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Population genomic insights into invasion success in a polyphagous agricultural pest, *Halyomorpha halys*

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Abstract

Invasive species are increasingly threatening ecosystems and agriculture by rapidly expanding their range and adapting to environmental and human-imposed selective pressures. The genomic mechanisms that underlie such rapid changes remain unclear, especially for agriculturally important pests. Here, we used genome-wide polymorphisms derived from native, invasive, and intercepted samples and populations of the brown marmorated stink bug (BMSB), *Halyomorpha halys*, to gain insights into population genomics processes that have promoted the successful global invasion of this polyphagous pest. Our analysis demonstrated that BMSB exhibits spatial structure but admixture rates are high among introduced populations, resulting in similar levels of genomic diversity across native and introduced populations. These spatial genomic patterns suggest a complex invasion scenario, potentially with multiple bridgehead events, posing a challenge for accurately assigning BMSB incursions to their source using reduced-representation genomic data. By associating allele frequencies with the invasion status of BMSB populations, we found significantly differentiated single nucleotide polymorphisms (SNPs) located in close proximity to genes for insecticide resistance and olfaction. Comparing variations in allele frequencies among populations for outlier SNPs suggests that BMSB invasion success has probably evolved from standing genetic variation. In addition to being a major nuisance of households, BMSB has caused significant economic losses to agriculture in recent years and continues to expand its range. Despite no record of BMSB insecticide resistance to date, our results show high capacity for potential evolution of such traits, highlighting the need for future sustainable and targeted management strategies.

KEYWORDS
gene flow, insect pest, invasion genomics, invasiveness, odorant binding proteins, pesticide resistance

1 | INTRODUCTION

Recent human activities have promoted the transport and introduction of species to new areas outside their native ranges. Some alien species can establish and become invasive in their introduced range, causing dramatic ecosystem disruptions and significant ecological and economic damage (Gippet et al., 2019; Kirk et al., 2013). In the newly colonized environment, invasive species

may experience differences in biotic interactions—such as predator pressure (Cuthbert et al., 2018) or parasite infections (Gozzi et al., 2020)—and abiotic conditions, such as climate variability (Colautti & Barrett, 2013) or pest eradication practices (Pélissié et al., 2022). Exposure to these novel conditions can often drive adaptive evolutionary change in invaders, a key feature that can facilitate their successful post-introduction proliferation and spread (Colautti & Lau, 2015; Sakai et al., 2001). Although a growing body of literature has reported evidence of rapid evolutionary shifts in morphology (Brandenburger et al., 2019), behaviour and life history traits (Ruland & Jeschke, 2020) during invasion, the genomic basis of such adaptations has remained largely unexplored—mainly due to the poor availability of genomic resources for invasive species (Matheson & McGaughran, 2022). Understanding the genomic underpinnings of adaptation in invasive species can provide insights into long-term effects and sustainability of various pest control strategies (Sethuraman et al., 2020).

Two distinct evolutionary mechanisms can control the rapid response of invasive populations to ecological changes in novel environments (Hawkins et al., 2019). First, de novo mutations can quickly spread in invaded ranges due to positive selection, for example on single genes conferring pesticide resistance (Rolim et al., 2021) or on master regulatory genes leading to upregulation of resistance pathways (Pélissié et al., 2022). Second, selective forces can act on standing genetic variation to rapidly increase the frequency of pre-existing alleles (in a single-gene or across genes for a polygenic trait) in newly invaded areas (Hawkins et al., 2019; Pritchard & Di Rienzo, 2010). These two mechanisms leave significant footprints on the genome. For instance, during rapid fixation of de novo mutations, variation at linked sites will be purged (Pritchard et al., 2010) and only a few master regulatory genes will be differentially expressed in invasive populations (Pélissié et al., 2022). However, with selection on standing variation many alleles of small effect can become fixed (Barrett & Schluter, 2008) and multiple genes in the same molecular pathway can be differentially expressed in invasive populations (Pélissié et al., 2022).

Identifying the relative contribution of standing versus de novo variation to the rapid adaptation of invasive pests is difficult, with so-called "selective sweep" analyses requiring high genomic marker density and reference genome contiguity. The degree to which de novo mutations can impact invasive success over the short timescale of invasion is also unclear, while disentangling the effects of both mechanisms from the influence of neutral demographic events remains a challenge (Pélissié et al., 2018, 2022; Weissman & Barton, 2012).

However, the increasing availability of functionally annotated pest genomes (e.g., i5K Consortium, 2013), the affordability of high-throughput sequencing and the development of sophisticated population genomic statistical approaches together provide novel opportunities to study evolutionary underpinnings of rapid adaptation in insect pests (Pélissié et al., 2018). In particular, genome scan methods can detect shifts in allele frequency or elevated differentiation at particular loci between different populations (Welles & Dlugosch, 2019). Specifically, for invasive species, the historical origin of populations (i.e., invasive vs. native) can be considered as a binary covariate in genome-scan analyses to characterize the association of genomic variants with the invasive status of populations and identify significant allele frequency differences between invasive and native populations (e.g., C2 statistic; Olazcuaga et al., 2020). Functional annotation of loci identified under this approach can provide insights into traits and physiological pathways associated with invasion (Estoup et al., 2016; Olazcuaga et al., 2020).

The brown marmorated stink bug (BMSB), *Halyomorpha halys* (Stål, 1855) (Hemiptera: Pentatomidae), is a highly invasive pest native to east Asia, including China, Japan and Korea (Figure 1a). BMSB is a polyphagous fruit-piercing bug, capable of feeding on >100 plant hosts, many of which are economically important crops (Lee et al., 2013). Gregarious in nature, it has a high dispersal capacity and high potential to compete with endemic species, making it a serious pest for agriculture and horticulture and a nuisance of households (Sparks et al., 2020; Yan et al., 2021). BMSB is an opportunistic hitchhiker on commodities and a large number of adults can aggregate in shipping containers and imported fruit and wood (Duthie, ; Gariepy et al., 2015; Wermelinger et al., 2007). This ability to hitchhike on material other than specific host plants, along with shelter-seeking behaviour, has facilitated the movement and spread of BMSB across different countries. Indeed, BMSB was first reported outside its native range in Allentown, Pennsylvania, in 1996 (Hoebeke & Carter, 2003) and has since established in other parts of the USA, Canada (in 2008; Bercha, 2008), Chile (in 2017; Faúndez & Rider, 2017) and Europe (since 2004; Haye et al., 2014). Single-locus or genome-wide single nucleotide polymorphism (SNP) data have revealed highly divergent lineages among native populations in east Asia. China is suggested as the most likely source of global spread, with evidence of multiple out-of-China invasions, while bridgehead events from the USA to Europe and Chile have also been identified (Valentin et al., 2017; Yan et al., 2021).

Control and eradication of BMSB involves use of a wide range of insecticides (Kuhar & Kamminga, 2017; Lee et al., 2013), pheromone lures (Weber et al., 2014) and botanical odorant lures (Zhong et al., 2022). Despite these efforts, BMSB continues to cause damage to agriculture (e.g., Bariselli et al., 2016). Although recently eradicated in Australia (Horwood et al., 2019), it is currently regularly intercepted at the border of multiple countries, including New Zealand, Norway and the UK (EPPO Global Database, 2022). Ecological niche modelling has highlighted northern Europe, northeastern North America, southern Australia and the North Island of New Zealand as being at high risk for further colonization of BMSB (Kistner, 2017; Zhu et al., 2012). Rising temperatures under future climatic scenarios are likely to facilitate this range expansion by accelerating population growth, potentially increasing the number of generations BMSB can produce annually (Kistner, 2017). Thus, uncovering the genomic characteristics that confer adaptation and establishment of BMSB in invaded areas will be important for

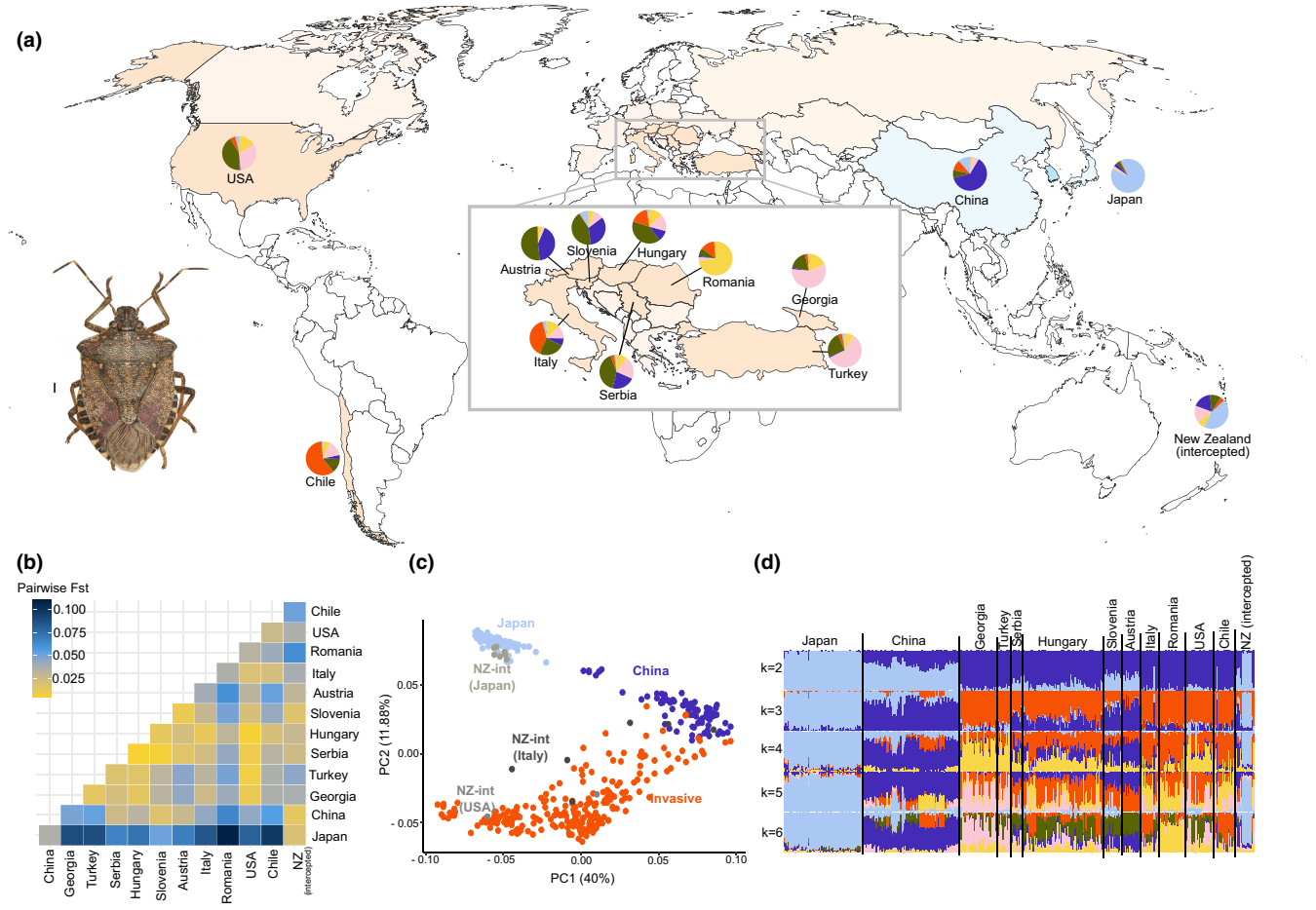

FIGURE 1 Global genomic structure of *Halyomorpha halys*. (a) Native (blue shade on map) and invaded (pink shades on map) distribution range of *H. halys*. New Zealand samples were intercepted at the border and therefore do not represent a single "population." Pie charts represent the proportion of individual genotypes in each population based on admixture proportions, estimated at $k = 6$ with sparse non-negative matrix factorization analysis [see also (d)]. (b) Heat map of pairwise F_{ST} values for 13 studied populations of *H. halys*. Dark blue colours indicate higher genome-wide differentiation between populations, according to the provided colour key. (c) Principal component analysis showing SNP variation among individuals across native, invasive and New Zealand-intercepted (NZ-int) individuals—in the latter case, the country that the cargo containing these intercepted samples came from is indicated in parentheses. (d) Admixture plots showing hierarchical population structure based on 14,172 neutral SNPs in 404 individuals across different *k* values. Each vertical bar represents an individual and colours represent admixture proportions. BMSB photo credit: Birgit Rhode, Manaaki whenua—Landcare research, New Zealand. Abbreviations: BMSB, brown marmorated stink bug; SNP, single nucleotide polymorphism.

identifying new genome-based management targets to help minimize the impacts of future invasions, while also furthering fundamental understanding of adaptive processes that underpin global population expansion in invasive pests.

Here, we take advantage of the recently published BMSB annotated whole genome (Sparks et al., 2020), as well as published population genomic data from the global invasion of BMSB (Yan et al., 2021) to scan for divergent loci between native and invasive populations. We investigate how allele frequency of outlier SNPs changes in invaded areas and use this information to highlight genes that lie in close proximity to outlier SNPs and therefore may be of potential invasive interest. Further, we use BMSB individuals intercepted at the New Zealand border to test whether the expected country of origin (based on associated shipping cargo information) is identifiable in their genomic data.

2 | MATERIALS AND METHODS

2.1 | Sample collection and SNP calling

We obtained genomic data from two native and 10 invasive BMSB populations (Figure 1a; Table S1) using previously published double digest restriction-site associated DNA sequencing (ddRADseq) data (NCBI Sequence Read Archive project ID PRJNA675311; Yan et al., 2021). We excluded one sample from China from this data set as it shows high levels of missing data. Sixteen intercepted samples, new to this study, were collected at the New Zealand border and were labelled according to the country of their shipping cargo (NCBI Sequence Read Archive BioProject ID PRJNA889079).

DNA extraction and ddRADseq library preparation of the New Zealand intercepted samples followed the protocol described in Yan

et al., (2021). Briefly, total genomic DNA was extracted from the head and thorax of each individual using a QIAGEN DNeasy Blood & Tissue Kit with QIAGEN RNase A treatment (Qiagen) following the manufacturer's protocol. We then used standard ddRADseq library preparation protocols (Peterson et al., 2012) using *Eco*RI and *Msp*I restriction enzymes (NEB). Genomic DNA from each sample (500 ng) was digested at 37°C for 5 h using 10 units of the two selected restriction enzymes and deactivated at 65°C for 20 min, followed by the ligation of Illumina adapter sequences and unique 8-bp barcodes. Individual libraries were then pooled and 220- to 450-bp fragments were manually excised and purified using a Zymoclean Gel DNA recovery kit (Zymo Research). Polymerase chain reaction (PCR) was carried out on DNA pools using 5 μl of 5× Reaction buffer, 5 μl of 5× High GC enhancer, 0.25 μl of Q5 polymerase, 5 nM of library DNA and a unique indexing primer for each pool that corresponded to the standard Illumina multiplexed sequencing protocol. The PCR protocol followed one initial denaturation at 98°C for 30 s, then 14 cycles of denaturation at 98°C for 15 s, annealing at 65°C for 30 s and extension at 72°C for 30 s, and a final extension at 72°C for 5 min. We finally combined library pools in an equimolar concentration to form a single genomic library for sequencing on one lane of a HiSeq X Ten Illumina sequencer (paired-end, 2 × 150 bp) by Personalbio.

Raw reads for all samples were mapped to the *H. halys* reference genome, Hhal_2.0 (NCBI assembly accession GCF_000696795.2; Sparks et al., 2020), using BWA-MEM version 0.7.17 (Li & Durbin, 2009) with default features and the *M* and *R* flags to mark secondary reads and add read groups, respectively. SAMTOOLS version 1.15.1 (Li et al., 2009) was used to convert sequence alignment map (SAM) files into sorted binary alignment map (BAM) files and to mark duplicates. Variants were called using the *mpileup* and *call* modules of BCFTOOLS version 1.13 (Li, 2011), using the default calling method, outputting only variant sites (*-mv*) and including variants with minimum mapping qualities (*--min-MQ*) and minimum base qualities (*--min-BQ*) of 20. We then removed all indels, nonbiallelic SNPs, and SNPs with a minimum allele frequency of <5% using BCFTOOLS. Further filtering of the resulting variant call file (VCF) included using PLINK version 2 (Chang et al., 2015) to keep SNPs with a 90% genotyping rate (*--geno 0.1*) and remove highly correlated SNPs in 50-kb windows (*--indep-pairwise 50 5 0.2*), and using VCFTOOLS version 0.1.15 (Danecek et al., 2011) to exclude individuals with >90% missing data (*--missing-indv*). The hard-filtered VCF that contained all SNPs, including neutral and adaptive, consisted of 14,235 SNPs distributed along 2540 scaffolds. By removing SNPs potentially under selection (see Section 3), we also generated a putatively neutral data set for population diversity, structure and assignment analysis, resulting in a VCF with 14,172 SNPs distributed across 2534 unique genomic scaffolds.

2.2 | Genetic diversity and population structure

We used the *populations* module of STACKS version 2.58 (Rochette et al., 2019) to calculate overall nucleotide diversity (π), average observed and expected heterozygosity (H_O and H_E), and average inbreeding coefficient F (F_{IS}; Wright, 1949) for each population. We used the R package StAMPP version 1.6.3 (Pembleton et al., 2013) to calculate population pairwise fixation indices (F_{ST}), according to the method proposed by Wright (1949) and updated by Weir and Cockerham (1984), using 100 bootstraps. We evaluated patterns of linkage disequilibrium (LD) decay across SNPs in each population with PopLDdecay version 3.42 (Zhang et al., 2019), using default parameters except changing the maximum distance between two SNPs setting to 1 kb to account for the lack of dense SNPs along short genomic scaffolds in our data set.

To explore SNP variation among individuals of native and invasive populations, we performed a principal component analysis (PCA) using the *glPca* function in the r package adegenet version 2.1.1 (Jombart, 2008). To infer individual ancestry coefficients and evaluate population structure and admixture, we applied the sparse non-negative matrix factorization (*sNMF*) algorithm implemented in the R package LEA version 2.8.0 (Frichot et al., 2014; Frichot & François, 2015) to analyse 13 values of *k* with 20 iterations per *k*-value. The number of ancestral populations was evaluated using a cross-entropy criterion. The cross-entropy plot of *sNMF* showed a "knee-point" at $k = 6$, with equally low cross-entropies at higher *k* values (Figure S1), limiting our ability to choose the optimal number of clusters. However, because inferring the true *k*-value in structure-like analysis is often a conservative procedure and can be unreliable (Kalinowski, 2011; Lawson et al., 2018), we here explore a range of *k* values to provide a better understanding of putative hierarchical population structure. Finally, we inferred phylogenetic relationships between native and invasive populations by constructing an unrooted maximum-likelihood tree with 2000 bootstraps using IQTREE version 2.0.3 (Minh et al., 2020). To find the best model of nucleotide substitution, we used the *ModelFinder* option implemented in IQTREE, selecting the best model (SYM+R6) based on a Bayesian information criterion.

We assessed directionality in contemporary gene flow (i.e., over the past few generations) between native and invasive populations (excluding the New Zealand intercepted samples) using the Bayesian inference approach of BAYESASS version 3 (Wilson & Rannala, 2003). BAYESASS uses individual multilocus genotypes to estimate recent effective gene flow among populations. We followed the user manual to adjust Markov Chain Monte Carlo (MCMC) mixing parameters for allele frequencies and inbreeding coefficients to achieve an optimal acceptance rate between 20% and 60%. We ran three independent analyses with different seed values, using 3 million iterations and 1000 sampling intervals, and discarding the first 1 million iterations as burnin. The final gene flow estimates were averaged over the three independent runs. Additionally, we assessed directional relative migration rates using the *divMigrate* function (Sundqvist et al., 2016) implemented in the R package diversity version 1.9.90 (Keenan et al., 2013). *divMigrate* defines a hypothetical pool of migrants for a given pair of populations and estimates genetic differentiation between each of the two populations and the hypothetical pool (Sundqvist et al., 2016). It then uses this information to calculate

relative levels of migration between the two populations and hence identifies putative source and sink regions and asymmetries in gene flow (Sundqvist et al., 2016). We used Nei's genetic differentiation statistic (G_{ST}; Nei, 1973) as a measure of population genetic differentiation to estimate relative migration between populations. Nei's G_{ST} is a coefficient of genetic differentiation and measures the proportion of genetic diversity that resides among populations; it is frequently used to estimate gene flow among demes (Culley et al., 2002).

2.3 | Population assignment of intercepted samples

To genetically confirm the source location of the 16 New Zealand border-intercepted BMSB individuals, we applied a machine-learning approach in the R package assignPOP version 1.2.4 (Chen et al., 2018). We first performed data evaluation on all non-intercepted samples (i.e., reference samples) in order to check whether the population genomic data (ddRADseq loci) for these samples had enough discriminatory power. Data evaluation of reference samples included randomly dividing individuals into training and test sets and performing Monte Carlo cross-validation to estimate assignment accuracies of reference samples (functions *assign.MC* and *accuracy.MC*). We performed this procedure using the following parameters for the training data set: proportion of random individuals from each population: 0.5 and 0.9; proportion of loci: 0.5, 0.9 and 1; loci sample method: F_{ST}; iterations: 50; and model: support vector machine (svm). Finally, we performed an assignment test on intercepted individuals and created membership probability plots using the function *assign.X*.

2.4 | Genome-wide scan for association with invasiveness

To estimate the contrast of allele frequencies between BMSB's native and invasive populations, we used BAYPASS version 2.3 (Gautier, 2015; Olazcuaga et al., 2020). BAYPASS implements a Bayesian hierarchical model (Coop et al., 2010; Gautier, 2015) to estimate overly differentiated loci among populations while accounting for confounding effects of shared demographic events by using a neutral covariance matrix, Ω, constructed from population allele frequencies (Gautier, 2015). We used invasive status of populations (native vs. invasive) as a binary covariable and identified SNPs that showed allele frequency differences between native and invasive populations by estimating the contrast statistic, C2 (Olazcuaga et al., 2020).

We ran the BAYPASS core model with default parameters, comparing established invasive populations (i.e., excluding New Zealand intercepted samples) against China (putative source of BMSB worldwide invasion). Using this approach, we contrasted the sum of standardized allele frequency of these two groups of populations defined according to their historical status and considering $c_j = 1$ for China, $c_j = -1$ for each established invasive population, and $c_j = 0$ for the excluded populations (Japan and New Zealand) in the *.ecotype* input file of BAYPASS (after Olazcuaga et al., 2020).

Histograms indicated that *p*-values associated with the C2 statistic were well-behaved (i.e., being close to uniform for higher *p*-values; Olazcuaga et al., 2020) (Figure S2). We controlled for multiple testing by calculating *q*-values for each individual SNP using the R package qvalue version 2.26.0 (Storey & Tibshirani, 2003). SNPs with *q*-values <.1 were considered as the best outliers in BMSB's invaded range. To assess convergence and the reproducibility of the MCMC estimates, we ran three additional independent BAYPASS runs using different seeds. We checked the consistency of the results of independent runs by calculating Forstner and Moonen Distance (FMD) (Förstner & Moonen, 2003) between pairs of covariance matrices (Ω) using the R function *fmd.dist* (distributed within the BAYPASS package; see Table S8 for results) and the correlation of both the Ω parameter and the XtX parameter across different runs.

2.5 | Analysis of genes of interest

We used SNPEFF version 4.3 (Cingolani et al., 2012) to investigate potential downstream functional implications of outlier SNPs by manually adding a database built from the *H. halys* reference genome. To search for genes in or within 10 kb distance from outlier SNPs, we first used BEDTOOLS version 2.29.2 (Quinlan & Hall, 2010) to create *bed* files containing flanking sequence position information from the Hhal_2.0 *H. halys* genome assembly (NCBI assembly accession GCF_000696795.2). Next, we used the UCSC Table Browser (https://genome.ucsc.edu/, accessed May 2022) to retrieve exons and coding DNA sequences located at these flanking regions. The UCSC Table Browser provided a list of transcript IDs corresponding to identified genes using the BMSB annotated genome. We searched the NCBI Nucleotide database to extract *H. halys* gene IDs and predicted protein descriptions for each transcript ID. When transcripts were not annotated (i.e., *H. halys* uncharacterized proteins in the NCBI Nucleotide database), we looked for homologous proteins using the UniProt BLAST tool (https://www.uniprot.org/blast/, accessed May 2022). To better understand the predicted function of identified genes, we also evaluated homologous gene functions in the *Drosophila melanogaster* database (https://flybase.org/, accessed May 2022).

Finally, we examined the identified genes using a gene ontology (GO) analysis. We first used INTERPROSCAN version 5.51 (Jones et al., 2014) to extract GO annotations for all genes, resulting in a complete set of GO terms as a reference for the enrichment analysis. We then used the R package topGO version 4.2 (Alexa & Rahnenfuhrer, 2022) to check which of the GO terms were significantly over represented in our identified gene set. We used the weight01 algorithm and Fisher's exact test, and retained enriched GO terms with a *p*-value of <.05.

3 | RESULTS

3.1 | Population differentiation and contemporary gene flow

The BMSB whole genome assembly used in this study consists of 16,639 scaffolds with a total ungapped length of 996,505,068 bp. The genome size of BMSB has previously been estimated to be 1.143 ± 0.019 Gb ($n = 4$) and 1.095 ± 0.023 Gb ($n = 4$) for a female and male specimen, respectively (Sparks, Bansal, et al., 2020). A histogram of the distribution of ddRAD tags along genomic scaffolds showed that the majority of scaffolds contained fewer than five SNPs (Figure S3). Neutral SNP data (14,172 hard-filtered SNPs from 404 individuals obtained from two native and 10 invaded countries, as well as the New Zealand intercepted samples) showed similar levels of nucleotide diversity across native and invasive populations of BMSB (π ranging from 0.23 to 0.24), slightly higher observed heterozygosity estimates among invasive populations (mean $H_O = 0.278$ and 0.291 in native and invasive populations, respectively), and negative inbreeding coefficients for all populations (Table S1). The highest genomic differentiation was observed between Japan and all invaded countries (F_{ST} ranging from 0.0519 to 0.107; Figure 1b; Table S2). However, the genomic distance between China and invasive populations was relatively lower (F_{ST} ranging from 0.0189 to 0.0646). Among invasive populations, Romania was highly differentiated and showed the largest F_{ST} values (F_{ST} ranging from 0.0314 to 0.107) when compared to native and other invasive populations (Figure 1b). We found similar patterns of LD decay for the studied ddRAD tags across native and invasive populations (Figure S4).

Spatial genomic analyses revealed Japan as a highly divergent population, with individuals from China clustering closer to invasive populations in a PCA (Figure 1c). The distribution of SNP variation along the first PC axis (accounting for 40% of the total variation) showed that Chinese samples overlapped with invasive samples along the right-hand edge of the invasive PC space, but the invasive groups have a much wider span, indicating higher levels of genomic variation among invaded countries. SNP variation along the second PC axis (11.88% of total variation) indicated a smaller genetic distance between Japan and China compared with the distance between Japan and invasive populations. Six individuals from China showed a signature of shared ancestry/admixture with Japan—lying approximately equidistant from the two countries in the PCA (Figure 1c; Figure S5). There was no geographically linked structure among the invasive populations (Figure S5).

Admixture (sNMF) plots revealed a signal of spatial segregation of native populations consistent with the PCA results, with China and Japan forming separate clusters, and a consistent signal of significant admixture between China and all invasive populations at various values of k (Figure 1d; Figure S1). The six outlier individuals from China were exceptionally admixed with Japan (ancestry proportions >0.5). At $k = 3$, Japan, China and all established invasive populations presented as separate clusters. Higher values of k distinguished finer-scale spatial structure across the invaded range amid high admixture. Among established invasive populations, Austria and Slovenia showed the highest admixture rates with China, while Romania represented a highly divergent cluster compared to other invasive populations (Figure 1d; Figure S1). A maximum-likelihood tree confirmed these patterns, showing China and Japan as two distinct lineages, lacking distinct spatial units within the invaded range, and indicating a close phylogenetic relationship between the Chinese and invasive populations (Figure S6).

BAYESASS showed that contemporary effective gene flow rates were low from native ranges towards invasive ranges and vice versa (mean posterior distribution <0.01), but high among most of the invaded countries (ranging from 0.01 to 0.15), particularly from different invaded countries towards the USA and Georgia (Figure 2a; Table S3). DI *divMigrate* showed relative migration between all pairs of populations, with low rates ($G_{ST} < 0.5$) between China and the invasive populations (Figure 2b; Table S4). Migration between Japan and all invasive populations was also low (G_{ST} ranging from 0.089 to 0.216). Among invaded ranges, high relative migration ($G_{ST} > 0.5$) to Hungary was observed from Italy, the USA, Serbia, Slovenia and Georgia; as well as to the USA, with migration from Hungary, Turkey and Georgia (Figure 2b; Table S4).

3.2 | Assignment of intercepted populations

We evaluated 16 samples that were intercepted at the New Zealand border from cargo containers arriving from Italy, USA and Japan to determine whether we could correctly identify the source population of each sample. Overall, the assignment approach (*assignPOP*) showed higher accuracy in determining the source population for samples of native origin (Figure S7), with all eight BMSB samples that were intercepted from Japan correctly assigned as such with high posterior probability (posterior probabilities >0.7; Figure 3; Table S5). However, Hungary and Georgia were incorrectly identified as the most likely sources of the New Zealand intercepted samples found in cargo shipped from the USA (although posterior probabilities were low: 0.29 and 0.41; Figure 3; Table S5). Similarly, the six samples that were found in cargo from Italy were misassigned to Slovenia, China and Hungary source populations, with moderate to high assignment posterior probabilities in each case (posterior probabilities ranging from 0.3 to 0.72; Figure 3; Table S5).

3.3 | Outlier SNPs and identified genes of interest

Genome-wide scans identified 63 outlier SNPs that differentiated invasive populations from the native populations in China. Outliers were located along distinct scaffolds, except a single case where two SNPs co-located to the same scaffold. Variant annotation analysis (*snpEff*) showed that ~24%, ~15% and ~1.5% of these SNPs were in transcript, up- or downstream gene regions, and exonic regions of the genome, respectively (Table S6). The remainder were in intergenic regions (~36%) or introns (~23%) (Table S6).

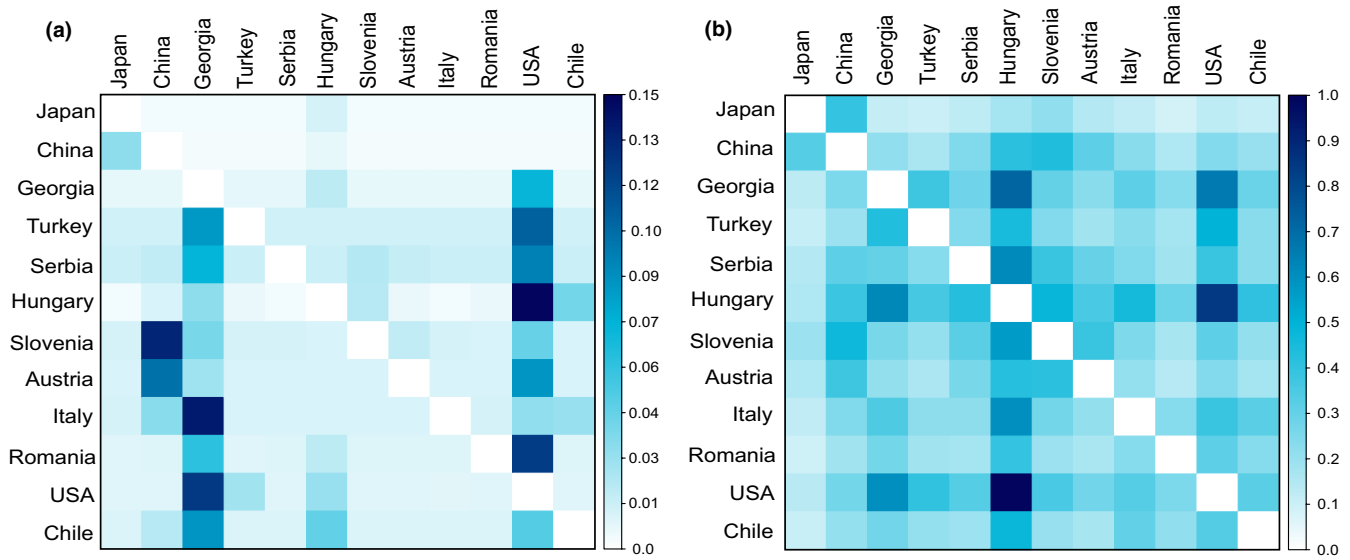

FIGURE 2 Comparison of contemporary gene flow patterns with directional relative migration rates between different pairs of populations of *Halyomorpha halys*. (a) Matrix of current gene flow inferred with BAYESASS, showing mean posterior estimates of gene flow. Higher values indicate high levels of contemporary gene flow between populations. See Table S3 for the numerical values. (b) Matrix of relative migration patterns inferred with divMigrate and calculated based on G_{ST} genetic distance. Higher G_{ST} values indicate higher relative migration rates between populations. See Table S4 for the numerical values.

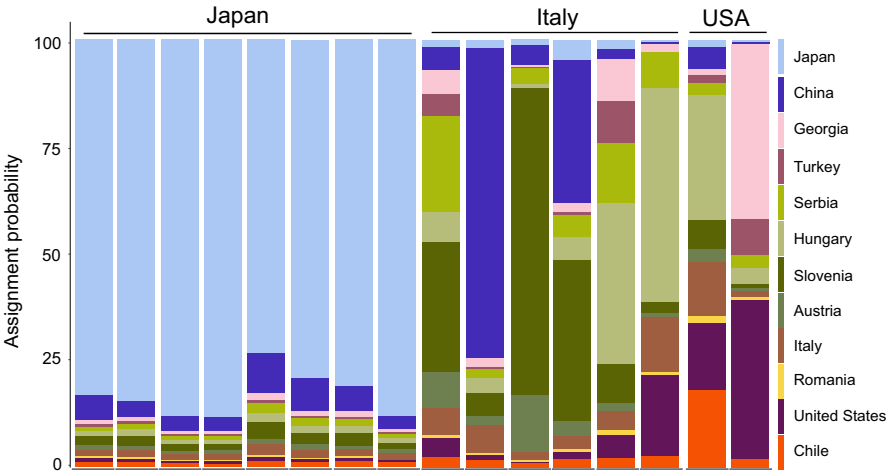

FIGURE 3 Membership probability plots showing predicted source populations of New Zealand intercepted samples of *Halyomorpha halys* that were found in cargo containers shipped from Japan, Italy and the USA. Each bar represents a single individual, with the colour key to the right indicating the predicted assignment country, and the actual origin of the intercepted samples specified at the top of the plot. The highest (and most accurate) assignment probabilities were obtained for intercepted samples from Japan.

Exons were located within 10 kb (up- or downstream) of 22 of the outlier SNPs. Using the *H. halys* genome assembly available at the UCSC Table Browser tool, we annotated 55 unique transcripts for these exons, including transcript variants due to alternative splicing of pre-mRNAs transcribed from a specific gene. Several of the associated genes had products of potential adaptive importance in invasion, including insecticide resistance, detoxification, fatty-acid metabolism and sensory perception (Table 1; Table S7). GO analysis of the 55 unique transcripts showed significantly enriched pathways ($p < .05$) in three molecular functions, including oxidoreductase activity (GO:0016491), odorant binding (GO:0005549) and protein binding (GO:0005515), as well as one biological process (cellular protein modification process; GO:0006464). No significant GO terms were detected for cellular components.

4 | DISCUSSION

We utilized the recent publication of the BMSB genome (Sparks, Bansal, et al., 2020), along with genome-wide SNP data, to illustrate a pattern of spatial structure across native and introduced ranges, and a high degree of shared ancestry and/or gene flow between populations from invaded regions around the world and China. Further, we demonstrated that multiple incursions and migration events, as well as contemporary gene flow among populations, can greatly reduce our ability to accurately distinguish sources of incursions using reduced-representation genomic data alone, and we identified differentiated SNPs in close proximity to genes potentially contributing to insecticide resistance, although such resistance is not currently reported for BMSB.

TABLE 1 Ten key identified genes located in or within 10 kb of outlier SNPs identified from genome scan analysis for native (China, as the main source of BMSB global invasion) and invasive populations of *Halyomorpha halys*

Allele frequency REF allele ALT allele *Native* *Invasive* *Intercepted* *CN* *AT CL GE HU IT RO RS SI TR US* *NZ*	**Outlier position / Gene ID / Gene position (start-end)**	**Predicted gene description**	**Predicted gene function** (based on the information for homologous genes in *Drosophila melanogaster*)
	NW_020110236.1: 179165 / LOC106680062; LOC106680070 / NW_020110236.1 (177108-356140); NW_020110236.1 (177086-355014)	glutathione S transferase	detoxification
	NW_020113526.1: 21559 / LOC106691423 / NW_020113526.1 (12476-37171)	sodium channel protein 60E	encodes a voltage-gated calcium-selective cation channel that likely modulates the stability of neural circuits, particularly under environmental stresses
	NW_020110345.1: 672507 / LOC106681914 / NW_020110345.1 (648379-674370)	vam6/Vps39-like protein	involved in autophagy, vesicle-mediated transport and cellular response to starvation
	NW_020111329.1: 81026 / LOC106693021 / NW_020111329.1 (69097-89018)	fatty acid amide hydrolase 2	involved in fatty acid catabolic process
	NW_020111843.1: 183884 / LOC106684563 / NW_020111843.1 (172401-192996)	odorant binding protein	involved in sensory perception of chemical stimulus
	NW_020110618.1: 467033 / LOC106692730 / NW_020110618.1 (397109-474900)	GTP-binding protein RAD	enables calcium channel regulator activity, involved in nervous system process, behaviour, signalling and response to stimulus
	NW_020110192.1: 859087 / LOC112210356 / NW_020110192.1 (800014-891918)	myosin	enables structural constituent of muscle, involved in muscle development and locomotion
	NW_020110248.1: 86248 / LOC106679719 / NW_020110248.1 (17524-167027)	tensin-1	Involved in cell-cell adhesion and development
	NW_020110322.1: 80259 / LOC106679052 / NW_020110322.1 (49152-91036)	tubulin glycylase 3A	enables protein-glycine ligase activity
	NW_020110743.1: 51494 / LOC106679862; LOC106679863 / NW_020110743.1 (59359-147336); NW_020110743.1 (104-43430)	UBX domain-containing protein 6; protein Wnt-5b	involved in development, response to stimulus and signalling

Note: For each gene, pie charts demonstrate variations in allele frequencies among different populations for outlier SNPs (CN = China, AT = Austria, CL = Chile, GE = Georgia, HU = Hungary, RO = Romania, RS = Serbia, SI = Slovenia, TR = Turkey, US = USA, NZ = New Zealand), and the outlier position/gene ID/gene position, and predicted gene description and function are listed. See Table S7 for the full list of identified genes.

Abbreviations: BMSB, brown marmorated stink bug; SNP, single nucleotide polymorphism.

4.1 | Spatial structure and contemporary gene flow

Previous population genetic analyses using mitochondrial markers reported high haplotype diversity and spatial differentiation across BMSB's native range (Cesari et al., 2015; Valentin et al., 2017; Xu et al., 2014; Yan, Pal, et al., 2021). Genome-wide SNP data in our study confirmed these findings, showing China and Japan as two highly divergent clusters. Such remarkable genetic divergence in the native range can be attributed to historical demographic events, initiated after the last glacial maxima (Xu et al., 2014) and intensified via isolation of the two countries (Yan, Vétek, et al., 2021). Although China and Japan were clustered in two divergent groups, we found evidence of bidirectional gene flow between the two, with higher genomic exchange from Japan towards China. Passive dispersal of individuals via human-mediated transport or "hitchhiking" may explain these patterns of asymmetrical contemporary gene flow

(Yan, Vétek, et al., 2021), and may account for the six individuals of Chinese origin that show >50% genotypic similarity to samples from Japan.

Across the invaded range, we found that the genotype composition of invasive populations was more similar to China, confirming that China is the probable main source of BMSB's worldwide invasion (Yan, Vétek, et al., 2021). This pattern aligns with previous reconstructions of BMSB invasion routes based solely on *COI* data (Valentin et al., 2017), which suggested separate invasion events from China to the USA and Europe. Higher global trade from China may have contributed to these patterns, potentially explaining the higher genetic similarity of China, versus Japan, to the invasive populations.

Global admixture events can potentially release invasive populations from environmental constraints that exist in the native range (Smith et al., 2020) by increasing genetic diversity and enhancing adaptive potential (North et al., 2021). Anthropogenic or natural long-distance dispersal events can aid colonization success by increasing propagule pressure (Crawford & Whitney, 2010; Dlugosch et al., 2015), potentially resulting in the rapid introduction of genetic variation into invaded areas (Lockwood et al., 2005; Wilson et al., 2009). Supporting this scenario, we found admixed lineages in the invaded range of BMSB, and levels of within-population neutral genomic diversity across the invaded range that were comparable to those of native populations. Strong flight capacity over long distances (Lee & Leskey, 2015; Wiman et al., 2015) has probably facilitated the spread of BMSB individuals at local scales (e.g., within invaded countries).

Other single-locus studies have also reported shared *COI* haplotypes between the different invaded countries (Gariepy et al., 2015) and indicated that secondary invasions from successfully invaded ranges (i.e., the invasive bridgehead effect; Lombaert et al., 2010) may explain these genetic patterns, including the presence of highly admixed genotypes of BMSB in multiple countries, including Hungary and Italy (Valentin et al., 2017). Our reconstruction of relative migration patterns using *divMigrate* supported these findings, for example showing widespread migrations and secondary invasions of Hungary from Slovenia, Italy, Romania, Georgia and the USA. However, BAYESASS showed that a high level of recent gene flow was observed only among a few invasive populations. These contrasting findings probably indicate that the observed spatial genomic patterns in BMSB are the result of historical shared diversity before secondary incursion events took place.

4.2 | Assigning potential sources of intercepted samples

Genome-wide SNP data obtained from reduced-representation sequencing methods, such as RADseq (Elshire et al., 2011), have enabled the precise assignment of invaded individuals to their source populations for a variety of invasive insect species (e.g., Popa-Báez et al., 2021; Schmidt et al., 2019). Successful identification of incursion sources, however, depends primarily on the complexity of invasion history, with multiple introductions, very recent timescales and demographic stochasticity potentially diminishing assignment accuracy (Sherpa & Després, 2021). In BMSB, multiple bridgehead events and recurrent movement of individuals between different invaded countries has created a complex invasion scenario that limited the ability to assign New Zealand intercepted samples from Europe to their correct country of origin in our study. Most of the invasive BMSB populations shared alleles and there was a lack of clear geographical delineation of populations to a specific country or region. However, native BMSB populations were spatially structured and could be well-distinguished from each other and from introduced populations. These spatial patterns suggest that, when using reduced-representation methods to identify sources of invasive species incursions, assignment probabilities will be highly accurate if such incursions have originated directly from the native range. In our study, consideration of the cross-validation results of the *assignPOP* analysis (Figure S7) showed that, for BMSB ddRAD loci, the highest assignment accuracies (>99%) could be obtained when genomic differentiation (F_{ST}) was at least 4% (see Table S2 for population F_{ST} values for Japan and China).

In the absence of discrete populations within the introduced range of the invasive species under study, tracing the source of incursion is likely to be challenging. In our case, the origin of the New Zealand intercepted samples was known a priori, but such knowledge is commonly missing, such as for intercepted samples not associated with cargo, or for those collected in the field post-introduction. Applying a higher number of SNPs (e.g., using whole genome-resequencing approaches), or incorporating fixed genome-wide differences, could potentially improve assignment accuracies in such cases by identifying rare or recent markers associated with local differentiation.

4.3 | Proximity of outlier SNPs to genes of potential invasive interest

Although non-equilibrium demographic conditions, such as repeated bottlenecks, can profoundly affect allele frequency changes in invasive populations, the C2-statistic approach used here has been shown to be robust to demographic events typical of biological invasions (Olazcuaga et al., 2020). This methodological approach accounts for the neutral evolutionary history of different populations when contrasting SNP allele frequencies between native and invasive populations by using the scaled covariance matrix of the population allele frequencies (Ω matrix), as well as the across-population (i.e., ancestral) allele frequency (Olazcuaga et al., 2020). One important caveat regarding our approach, however, is our use of one population from China as the sole point of reference when identifying highly differentiated alleles in invasive populations. The spatial genomic structure and genome-wide diversity rates across the invaded ranges of BMSB we identified, in line with previous mitochondrial DNA studies (Cesari et al., 2015; Valentin et al., 2017; Yan,

Pal, et al., 2021), suggests that other unsampled source population(s) might contribute to allele frequency variation in BMSB invasive populations. Future studies incorporating samples from different native populations within China, or other unsampled invasive populations, are essential to provide further insights into the potential role of genetically divergent source populations in invasion success.

Experimental evidence suggests that populations of introduced species can experience adaptive evolutionary changes that can contribute to their invasion success, for example by selection acting on insecticide and stress resistance alleles (Cattel et al., 2020; Fouet et al., 2012; Pélissié et al., 2022). Among arthropods, glutathione *S*-transferase (GST) and sodium channel genes are among the important targets of natural selection on insecticide-resistance phenotypes (Dong, 2007; Pavlidi et al., 2018). GSTs comprise a multifunctional enzyme family that participates in the metabolism and detoxification of insecticides (Cao et al., 2015; Sparks et al., 2017; Sparks, Nelson, et al., 2020) and in protection against oxidative stress (Ranson et al., 2002). Sodium channels are involved in the generation and propagation of action potentials and membrane excitability and can be sensitive to a variety of neurotoxins, including insecticidal pyrethroids (Du et al., 2016). Particularly for BMSB, pyrethroids have been the most widely used insecticides due to their availability, effectiveness and relatively low cost (Kuhar & Kamminga, 2017). We found that, compared to native populations, invasive BMSB populations carried differentiated SNPs located in close proximity to GST and sodium channel genes. These outlier SNPs showed a notable change in allele frequencies in introduced populations, with lower frequencies of the alternative allele in invasive populations compared to China, suggesting the possibility of resistance-related genomic changes building from standing genetic variation across BMSB's invaded range. Current management of BMSB relies widely on the application of neurotoxic broad-spectrum pesticides, including pyrethroids (Kuhar & Kamminga, 2017; Rice et al., 2014). Although insecticide resistance has not yet been documented for BMSB (Sparks, Bansal, et al., 2020) and selection pressure for resistance in BMSB has been reported to be low due to its polyphagy and high mobility (Kuhar & Kamminga, 2017), the presence of outlier SNPs in the proximity of genes that confer insecticide resistance warrants further investigation on how such genes could contribute to invasion success in this species.

In addition to the chemical control of BMSB using insecticides, recent management methods rely on "attract-and-kill" strategies, which utilize *H. halys* aggregation pheromones (with or without botanical attractants) to attract insects to traps for elimination via specific killing agents (Morrison et al., 2016; Zhong et al., 2022). Aggregation pheromones essentially target the insect olfaction system, attaching to odorant binding proteins in the antennae to control the insects' semiochemical recognition (e.g., in BMSB; Rice et al., 2014) and manipulate its behaviour away from host plants (Venthur & Zhou, 2018). We detected outlier SNPs in close proximity to odorant-binding protein genes and identified molecular pathways significantly enriched for stimulating olfactory perception in the introduced populations of BMSB. These findings suggest that BMSB may be undergoing selective responses to currently utilized odorant baits. Adaptive evolution of odorant binding proteins has been reported to modify olfactory and gustatory avoidance behaviour in other insects, such as *Drosophila* species (Whiteman & Pierce, 2008). Alternatively, the proximity of outlier SNPs to genes associated with chemoreception we identified may indicate selection on behavioural traits, such as perception of the surrounding environment, foraging, and mate or predator recognition, which are all critical for the survival of insects (Vieira & Rozas, 2011; Yuan et al., 2016).

Finally, we identified differentiated SNPs around several genes involved in development, metabolism, and other physiological and cellular functions. Unfortunately, we lack information on the putative adaptive functions of these genes, or on their role in invasion success more generally. Nevertheless, as examples of potentially advantageous genes that may have implications for survival of invasive insects, they should be targets for future quantitative genetic studies that aim to characterize functional and/or phenotypic differences between native and invasive populations. In BMSB, for instance, individuals can become bivoltine (have two generations per year) in introduced ranges, especially in warmer climates (Costi et al., 2017; Stoeckli et al., 2020). Future research could investigate whether the genes we have identified could play a role in fecundity and/or phenology of BMSB throughout its invaded range.

5 | CONCLUSIONS

Genome-wide SNP data allowed us to characterize the global invasion pattern of a highly polyphagous pest. The complex invasion history of BMSB included multiple colonization events and high levels of gene flow and admixture between introduced populations, resulting in an inefficiency to accurately assign several recent interceptions to their source populations. Whole genome data may provide a more fine-scale differentiation of such recent dispersal and mixing events, thus allowing population assignment in the absence of discrete populations within the introduced ranges of the invasive species. Additionally, we identified biologically meaningful genomic variants potentially associated with invasion success. These variants were located in close proximity of genes with well-understood functions for pesticide resistance and sensory perception. Although to the best of our knowledge no case of insecticide resistance has yet been reported for BMSB, our results suggest that resistance phenotypes may have the potential to evolve in BMSB from standing variation. Further research focused on understanding the genomic factors that facilitate invasion success will be particularly important as invasive species such as BMSB continue to expand their range.

AUTHOR CONTRIBUTIONS

Elahe Parvizi, Manpreet K. Dhami and Angela McGaughran conceived the study, Juncong Yan performed the DNA extraction and ddRADseq library preparation associated with the New Zealand intercepted samples, and Elahe Parvizi analysed the data and wrote the manuscript. All authors read and edited the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Raw demultiplexed ddRADseq reads from the New Zealand intercepted samples are available on NCBI's SRA database under BioProject ID PRJNA889079. All genomic data and metadata are available at the Dryad Digital repository (https://doi.org/10.5061/dryad.w9ghx3fsk) and related scripts are available at GitHub (https://github.com/Elahep/BMSB-popgenomics).

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SUPPORTING INFORMATION

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