Population genomics of the invasive Argentine ant (*Linepithema humile*) – adaptive evolution in introduced supercolonies despite low genetic diversity

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Abstract

The Argentine ant (*Linepithema humile*), native to South America, has spread globally over the past 150 years, forming extremely large supercolonies in its introduced range. Despite the recent demographic history, including founder effects, Argentine ants thrive in the introduced range and displace native ant species. We adopted a comprehensive approach to investigate selection signals across the whole genome of this highly invasive species, with a specific focus on introduced supercolonies. We also investigated genome-wide diversity and divergence patterns and compared the results with earlier microsatellite marker data studies. We used pooled whole-genome sequence data from 100 workers from the species' native range and each of the three invasive supercolonies – European Main, Catalonia, and Chile. Invasive supercolonies harboured low genetic diversity and were genetically highly differentiated. Despite this, we could detect signs of positive selection in their genomes. Some of the selected genes showed parallel adaptive evolution in invasive supercolonies. Furthermore, there were no signs that a social organisation based on unrelated workers had led to impaired adaptability (genetic meltdown). We conclude that introduced Argentine ant supercolonies evolve adaptively, indicating that founder effects, low genetic diversity and supercolony social organisation do not always hamper species adaptability.

Keywords: pool-seq, demographic history, founder effect, genetic drift, selective pressure

1. Introduction

Invasive species increasingly threaten biodiversity and ecosystems globally (Mollot et al., 2017; Seebens et al., 2017). In the most harmful situations, they cause local extinctions, permanently changing the nature of colonised areas (Holway et al., 2002; Mack et al., 2000). However, the factors contributing to the success of invasive species are still poorly understood, as are their long-term evolutionary prospects in the new ranges, which makes the possibility of controlling these species and mitigating their detrimental effects challenging (Estoup et al., 2016; Pérez et al., 2006; Sherpa & Després, 2021).

Ants exhibit enormous species richness, inhabit diverse ecological niches, and play a crucial role in many ecosystems (Hölldobler & Wilson, 1990; Moreau et al., 2006; Wilson & Hölldobler, 2005). Many ant species are also among the most harmful invasive species (Holway et al., 2002; Lester & Gruber, 2016; McGlynn, 1999). One of these, the highly invasive Argentine ant (*Linepithema humile*), has spread, by accidental human introduction, from its original habitat in South America to all continents except Antarctica during the past 150 years (Suarez et al., 2001; Wetterer et al., 2006, 2009; Wetterer & Wetterer, 2006). Typical of invasive ant species, the Argentine ant also forms large polygynous (multi-queen) and polydomous (multi-nest) societies, known as supercolonies (Pedersen et al., 2006), in which territorial borders between nests are absent over large areas, allowing individuals to move freely between them. In both the native and introduced ranges, these supercolonies form closed breeding units where mating occurs within the nest, and colonies spread by budding (Helanterä, 2022; Pedersen et al., 2006; Vogel et al., 2009). In the introduced range, Argentine ants dominate competition between species, destroy local ecosystems, and cause species extinctions (Giraud et al., 2002; Holway et al., 2002; Sanders et al., 2001, 2003). The Argentine ants' supercolony size in the introduced range can be enormous, e.g., the European Main supercolony spans over 6,000 kilometres from the Mediterranean coast in Italy to the Spanish Atlantic coast (AntWeb, 2026; Giraud et al., 2002).

Previous research using microsatellite marker data indicated that introduced Argentine ant supercolonies harbour low genetic diversity and are genetically highly differentiated from each other and from the native

range supercolonies (Blight et al., 2012; Brandt et al., 2009; Giraud et al., 2002; Jaquiéry et al., 2005; Tsutsui et al., 2000; Vogel et al., 2010). These introduced supercolonies originate from a small number, in some cases only a dozen, of reproducing individuals (Giraud et al., 2002; Vogel et al., 2010), indicating strong founder effects, i.e., loss of genetic variation. Genetic drift (random fluctuations in allele frequencies, often causing allele fixation or loss) is amplified in these small, newly established founder populations, leading to even greater differentiation between populations (Keller & Passera, 1993; Nei et al., 1975). Low initial diversity, combined with strong drift driven by small effective population sizes, should impede adaptive evolution in the introduced Argentine ant supercolonies. Moreover, the general inefficiency of selection on worker traits in supercolonies with low relatedness, due to multiple egg-laying queens, increases the accumulation of deleterious mutations and decline in fitness (genetic meltdown) (Helanterä et al., 2009; Linksvayer & Wade, 2009). However, the success and dominance of Argentine ants in the introduced range (Vogel et al., 2010) suggest local adaptation to the new environments. This success in novel ranges despite small effective population sizes and decreased selection efficacy raises an important question about the effects of natural selection on the evolution of these ants.

Our earlier population genetic study, focusing on the evolution of immune genes in 18 Argentine ant supercolonies worldwide, including the invasive supercolonies of this study, indicated that, despite recent demographic history, positive selection has affected the evolution of immune genes in the introduced range (Holmberg et al., 2024). In this study, we adopted a more comprehensive approach to investigate signals of selection across the whole genome. We studied native-range supercolonies and three invasive supercolonies from different parts of the world using pooled whole-genome sequence data from 100 workers from the native range and from each of the three invasive supercolonies. We aimed to investigate: i) the overall genome-wide patterns of selection in invasive Argentine ants, i.e., whether signatures of selection could be detected in their genomes, ii) signatures of parallel adaptive evolution among the three invasive supercolonies, and iii) whether genome-wide data confirms the earlier findings, based on microsatellite marker data, about demographic changes during introductions, supercolonial diversity and divergence.

2. Materials and Methods

2.1. Sampling

We analysed four samples of Argentine ants. One of the samples represents native-range supercolonies, and three samples represent invasive supercolonies, one originating from South America and two from Europe (Table S1) (Wild, 2004). All samples include 100 diploid workers. The sample representing the native-range supercolonies was collected in Argentina, while the samples representing the three invasive supercolonies were collected in France, Spain and Chile. The three sampled invasive supercolonies arose from different primary introductions from the native range (Vogel et al., 2010). The two European samples were collected from the two known, separate supercolonies: the European Main supercolony (European Main; establishment recorded 1906) and the Catalonian supercolony (Catalonia; 1916), which live partly next to each other along the Mediterranean coastline (Giraud et al., 2002). The third invasive sample from the Chilean supercolony (Chile; 1965) was sampled from the only recognised supercolony in the country (Vogel et al., 2010). For each of the three samples representing the introduced ranges, ten individuals were collected from each of ten different nests within each supercolony (i.e., 100 individuals per supercolony). In the introduced ranges, ten nests were always close together at a single location. For the native-range sample, ten individuals were collected from ten nests each from a separate supercolony from four separate localities (i.e., a total of 100 individuals per ten supercolonies) to capture the total genetic diversity in the species' natural range (López et al., 2025) (Table S1).

2.2. DNA extraction and sequencing

Genomic DNA was extracted individually from each ant using the DNeasy Blood & Tissue Kit (QIAGEN). Equal amounts of DNA from ten individuals per nest were pooled and genome-amplified using REPLI-g Mini Kit (QIAGEN). Finally, all the genome-amplified sub-samples were pooled so that each final sample represented 100 individuals. The samples were sent to BGI Genomics for library preparation and paired-end sequencing using an Illumina Hiseq™ 2000 sequencer, with a read length of 90 base pairs (bp) and an

120 insert size of 200 bp. The clean reads provided by BGI Genomics were filtered to remove adapters,
121 contaminants, and low-quality sequences.

122 2.3. Data processing

123 The quality encoding of the sequenced raw reads was converted from Phred 64 to Phred 33 (also known as
124 Sanger), as it is more widely used and required in many software programs. The conversion was done using
125 the Seqtk tool (version 1.3) (*Seqtk*, 2018). After this, raw reads were filtered using trim-fastq.pl script from
126 the basic pipeline of PoPoolation (version 1.2.2) (Kofler et al., 2011). The reads were filtered using an
127 average minimum base quality of 20 and a minimum read length of 70 bp. The quality of the reads was
128 verified using FastQC (version 0.11.8) analyses after filtering (Andrews, 2010).

129 Filtered reads were aligned to the reference genome (Genome assembly Lhum_UNIL_v1.0, Pan et al., 2024)
130 using the BWA-MEM algorithm from the BWA software package (version 0.7.17) with default settings (Li &
131 Durbin, 2009). The resulting SAM files were sorted, quality-filtered and converted to more compressed
132 binary versions (BAM files) using the view command of SAMtools (version 1.10) (Li et al., 2009). Only
133 aligned reads with a mapping quality of at least 20 and a SAM flag "properly paired" were saved. Duplicates
134 were removed using Picard's MarkDuplicates tool (version 2.21.4) (*Picard Toolkit*, 2019). RepeatModeler
135 (version 2.0.7) was used to identify repeats, and RepeatMasker (version 4.1.9) was used to mask the
136 identified repeats in the reference genome (Smit & Hubley, 2015). Degeneracy of sites in coding regions
137 was annotated with degenotate (version 1.2.4) (Mirchandani et al., 2024).

138 2.4. Population genetic analyses

139 2.4.1. Genomic diversity

140 The genomic diversity of supercolonies was evaluated for the whole genome, as well as separately for four-
141 fold and zero-fold degenerate sites in coding regions. Two genetic diversity estimators, Tajima's π (π) and
142 Watterson's Θ (Θ_w), were computed using Grenedalf's (version 0.6.3) diversity command (Czech et al.,
143 2024). Aligned reads were subsampled to a maximum sequencing depth of 200 using the subsampling

144 method subscale. A minimum sequencing depth of four and a minor allele count of two were required per
145 sample. We also estimated microsatellite marker diversity, expected heterozygosity (H_{exp}) and allelic
146 richness (k') for five variable microsatellite loci obtained from Vogel et al. (2010), applying a similar sample
147 size and design as the genomic samples (see Text S2).

148 2.4.2. Genomic differentiation

149 To evaluate the genomic differentiation of supercolonies, we calculated Hudson's estimator of F_{ST} using
150 Grenedalf´s fst command (Czech et al., 2024). A minimum sequencing depth of four and a minor allele
151 count of two were required per sample. We also estimated microsatellite marker differentiation using
152 pairwise F_{ST} for five variable microsatellite loci obtained from Vogel et al. (2010), applying a sample size and
153 design similar to those of the genomic samples (see Text S2).

154 2.4.3. Population structure and adaptive evolution

155 We used the population genomics software BayPass (version 2.31), which utilises a Bayesian framework to
156 identify SNPs subjected to selection and associated with population-specific covariates (Gautier, 2015;
157 Olazcuaga et al., 2020). The different models of BayPass estimate and account for the neutral covariance
158 structure among population allele frequencies resulting from their shared history.

159 To evaluate population structure and identify SNPs under selection among invasive supercolonies, the
160 analysis was first run in core model mode with default settings. The differentiation outlier statistics, XtX,
161 consider all analysed populations simultaneously and identify SNPs that show unusually high differentiation
162 between populations relative to neutral expectations based on population structure and drift, and thus are
163 potential targets of selection in one or more populations. We analysed the three invasive supercolonies to
164 identify differentiated SNPs in at least one of them, making these SNPs candidates for selection. As this
165 analysis is based on differences in allele frequencies and includes solely invasive supercolonies, it only
166 identifies SNPs that have experienced different selective pressures in at least one of the studied
167 supercolonies, rather than SNPs that have a shared selective regime across all three invasive supercolonies
168 (these SNPs were identified with a different method, see below). XtX statistics were calibrated using a

169 simulated neutral dataset, i.e., a pseudo-observed data set (POD). For neutral data simulation, SNPs were
170 thinned into 20 subsets, each comprising approximately 42K SNPs. These thinned SNP sets were used to
171 estimate the covariance matrix, i.e., Ω of population allele frequencies resulting from their demographic
172 history, which were then used to simulate PODs of 50K SNPs. PODs were then run in core model mode, and
173 the 99th percentiles of XtX differentiation outlier statistics were calculated; the average of these
174 percentiles serves as a threshold to identify outlier SNPs, i.e., candidates for selection.

175 Furthermore, a contrast model mode, C2 statistic, was run to estimate whether SNPs are associated with
176 invasiveness. The C2 statistics contrast and compare allele frequencies between groups of populations
177 defined by the binary covariable of interest, testing for a consistent allele frequency difference between
178 groups. Hence, we contrasted the native-range sample with the group of three invasive supercolones. This
179 analysis identifies SNPs that share similar allele frequencies across invasive supercolonies and
180 simultaneously differ from those in natives. However, note that the association does not require complete
181 similarity in allele frequencies across all invasive supercolonies, two might be enough. The C2 statistics
182 were calibrated using PODs as described above to indicate whether outlier SNPs were associated with
183 invasiveness. Both models accounted for population structure estimated as Ω of population allele
184 frequencies.

185 Genes containing outlier SNPs with high XtX values were considered as potential targets of positive
186 selection in one or more invasive supercolonies. Genes containing outlier SNPs with high C2 values were
187 associated with invasiveness. We performed gene enrichment analysis using the genes identified as
188 potential targets of positive selection as a test set and the annotated genes of the reference genome
189 (Annotation GCF_040581485.1-RS_2024_08) as a reference set, using the ShinyGO tool (version 0.85) (Ge
190 et al., 2020). Similarly, genes associated with invasiveness were analysed for enrichment. Moreover, genes
191 identified by both the XtX and C2 statistics were analysed for enrichment.

192 3. Results

193 3.1. Properties of the data

194 Sequencing reads covered 92.78%, 93.11%, 82.71%, and 92.38% of the reference genome in native-range
195 sample, Main, Catalonia and Chile, while the mean sequencing depths were 87, 98, 61, and 78, respectively.
196 Repetitive regions, which comprised 31% of the reference genome, were removed from all downstream
197 analyses.

198 3.2. Introduced supercolonies are expanding and harbour low genetic diversity

199 We evaluated the genetic diversity of supercolonies with two genetic diversity estimators, Tajima's pairwise
200 nucleotide diversity (π) and Watterson's theta (Θ_w), describing the population mutation rate. To ensure
201 comparability, we accepted only sites with data from all supercolonies for diversity calculations. These sites
202 contained 502,659 whole-genome SNPs, of which 59,575 were 4-fold SNPs, and 122,678 were 0-fold SNPs.
203 SNPs were identified simultaneously across the entire data set.

204 According to π, the native-range supercolonies were more genetically diverse than the invasive
205 supercolonies (p-values < 0.05 in all pairwise comparisons, see details in Table S3; Table 1). Both expected
206 heterozygosity (H_{exp}) and allelic richness (k') estimates derived from microsatellite marker diversity yielded
207 similar results to π – the sample of native-range supercolonies harbours higher diversity than the invasive
208 supercolonies (Table S4, Figure S5). Instead, Θ_w indicated that Catalonia had the highest genetic diversity
209 (p-values < 0.05 in all pairwise comparisons, see details in Table S3; Table 1). The Catalonia supercolony
210 harboured an excess of rare alleles, as evidenced also by the high peaks on the left side of the folded site
211 frequency spectrum (Figure 1). For each supercolony, Θ_w was always higher than π, especially pronounced
212 in the invasive supercolonies, indicating expanding population sizes (p-values < 0.05 in all pairwise
213 comparisons, see details in Table S3; Table 1). Moreover, four-fold sites had consistently higher diversity
214 than zero-fold sites, as expected (p-values < 0.05 in all pairwise comparisons, see details in Table S3; Table
215 1).

216 3.3. Introduced supercolonies are genetically different from each other

217 We used pairwise F_{ST} values to evaluate genetic differentiation between supercolonies. The results
218 indicated that supercolonies were genetically highly differentiated from each other (Table 2). The pairwise

219 F_{ST} values were consistently highest between Catalonia and the other supercolonies, indicating that
220 Catalonia was the most genetically differentiated supercolony (Table 2). The microsatellite marker data also
221 revealed genetic differences between supercolonies (Table S6, Figure S7). The marker data indicated that
222 invasive supercolonies were more differentiated from each other than from the native-range supercolonies
223 (Table S6, Figure S7) – a pattern that we did not observe in the genomic data.

224 3.3. Argentine ants can adapt to new environments

225 The core model and the XtX statistics of the BayPass software were used to identify candidate genes for
226 positive selection among invasive supercolonies. 1220 genes (see Table S8) contained one or more SNPs
227 with an XtX value greater than the calibrated threshold (6.3825), indicating them as outlier loci in the
228 genome scan for adaptive differentiation, and thus local adaptation in one or more of the invasive
229 supercolonies. The XtX outlier SNPs were distributed across the genome (Figure S9). Enriched molecular
230 function and biological process GO terms among the candidate genes were mainly related to nervous
231 system development, ion transport, signalling-related processes, and transcriptional regulation (Table S10).

232 Contrast analysis based on C2 statistics of the BayPass software were used to identify genes associated with
233 invasiveness. 285 genes (see Table S11) contained one or more SNPs with a C2 value greater than the
234 calibrated threshold (4.7973), indicating them as outlier loci in the genome scan for association with
235 invasiveness. Thus, these genes showed signs of parallel adaptive evolution across invasive supercolonies.
236 These C2 outlier SNPs were also distributed across the genome (Figure S12). Enriched molecular function
237 and biological process GO terms among genes associated with invasiveness were mainly related to ion
238 transport, cellular signalling and communication, and gene regulation and transcriptional processes (Table
239 S13). Notably, 97 genes were identified by both XtX and C2 analyses. These genes showed both high
240 differentiation between invasive supercolonies and an association with invasiveness, indicating parallel
241 adaptive evolution at each gene in two out of the three invasive supercolonies studied. One molecular
242 function GO term, GO:0030125 Semaphorin receptor binding, was enriched among these genes (Table S14).

243 The remaining 188 genes associated with invasiveness (high C2) were those that showed parallel adaptive
244 evolution across all three invasive supercolonies (as not identified with the XtX).

245 Both models estimated and accounted for the covariance structure among population allele frequencies
246 resulting from their shared history. The SVD-based visualisation of the Ω matrix summarises the genetic
247 structure among the native-range sample and the three invasive supercolonies (Figure 2). PC1 explains
248 approximately 50% of the total genetic variation and distinguishes native-range supercolonies from invasive
249 ones. PC2 explains approximately 35% of the variation and distinguishes the Catalonia supercolony from
250 the other invasive supercolonies (Figure 2).

251 4. Discussion

252 This study aimed to shed light on the highly invasive Argentine ant's recent evolutionary history and
253 genome dynamics, specifically focusing on the introduced supercolonies. We searched for answers to the
254 following questions: i) can signs of selection be detected in the genomes of the highly invasive Argentine
255 ant?, ii) are there signatures of parallel adaptive evolution among invasive supercolonies?, iii) are we able
256 to verify, using genomic data, the earlier population genetic findings on diversity and divergence based on
257 microsatellite marker data?

258 Despite the recent demographic history, including strong founder effects, we detected signs of selection in
259 the invasive supercolonies, indicating adaptability. Numerous genes were identified as candidates for
260 positive selection among invasive supercolonies. This finding demonstrates local adaptation in introduced
261 ranges with novel selective pressures. Due to the global nature of the analysis considering allele frequency
262 differences, it cannot be said whether these genes were positively selected in one or more of the
263 supercolonies, or, if selected in more than one, whether the selected allele is the same or different. But it is
264 evident that positive selection shapes the evolution of invasive Argentine ant supercolonies, and that the
265 identified genes play a key role in local adaptation. Moreover, some genes were associated with
266 invasiveness, indicating parallel adaptive evolution in invasive supercolonies. Thus, selective regimes are
267 probably not entirely different between invasive supercolonies, and some selective pressures are shared

268 across invasive ranges. Whilst the Mediterranean-like climate is shared across the native and invasive
269 ranges of the Argentine ant (Roura-Pascual et al., 2011), other biotic and abiotic factors, such as pathogens
270 and competitors, likely differ between regions, leading to distinct local selective pressures and local
271 adaptation (Holmberg et al., 2024; Lester & Gruber, 2016).

272 We detected positive selection in several immune genes (emp, imd, hop, bsk, Trax, Toll-6, and Sp1) in the
273 whole-genome scanning. We could not find overlap between the positively selected immune genes
274 identified here and those reported in the earlier Argentine ant immune gene study, even though the
275 studied supercolonies are the same (worker specimens differ) (Holmberg et al., 2024). This might be due to
276 differences in sampling strategies and the methods used. However, together, these findings indicate that
277 immune genes play important roles in how invasive Argentine ants adapt to new ranges.

278 Wagner et al. (2023) reported that Argentine ants were excellent olfactory learners. They proposed that
279 efficient learning combined with other features of Argentine ants, such as rapid discovery of food sources
280 and other resources, and rapid recruitment, might provide a competitive advantage over local species in
281 introduced ranges (Wagner et al., 2023). Intriguingly, the positively selected genes include olfactory
282 learning (trp, mura, mnb, Mob2, cher, PKA-R1, Fas3, Fas1) and memory genes (eag, aPKC, dnc).

283 The enriched GO terms among the positively selected genes included a range of molecular functions. Some
284 of these overlap with GO terms for genes that have evolved under positive selection across the ant
285 phylogeny over a long evolutionary time (Barkdull & Moreau, 2023). These GO terms were GO:0015103
286 Inorganic anion transmembrane transporter activity, GO:0022836 Gated channel activity, GO:0022857
287 Transmembrane transporter activity, GO:0004930 G protein-coupled receptor activity, GO:0004672 Protein
288 kinase activity, GO:0005515 Protein binding, and GO:0008061 Chitin binding.

289 The general observation of low diversity and high divergence in the invasive supercolonies based on our
290 genome-wide data largely confirms the results of earlier marker data studies of Argentine ants (Blight et al.,
291 2012; Brandt et al., 2009; Giraud et al., 2002; Jaquiéry et al., 2005; Tsutsui et al., 2000; Vogel et al., 2010).
292 However, there were some discrepancies between the results of genomic data and the microsatellite loci

293 obtained from Vogel et al. (2010). Catalonia appeared to be even more differentiated from other
294 supercolonies based on the genomic data than the marker data suggested, with an excess of rare alleles
295 (high Θ_w). Similarly, in another invasive ant species, *Cardiocondyla obscurior,* genome-wide evidence
296 showed reduced genetic diversity in invasive populations (Errbii et al., 2021). Moreover, marker data have
297 demonstrated reduced genetic diversity in several other invasive ant populations of *Nylanderia fulva,*
298 *Pheidole megacephala, Solenopsis invicta*, *Solenopsis geminata*, and *Wasmannia auropunctata* (Fournier et
299 al., 2005, 2009, 2012; Ross et al., 1993, 1996; Wauters et al., 2018). Together, these results indicate that
300 introduced populations of invasive ant species typically harbour less genetic diversity than native
301 populations. This is in line with the typical supercolonial lifestyle of the invasive ants, i.e., the formation of
302 closed breeding units and the fact that populations in the introduced ranges usually comprise single
303 supercolonies.

304 Our results give no indication that the demographic and ecological changes that accompany an invasion,
305 namely the expansion of supercolonies in the absence of competition that drastically reduces the
306 relatedness between sterile workers and reproductive queens (Giraud et al., 2002; Helanterä, 2022;
307 Helanterä et al., 2009; Pedersen et al., 2006), would have amplified the predicted accumulation of harmful
308 mutations or hampered positive selection on worker traits (Linksvayer & Wade, 2009) in the invasive
309 supercolonies. This could be due to, firstly, the relatively short time span – less than 100 generations –
310 since introductions, or secondly, the rarity of genes only expressed in workers, where such mutation
311 accumulation is predicted and shown to occur (Linksvayer & Wade, 2009; Warner et al., 2017). The rarity of
312 such genes could mask any genome-wide effect, and testing this hypothesis in invasive supercolonies
313 requires high-quality gene expression data.

314 The high divergence between the invasive Argentine ant supercolonies included in this study may be
315 explained by the fact that they have originated from different primary introductions from the native range
316 without secondary reinforcements (Giraud et al., 2002; Vogel et al., 2010). Moreover, founder effect likely
317 initiated the first shift toward genetic differentiation within the introduced supercolonies, as the effective

318 queen number establishing the European Main as well as the Catalonian supercolonies has been estimated
319 to be between 6 to 13 individuals (Giraud et al., 2002; Vogel et al., 2010), while in the native range
320 supercolonies, it has been estimated to be extremely high, reaching infinity (Pedersen et al., 2006).
321 Subsequent gene flow between invasive supercolonies has been prevented by two factors: i) Argentine ant
322 workers are highly aggressive toward males originating from other colonies, and ii) there is considerable
323 geographic distance between the studied supercolonies, except the European Main and Catalonian
324 supercolonies, which live partly next to each other (Blight et al., 2012; Giraud et al., 2002; Jaquiéry et al.,
325 2005; Vogel et al., 2010). Although the European Main and Catalonia supercolonies live close to each other,
326 there is no gene flow between them (Blight et al., 2012; Giraud et al., 2002; Jaquiéry et al., 2005). In
327 addition, amplified genetic drift in small founder populations might have further increased fluctuations in
328 allele frequencies, contributing to diversification within expanding supercolonies (Nei et al., 1975; Vogel et
329 al., 2010). Especially in Catalonia, the excess of rare alleles might indicate both substantial expansion after
330 population foundation and strong purifying selection. Other social insects, such as the yellow-legged hornet
331 *Vespa velutina* and German wasp *Vespula germanica,* have also successfully invaded regions outside their
332 native range despite low genetic diversity (Arca et al., 2015; Brenton-Rule et al., 2018; Eloff et al., 2020;
333 Takeuchi et al., 2017). In the yellow-legged hornet, successful invasion possibly originated from as few
334 individuals as just one (one queen mated with multiple males) (Arca et al., 2015; Takeuchi et al., 2017). In
335 addition, other non-social insects, such as the African fig fly *Zaprionus indianus* (Comeault et al., 2020), and
336 other species, such as the invasive wart comb jelly *Mnemiopsis leidyi* (Jaspers et al., 2021) have also proven
337 that invasion success does not require high genomic diversity. Thus, the general assumption of invasive
338 populations' lower adaptive potential is incorrect, as the founder effect and low diversity do not always
339 prevent invaders' success.

340 The success of a wide range of invasive species populations with low adaptive potential due to low genetic
341 diversity has been explained by factors such as gene flow, stress-induced accelerated mutation rate or TE-
342 activation, epigenetic changes and the release from natural pathogens and enemies (Errbii et al., 2021;
343 Manfredini et al., 2019; Marin et al., 2019; North et al., 2021; Schrader et al., 2014). Despite the low genetic

344 diversity, the invasive Argentine ants continue to evolve adaptively. Pre-adaptation in the native range has
345 recently received more attention across species (Davidson et al., 2011; Elst et al., 2016; Estoup et al., 2016;
346 Guo et al., 2014; Hufbauer et al., 2012), and we suggest that this might also play a role in the initial invasive
347 success of the Argentine ant. The unstable environment in the native range of the Argentine ant,
348 characterised by frequent flooding (LeBrun et al., 2007), may enhance the species' adaptive potential.
349 Balancing selection, which maintains alternative alleles in fluctuating conditions, could contribute to their
350 continued and long-term success by enabling rapid adaptation to new habitats following introductions as
351 indicated here. The exact roles of all selected genes must be carefully resolved among the complex
352 biological processes and pathways in upcoming genomic surveys, such as comparative population genomic
353 studies between native and introduced supercolonies using both high-quality genomic and transcriptomic
354 data at the individual level. Our study provides an excellent groundwork and frame for future studies of the
355 Argentine ant in the field of invasion genomics.

356 Tables and Figures

357 Table 1. The average per-site diversity estimators, π and Θ_W, for whole-genome, four-fold sites, and zero-fold
358 sites.

	Sample	π	Θ_W
whole-genome	Native	0.00094	0.00203
	Main	0.00048	0.00200
	Catalonia	0.00058	0.00593
	Chile	0.00056	0.00210
4-fold	Native	0.00220	0.00521
	Main	0.00120	0.00486
	Catalonia	0.00124	0.01219
	Chile	0.00127	0.00544
0-fold	Native	0.00049	0.00237
	Main	0.00031	0.00221
	Catalonia	0.00043	0.00550
	Chile	0.00029	0.00246

359

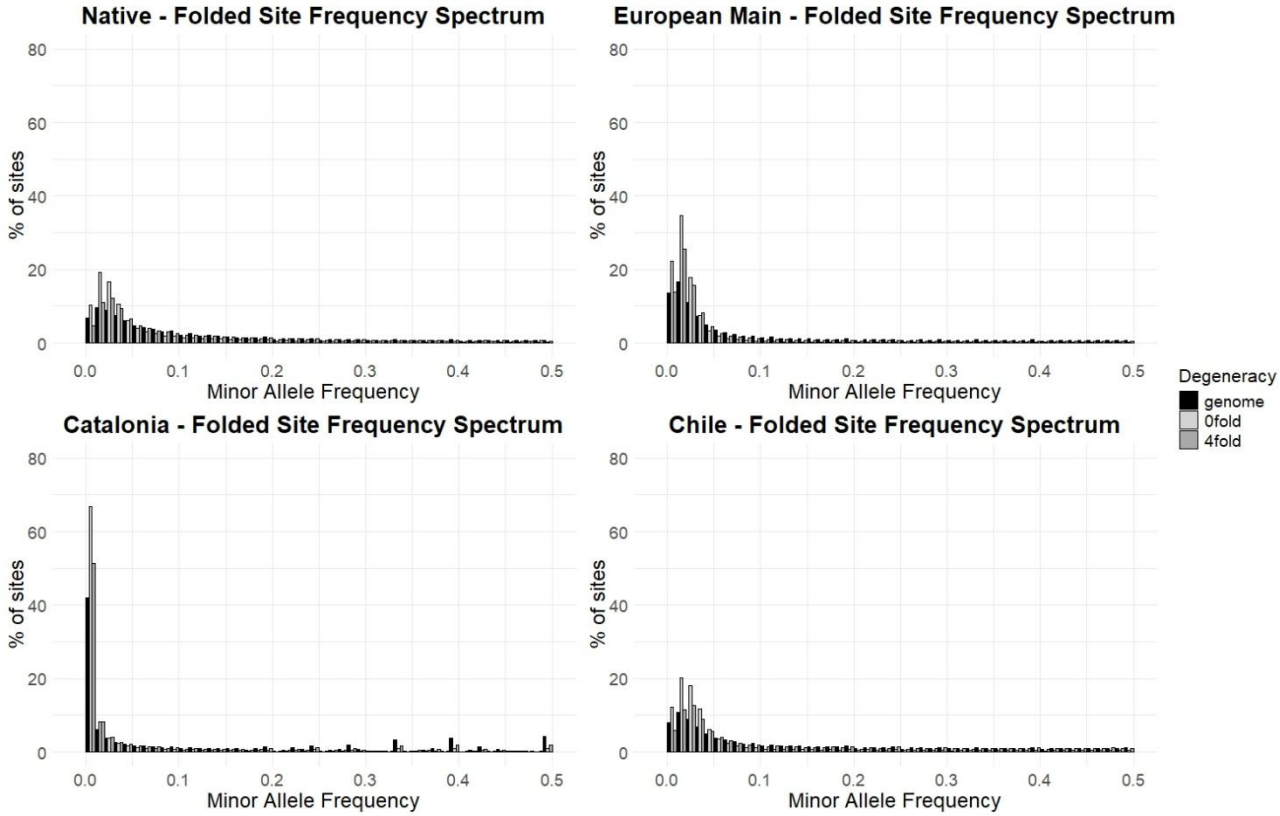

Figure 1. Folded site frequency spectra for Native, Main, Catalonia, and Chile.

Table 2. Genetic differences measured as pairwise F_{ST} values, genome-wide average.

F_{ST}	Native	Main	Catalonia	Chile
Native	0	0.2812	0.4434	0.2670
Main		0	0.5034	0.2507
Catalonia			0	0.5148
Chile				0

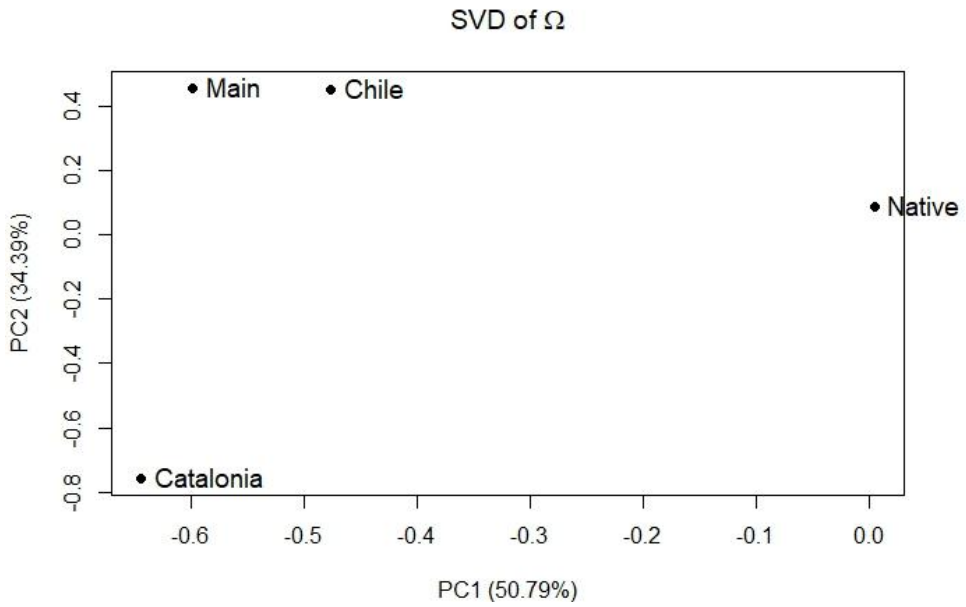

Figure 2. The SVD-based visualisation of the covariance matrix, i.e., Ω of population allele frequencies.

Author contribution

JSP, HH, and LV designed the research. JP did the lab work. IP analysed the data and wrote the manuscript, and all authors contributed to editing and revising.

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598 Data Accessibility Statement

599 Raw sequence reads are deposited in the SRA (BioProject PRJNA846165).

600 Benefit-Sharing Statement

601 Benefits from this research accrue from sharing our data and results on public databases as described

602 above.