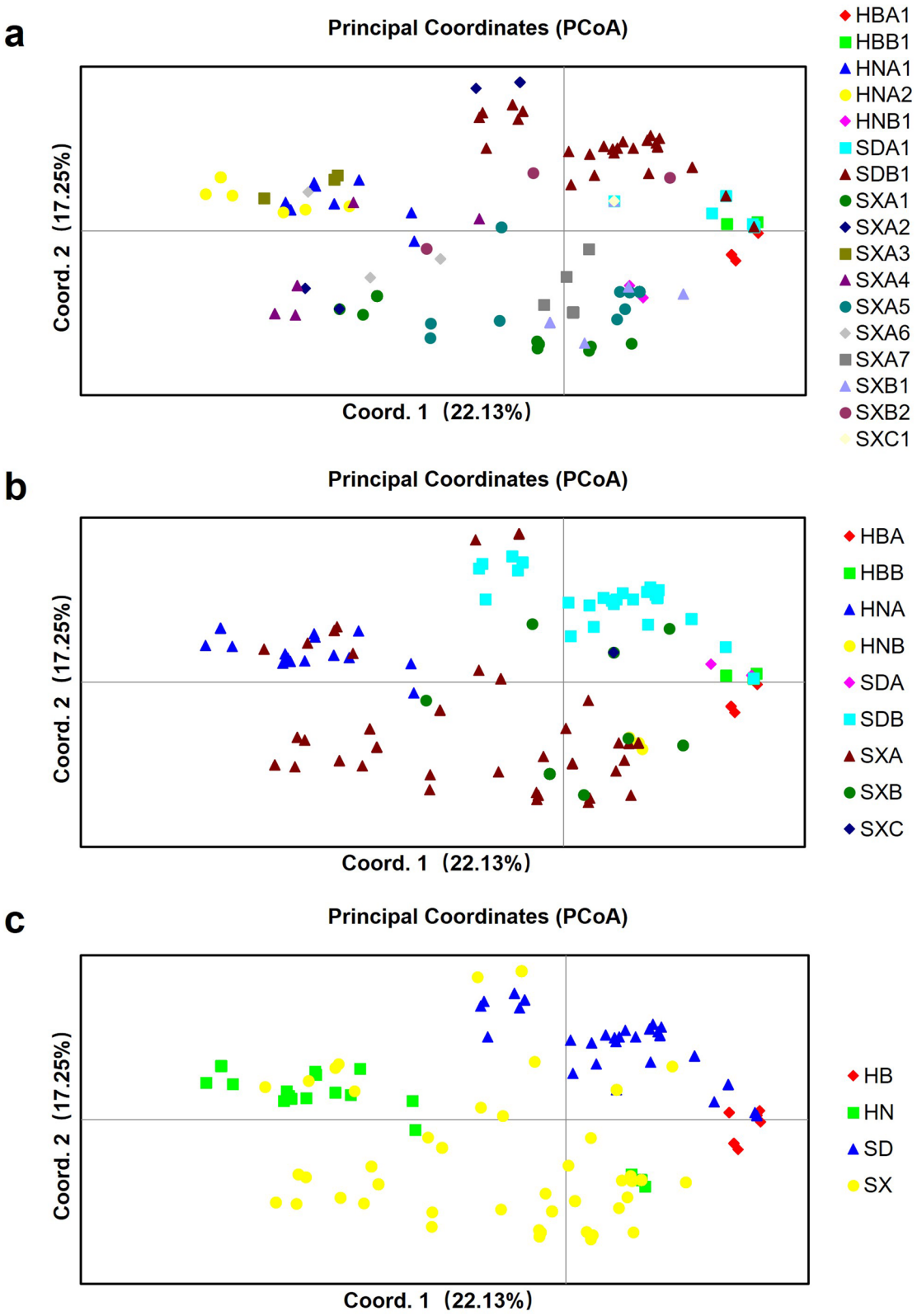

Fig. 3 (See legend on previous page.)

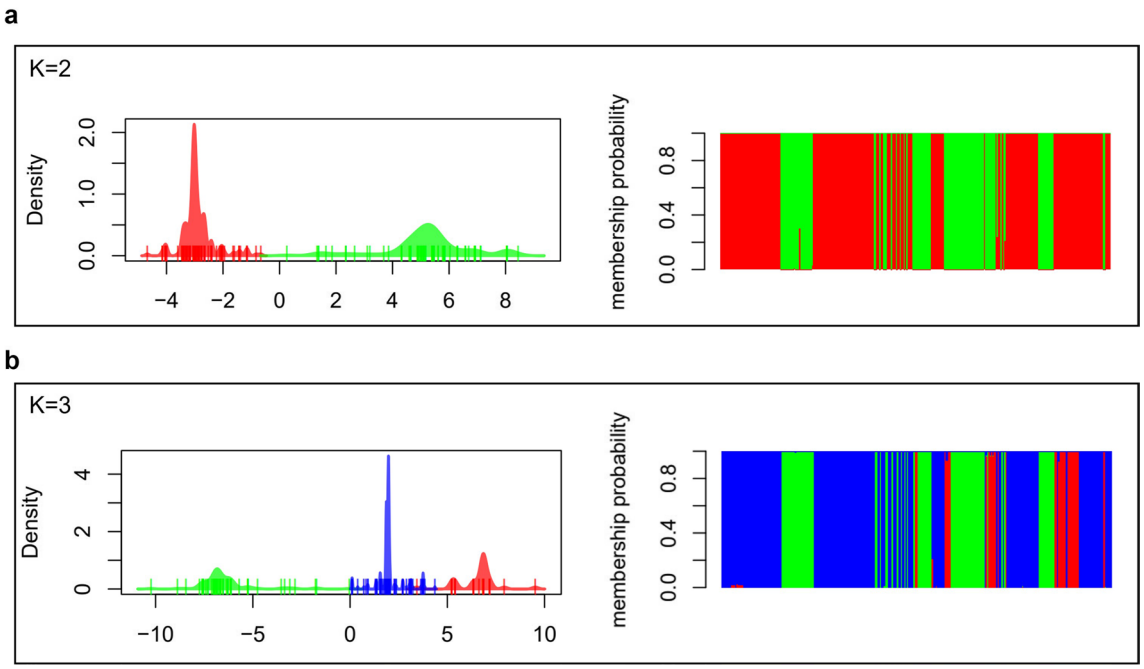

Fig. 4 Genetic structure analysis results of *Puccinia striiformis* f. sp. *tritici* populations obtained by the "Adegenet" function in "Poppr" package in R program 4.2.1. **a** Densities of populations on a given discriminant function with different colors for different populations (on the left side) and bar plot with assignment of samples into different clusters when K = 2 (on the right side). **b** Densities of populations on a given discriminant function with different colors for different populations (on the left side) and bar plot with assignment of samples into different clusters when K = 3 (on the right side)

disease epidemics in the region, which is consistent with previous empirical conclusions (Chen et al. 2014).

The findings of phylogenetic clustering revealed that *Pst* populations in four provinces were included in a mixed group on the phylogenetic tree, suggesting the considerable urediniospores exchange between the Shaanxi province and the North China Plain. The phylogenetic tree revealed a closer genetic relationship between *Pst* populations from Shaanxi and Henan provinces. It is likely that the two provinces are adjacent geographically and the *Pst* populations exchange more frequently than other provinces.

The Shaanxi subpopulations exhibited the highest level of dispersion in the PCoA, with notable overlaps observed with the Henan and Shandong subpopulations, suggesting a substantial population exchange between these regions. Conversely, the Hebei subpopulations only showed overlap with the Shandong subpopulations. The DAPC further supported these findings, revealing that the Shaanxi subpopulations displayed the greatest complexity and possessed a unique demographic component. In contrast, Hebei and Shandong subpopulations shared a singular population composition, while Shaanxi subpopulations showed the closest resemblance to that of Henan subpopulations. These results support the hypothesis of the genetic differentiation occurring from south to north and from west to east of China, following the routes from Shaanxi to Henan, Shandong, and then via Shandong to Hebei.

In addition, we provided evidence that the dispersal of *Pst* from Shaanxi to the North China Plain occurred gradually, involving intermediary regions such as Henan and Shandong provinces, before reaching Hebei province. Notably, the spread of *Pst* from Henan to Hebei province was negligible. Shandong province played a pivotal role as a bridge connecting Shaanxi and Hebei subpopulations, contributing to the spring epidemic in North China. The unique geographical ecology of Shandong province is believed to be a major factor. Being a coastal province, Shandong province experiences seasonal variations with wind movement from sealand (Yao et al. 2019), exerting a substantial influence on the spring epidemic in North China.

The shared MLGs, the decline in genetic diversity from west to east of China, and the absence of linkage disequilibrium indicated that Shaanxi province served as the origin of wheat stripe rust in the studied region. The route of pathogen dispersal between regions can be inferred based on the principle that the genetic diversity of the source population is typically greater than that of downstream populations (Savolainen et al. 2002; Ali et al. 2014). Previous studies on wheat stripe rust have proposed various

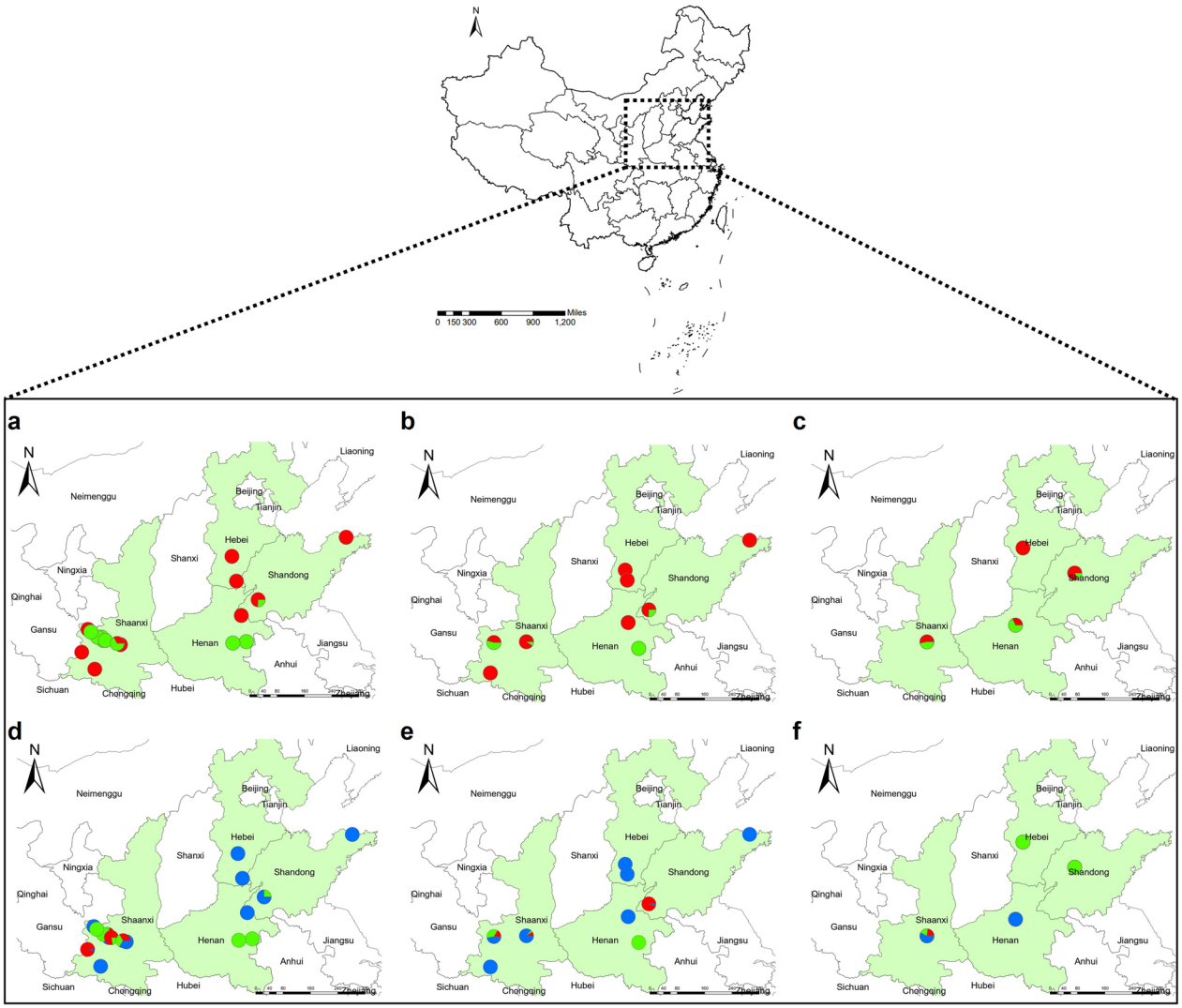

Fig. 5 Discriminant analysis of principal components (DAPC)-based geographical distributions by the "Adegenet" function in "Poppr" package in R program 4.2.1. **a–c** correspond to the DAPC-based assignment in group of counties group of prefecture and group of province respectively when K = 2, and **d–f** correspond to the DAPC-based assignment in group of counties, group of prefecture and group of provinces respectively when K = 3

sources and directions of dispersal. For instance, Ali et al. (2014) suggested that the genetic diversity of the Himalayas and surrounding regions have contributed to the emergence of wheat stripe rust. Wan et al. (2015) identified Gansu province as a primary source, with dispersal towards Qinghai and Xinjiang regions. Wang et al. (2020) found that Hubei province had the highest genotype diversity, and the predominant flow was from Hubei province to North China. Alam et al. (2021) identified Dehong, Dali, Lincang, and Baoshan regions as potential sources of *Pst* in Yunnan province of China. In our study, the high genetic diversity observed in the Shaanxi subpopulations, coupled with the gradual decrease in diversity from west to east and south to north, suggests that Shaanxi is a likely source of wheat stripe rust dispersal. Furthermore, the linkage disequilibrium in Shaanxi province indicated the presence of recombinant variation, possibly contributing to genetic diversity. The shared MLGs among populations can also serve as molecular evidence of dispersal (Liang et al. 2013; Wan et al. 2015; Liu et al. 2021). Shaanxi subpopulations exhibited the broadest distribution of shared MLGs with Henan and Shandong subpopulations, further supporting that Shaanxi province is likely the *Pst* inoculum source to the other three provinces. Geographically, Shaanxi is located in the western part of the studied regions, and

potentially receives the oversummering inoculum source earlier (Additional file 1: Table S1).

The role of Southwestern oversummering regions in the nationwide epidemic is also worthy of attention. Southwestern oversummering regions were previously considered to be an independent epidemic region of wheat stripe rust with no exchange with other epidemic regions (Zeng and Luo 2006). Recent evidence has proven that there was an exchange of *Pst* inoculum between Yunnan and Hubei, Jiangsu, Zhejiang regions, and the middle and lower reaches of the Yangtze River (Li et al. 2021; Huang et al. 2022; Ju et al. 2022). Of greater significance, Yan et al. (2023) found that the south of Hubei served as a "stopover" station for the inoculum sources from Yunnan to Zhejiang province. Therefore, it is possible that *Pst* inoculum on the North China Plain could come from Southwestern oversummering regions. The related study should be a key focus in future research.

The results of $\overline{r}_d$ values indicated that the *Pst* pathogen may have possibly completed the sexual phase of the fungi in certain areas of Shaanxi and Henan provinces (Additional file 2: Figure S3). Earlier reports suggested that under natural conditions, *Pst* could infect the *Berberis* spp., where some *Pst* populations have sexual recombination (Zhao et al. 2013; Wang et al. 2016). Indeed, *Berberis* spp. are distributed throughout the entire central and southern regions of Shaanxi province and the western regions of Henan province. Based on the distribution of *Berberis* spp. and linkage disequilibrium analysis, it could be inferred that there was a high likelihood of sexual recombination of *Pst* occurring in Shaanxi province.

The warm winters attributed to climate change have facilitated the favorable overwintering conditions for wheat stripe rust in Shaanxi province, consequently promoting the winter reproduction of *Pst* (Hu et al. 2020). The continuous occurrence of wheat stripe rust in Shaanxi Province significantly influences the overall epidemic of this disease in China, representing a prominent core epidemic system (Wu et al. 2016). Population genetic analysis provides valuable insights into the role of *Pst* in the Shaanxi province during the 2022 spring epidemic, which extended across a substantial portion of the North China Plain.

Conclusions

In this study, we performed analyses of the population genetic structure in four provinces (Shaanxi, Henan, Hebei, and Shandong) and concluded that the spread of *Pst* to Henan and Shandong province occurred via Shaanxi province originally, followed by subsequent transmission to Hebei province through Shandong province. It is therefore of great theoretical and practical significance to pay attention to the initial inoculum of *Pst* in these regions to control the spring prevalence of wheat stripe rust.

Methods

Pst isolate sampling

From February to June of 2022, fresh *Pst*-infected leaves were collected from Shaanxi, Henan, Hebei, and Shandong provinces in China. To give a representative number of isolates, each sampling site was separated at least two kilometers. In each site, at least three field plots were sampled with 2–5 leaf samples per field plots. The *Pst*-infected leaves were packed separately into sulfuric acid paper bags and stored in a 4°C dryer for later use. A single lesion from the *Pst*-infected leaves was cut and placed in a 2 mL centrifuge tube for DNA extraction (Ali and Hodson 2017). A total of 302 *Pst* isolates were collected and the geographic information was listed in Additional file 1: Table S1.

DNA extraction and SSR amplification of *Pst*

The genomic DNA of wheat stripe rust was extracted by the cetyltrimethylammonium bromide (CTAB) method described by Wan et al. (2015). For genotype amplification, thirteen pairs of published SSR primers were selected (Enjalbert et al. 2002; Bahri et al. 2009; Chen et al. 2009b; Zhan et al. 2015) (Additional file 1: Table S6). Fluorescent labeling was synthesized by fluorescent modification of each pair of SSR primers and followed an amplification protocol as described by Wang et al. (2021). All PCR products were sent to Beijing Tsingke Biotechnology Co., Ltd. for capillary electrophoresis, and the electrophoresis process was carried out on Applied Biosystems 3730xl DNA analyzer. GeneMarker 2.2.0 was used to view the electrophoresis results from the Peak map file in .fsa format. The size of the target band was judged by the following criteria: (1) The fluorescence value should be higher than 500; (2) The loci with three or more obvious amplification peaks were recorded as deletion (Berlin et al. 2013); (3) If two peaks occur with the intensity of one lower than one-third of the other, only the highest peak was recorded. The band size matrix was organized to the format required by GenAlEx 6.5 (Peakall and Smouse 2012) and was converted to the .csv data format for analysis by "Poppr" package in R program 4.2.1 (Kamvar et al. 2015).

Genetic diversity and genotypic diversity analysis

To calculate genetic diversity, number of polymorphic alleles (*Na*), number of effective alleles (*Ne*), Shannon's information index (*I*), observed heterozygosity (*Ho*),

and expected heterozygosity (*He*) were obtained using GenAlEx 6.5 (Peakall and Smouse 2012). The multi-locus genotype (MLG), effective multi-locus genotype (eMLG), Shannon-Wiener index (*H*), Stoddart and Taylor's index (*G*), and Simpson's Index (λ) were calculated by "Poppr" package in R program 4.2.1(Kamvar et al. 2015) for genotypic diversity evaluation.

Population differentiation

GenAlex 6.5 (Peakall and Smouse 2012) was used to calculate the genetic divergence indexes to clarify the genetic divergence using the analysis of molecular variance (AMOVA) and fixation index (F_{ST}). Number of migrations (*Nm*) based on $Nm = (1\text{-}F_{ST})/4F_{ST}$ was calculated to observe gene flow between populations. The shared MLGs that were detected in two populations were also statistical to infer gene flow.

Phylogenetic analysis

Based on Nei's genetic distance matrices obtained from GenAlex 6.5 (Peakall and Smouse 2012), MEGA 11.0 was used to construct a circular phylogenetic tree using the UPGMA method to determine the hypothetical clustering of molecular groups.

Population structure analysis

Three methods were adopted here: (1) PCoA in GenAlEx 6.5 software was used to observe the two-dimensional spatial distribution of each population based on the triangular matrix of Nei's genetic distance between individuals, and the nonparametric model was used to output the principal coordinates. (2) DAPC was generated by the "Adegenet" function in "Poppr" package in R program 4.2.1 (Jombart et al. 2010). (3) STRUCTURE 2.3.3 software was used to group individuals according to their genetic structure. The mixed ancestor model that did not consider the source of the individual population was selected. The putative K was set from 2 to 10 with 20 iterations. The length of the burn-in period was set to 2000 and the number of Markov chain Monte Carlo (MCMC) repetitions after burn-in was 10,000.

Detection of reproductive mode

In order to test possible sexual recombination, the index of association (I_A) and the standardized index of association ($\bar{r}_d$) of all county-level subpopulations were calculated. The significance of linkage disequilibrium was evaluated by 999 random stimulations in "Poppr" package in R program 4.2.1. The null hypothesis is that the gene linkage between populations was balanced, and populations were randomly recombined (Kamvar et al. 2015).

Abbreviations

AMOVA	Analysis of molecular variance
DAPC	Discriminant analysis of principal components
eMLG	Effective multi-locus genotype
F_{ST}	Fixation index
G	Stoddart and Taylor's index
H	Shannon-Wiener index
He	Expected heterozygosity
Ho	Observed heterozygosity
I	Shannon's information index
I_A	Index of association
λ	Simpson's index
MCMC	Markov chain Monte Carlo
MG	Molecular group
MLG	Multi-locus genotype
MLG ratio	Ratio of multi-locus genotype to total individual numbers
N	Number of individuals
Na	Number of polymorphic alleles
Ne	Number of effective alleles
Nm	Number of migrants
PCoA	Principal coordinate analysis
Pst	*Puccinia striiformis* f. sp. *tritici*
SSR	Simple sequence repeat
$\bar{r}_d$	Standardized index of association
UPGMA	Unweighted pair group method with arithmetic mean

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42483-024-00231-2.

Additional file 1: Table S1. Geographic information of *Puccinia striiformis* f. sp. *tritici* samples. **Table S2.** The fixation index (F_{ST}) and number of migrants (*Nm*) at the county level. **Table S3.** The fixation index (F_{ST}) and number of migrants (*Nm*) at the prefecture level. **Table S4.** The fixation index (F_{ST}) and number of migrants (*Nm*) at the province level. **Table S5.** Number of multi-locus genotypes (MLGs) detected in county-level populations. **Table S6.** Information of 13 pairs of simple sequence repeat (SSR) primers.

Additional file 2: Figure S1. K value diagram with optimal K = 3 by Bayesian analysis based on STRUCTURE 2.3.3 software. **Figure S2.** Population structure of *Puccinia striiformis* f. sp. *tritici* populations based on STRUCTURE 2.3.3 software when K = 2 and K = 3 (From No. 1 to No. 17, they represent populations from Ningjin (HBA1), Daming (HBB1), Dancheng (HNA1), Xihua (HNA2), Lankao (HNB1), Fushan (SDA1), Yuncheng (SDB1), Mei (SXA1), Qishan (SXA2), Fengxiang (SXA3), Fufeng (SXA4), Long (SXA5), Qianyang (SXA6), Feng (SXA7), Xiyi (SXB1), Zhouzhi (SXB2), and Chenggu (SXC1), respectively). **Figure S3.** Histograms obtained by "Poppr" package in R program 4.2.1 showing Dancheng (HNA1), Fengxiang (SXA3), and Zhouzhi (SXB2) populations with the possibility of sexual recombination.

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Author contributions

ZM and QS designed the research; MD and YB provided sampling help; ZY and ZW analyzed the data; XL and XQ provided assistance for experiment; CZ and AA wrote the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Not applicable.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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