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Tracking the North American Asian Longhorned Beetle Invasion With Genomics

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ABSTRACT

Biological invasions pose significant threats to ecological and economic stability, with invasive pests like the Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky, ALB) causing substantial damage to forest ecosystems. Effective pest management relies on comprehensive knowledge of the insect's biology and invasion history. This study uses genomics to address these knowledge gaps and inform existing biosurveillance frameworks. We used 2768 genome-wide single nucleotide polymorphisms to compare invasive *A. glabripennis* populations in North America, using genomic variation to trace their sources of invasion and spread patterns, thereby refining our understanding of this species' invasion history. We found that most North American *A. glabripennis* infestations were distinct, resulting from multiple independent introductions from the native range. Following their introduction, all invasive populations experienced a genetic bottleneck which was followed by a population expansion, with a few also showing secondary spread to satellite infestations. Our study provides a foundation for a genome-based biosurveillance tool that can be used to clarify the origin of intercepted individuals, allowing regulatory agencies to strengthen biosecurity measures against this invasive beetle.

Mingming Cui and Amanda D. Roe are joint first authors.

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1 | Introduction

Biological invasions pose a significant threat to the ecological stability of our forests (Aukema et al. 2011; Pejchar and Mooney 2009; Pyšek et al. 2020) and are considered one of the greatest threats to biodiversity (Clavero and Garcia-Berthou 2005; Mainka and Howard 2010). Costs of biological invasions are equivalent to natural disasters (Turbelin et al. 2023) and recent invasions of the emerald ash borer (*Agrilus planipennis*) and hemlock wooly adelgid (*Adelges tsugae*) in North America have highlighted the devastating long-term impacts of invasive insects once these pests become established (Eschtruth, Evans, and Battles 2013; Herms and McCullough 2014; Holmes et al. 2009). Therefore, we must focus on preventing invasions and rapidly responding to new invasive pests to reduce the likelihood of their establishment (Epanchin-Niell and Liebhold 2015). However, these proactive management approaches require detailed knowledge of each pest and its invasion pathway to establish strategies that will reduce the likelihood of future introductions (Bilodeau et al. 2019; Hamelin and Roe 2020; Roe et al. 2019).

Genomics, when integrated into a robust biosurveillance framework, can fill critical knowledge gaps, support proactive management of invasions, and improve global biosecurity (Roe et al. 2019; van Rees et al. 2022). Highly abundant genomic markers, such as single nucleotide polymorphisms (SNPs) obtained through genotyping-by-sequencing (GBS) (Elshire et al. 2011), can provide detailed knowledge on invasive pest biology, including insights to the invasion history, pathways of introduction, and the regional sources of invasion (Hamelin and Roe 2020). For example, genome-wide SNPs resolved invasion pathways for *Aedes aegypti* and showed that many individuals had signatures of insecticide resistance, highlighting the risk of relying solely on these products to prevent their spread (Schmidt et al. 2019). In another invasive mosquito, *Aedes albopictus*, human-assisted transport and road corridors were identified as important pathways for spread using highly variable genomic markers (Sherpa et al. 2020). Picq et al. (2018) showed that genome-wide markers could reliably trace the population sources for *Lymantria dispar asiatica* and *L. d. japonica* and then used these data to identify the sources of intercepted moths, providing detailed knowledge of historic invasions and a foundation for a genomic-based assay (Picq et al. 2023). These studies, among many others, highlight the breadth of knowledge that can be gained from genomic data on the invasion process and its ability to inform management responses to these threats.

The Asian longhorned beetle (Cerambycidae: *Anoplophora glabripennis* Motschulsky) is a polyphagous wood-boring beetle introduced to hardwood forests in North America and Europe (Blackburn et al. 2020; Javal et al. 2017; Meng, Hoover, and Keena 2015). Recent work by Cui et al. (2022) described native *A. glabripennis* population variation using genome-wide SNPs and delineated distinct population structure among regional populations. They successfully assigned *A. glabripennis* individuals to regional groups with a limited number of SNPs, demonstrating the ability to use these genomic markers to trace individuals to known source populations.

Since its discovery in 1996 in Brooklyn, New York (USA), a number of *A. glabripennis* infestations have been detected in North

America (Figure 1a). Knowledge of the source and pathway of introduction for each infestation can provide valuable knowledge to guide management efforts and regulation of this species. Eradication is used to manage *A. glabripennis* in North America (Smith et al. 2009; Trotter III and Hull-Sanders 2015; Turgeon et al. 2022) and while established *A. glabripennis* populations have been successfully eradicated in several locations (Eyre and Barbrook 2021; Liebhold et al. 2016), these efforts are still ongoing in other infestations (Coyle et al. 2021). When a new infestation is detected, it is necessary to distinguish between unique invasions and satellite infestations caused by secondary spread during these control efforts. The possible source(s) of invasive *A. glabripennis* populations were previously explored using a combination of microsatellites and mitochondrial DNA by Carter, Smith, and Harrison (2010), and they suggested that separate introduction events were responsible for many North American and European populations but were unable to pinpoint the probable source populations. Similarly, Javal et al. (2019) suggested that multiple independent introductions were responsible for most European populations from the native range, and although at least one European population was founded from North America. However, confidence in determining the sources for the invasive North American populations was hampered by complex population variation, limited information in the selected genetic markers, and low sample size (Carter, Smith, and Harrison 2010; Javal et al. 2019). Genomic markers, like those used in Cui et al. (2022), are highly variable and can provide a valuable insight to the history and spread of invasive *A. glabripennis* populations, thereby informing future regulatory response plans (Bilodeau et al. 2019; Hamelin and Roe 2020; van Rees et al. 2022).

Here, we explored the *A. glabripennis* invasion in North America using genome-wide SNPs. We used genomic markers, and the native population structure described by Cui et al. (2022) to (1) characterize population structure among North American *A. glabripennis* populations, (2) trace the sources of invasion from the native range, and (3) quantify secondary spread within North America. Collectively, these data provide a clearer picture of the invasion history of *A. glabripennis* in North America.

2 | Methods

2.1 | Study Organism

The native range of the *A. glabripennis* is limited to China and the Korean Peninsula. The first breeding populations discovered outside of this native range occurred in 1996 in North America (Figure 1) and 2001 in Europe (Haack et al. 1996, 1997; Poland 1998; Lingafelter and Hoebeke 2002; Krehan 2002; Javal et al. 2017). It has been recorded on > 100 hardwood tree species (Sjöman, Östberg, and Nilsson 2014) with preference for *Acer*, *Populus*, *Salix*, and *Ulmus* (Haack 2006; Meng, Hoover, and Keena 2015; Turgeon et al. 2021). In China, *A. glabripennis* is considered a serious forest pest and is responsible for nearly 12% of the total losses attributable to forest pests and diseases, costing an estimated \$1.5 billion annually (Hu et al. 2009). As such, *A. glabripennis* is considered a high-risk invasive beetle in both native and introduced ranges (Haack et al. 2010). The typical life cycle of *A. glabripennis* spans 1 year in most regions

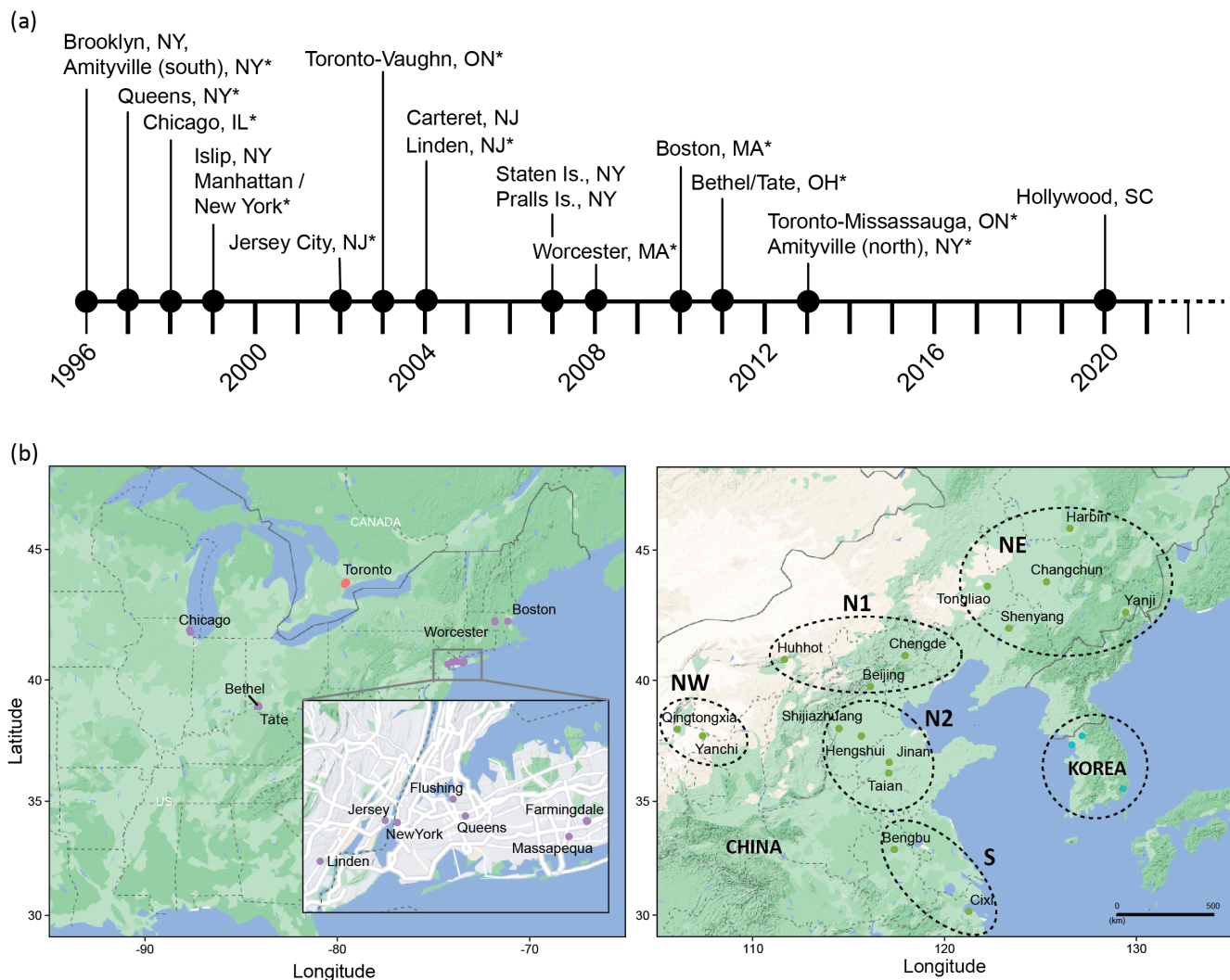


FIGURE 1 | Detection history of the North American *A. glabripennis* infestations and location of sampling areas for this study. (a) Date of detection and location of *A. glabripennis* infestations in North America. Infestations with (*) were included in the genomic analysis. MA, Massachusetts; OH, Ohio; IL, Illinois; NJ, New Jersey; NY, New York; SC, South Carolina. (b) Sampling map. The left panel shows geographic sampling in the invasive range, USA (purple) and Canada (red). Toronto (includes Toronto/Vaughan and Toronto/Mississauga), Amityville (south) (includes Massapequa, NY), Amityville (north) (includes Farmingdale, NY). The right panel shows sampling in the native range: China (green) and Korea (cyan). The different regions within China are illustrated by dashed ovals: North Plain region (N1, N2), Northwest (NW), Northeast (NE), South (S), as defined in Cui et al. (2022).

of China, although this is strongly dependent on environmental conditions (Lingafelter and Hoebeke 2002; Wang et al. 2023). For example, in the coldest regions in China, larvae typically require 2 years to complete their development (Lingafelter and Hoebeke 2002) and up to 3 years in cooler climates (Straw et al. 2015); while warmer locations have a synchronous univoltine life cycle with a single generation per year, similar to the native range (Schmitt 2023). The development time is relatively long compared to other cerambycid beetles (Lu et al. 2013; Bybee et al. 2004) and may influence the invasion dynamics of this species (Schmitt 2023).

2.2 | Sampling and DNA Preparation

To determine the source(s) of the invasive populations found in Canada and the United States of America, we obtained 266

specimens over multiple years (1999–2017) (Figure 1; Table S1). We also used previously published *A. glabripennis* data (BioProject ID PRJNA824548) from China and South Korea to generate a native reference collection to define possible source populations (Cui et al. 2022).

A single leg or larval thoracic muscle was used for DNA extraction from each specimen. The tissue was surface sterilized using 95% ethanol and flash frozen in liquid nitrogen before being ground using a mixer mill (Retsch MM400, Germany) at 29 Hz for 1 min. DNA was extracted from this homogenate using the DNeasy 96 Blood & Tissue Kit (Qiagen, Hilden, Germany) with an added RNAase treatment following the manufacturer's instructions. We measured DNA quality and quantity using the NanoDrop ND-1000 spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA) and Qubit 2.0 Fluorometer (Thermo Fisher Scientific, Wilmington, DE, USA), respectively.

2.3 | Genotyping and Bioinformatics Processing

GBS libraries and Ion Torrent sequencing were performed at the *plateforme d'analyses génomiques* of the *Institut de Biologie Intégrative et des Systèmes* (IBIS, Université Laval, Québec, QC, Canada). Libraries for Ion Proton GBS were prepared using the procedure described by Abed et al. (2019) with the modification to include NsiI to the double digest PstI/MspI as described in de Ronne et al. (2023). Libraries were prepared for sequencing using an Ion CHEF, Hi-Q reagents, and P1 V3 chips (ThermoFisher Scientific, Waltham, MA, USA), and the sequencing was performed over 300 flows on an Ion Proton instrument (ThermoFisher Scientific), following manufacturer's instructions.

We used the Fast-GBS v1.0 pipeline to process raw sequencing reads (Torkamaneh et al. 2017; Torkamaneh, Larocche, and Belzile 2016). In this pipeline, it followed several steps to process the sequencing data. First, SABRE v1.0 was used to demultiplex single-end, 150bp barcoded reads (Joshi 2011) and Cutadapt v2.1 (Martin 2011) was applied to remove the GBS adapter sequences. We aligned the trimmed reads, with a minimum length of 50bp, to the *A. glabripennis* reference genome (GCA_000390285.1) (McKenna et al. 2016) using Burrows-Wheeler Aligner v0.7.17 (Li 2013). Samtools v1.8 (Li et al. 2009) was utilized to convert the SAM files to BAM format for indexing, and finally, PLATYPUS v0.8.1.1 was used to call variants within the pipeline, using a minimum mapping quality of 10 and maximum read length of 250bp (Rimmer et al. 2014). SNP variants were filtered using VCFtools v0.1.16 (Danecek et al. 2011) and PLINK v2.0 (Chang et al. 2015). We applied basic filters to retain biallelic SNPs and variants with a PASS flag, retaining loci with <50% missing data and individual samples with <20% missing data. Furthermore, we kept loci with <10% missing data per site, a read depth > 5, and minor allele frequency > 0.05. We then pruned SNPs in a sliding window of 50 SNPs (advanced by 5 SNPs each time) with $r^2 < 0.4$. Finally, we removed samples based on relatedness using the KING method (Manichaikul et al. 2010) integrated in PLINK, with a cutoff of 0.25 to remove full siblings.

2.4 | Genetic Diversity and Population Structure

To assess genetic diversity, we calculated observed heterozygosity (H_o) and expected heterozygosity (H_e) for individual native and invasive populations using STACKS v1.48 (Catchen et al. 2013) and then employed the Mann-Whitney U nonparametric test to compare the genetic diversity between the native and invasive populations. We also measured pairwise F_{ST} between populations using STACKS.

We performed principal component analyses (PCA) in adegenet v2.1.2 (Jombart 2008) to characterize genetic differentiation among all samples. We applied the maximum likelihood estimation method Admixture v1.3.0 (Alexander, Novembre, and Lange 2009) to estimate individual ancestry membership. This approach employs a cross-validation to identify the optimal K . We ran models with an ascending number of ancestral populations, ranging from 2 to 20, using a default fivefold cross-validation and selected the optimal K based on the lowest cross-validation error.

2.5 | Population Assignment

We applied a discriminant analysis of principal components (DAPC) in adegenet v2.1.2 (Jombart 2008; Jombart, Devillard, and Balloux 2010) to assign invasive *A. glabripennis* samples to populations from the native range. We ran the “dapc” function on all native *A. glabripennis* samples, retaining five principal components and three discriminant functions for the discriminant analysis. Based on the DAPC results obtained from the native dataset, we used the “predict.dapc” function to predict group membership results for all invasive *A. glabripennis* samples and visualized the assignment results in a contingency table.

To further explore the evolutionary relationships among samples, we computed a maximum likelihood (ML) phylogeny using 1000 bootstrap replicates under the GTRGAMMA model in RAxML v8.2.9 (Stamatakis 2014).

2.6 | Invasion History and Recent Gene Flow

To reconstruct the invasion history of North American *A. glabripennis*, we compared different invasion scenarios using an approximate Bayesian computation (ABC) method, implemented in DIYABC v2.1.0 (Cornuet et al. 2014). This approach simulates datasets for *a priori* invasion history models and compares these simulated datasets with the observed dataset. We followed a step-by-step procedure as previously described by Sherpa et al. (2019). We guided our scenario selection using results from previous genetic studies (Cui et al. 2022; Javal et al. 2019) and our current results.

The first three steps sequentially defined the divergence history of the native populations, while the next five steps identified the optimal invasion scenario for each invasive population (see Appendix S1 for further details). We only considered invasive populations with more than four individuals and a uniform genetic composition, that is, populations in which all individuals had a similar genetic composition; hence, we excluded populations from New York and New Jersey due to their demonstrated genetic complexity (see Admixture results). Based on the estimated population structure, we did not include a migration scenario in our DIYABC analyses. In the final step, we synthesized the previously inferred origins of each invasive population to construct a comprehensive evolutionary scenario. This scenario integrated all populations, and we then estimated posterior parameters, such as effective population sizes, population divergent time, and bottleneck duration. We simulated 20,000 datasets for each scenario, selecting all summary statistics for SNP loci in DIYABC. We evaluated each model (scenarios and/or associated priors) using PCA. In this process, we projected both the observed and simulated datasets onto a PCA space using the genetic summary statistics as components of the feature vector. We anticipated overlap between the observed and simulated datasets, supporting the validity of our models. For model selection and parameter estimation, we used 1000 trees simulated in DIYABC Random Forest v1.1.27 (Collin et al. 2021), an extended version of DIYABC that employs decision trees to facilitate model selection (Pudlo et al. 2016). This method generated classification

votes for each scenario and allows us to estimate the posterior probability for the selected scenario.

We measured recent migration rates between populations (the proportion of individuals that are immigrants per generation) using BA3-SNPS v1.1 (Mussmann et al. 2019), modified from BayesAss v3.04 (Wilson and Rannala 2003), which estimates recent gene flow between populations using Bayesian Markov Chain Monte Carlo resampling. We included only populations that contains more than 15 individuals, as BayesAss assumes low migration rates, which can be difficult to estimate accurately with smaller sample sizes (Meirmans 2014). First, we ran the analysis with the default value of each mixing parameter (i.e., 0.1). Based on the acceptance rates, we adjusted the mixing parameters until acceptance rates fell within the suggested range of ~0.2–0.6 (Wilson and Rannala 2003). We then performed 10 longer, independent runs with adjusted mixing parameters for allele frequencies of 0.5 and inbreeding coefficient of 0.01. Each run consisted of using 20 million iterations, with a burn-in of five million, sampled every 1000 iterations, and produced trace files with the -t flag. We calculated the Bayesian deviance as suggested by Meirmans (2014) to select the best run. Run #5 (Figure S1) had the lowest deviance value and was selected for downstream parameter estimation of migration rates between *A. glabripennis* populations.

3 | Results

3.1 | Sequencing and Genotyping

We generated ~335 million raw reads for all invasive *A. glabripennis* samples using GBS with a triple digest library. In sum, we obtained 969,515 SNP variants through the Fast-GBS pipeline. After variant filtering and quality control, 2768 SNPs and 490 individuals were retained. Our dataset included 156 invasive samples from North American infestations, which we combined with 331 previously published reference individuals from 16 sites in China and three putative native samples from Korea (Cui et al. 2022). A detailed summary of the number of individuals and SNPs retained after each filtering step is shown in Table S2.

3.2 | Genetic Diversity and Population Structure

We found that genetic diversity was generally lower in the invasive populations compared to those in the native range. H_o ranged between 0.259 and 0.326 for native populations and 0.151 and 0.270 for invasive North American populations; H_e ranges between 0.217 and 0.295 for the native populations and 0.132 and 0.235 for the invasive populations (Table 1; Table S3). The Mann–Whitney U -test confirmed such differences for both H_o and H_e estimates. Specifically, the H_o in native populations (mean = 0.291) was significantly higher ($p = 8.58e^{-07}$) compared to invasive populations (mean = 0.223). Similarly, H_e in native populations (mean = 0.260) was also significantly higher than in invasive populations (mean = 0.184, $p = 2.51e^{-06}$). Genetic distance between populations was represented by pairwise F_{ST} values (Figure 2a). The average F_{ST} between the invasive populations was 0.1547 ± 0.0075 , while between native reference populations, it was lower (0.0598 ± 0.0021), and between native and invasive populations, it was 0.096 ± 0.0021 (Table S4).

The native *A. glabripennis* reference collection samples were divided into distinct regional clusters previously delimited by Cui et al. (2022) (Figure S2; Figure 1b): (1) Northeast region (NE), bordered by the Greater Khingan Range to the west; (2) Northwest region (NW), bordered by the Helan Mountains to the east; (3) North Plain (divided into two regions, N1 & N2); (4) the South (S), bordered by the Huai River basin in the north; and (5) South Korea. They also showed that although Shijiazhuang (SHI) is geographically located in the North Plain, it is genetically more similar to the NW region, with SHI grouping with populations QI and YC rather than with geographically proximate populations in the North Plain. When we included the invasive samples (Figure 2b; Figure S3), we observed that no North American samples were associated with native Korean populations, USA samples formed groups nested within regions in China, and Toronto samples formed a single distinct cluster (Figures S3–S5).

In our admixture analysis, we selected $K=14$ as the optimal value for the combined dataset of native and invasive populations (Figure S6, showing K values from 3 to 14). Both our admixture results (Figure 2c) and PCA clustering (Figure S5) were largely congruent for the invasive populations, with a few exceptions. Three of our invasive populations (TOR, OH, IL) formed distinct and uniform admixture plots and PCA clusters across sites and sampling years (Figure 2c; Figure S5). The MA population showed a distinct and uniform admixture plot; however, we observed temporal variation among individuals in the PCA plots (Figure S5c). For example, all individuals collected from Worcester, MA, in 2008 formed a tight group nested within the South cluster, along with two individuals from Boston, MA, in 2010. The remaining samples (Worcester 2009 and Boston 2010) formed a loose group with no clear source (Figure S5c).

We also observed greater genetic complexity in our NY and NJ samples compared to the other invasive populations. The NY infestation was the oldest and most extensive, with samples spanning 14 years (1999–2013), and we observed spatial and temporal genetic variation among collection locations and time points. For example, the early samples from New York City (1999–2009) were admixed and formed a large mixed cluster in the PCA (Figure 2c; Figure S5b). Farmingdale (2013), however, formed a distinct group, separate from the remaining New York samples in both the admixture plot and PCA. Massapequa (2005–2007), Queens (1999–2001), Flushing (2004) and New Jersey (2003, 2006) showed variable levels of admixture and clustering within the PCA analyses (Figure 2c; Figure S5b,e).

3.3 | Population Assignment

To further refine our population assignments, we assigned invasive individuals to native reference population clusters using DAPC discriminant functions derived from a reference DAPC model (Figure 3a; Figure S7). We summarized these individual assignments in a contingency table (Figure 3b), with assignment results for each individual and their posterior membership probabilities shown in Table S5. Most invasive individuals were assigned to the N2 region in China, including all individuals in TOR, OH, and IL, as well as some individuals from MA, NJ, and NY. The remaining NY individuals were assigned to N1, including all individuals from Farmingdale, NY. A similar pattern

TABLE 1 | Sampling location and genetic diversity of *A. glabripennis* infestations in North America.

Country	State/ Province	Population	ID	N	Year sampled	H_o	H_e
USA	IL	Chicago	Chi	18	1999	0.254±0.005	0.235±0.004
		Boston	Bos	6	2010	0.204±0.006	0.153±0.004
	MA	Worcester	Wor	5	2008	0.234±0.006	0.183±0.004
		Worcester	Wor	3	2009	—	—
		Jersey City	Jers	2	2003	—	—
	NJ	Linden	Lin	4	2006	0.225±0.006	0.165±0.004
		Farmingdale	Far	12	2013	0.270±0.006	0.218±0.004
	NY	Flushing	Flush	4	2000	0.211±0.006	0.163±0.004
		Massapequa	Massap	14	2005	0.254±0.005	0.235±0.004
		Massapequa	Massap	1	2006	—	—
		Massapequa	Massap	4	2007	0.236±0.006	0.184±0.004
		NYC	NYC	7	2003	0.205±0.005	0.183±0.004
		NYC	NYC	1	2004	—	—
		NYC	NYC	1	2005	—	—
		NYC	NYC	4	2008	0.227±0.006	0.170±0.004
		NYC	NYC	5	2009	0.157±0.006	0.120±0.004
		Queens	Qu	3	1999	—	—
		Queens	Qu	4	2000	0.206±0.006	0.165±0.004
		Queens	Qu	8	2001	—	—
	OH	Bethel	Beth	5	2011	0.257±0.006	0.214±0.004
		Bethel	Beth	4	2012	0.244±0.006	0.200±0.004
		Bethel	Beth	2	2013	—	—
		Bethel	Beth	3	2014	—	—
		Bethel	Beth	16	2015	—	—
		Tate	Tate	1	2017	—	—
		Tate	Tate	1	2017	—	—
Canada	ON	Toronto/Vaughan	TOR1	32	2004	0.234±0.005	0.220±0.004
		Toronto/Mississauga	TOR2	5	2013	0.151±0.005	0.132±0.004

Note: Standard errors are presented for each value. Values for populations with a sampling size fewer than four were not calculated. Indices for native populations are provided in Table S3.

Abbreviations: H_e , expected heterozygosity; H_o , observed heterozygosity; N , number of individuals.

was observed in NJ, with individuals assigned to both N1 and N2 clusters, but with the addition of one individual assigned to the NE cluster—the only North American individual associated with this region. The MA infestation also had individuals assigned to N2, with six individuals assigned to S. This is consistent with the PCA results reported earlier (Figure S5c). Notably, no invasive individuals were assigned to the NW cluster.

To further clarify relationships between invasive individuals and native populations, we constructed an ML tree using our SNP dataset (2768 SNPs) (Figure 4). A few invasive populations were nested within native lineages with high support.

Individuals from TOR and OH were well supported within the N2 lineage and MA individuals were nested within the S clade. Individuals from Farmingdale were nested within the N1 clade. The remaining individuals from NY, IL, and NJ formed a single clade with low support values, and there was no clear, well-supported relationship to any native lineage.

3.4 | Invasion History and Recent Gene Flow

We used DIYABC to reconstruct the invasion history and population demographics of five North American populations

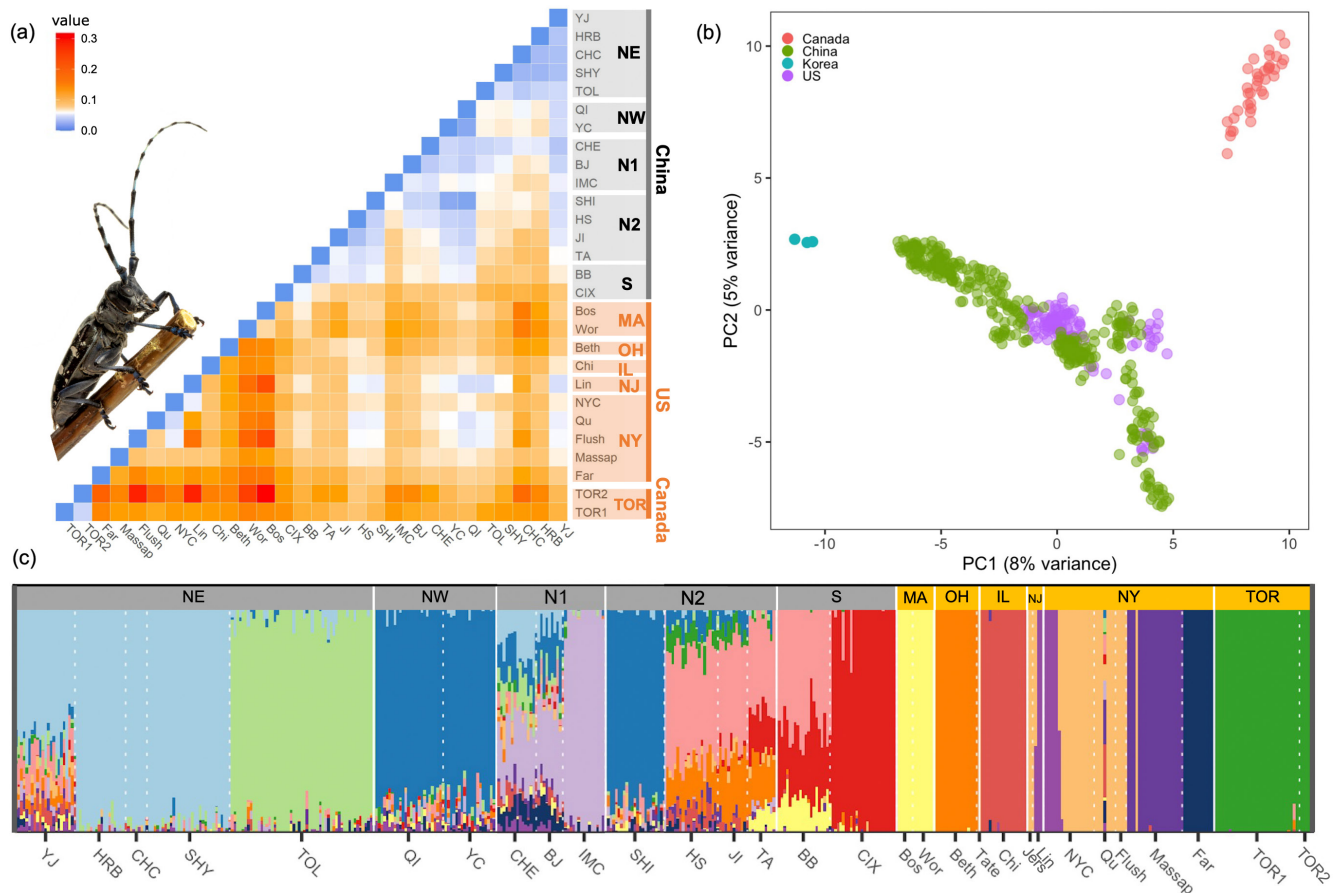


FIGURE 2 | Population structure of native and North American invasive *A. glabripennis*. (a) Pairwise F_{ST} between populations (populations with <4 individuals not shown), with a color ramp indicating degree of differentiation (blue=low, red=high) (see Table S4 for F_{ST} values). The native range includes YJ, Yanji; HRB, Harbin; CHC, Changchun; SHY, Shenyang; TOL, Tongliao; QI, Qingtongxia; YC, Yanchi; CHE, Chengde; BJ, Beijing; IMC, Huhhot; SHI, Shijiazhuang; HS, Hengshui; JI, Jinan; TA, Taian; BB, Bengbu; CIX, Cixi. Invasive range includes Bos, Boston; Wor, Worcester; Beth, Bethel; Chi, Chicago; Lin, Linden; NYC, New York; Qu, Queen; Flush, Flushing; Massap, Massapequa; Far, Farmingdale; TOR, Toronto. See Figure 1 for locations. (b) Principal component analysis of all *A. glabripennis* populations, color-coded by country. (c) Admixture bar plots showing the proportion of genetic membership for each individual, represented as vertical bars colored according to their estimated ancestry within each cluster. Optimal clustering is at $K=14$ (see Figure S6 for $K=3$ to $K=14$). Image of an *A. glabripennis* adult was provided by Dr. Brent Sinclair.

(MA, OH, IL, TOR, Far). Using an eight-step approach to DIYABC model selection, we selected a single optimal population history model for each population (Figure S8) and a combined native + North American invasion scenario (Figure 5). The observed dataset overlapped with the simulated datasets in the PCA (Figure S9). We selected scenarios in each step with the highest classification votes. Based on this optimal model, the average introduction time of invasive populations ranged from 14 (OH) to 25 (Farmingdale) years prior to the time of sample collection (i.e., the contemporary time in the DIYABC analysis), and the estimated year of introduction for these invasive populations span from 1979 (Farmingdale, NY; IL) to 2009 (OH) (95% confidence interval) (Figure 5; Table S6). The mean predicted founding population size for the invasive populations ranged from 53 (IL) to 55 individuals (TOR) but could have started from as few as 13 individuals (OH) (Table S6). Bottleneck events lasted between 10 and 19 years (mean bottleneck duration) but could have lasted as short as 2 years (IL, TOR, MA and OH) or as long as 36 years (Farmingdale). Between the time of introduction and the sampling date, the invasive populations expanded as they grew

and spread, with an average effective population size ranging from 494 (Farmingdale) to 519 (IL).

We also measured migration rates between populations in both the native and invasive ranges, calculating the proportion of individuals in a population that are immigrants from other populations per generation. This reflects recent migration or colonization events. We selected Run five (Figure S1) based on its Bayesian deviance to generate point estimates and calculated the migration rate within and among native and invasive populations (Figure 6). We observed evidence of gene flow from the native range to the invaded range, with an observed migration rate of 0.0161 (proportion of individuals) from Chengde (CHE, N1) to Queens (Qu, New York), while all other rates were <0.0123. Within the invasive range, we observed more frequent gene flow between populations, including Worcester to Boston (0.0339), New York City to Linden (0.0206), and from the first infestation of Toronto to the second (0.0196). We saw little to no contemporary gene flow from the invasive range back to the native range or among the major infestations in North America.

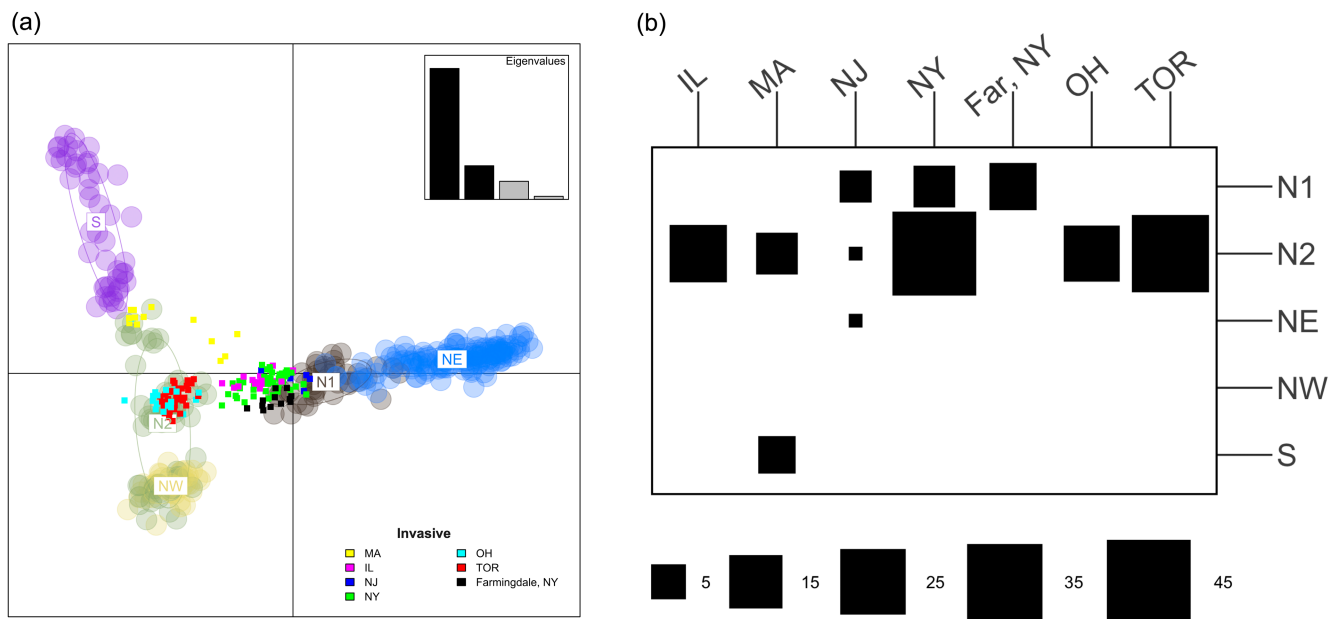


FIGURE 3 | Population assignment of invasive *A. glabripennis* individuals. (a) Scatterplot of two discriminant functions showing the clustering of invasive individuals (solid squares) with reference native populations (light circles). (b) Contingency table of individual assignments to a *priori* reference native populations based on DAPC discriminant functions. Square size indicates the number of invasive individuals (columns) assigned to each native population cluster (rows). MA, Massachusetts; OH, Ohio; IL, Illinois; NJ, New Jersey; NY, New York; TOR, Toronto; N1, North Plain region one; N2, North Plain region two; NW, Northwest; NE, Northeast; S, South. Single individuals from the NJ infestation were assigned to N2 and NE. Farmingdale (Far, NY) was treated separately from other NY samples based on the admixture results.

4 | Discussion

The Asian longhorned beetle is an invasive insect that poses a significant threat to hardwood forests throughout its invasive range. Genome-wide markers obtained from reduced representation libraries provide insight to the population variation among invasive *A. glabripennis* populations in North America. We showed that North American populations were structured, with multiple independent introductions from four sources in the native range. We also showed that secondary spread from initial introductions created new satellite infestations, which were likely human assisted given the relatively poor dispersal abilities of *A. glabripennis*. Finally, during their invasion, these populations experienced genetic bottlenecks followed by population expansion, demonstrating their resilience to founder effects. Collectively, our data fill important knowledge gaps about the invasion history of *A. glabripennis* in North America and can help inform future biosurveillance approaches and eradication efforts for other active infestations and in the event new breeding populations are discovered.

4.1 | Genetic Structure and Bottlenecks in the North American *A. glabripennis* Invasion

High genetic diversity typically provides populations with the evolutionary potential to adapt to new environments. However, introduced *A. glabripennis* populations in North America (Carter, Smith, Turgeon, et al. 2009; Javal et al. 2019) and in Europe (Javal et al. 2019) showed reduced genetic diversity relative to the native populations. This phenomenon was confirmed in our results (Table 1; Table S3), and based on these findings,

we included genetic bottlenecks during the initial founding within our demographic analyses (Figure 5). In fact, our demographic modeling predicted that the invasive populations were founded by relatively few individuals (Table S6). Despite this loss of diversity and limited number of founders, *A. glabripennis* populations established and expanded successfully following their introductions, as assumed in our DIYABC modeling and observed in various control efforts (e.g., Turgeon et al. 2022).

This phenomenon reflects a well-explained “genetic paradox” where invasive species are highly successful despite their initially low genetic diversity due to bottleneck effects (Estoup et al. 2016; Schrieber and Lachmuth 2017). One explanation for this paradox is the occurrence of multiple introductions, which can restore the reduced genetic diversity during the initial invasion by mitigating inbreeding and reintroducing genetic variation (Kolbe et al. 2004). This process is common among invasive insects (Garnas et al. 2016), with recent examples in termites (Blumenfeld et al. 2021; Eyer et al. 2021), *Spodoptera frugiperda* (Tay et al. 2022), *Trichocorixa verticalis* (Ortego et al. 2021), the invasion of *Lycorma delicatula* in South Korea (Kim et al. 2021), *Roeseliana roeselii* (Kaňuch et al. 2022) and *Bemisia argentifolii* (Wongnikong, Hereward, and Walter 2021).

Interestingly, however, the restoration of genetic diversity through admixture is not a prerequisite for invasion success, as demonstrated by our findings, where most of the invasive populations appeared to have resulted from independent introduction events and thus remain genetically distinct. Similar to our study, successful invasions can occur from independent introductions, such as for the invasive Hawaiian crickets *Teleogryllus oceanicus* (Zhang et al. 2021), small hive beetles *Aethina tumida* (Liu et al. 2021), and the melon fly *Bactrocera cucurbitae* (Dupuis

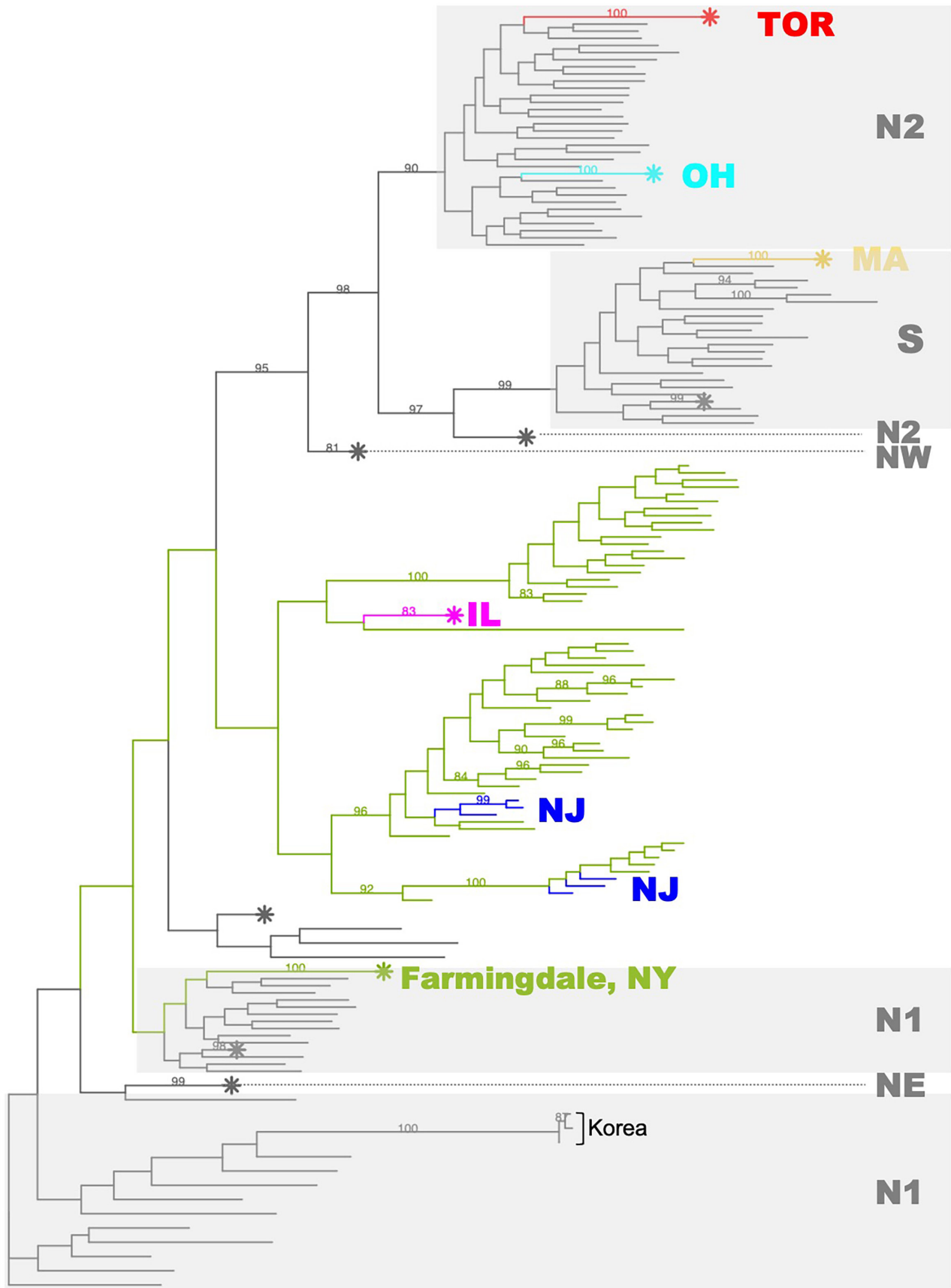


FIGURE 4 | Maximum likelihood phylogenetic tree (unrooted) of the complete *A. glabripennis* dataset ($n=2768$ SNPs). MA, Massachusetts; OH, Ohio; IL, Illinois; NJ, New Jersey; NY, New York; TOR, Toronto; N1, North Plain region one; N2, North Plain region two; NW, Northwest; NE, Northeast; S, South. Native lineages are colored in gray, while invasive populations are colored as in Figure 3. Branches marked with a “*” are collapsed clades containing multiple individuals. Branches with bootstrap values $> 80\%$ are labeled above the nodes.

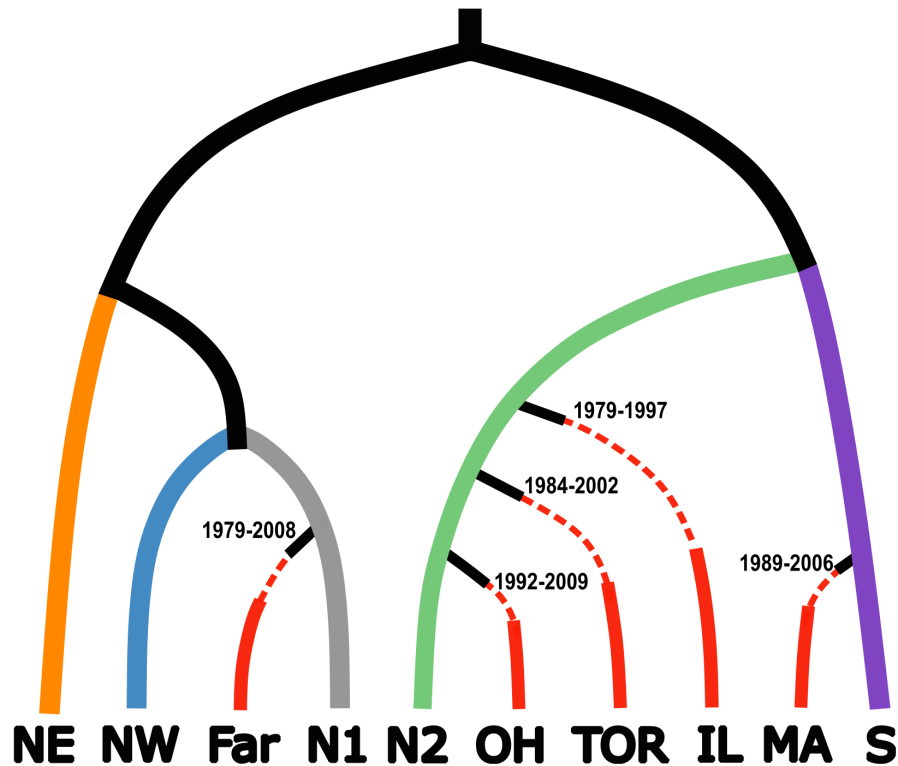


FIGURE 5 | Invasion history of North American *A. glabripennis* populations. MA, Massachusetts; OH, Ohio; Far, Farmingdale, New York; TOR: Toronto; N1, North Plain region one; N2, North Plain region two; NW, Northwest; NE, Northeast; S, South. Each native region is colored individually, while all invasive populations are in red. Invasive populations experienced a bottleneck event (dashed line) followed by population expansion (solid line). The unsampled ancestry population is shown in black. Confidence intervals (95% CI, in exact years) are indicated at the point of introduction date for each invasive population (time not to scale).

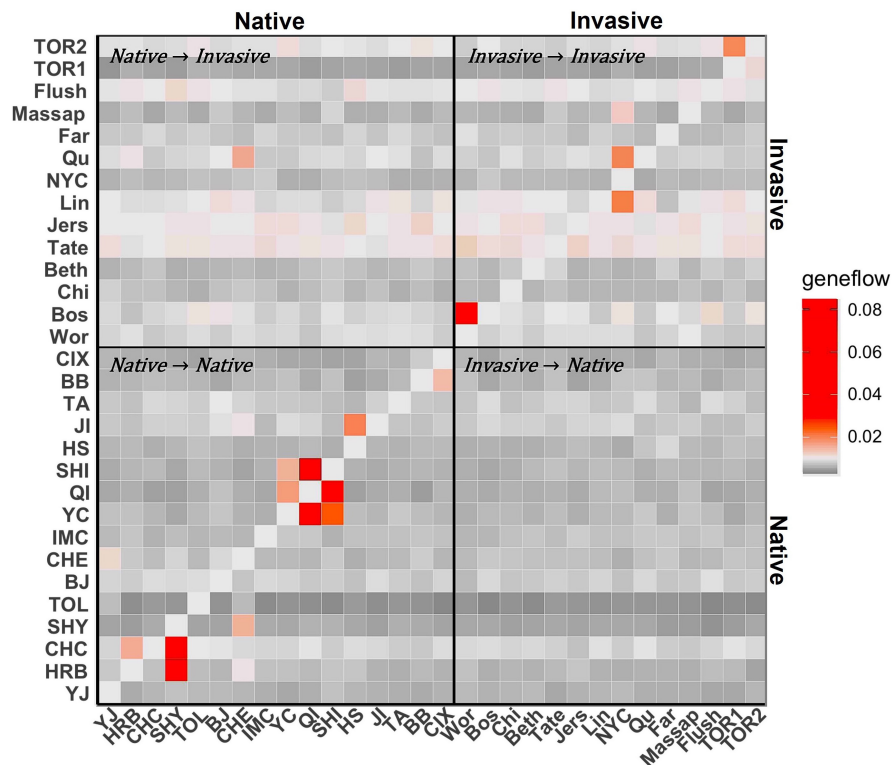


FIGURE 6 | Gene flow between and within *A. glabripennis* collection sites. See Figures 1 and 2 for the locations and full names of the populations. The direction of migration is read from populations on the horizontal axis to populations on the vertical axis. The color gradient indicates migration rates, from little to no migration (gray) to increasing levels of migration (red).

et al. 2018). These invasive populations may possess preadapted traits that are favorable in the invaded region, contributing to their invasion success (Estoup et al. 2016). In our study, invasive *A. glabripennis* may have benefited from the climate and host plants that are similar to those in its native range. Additionally, introduced species can undergo rapid evolutionary change (Whitney and Gabler 2008), particularly insects, which are further favored by their short generation times (Loxdale 2010; McCulloch and Waters 2023). For instance, the invasive Asian honeybee *Apis cerana* population in Australia was founded by only one colony despite a severe bottleneck, and signatures of positive selection were detected on standing genetic variation during the first few years after its invasion (Dogantzis et al. 2024). Therefore, preadaptation and/or rapid spread of advantageous alleles in the invasive populations may have contributed to the invasion success of North American *A. glabripennis*. Future studies could benefit from a more targeted approach, such as scanning for genomic signatures of adaptation on a genome-wide scale. The presence of multiple independent introductions offers a unique opportunity to study parallel adaptation, which could provide valuable insights to the pattern, mechanism, and rate of evolutionary change in these populations.

4.2 | Invasion Source

Successful identification of an invasion source is dependent on levels of population structure in the native range and the ability for markers to resolve this structure (Roe et al. 2019; Hamelin and Roe 2020). We detected similar invasion patterns in our North American populations as observed in previously studied European infestations (Javal et al. 2019): the European infestations were predicted to have arisen from multiple, independent introductions from the native area, and Northern populations in China are the most probable sources. However, earlier approaches were unable to achieve adequate resolution due to marker variability and low sample size (Carter, Smith, and Harrison 2009, 2010; Javal et al. 2019). Cui et al. (2022) previously delineated six native *A. glabripennis* populations within China and Korea using genome-wide SNP markers, which we used as source populations to reconstruct the invasion history of North American populations. Using the same genome-wide approach, we showed that four native *A. glabripennis* populations acted as potential sources for the North American invasion (N1, N2, NE, S; Figures 3–5). These results are of much higher resolution than those reported in Javal et al. (2019).

Genome-wide markers allowed us to characterize subtle differences between invasive *A. glabripennis* populations. The genetic distances between invasive populations were more pronounced than between native populations or between invasive populations and their native sources (Figure 2). These differences may arise from stochasticity during the colonization process, including random differences in initial allele frequency, number of founders, or subsequent genetic drift (Dlugosch et al. 2015; Dlugosch and Parker 2008). A similar pattern was observed by Ciosi et al. (2008) in the invasive beetle *Diabrotica virgifera* where invasive populations showed marked genetic differences between invasive populations, even though they originated from the same source region. This variability provides an

opportunity to develop biosurveillance markers that will allow us to track secondary movement and spread in *A. glabripennis*, as well as detect potential bridgehead events in *A. glabripennis* invasions (Lombaert et al. 2010).

Tracing the source of an invasion provides useful knowledge on the history and the frequency of introductions from specific regions (i.e., propagule pressure) (Simberloff 2009). To understand the observed pattern of invasion, it is important to contextualize these results with the history and population dynamics of *A. glabripennis* within the native range. Since the 1980s, *A. glabripennis* populations have rapidly expanded in China (Yan 1985). This population growth was linked with afforestation efforts in northern China as part of the Three North Shelterbelt Forest program (TNRSF) (Luo, Wen, and Xu 2003; Zhang et al. 2016). Outbreaks of *A. glabripennis* then expanded beyond the boundaries of the TNRSF project into southern regions, and *A. glabripennis* is now considered a widespread pest throughout temperate China (Haack et al. 2010). We hypothesize that the increased prevalence of *A. glabripennis* in the native range contributed to higher invasion risk and more likely invasion outcomes. Our sampling in the native range included sites within (NW, N1, NE) and outside (N2, S) the TNRSF. The earliest *A. glabripennis* detections in NY and NJ were traced to the N1, N2, and NE region, which includes both TNRSF and non-TNRSF locations. Later infestations, such as those associated with TOR, OH, and MA, were entirely from sources outside of the TNRSF region. The N2 source region has experienced severe population outbreaks since the early 2000s (Huang et al. 2021), and this population growth in China coincides with the timing of some later invasions in North America (Figure 1). High native population density of a potential invasive increases propagule pressure and increases the probability for successful establishment of an invasive population (Lockwood, Cassey, and Blackburn 2009; Simberloff 2009). The spatiotemporal timing of native outbreaks tracks shifts in source populations for the North American incursions of *A. glabripennis* and a detailed spatiotemporal analysis of the global invasion history will provide greater insight to this hypothesis.

Human-assisted dispersal is key to the global movement of many invasive insects, including *A. glabripennis* (Haack 2006; Ladin et al. 2023; Short et al. 2019). Larvae are found within the heartwood and can be readily transported in solid wood packing material, which includes pallets, dunnage, and spools (Greenwood et al. 2023). Port inspections continue to discover infested packaging material (Krishnankutty et al. 2020; Wu et al. 2017), despite phytosanitary measures established to curb the spread of wood-boring invasives (Aukema et al. 2010). Our results, combined with increasing global connectivity and continued interceptions (Garnas et al. 2016; Roques et al. 2016; Wu et al. 2017), show that the risk of future *A. glabripennis* introductions remains high. Our data identified a high-risk source region (N2: Shandong and Hebei provinces) and could help guide targeted inspections and surveillance protocols to mitigate the risk of future *A. glabripennis* introductions.

4.3 | Secondary Spread of *A. glabripennis*

Following introduction and establishment, expansion of an invasive species is driven by secondary spread into neighboring

habitats (Blackburn et al. 2011). Limiting secondary spread is often a critical component of invasive species control and management (Garnas et al. 2016; Pyšek and Richardson 2010). Adult *A. glabripennis* are considered relatively stationary and rarely disperse beyond natal or nearby hosts when conditions are favorable (Zhou, Zhang, and Lu 1984), with 98% of the individuals recaptured within 920 m of the release site (Smith et al. 2004). Unlike many invasives, eradication of *A. glabripennis* is possible and due primarily to this limited dispersal capacity (Smith et al. 2001, 2004; Turgeon et al. 2022) and relatively low reproductive rate in the invasive area (Keena 2002; but see Coyle et al. 2021). Human-assisted movement, together with occasional natural dispersal over longer distances (Hull-Sanders et al. 2017; Lopez et al. 2017; Javal et al. 2018), can undermine these eradication activities and cause pests to breach regulated quarantine zones (Hulme 2009; Rassati et al. 2018). For instance, Brooklyn is considered the original infestation in the New York region where it was first detected in 1996 (Sawyer 2007). Central Long Island includes several infestations which were predicted to be a result of secondary spread from the original Brooklyn population (Haack et al. 1997). Our genomic results support this hypothesis, with evidence of gene flow from NYC to the Long Island area (i.e., Massapequa, Figure 6).

Distinguishing between new introductions and satellite populations founded by secondary spread helps regulatory agencies evaluate the success of eradication efforts, establish appropriate quarantine zones, and identify high risk pathways of movement (Garnas et al. 2016). For example, we showed contemporary gene flow from Worcester to Boston (Figure 6), suggesting that Boston was a satellite population founded from secondary spread out of the Worcester infestation. Worcester is a large infestation (Dodds and Orwig 2011; Meng, Hoover, and Keena 2015) and Boston is beyond the dispersal range previously recorded in *A. glabripennis* (Smith et al. 2001, 2004); thus, it is reasonable to assume that the spread was due to human activity. Similarly, the Toronto/Mississauga infestation in 2013 (TOR2) was thought to be a satellite of the population discovered in 2003 (Turgeon et al. 2015). Our results confirmed this hypothesis, as we observed migration from Toronto/Vaughn (TOR1) into TOR2 as well as lower genetic diversity in TOR2, which would be consistent with a genetic bottleneck resulting from eradication efforts and/or founder effects. Our genomic data show that distant satellite populations can arise well beyond the dispersal range of *A. glabripennis* (<3 km, Smith et al. 2004), and beyond the typical regulated area of an infestation (e.g., Fournier and Turgeon 2017). Knowledge of invasion pathways helps reduce uncertainty of spread dynamics and can assist with the deployment of limited surveillance resources (Melbourne and Hastings 2009; Yemshanov et al. 2017). Our data on the nature of satellite populations and secondary spread provides further support for the scenario-based surveillance approach, which includes surveys well beyond the boundaries of the quarantine zone to capture distant, low probability spread events (Yemshanov et al. 2017).

Even with secondary spread within the North American invasion, there is limited evidence of admixture among the invasive populations (Figure 2). Admixture can increase genetic diversity and create new allele combinations that could affect

the evolutionary trajectory of an invasive population (Dlugosch and Parker 2008; Rius and Darling 2014). Admixture is predicated on contact between divergent lineages and although we did not detect admixture in the majority of our populations, we observed such patterns in both the NY and NJ populations (Figure 2) which require further exploration. Given the distinct genomic signatures of each invasive population, secondary spread between infestations could potentially increase admixture within the invasive range and alter the evolutionary potential and inherent risk posed by these infestations. Admixed invasive populations have been identified as important drivers of global invasions and are frequently detected in bridgehead invasion scenarios (Lombaert et al. 2010). Bridgehead events (*sensu* Lombaert et al. 2010) occur when a successful invasive lineage acts as a source for new invasive populations, a phenomenon frequently reported in other invasive groups (Bertelsmeier 2021; Blumenfeld et al. 2021; Garnas et al. 2016; Kim et al. 2021; Ortego et al. 2021; Rius and Darling 2014). In *A. glabripennis*, a bridgehead scenario from invasive USA populations was predicted for Gien, France (Javal et al. 2019), although we cannot yet assess whether a similar situation happened in North America. A global survey of invasive *A. glabripennis* populations is needed to clarify whether additional bridgehead invasion scenarios have occurred and the nature of admixture in these two invaded regions. If *A. glabripennis* infestations are not eradicated and are allowed to persist, the risk of admixture increases, particularly if secondary spread and gene flow occurs between populations with distinct sources and unique genetic diversity. Our genomic data provide a historic baseline which can be used to assess whether genetic structure, diversity, and admixture in invasive *A. glabripennis* populations change over time.

5 | Conclusion

The Asian longhorned beetle is a high-risk invasive species that continues to threaten temperate forests in North America, Europe, and other parts of Asia. Over 30 global incursions of *A. glabripennis* have occurred (Haack et al. 2010), with recent invasions discovered in South Carolina and Japan (Akita et al. 2021; Coyle et al. 2021). While eradication is possible, active infestations are still being controlled and live *A. glabripennis* continue to be intercepted along trade pathways (Wu et al. 2017; Krishnankutty et al. 2020). Although high-risk wood packaging material is targeted for inspection, live insects are still found in ISPM-15 stamped material (Haack et al. 2014; Greenwood et al. 2023). As we show, knowledge derived from genomic data can elucidate *A. glabripennis* invasion pathways, providing information that can further guide surveillance and management efforts. Our SNP markers can be translated into a target-enriched screening tool (Altmüller, Budde, and Nürnberg 2014; Diepenbroek et al. 2020) that would be able to rapidly reconstruct the invasion history of new or existing *A. glabripennis* populations or for intercepted individuals. With such a tool, we can also re-examine global invasion scenarios for other *A. glabripennis* populations (Javal et al. 2019; Lee, Lee, and Lee 2020) to refine our understanding of the invasion history of this important pest. By harnessing the power of genomic data and our refined understanding of *A. glabripennis* invasions, we pave the way toward innovative

genomic biosurveillance (Bilodeau et al. 2019) and evidence-based management strategies that will reduce the risk posed by this invasive pest.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The resources supporting the findings of this study are openly available. The individual genotype data are deposited in the Dryad Digital Repository and can be accessed via the Dryad <https://doi.org/10.5061/dryad.280gb5n05>. Raw sequence data are available at the Sequence Read Archive (SRA) with the BioProject ID PRJNA824548. The script utilized for analysis is accessible via GitHub at the following URL: <https://github.com/mimingcui/invasiveALB>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.