


ORIGINAL ARTICLE

Inbreeding tolerance as a pre-adapted trait for invasion success in the invasive ant *Brachyponera chinensis*

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Abstract

Identifying traits that facilitate species introductions and successful invasions of ecosystems represents a key issue in ecology. Following their establishment into new environments, many non-native species exhibit phenotypic plasticity with post-introduction changes in behaviour, morphology or life history traits that allow them to overcome the presumed loss of genetic diversity resulting in inbreeding and reduced adaptive potential. Here, we present a unique strategy in the invasive ant *Brachyponera chinensis* (Emery), in which inbreeding tolerance is a pre-adapted trait for invasion success, allowing this ant to cope with genetic depletion following a genetic bottleneck. We report for the first time that inbreeding is not a consequence of the founder effect following introduction, but it is due to mating between sister queens and their brothers that pre-exists in native populations which may have helped it circumvent the cost of invasion. We show that a genetic bottleneck does not affect the genetic diversity or the level of heterozygosity within colonies and suggest that generations of sib-mating in native populations may have reduced inbreeding depression through purifying selection of deleterious alleles. This work highlights how a unique life history may pre-adapt some species for biological invasions.

KEYWORDS

colony breeding system, genetic bottleneck, inbreeding, invasive species, sib-mating

1 | INTRODUCTION

The persistence of a population generally relies on the maintenance of genetic variability across generations of successful reproduction. Introduced populations almost inevitably experience genetic bottlenecks reducing their genetic diversity and their level of heterozygosity relative to native populations (Schrieber & Lachmuth, 2017). This usually results in inbreeding depression, increasing the frequency of detrimental phenotypes due to recessive deleterious mutations (Fauvergue, Vercken, Malausa, & Hufbauer, 2012; Kirkpatrick & Jarne, 2000; Nei, Maruyama, & Chakraborty, 1975), which, in turn, reduces the fertility, survival and growth rates of individuals with high inbreeding coefficients (Charlesworth & Willis, 2009). In this context, it is puzzling how often genetically impoverished introduced species seem to circumvent or overcome genetic depletion to successfully establish and achieve local dominance in a new environment (Frankham, 2004; Lee, 2002; Pérez, Nirchio, Alfonsi, & Muñoz, 2006; Roman & Darling, 2007; Simberloff, 2009).

Social insects are among the most successful animal species at invading new environments, probably due to their ability to overcome a broad range of ecological pressures through colony-level responses in addition to their individual-level responses (Moller, 1996; Suarez, Holway, & Tsutsui, 2008). The colony-level responses of social insects may even turn inbreeding into an advantage (Tsutsui, Suarez, Holway, & Case, 2000). In many social insects, the overall genetic impoverishment following invasion is associated with a reduction in the genetic variation among colonies, and thus, a decrease in within-colony relatedness. This may lead to a loss of nestmate recognition and a collapse of colony boundaries (Giraud, Pedersen, & Keller, 2002; Suarez et al., 2008), supporting the development of supercolonies: widespread colonies formed of several interconnected nests containing several, up to thousands of queens (Helanterä, Strassmann, Carrillo, & Queller, 2009; Holway, Lach, Suarez, Tsutsui, & Case, 2002; Suarez et al., 2008). This social organization provides colonies rapid growth, a higher probability of survival and an earlier onset of the reproduction stage (Boomsma, Huszár, & Pedersen, 2014; Boulay, Arnan, Cerdá, & Retana, 2014). Ultimately, unicoloniality provides a strong ecological advantage and raises the likelihood of invasion by allowing such colonies to reach high worker densities and lower intraspecific competition, resulting in interspecific dominance (Holway & Suarez, 2004; Le Breton, Jourdan, Chazeau, Orivel, & Dejean, 2005). However, unicoloniality in social insects is paradoxical, as the loss of colony boundaries and the high number of queens reduce relatedness between colony members (Cremer et al., 2008; Fournier, De Biseau, & Aron, 2009; Tsutsui et al., 2000), and thus workers' indirect fitness (Hamilton, 1964), calling into question the evolutionary stability of these invasive populations (Helanterä et al., 2009). In addition, in the long-term inbreeding has the potential to pose additional costs to the social Hymenoptera, such as increased male sterility through the production of diploid males (van Wilgenburg, Driessen, & Beukeboom, 2006; Zayed & Packer, 2005) as occurs in introduced populations of the fire ant *Solenopsis*

invicta Buren (Krieger, Ross, Chang, & Keller, 1999; Ross, Vargo, Keller, & Trager, 1993).

Native to eastern Asia, the Asian needle ant, *Brachyponera chinensis* (Emery), was first recorded in eastern North America in the early 1930s. Since its arrival, this species has spread and is now present in most south-eastern states of the US and is known to disrupt native ant and plant communities both in disturbed and relatively intact habitats (Bertelsmeier, Guénard, & Courchamp, 2013; Guénard & Dunn, 2010; Rodriguez-Cabal, Stuble, Guénard, Dunn, & Sanders, 2012). In its invasive range, *B. chinensis* seems to form dense and expansive colonies (Guénard & Dunn, 2010), but it is unclear if these colonies differ in their social organization and spatial expansiveness from colonies in the native range. To help elucidate the evolutionary factors underlying its invasion success, we compared the population structure and the colony breeding system between native and introduced ranges of the Asian needle ant. We used 20 microsatellite markers and a mitochondrial DNA locus to characterize the genetic diversity in both native and introduced ranges to determine the extent of the bottleneck following its introduction. We investigated how populations of the Asian needle ant are structured across Japan and the US, to investigate whether invasion induced a shift in reproductive strategies of *B. chinensis* colonies.

We found that invasion has lowered the genetic diversity in introduced populations but did not induce a shift in colony breeding system with populations comprising several large polygynous and polydomous colonies. Remarkably, we uncovered that inbreeding is not a consequence of the bottleneck, but it is due to sib-mating that pre-exists in native populations. The bottleneck hence did not affect the genetic diversity or the level of heterozygosity within colonies in the invasive range. Further, generations of sib-mating in native populations may have purged deleterious alleles thereby reducing inbreeding depression and acting as a pre-adapted trait to favour invasion success.

2 | MATERIALS AND METHODS

2.1 | Sample collection

Three populations of *B. chinensis* in its native range in Japan (Kyoto, Okayama and Okinawa) and one population in the introduced range in the US (Raleigh) were extensively sampled (Figure 1). Within each population, we laid out 10 × 200 metres transects along which we collected all nests encountered inside wood debris (downed logs and branches). Thirty-nine nests from four transects were sampled in Raleigh, and in Japan, 29 transects (63 nests from five transects in Kyoto; 20 nests from six transects in Okayama and 14 nests from four transects in Okinawa) were sampled. All workers, queens, males and brood were directly stored in pure ethanol until subsequent genetic analyses. In addition, 1–2 workers from six additional populations spread across Japan were sampled for phylogeographic analyses. Sample localities and Accession nos. are given in Table S1.

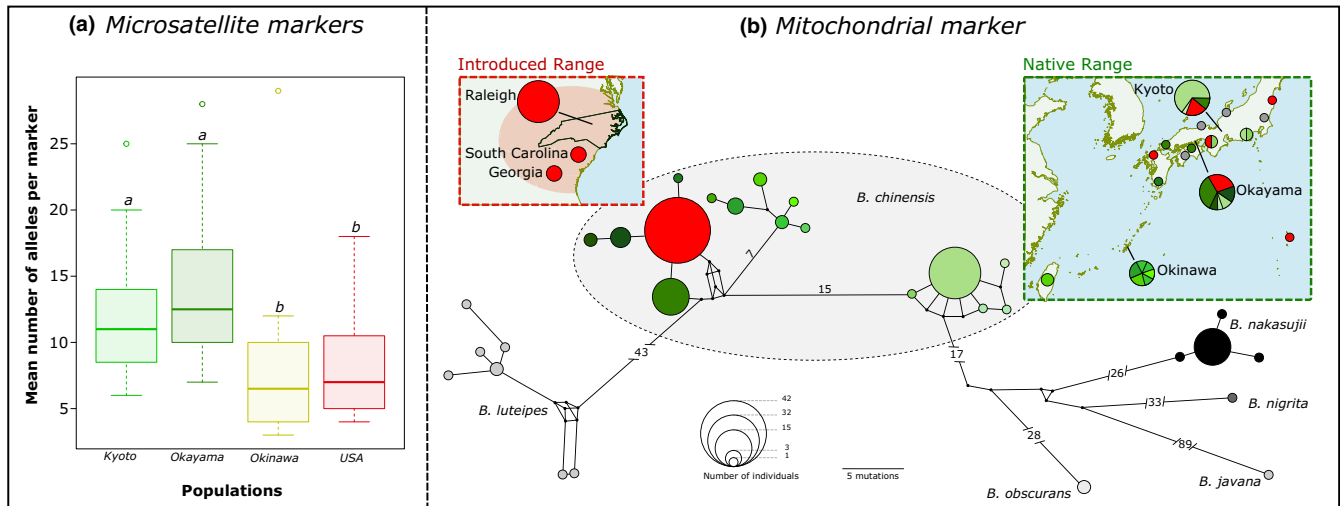


FIGURE 1 (a) Mean number of alleles per microsatellite marker for each population. Box plots show median and 1st and 3rd quartile; whiskers include 95% of all observations; outliers are plotted as individual dots. Mean allele number with different lower case letters differed significantly. (b) Haplotype network for the COI mitochondrial marker of *B. chinensis* in its native and introduced populations. Circle sizes are proportional to the number of sequences observed in the data set and the branch lengths indicate the number of mutations between haplotypes. *Brachyponera nakasujii*, *B. luteipes*, *B. obscurans*, *B. javana* and *B. nigrita* are used as outgroups. Geographic distribution of haplotypes is represented on the sampling map [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Genetic procedures

Total genomic DNA was extracted from each individual using a modified Gentra Puregene extraction kit (Gentra Systems, Inc. Minneapolis, MN, USA). Twenty-five new microsatellite markers (Bch01 to Bch25; Table S2) were developed for *B. chinensis* running a pool of 10 individuals originating from the Raleigh, NC population through one lane of Illumina HiSeq. Sequences were assembled after trimming of adapters and low-quality bases (Q score <25) using Trimmomatic (Bolger, Lohse, & Usadel, 2014). Trimmed reads were then assembled using ABySS (version 1.9.0) (Simpson et al., 2009). A total of 73189 reads containing microsatellite repeat motifs were identified among the 461419 sequences analysed using Msatcommander v. 0.8.2.0 (Faircloth, 2008). Among these, we selected a set of 25 loci (3, 12 and 10 with di, tri and tetranucleotide repeats, respectively) and designed the corresponding primers using the online Primer3 software (<http://www.simgene.com/Primer3>). Twenty-one out of the 25 primer pairs were successfully amplified on six *B. chinensis* workers in standard simplex PCR and visualized on agarose gels. One microsatellite marker (Bch17) was later discarded due to the presence of null alleles and inconsistent amplification. No evidence of linkage disequilibrium for any pair of the remaining loci was observed after corrections for multiple testing. The subsequent analyses were therefore performed on multi-locus data from all 20 microsatellites for all populations. For these 20 microsatellite loci, we used the M13-tailed primer method (Boutin-Ganache, Raposo, Raymond, & Deschepper, 2001) to label amplicons. The M13 tails were 5'-fluorescently labelled with 6-FAM, VIC, PET or NED to facilitate multiplexing. Primer sequences, GenBank Accession nos. PCR conditions and multiplexing arrangements are given in the online supplementary material (Table S2). Amplicons were amplified

using a Bio-Rad thermocycler T100 (Bio-Rad, Pleasanton, CA) and visualized on an ABI 3500 capillary sequencer against LIZ500 internal standard (Applied Biosystems, Foster City, CA, USA). Allele scoring was carried out using Gene Marker[®] HID (Holland & Parson, 2011). For mitochondrial analyses, we sequenced a fragment of the COI mitochondrial gene using the C13 and C14 primer pair, specific for *B. chinensis* species (Yashiro, Matsuura, Guénard, Terayama, & Dunn, 2010). PCR products were purified with EXOSAP-it PCR purification kit (Affymetrix), followed by sequencing with the ABI BigDye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems). Sequencing was performed on an ABI 3500 Genetic Analyzer (Applied Biosystems). Base calling and sequence reconciliation were performed using CodonCode Aligner (CodonCode Corporation, Dedham, MA, USA).

2.3 | Population structure and evidence of genetic bottleneck

For mitochondrial analyses, new mitochondrial sequences were characterized for one worker per nest for each transect within each population, as well as for 1–2 workers from the six additional populations spread across Japan and Taiwan. In addition, we integrated 25 sequences of *B. chinensis* from GenBank covering nine native populations in Japan (Fukuoka, Hyogo, Kagawa, Kagoshima, Kanagawa, Okayama, Okinawa, Tochigi and Yamaguchi) and Taiwan (Nantou), and nine sequences from three introduced populations in the US (Georgia, South and North Carolina; Figure 1) (Yashiro et al., 2010). Overall, our sampling included 91 samples in 12 native populations and 25 samples in three introduced populations for *B. chinensis*, as well as 21, 9, 2, 1 and 1 sample of the closely related species *B. nakasujii*, *B. luteipes*, *B. obscurans*, *B. javana* and *B. nigrita*, respectively, which were used as outgroups. Phylogeographic

relationships between haplotypes were represented on networks produced by the median-joining method (Bandelt, Forster, & Röhl, 1999) implemented in the program NETWORK v.4.6.1.1 (available at <http://www.fluxus-engineering.com/>). Comparisons within and between populations were performed based on nucleotide diversity and genetic divergence using MEGA v. 5.0 (Tamura et al., 2011).

For microsatellite analyses, six workers per nest were genotyped at the 21 microsatellite markers in each transect within the four populations ($X \pm SD = 5.56 \pm 2.06$; $N_{\text{workers}} = 729$; $N_{\text{nests}} = 131$). Allele frequencies, measures of observed and expected heterozygosity and F -statistics were estimated using FSTAT (Goudet, 1995). To detect the occurrence of a bottleneck, we investigated a loss of genetic diversity in introduced populations comparing the mean number of alleles per marker between populations using the Kruskal–Wallis test. In recently bottlenecked populations, gene diversity (sensu Nei, 1973) is larger than expected from the number of alleles at mutation–drift equilibrium since allele number decreases faster than gene diversity after a founder effect. This results in heterozygosity excess in introduced populations (Cornuet & Luikart, 1996). We thus tested for a bottleneck effect in the Raleigh population by performing a Wilcoxon test on heterozygosity excess using Bottleneck 1.2.02 (Piry, Luikart, & Cornuet, 1999) with a two-phase model of mutation (TPM) (Cornuet & Luikart, 1996). In addition, we identified recent bottlenecks through the mode-shift distortion in the distribution of allele frequencies they induced (Luikart, Allendorf, Cornuet, & Sherwin, 1998). Populations with stable size are characterized by an L-shaped distribution (i.e., indicative of many alleles with low frequencies) while bottlenecked populations show a mode shift to more alleles at intermediate frequencies, resulting from the purging of rare alleles by a founder effect. We use this graphical approach to identify recently bottlenecked populations (Luikart et al., 1998).

2.4 | Colony structure

We determined colony identity within each transect using three methods. First, we investigated population structure by plotting [$F_{ST}/(1 - F_{ST})$] coefficients between pairs of nests against the \ln of their geographic distance (Slatkin, 1993). Mantel tests implemented in GENEPOP ON THE WEB (Rousset, 2008) were used to test the significance of the correlation. F_{ST} coefficients between pairs of nests were then visualized on nest-by-nest F_{ST} matrices. Second, to determine whether different nests belonged to the same genetic entity (i.e., colony), genotypic frequencies at all nests within transects were compared using a log-likelihood (G)-based test of differentiation using GENEPOP ON THE WEB (Rousset, 2008). Overall significance was determined using a Fisher's combined probability test after a Bonferroni correction was applied to account for multiple comparisons. Finally, the clustering of different nests under unique colony entities was represented for each transect by the inference of genetic clusters (K) in our sampling using Bayesian clustering implemented in Structure v.2.3 (Pritchard, Stephens, & Donnelly, 2000). The simulations were run with values of K from 1 to the number of nests encountered within each of the populations studied and

repeated 20 times for each number of K. A different simulation was run for each population. A combination of an admixture and a correlated allele frequency model was used for the analysis. Each run included a 5×10^4 burn-in period followed by 1×10^5 iterations of the MCMC. The most likely number of groupings was evaluated using ΔK (Evanno, Regnaut, & Goudet, 2005) and log-likelihood value by Structure Harvester v.0.6.8 (Earl & vonHoldt, 2012).

For each colony uncovered by this method (in most cases comprising multiple nests, see section 3 below), the minimum number of queens was determined from field observations. Queen-mating frequency was estimated from mother–offspring genetic analyses in which male genotypes were inferred from the workers' genotypes. Each worker was assigned to a given patriline with the maximum-likelihood method implemented in the software COLONY 1.2 (Wang, 2004). Relatedness coefficients (r) were estimated using the program COANCESTRY v.1.0 (Wang, 2011), according to the algorithm described by Queller & Goodnight (Queller & Goodnight, 1989). Relatedness coefficients were calculated separately for each population to account for the differences in allele frequencies between populations. Relatedness coefficients were first estimated among colonies; colonies were weighted equally, and standard errors (SE) were obtained by jackknifing over colonies. Relatedness coefficients were then estimated (a) between queens within colonies, (b) between queens and their inferred males and (c) between the inferred males that mate with a given queen.

Despite finding multiple queens within colonies (up to 47), allelic diversity within colonies was surprisingly low and all workers from most of the colonies could be assigned to a single queen (see section 3). This finding prompted us to examine the possibility that queens use thelytokous parthenogenesis for the production of new queens, while sexual reproduction is conserved for worker production. A distinct mode of production for the different castes within colony is expected to yield a significant change in heterozygosity between queen and worker castes (Pearcy & Aron, 2006). We hence compared the mean observed heterozygosity (H_o) between the queens and the workers.

3 | RESULTS

3.1 | Loss of genetic diversity and evidence of a bottleneck

All microsatellite loci analysed were polymorphic in at least one population with the number of alleles varying between 8 for locus *Bch1* to 52 for locus *Bch25* marker ($X \pm SD = 19.7 \pm 9.7$; Table 1 and Table S2, Supplementary Information). The mean number of alleles per locus was significantly lower in the populations of Okinawa and Raleigh (7.9 and 8.4, respectively) than in the mainland Japanese populations of Kyoto and Okayama (11.8 and 14.1, respectively) ($p = 0.00$, Kruskal–Wallis rank test; $p < 0.05$, post hoc Dunn test) (Figure 1; Figure S1; Table 1). In addition, the allelic distribution in the invasive population of Raleigh revealed skewed distributions towards intermediate allele frequencies (Figure S2), probably resulting

TABLE 1 Average number of alleles per marker, mean number of alleles per colony, inbreeding coefficient F_{IS} , level of observed and expected heterozygosity and average F_{ST} between transect for each population

	Kyoto	Okayama	Okinawa	Raleigh	Overall
Number of alleles within population					
X	11.8	14.05	7.9	8.35	19.7
SD	5.0	5.8	5.8	4.2	9.7
Mean number of alleles per colony					
X	2.58	3.46	2.27	3.59	3.10
SD	1.07	1.12	0.67	0.77	1.09
Inbreeding index (F_{IS})					
X	0.383	0.248	0.525	0.398	0.478
SD	0.141	0.123	0.207	0.152	0.081
Heterozygosity obs (exp)					
X	0.444 (0.750)	0.603 (0.794)	0.228 (0.475)	0.414 (0.688)	0.423 (0.846)
SD	0.11 (0.09)	0.14 (0.08)	0.17 (0.28)	0.09 (0.09)	0.09 (0.04)
Average F_{ST} between transect					
X	0.208	0.191	0.147	0.167	0.188
SD	0.04	0.07	0.01	0.03	0.06
Relatedness (w-w)					
X	0.348	0.157	0.258	0.202	0.241
SD	0.182	0.176	0.222	0.107	0.171

from a loss of rare alleles during founder events (Luikart et al., 1998). The bottleneck test, however, failed to detect a recent bottleneck through an excess of heterozygotes ($p = 1.0$), as most of our loci exhibited heterozygote deficiency. The decrease in heterozygotes observed in this species most probably stems from its inbred mating strategy (see below) and therefore cannot be used to reliably estimate the occurrence of a bottleneck in this species. Though, the reduced number of alleles and their skewed distribution in the introduced population of Raleigh is indicative of a bottleneck event.

Our mitochondrial data set of *B. chinensis* included 543 bp COI sequences for 91 individuals from 12 native localities and 25 individuals from three introduced populations in the US (Figure 1). We uncovered 39 (7.18%) variable sites and detected 16 haplotypes of *B. chinensis*. The loss of genetic variation uncovered using microsatellite markers was also found in this mitochondrial marker, as all of the 16 haplotypes were found in the native areas but only one was found in the introduced areas (including Georgia, South and North Carolina). Furthermore, the number of haplotypes ranged from 1 to 6 among localities in the native range (4, 6 and 6 in Kyoto, Okayama

and Okinawa, respectively) and mean genetic distance within the native zone was 2.6%.

3.2 | Populations are strongly differentiated and comprise large polygynous and polydomous colonies

We found substantial genetic differentiation between transects in the invasive population of Raleigh ($F_{ST} = 0.167$). This value is significantly higher than 0 (expected when the whole population consists of a single supercolony), and it does not significantly differ from the mean F_{ST} between transects in the native range of *B. chinensis* (0.187; $p = 0.398$, Mann–Whitney test). In addition, the distribution of the genetic diversity is comparable between populations (Table 2), suggesting that dispersal strategies of this species remain similar between native and introduced ranges.

Within transects, the genetic differentiation between nests significantly increases with geographic distance in both the native and introduced populations. However, in most populations, the distribution of F_{ST} values is bimodal with genetic differentiation between

TABLE 2 Analysis of molecular variance (AMOVA) for each population of *B. chinensis*

Source of variation	Sum of squares			Variance components			Percentage variation		
	Kyoto	Okayama	USA	Kyoto	Okayama	USA	Kyoto	Okayama	USA
Among colonies	271.4	453.9	1000.1	1.797	1.929	2.152	35.76%	25.90%	29.96%
Among nests within colonies	52.7	41.4	161.5	0.052	0.282	0.198	1.04%	3.79%	2.75%
Within nests	421.6	995.1	2200.8	3.175	5.236	4.832	63.20%	70.31%	67.28%
TOTAL	745.7	1490.4	3362.4	5.02	7.447	7.182			

nests being either high or close to zero (Figure 2 and 3). Genotypic differentiation tests indeed reveal that several nests within most transects were not significantly different from each other (i.e., probably belonging to a single colony). The genotypic differentiation tests, F_{ST} matrices and STRUCTURE clustering showed that the introduced populations of Raleigh, as well as the native populations, consist of polydomous colonies of a few to several interconnected nests (Figure 2 and 3), in line with previous observations from the field (BG). Field observations revealed that colonies of *B. chinensis* were polygynous in both the native and introduced ranges, with mated queen number ranging from 1 to 47 (a maximum of 25 queens was found in a single nest).

3.3 | Colonies are highly inbred and produce supplemental queens that stay within colonies. They hence exhibit extremely low genetic diversity considering their numerous queens, preserving relatedness among nestmates

Remarkably, all populations showed departure from Hardy-Weinberg equilibrium at all loci, with a lower proportion of heterozygous individuals ($H_o \pm SD = 0.423 \pm 0.08$) than expected

($H_e \pm SD = 0.846 \pm 0.04$) yielding a significant overall F_{IS} index of 0.478 ($p < 0.01$; Table 1). Despite field evidence of polygyny, mother-offspring genetic inferences revealed that the genotypes of all workers in a colony match with the occurrence of a single matriline in most of the colonies analysed. Such a result is found even when a high number of workers per colony were genotyped (up to 130) with a high allelic diversity within the population (mean number of alleles per locus $X \pm SD = 11.8 \pm 5.0$). Despite the high number of reproductive queens within colonies and the high allelic diversity within populations, the number of alleles per colony was strikingly low ($X \pm SD = 3.10 \pm 1.09$; Table 1; Figure 4c).

The mean relatedness between nestmate queens was $r = 0.54$ in the introduced Raleigh population. This value is significantly higher than zero ($p < 0.01$), which is expected under the association of random founder queens. This result suggests that nestmate queens are descendants of the original foundress queen. This conclusion is supported by the presence of a single mtDNA haplotype present within each native colony. In addition, the mean relatedness coefficients observed between the queens and their male mates were significantly higher from the values expected under random mating ($r_{obs} = 0.244$ ($r_{exp} = -0.005$), 0.263 (0.010), 0.117 (-0.008) and 0.225 (0.039), in the Raleigh, Kyoto, Okayama

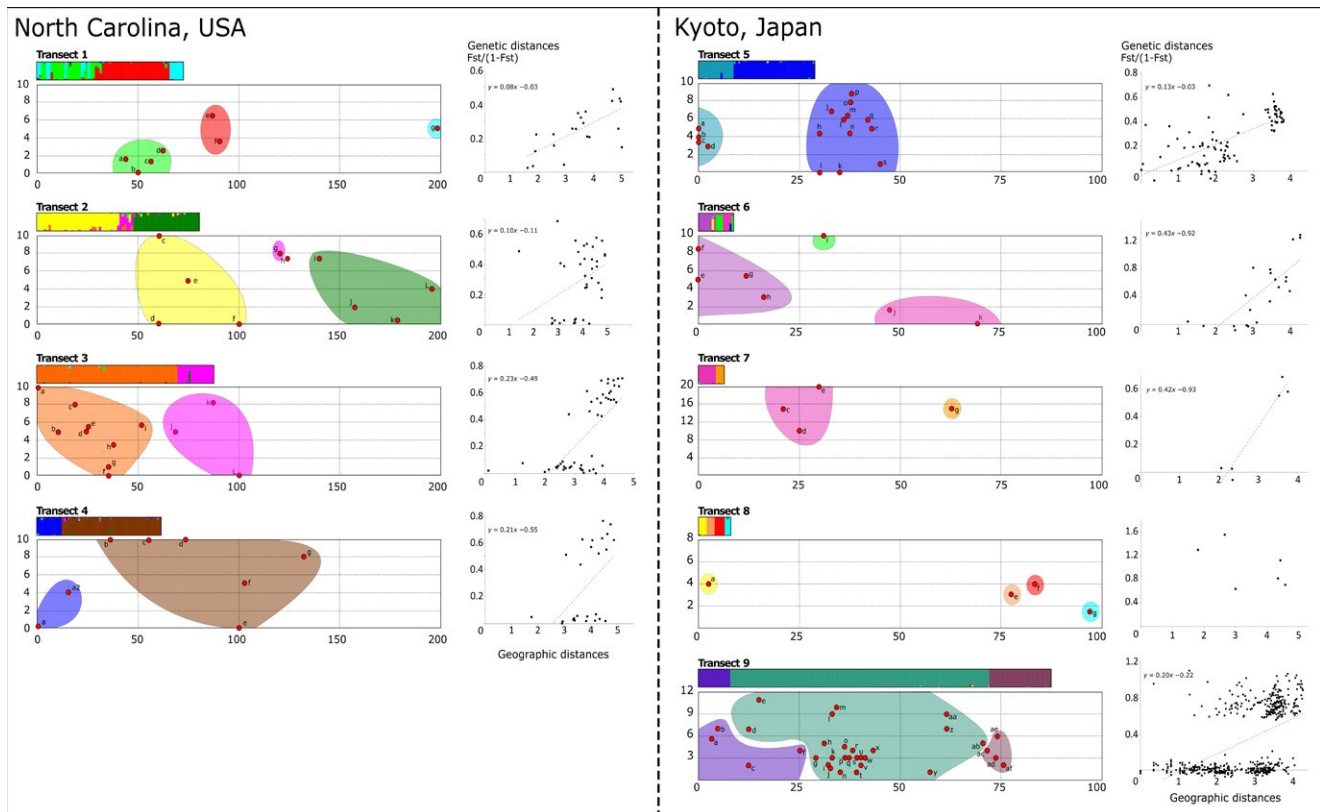


FIGURE 2 Transects in the introduced population of Raleigh and in the native population of Kyoto. In each transect, the location of each nest is represented by red dots. Nests' locations are indicated in metres in Table S1 (x,y). Coloured circles group nests that were not significantly different from each other (i.e., probably belonging to a single colony) based on genotypic differentiations tests, F_{ST} matrices and STRUCTURE clustering. STRUCTURE clustering and the correlations between genetic differentiation between nests and geographic distances are also given for each transect by plotting $[F_{ST}/(1 - F_{ST})]$ coefficients between pairs of nests against the \ln of their geographic distance [Colour figure can be viewed at wileyonlinelibrary.com]

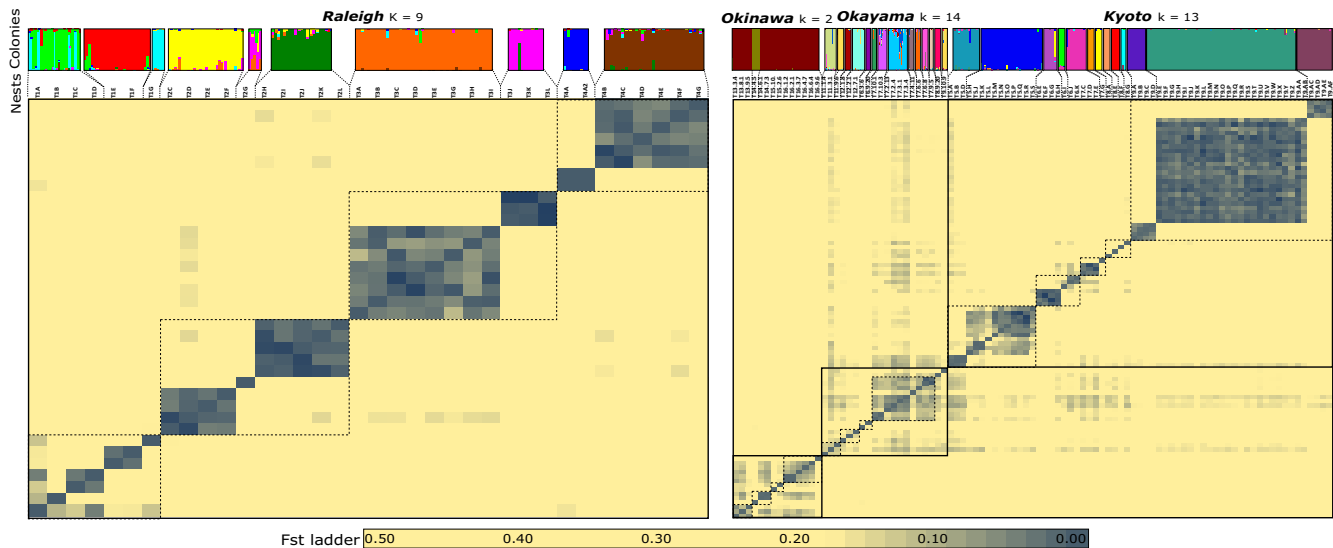


FIGURE 3 Results of the F_{ST} genetic differentiation tests are summarized using nest-by-nest matrices for native (a) and introduced (b) populations of *B. chinensis*. Cells are coloured according to the genetic differentiation between each pair of nests. STRUCTURE results shown on Figure 2 are also reported on this figure [Colour figure can be viewed at wileyonlinelibrary.com]

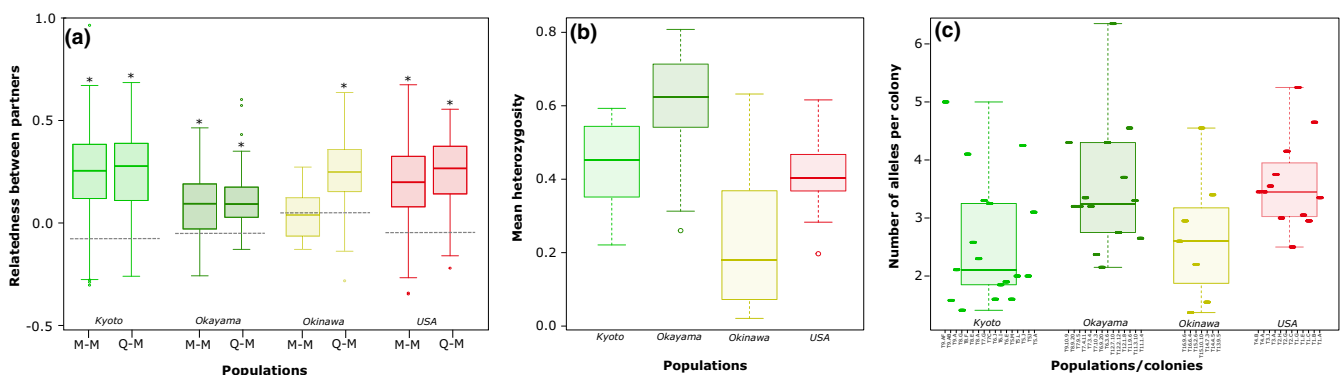


FIGURE 4 (a) Average relatedness between sexual individuals in each population. The mean relatedness between an inferred queen and their inferred mates (Q-M) and the relatedness between inferred males mated with an inferred queen (M-M) are represented. The dotted lines indicate the expected relatedness between partners in the case of random mating in each population as estimated by the program COANCESTRY. Asterisks indicate a significant difference between the observed and expected relatedness between partners. (b) Mean heterozygosity for each population. (c) Number of alleles uncovered in each colony and the average number of alleles per colony for each population [Colour figure can be viewed at wileyonlinelibrary.com]

and Okinawa populations, respectively; all $p < 0.01$; Figure 4a). Similarly, the values observed between the different males mated with the same inferred queen were significantly higher than expected under random mating ($r = 0.202, 0.245, 0.088$ and 0.042 ; all $p < 0.01$; except in the Okinawa population). This result indicated that mating occurred between relatives in both introduced and native ranges.

The mean ($\pm SD$) within-colony genetic relatedness among nest-mate workers was $r = 0.202 \pm 0.107$ for the introduced population of Raleigh and $r = 0.348 \pm 0.182, 0.157 \pm 0.176$ and 0.258 ± 0.222 for the native populations of Kyoto, Okayama and Okinawa, respectively (Table 1). These values were significantly lower than the 0.75 expected under monogyny and monandry (two-tailed t tests, all $p < 0.01$), but were still significantly different from zero (all $p < 0.01$).

Again, these results are consistent with colonies headed by numerous related queens.

3.4 | Bottleneck has no effect on inbreeding coefficient and within-colony diversity

Interestingly, the inbreeding coefficient in the introduced population of Raleigh ($F_{IS} = 0.398$) is not significantly higher than in the native populations ($F_{IS} = 0.383, 0.525$ and 0.248 for Kyoto, Okayama and Okinawa populations, respectively; Table 1). Similarly, observed heterozygosity did not differ between the introduced population (H_o Raleigh = 0.414) and the native populations ($H_o = 0.444, 0.603$ and 0.228 for Kyoto, Okayama and Okinawa populations, respectively; Figure 4b). Furthermore, the mean number of alleles per colony is

even slightly higher in the introduced population of Raleigh than in the native Japanese population of Kyoto ($p = 0.015$, Dunn test; Figure 4c) but not the Okayama and Okinawa populations ($p = 1.0$ and 0.13 , respectively, Dunn test) despite the fact that the overall number of alleles in the Raleigh population is almost twice as low as in the Okayama and Kyoto populations (Figure 1).

4 | DISCUSSION

We found that inbreeding tolerance in native populations acts as a pre-adapted trait for invasion success. We highlighted four major features of the life history traits of the Asian needle ant *Brachyponera chinensis* and how they may favour its ecological dominance, coping with genetic depletion subsequent to a founder event. First, a bottleneck has lowered the genetic diversity in introduced populations of this species by 30%–40% relative to native mainland Japanese populations. Second, the introduction of this species did not induce a major shift in the population genetic structure and colony breeding system. Both native and introduced localities comprise strongly differentiated populations of large polygynous colonies composed of several interconnected nests. Third, colonies are initiated by a single queen and then produce supplementary queens that subsequently reintegrate into their natal nest. Finally, we found an unusually high level of inbreeding in both the introduced and native populations, with queens of *B. chinensis* preferentially mating with related males. This reproductive strategy results in abnormally low within-colony genetic diversity and a low level of heterozygosity. Remarkably, these features were observed in introduced populations, as expected after a bottleneck event, but also in native populations of this species where genetic diversity is twice as high. This suggests that inbreeding is not a consequence of the bottleneck, but an active mate choice that pre-existed in native populations and might have pre-adapted this species to invasion. Further, generations of inbreeding in native populations may have purged deleterious alleles thereby possibly strengthening this species against genetic depletion by reducing inbreeding depression. Overall, these results highlight the long inbreeding history of this species that may underlie inbreeding tolerance and act as a pre-adapted trait to favour successful invasion.

The inbreeding level uncovered in our study is quite unusual among animals and one of the highest ever found in an ant species (Foitzik, Rüger, Kureck, & Metzler, 2011). Inbreeding is often due to small population sizes and/or restricted dispersal, but it may also stem from active mate choice for relatives (Keller & Waller, 2002; Templeton & Read, 1994). Surprisingly, high inbreeding levels were found in both introduced and native populations suggesting that inbreeding in this species is not a consequence of the founder effect following introduction, but instead a reproductive trait favoured by frequent mating between relatives. Inbred offspring usually experience reduced fitness, and so, natural selection has favoured many mechanisms whereby species can avoid inbreeding (Charlesworth & Willis, 2009; Keller & Waller, 2002). Yet, inbreeding avoidance may

also be costly in terms of high mortality rates during dispersal or missed mating opportunities (Kokko, Ots, & Tregenza, 2006). Inbred social systems may thus, at least in theory, be balanced by the benefits of group living such as cooperation in foraging, brood rearing and nest defence. Inbreeding also increases the proportion of shared alleles between parents, including those favouring inbreeding; thus, inbreeding may enhance social cohesion within groups as it increases relatedness and the indirect benefit of helping behaviour through kin selection (Charlesworth, 2006; Hamilton, 1964; Hill & Weir, 2007; Kokko et al., 2006; Thurin & Aron, 2009). Hence, in rare cases, inbred mating might be selected for when the costs of avoidance are higher than those of inbreeding depression (Waser, Austad, & Keane, 1986), or when the advantages of mating with close kin override the cost of inbreeding depression (Bengtsson, 1978; Kokko et al., 2006; Lehmann & Perrin, 2003; Parker, 2006; Thünken, Bakker, Baldauf, & Kullmann, 2007).

In ants, inbreeding is fairly rare as its costs are usually high and permanent due to their system of sex determination (Ross et al., 1993) and their partner commitment for life (Boomsma, 2009). In monogynous colonies, mating usually occurs through nuptial flights where sexuals from surrounding colonies are synchronously released, strongly limiting the risk of mating between relatives (Hölldobler & Wilson, 1990). In polygynous colonies with intranidal mating, queens within the colony may use kin discrimination to distinguish between nestmate and non-nestmate males, and to promote mating with unrelated males (Kaufmann, Boomsma, Passera, & Petersen, 1992; Keller & Passera, 1993; Passera & Keller, 1994). In the native and invasive ranges of the Argentine ant, intranidal mating is not associated with inbreeding (Ingram, 2002; Krieger & Keller, 2000), as colonies contain large numbers of unrelated queens that frequently move between nests (Jaquière, Vogel, & Keller, 2005; Pedersen, Krieger, Vogel, Giraud, & Keller, 2006). However, low to high levels of inbreeding have been reported in a few species (Cole & Wiernasz, 1997; Haag-Liautard, Vitikainen, Keller, & Sundstrom, 2009; Heinze, 2017; Heinze, Schrempf, Rakotondrazafy, & Fisher, 2014; Sundstrom, Keller, & Chapuisat, 2003; Thurin & Aron, 2009). In these species, inbreeding is mostly detrimental and affects several life history traits. In *Cardiocondyla obscurior* Wheeler, inbreeding results in lower queen lifespan and brood survival (Schrempf, Reber, Tinaut, & Heinze, 2005). In *Formica exsecta* Nylander, inbreeding is associated with reductions in queen lifespan, immune defence of new queens, male quality and colony survival (Haag-Liautard et al., 2009; Vitikainen & Sundström, 2011).

The complementary sex determination system present in the Hymenoptera can lead to high genetic loads in introduced populations. In this system, females, which are diploid, are heterozygous at the sex-determining locus (or loci), and males, which are normally haploid, are hemizygous (Whiting, 1943). However, males that are homozygous at the sex-determining locus (or loci) are diploid and generally sterile (Harpur, Sobhani, & Zayed, 2013). In the fire ant *S. invicta*, there appears to be only a single locus controlling sex determination and introduced populations in the U.S. show high levels of diploid male production compared to native populations due to a reduction in the

number of alleles at the sex-determining locus (Ross et al., 1993). A similar situation has been found in the invasive bee *Lasioglossum leucozonium* (Schränk) in Canada (Kukuk & May, 1990). In both of these species, invasive populations thrive despite the high fitness costs associated with the production of diploid males. In the present study, we did not investigate diploid male production because we found too few males present for a thorough genetic analysis. Additional studies are needed to determine whether diploid males are produced in *B. chinensis* and if so, whether introduced populations produce more than native populations.

Brachyponera chinensis colonies cover large surface areas and are composed of several interconnected nests. A polydomous nesting system has been previously suspected in this species. In one study, no aggressive behaviour towards non-nestmate workers was reported within populations, while between-population pairs of workers were highly aggressive to each other (Murata, Tsuji, & Kikuchi, 2017). In ants, polygyny could arise either through the production of new queens that reintegrate into their natal nests or through the integration of foreign queens into already established nests (Keller, 1995). In our study, the occurrence of a single mitochondrial DNA haplotype and the high levels of relatedness among nestmate queens within colonies in both the native and introduced populations strongly support the hypothesis that colonies are initiated by a single queen, and additional queens are subsequently recruited from their natal nest, providing genetic evidence for previous field observations.

Polygyny in *B. chinensis* may provide colonies rapid growth, a higher probability of survival and an earlier onset of reproduction (Boomsma et al., 2014; Boulay et al., 2014). This strategy may also enhance invasion success as it allows colonies to reach high worker densities and rapidly overcome interspecific competition (Holway & Suarez, 2004; Le Breton et al., 2005). However, high levels of polygyny are usually associated with a reduction in within-colony relatedness and thus lower workers' indirect fitness (Hamilton, 1964).

In invasive species, unicoloniality may be even more paradoxical as the high number of reproductive queens and the loss of colony boundaries eliminates relatedness between colony members. Within-colony relatedness is indeed close to zero in several invasive species (e.g., *Linepithema humile* (Mayr), (Tsutsui et al., 2000); *Lasius neglectus* Van Loon, Boomsma & Andrasfalvy, (Cremer et al., 2008); *Pheidole megacephala* Fabricius, (Fournier et al., 2009)). In *B. chinensis*, the newly produced queens mate with related males then reintegrate into their natal nests for colony growth. Colonies, therefore, keep their genetic identities and high relatedness within the colony even with a high number of reproductive queens. Inbreeding thus allows the development of populous and spatially expansive colonies, due to the presence of several reproductive queens, yet preserving workers' indirect fitness benefit and social cohesion within colonies (Haag-Liautard et al., 2009; Thurin & Aron, 2009; Thurin, Sery, Guimbretiere, & Aron, 2011; Trontti, Thurin, Sundström, & Aron, 2007).

A strategy similar to *B. chinensis* has also been reported in the ant species *Technomyrmex albipes* (revised as *T. brunneus*; Bolton, 2007)

and *Hypoponera opacior* (Forel) (Foitzik, Kureck, Rüger, & Metzler, 2010; Yamauchi, Furukawa, Kinomura, Takamine, & Tsuji, 1991). In *T. brunneus*, huge polydomous colonies are founded by winged females after a nuptial flight, but reproduction is then supplanted by inbred wingless intercastes that mate with related males within the nests (Yamauchi et al., 1991). In *H. opacior*, a second set of wingless sexuals emerge later during the season and mate within the nest, resulting in high inbreeding coefficients. These ergatoid queens are either recruited into the mother nest or found new colonies nearby through budding (Foitzik et al., 2010). This strategy also is analogous to the one encountered in many subterranean termite species. Colonies are founded by a monogamous pair of primary reproductives (queen and king), but secondary reproductives (neotenics) take over or supplement reproduction when the colony grows (Buchli, 1958). Neotenics develop from nymph or worker offspring of the primary pair. They stay and mate within the colony possibly for several generations, leading to high degrees of inbreeding (Vargo & Hunscheder, 2009; Vargo et al., 2013). Such a strategy has been reported in several invasive termite species (Dronnet, Chapuisat, Vargo, Lohou, & Bagnères, 2005; Leniaud, Dedeine, Pichon, Dupont, & Bagnères, 2010; Perdureau et al., 2015) and allows rapid growth of the colony without reducing the relatedness within colonies.

In *B. chinensis*, polygynous colonies exhibit an average of three alleles per microsatellite locus. This number is surprisingly low considering the high number of reproductive queens within colonies and probably stems from the inbred mode of reproduction. This weak within-colony diversity does not allow reliable estimates of the number of matings per queen, as the probability that two different males carry the same alleles at every locus is high. Polyandry or "indirect polyandry" (through several single-mated queens) may be selected in highly inbred species to reduce the risk of genetically incompatible matings, which may result in production of nonviable offspring and/or sterile diploid males (Cook & Crozier, 1995; Cornell & Tregenza, 2007; Duthie, Bocedi, & Reid, 2016; Michalczyk et al., 2011; Tarpay & Page, 2002; Tregenza & Wedell, 2002).

Social insects display a large array of reproductive strategies, including unorthodox reproductive modes involving clonal reproduction and hybridization. Some of which may favour invasiveness by acting as pre-adaptations against genetic depletion or the increased homozygosity due to bottlenecks during invasions (Pearcy, Goodisman, & Keller, 2011). In some populations of three invasive ant species, *Paratrechina longicornis* Latreille, *Wasmannia auropunctata* Roger and *Vollenhovia emeryi* Wheeler, workers arise from classical sexual reproduction, whereas queens are clones of their mothers and males are clones of their fathers (Fournier et al., 2005; Ohkawara, Nakayama, Satoh, Trindl, & Heinze, 2006; Percy et al., 2011). Male and female gene pools are completely segregated (Foucaud, Estoup, Loiseau, Rey, & Orivel, 2010; Kobayashi, Hasegawa, & Ohkawara, 2008), allowing queens to mate with their brothers inside the nest, yet maintain heterozygosity in the worker caste over an unlimited number of generations (Percy et al., 2011). In these species, a single-mated clonal queen may found an introduced population, producing 100% heterozygous workers and

circumventing the costs associated with inbreeding (Foucaud et al., 2010; Pearcy et al., 2011). In our study, the level of heterozygosity is lower than expected in both workers and queens of *B. chinensis*; but it did not differ significantly between the two castes. This indicates that they were both produced through classic sexual reproduction (Figure S3) and that the high level of inbreeding in *B. chinensis* arises from sib-mating rather than clonal reproduction of queens.

We found high inbreeding coefficients in both native and introduced populations of *B. chinensis* suggesting that inbreeding preference is not a shift in the reproductive strategy of the invasive population but instead the pre-existing condition in the species. This mating strategy may have favoured the invasive capacity of *B. chinensis* by reducing possible effects of inbreeding depression subsequent to its introduction to new areas. Native populations of this species naturally undergo inbreeding and are probably adapted to the potential deleterious effects of inbreeding. Consequently, genetic bottlenecks are less constrained by the costs of inbreeding depression than one might expect. In other terms, a long history of inbreeding in native populations may have already reduced the frequency of deleterious recessive alleles (Barrett & Charlesworth, 1991; Crnokrak & Spencer, 2002) and promoted the evolution of inbreeding tolerance (Kureck, Jongepier, Nicolai, & Foitzik, 2012). Theoretical simulations indicate that low levels of inbreeding over a long period efficiently purge deleterious alleles (e.g., Bijlsma, Bundgaard, & Boerema, 2000; Boakes & Wang, 2005; Day, Bryant, & Meffert, 2003; Hedrick, 1994; Miller & Hedrick, 2001), contrasting with invasive populations that often undergo intense inbreeding over a short period of time. Empirical studies also support that regularly inbred populations may be less prone to inbreeding depression (Charlesworth & Charlesworth, 1987; Lacy & Ballou, 1998). Furthermore, a computational study revealed that bottlenecks of intermediate size also purge the alleles that cause inbreeding depression under certain theoretical conditions (Glémin, 2003). In the ladybird *Harmonia axyridis* Pallas, bottlenecks have purged deleterious alleles, enabling invaders to maintain high fitness when inbred rather than posing a barrier to invasion as often assumed (Facon et al., 2011).

5 | CONCLUSION

To date, a number of studies on ants, as well as other widely diverse taxa, have reported a loss of diversity and a higher level of inbreeding as a consequence of a founder effect following introduction. Inbreeding tolerance as a pre-adapted trait for invasion success has not, however, been previously described. Colonies headed by closely related queens together with regular sib-mating in native populations of *B. chinensis* have probably strengthened its inbreeding tolerance and reduced inbreeding depression. This is achieved through purifying selection of deleterious alleles expressed in homozygous diploid individuals, as well as in haploid males (Antolin, 1999; Henter & Fenster, 2003). The introduced population of *B. chinensis* in the US has undergone a genetic bottleneck, drastically reducing genetic

diversity; however, it has not affected the genetic diversity or the level of heterozygosity within colonies and does not seem to impact its invasion success nor prevent its ecological dominance in introduced populations. To date, the effects of chronic inbreeding on queen longevity, diploid male production, colony productivity and survival remain unknown in this species. Based on our results, we hypothesize that dispersing queens generally mate with unrelated males during nuptial flights at the time of colony founding. After colony foundation, colony growth is accelerated by the production of additional queens, which remain in their natal colony and mate with their kin.

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DATA ACCESSIBILITY

DNA sequences: GenBank Accession nos. MH370616 to MH370732. Sampling locations and microsatellite genotypes: Dryad <https://doi.org/10.5061/dryad.rm3558f>.

AUTHOR CONTRIBUTIONS

The studies were designed by KT, KM, EV, BG and RD. Samples were collected by KK, YY, WS, CH, TY, KT, KM and EV. The microsatellites were developed by EV and PAE. All the genetic analyses were performed by PAE. The paper with contributions of EV, KT, KM, BG and RD was written by PAE.

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REFERENCES

- Antolin, M. F. (1999). A genetic perspective on mating systems and sex ratios of parasitoid wasps. *Researches on Population Ecology*, 41, 29–37. <https://doi.org/10.1007/PL00011979>
- Bandelt, H. J., Forster, P., & Röhl, A. (1999). Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, 16, 37–48. <https://doi.org/10.1093/oxfordjournals.molbev.a026036>
- Barrett, S. C. H., & Charlesworth, D. (1991). Effects of a change in the level of inbreeding on the genetic load. *Nature*, 352, 522. <https://doi.org/10.1038/352522a0>
- Bengtsson, B. O. (1978). Avoiding inbreeding: At what cost? *Journal of Theoretical Biology*, 73, 439–444. [https://doi.org/10.1016/0022-5193\(78\)90151-0](https://doi.org/10.1016/0022-5193(78)90151-0)

- Bertelsmeier, C., Guénard, B., & Courchamp, F. (2013). Climate change may boost the invasion of the Asian Needle Ant. *PLoS ONE*, 8, e75438. <https://doi.org/10.1371/journal.pone.0075438>
- Bijlsma, R., Bundgaard, J., & Boerema, A. (2000). Does inbreeding affect the extinction risk of small populations?: Predictions from *Drosophila*. *Journal of Evolutionary Biology*, 13, 502–514. <https://doi.org/10.1046/j.1420-9101.2000.00177.x>
- Boakes, E., & Wang, J. (2005). A simulation study on detecting purging of inbreeding depression in captive populations. *Genetical Research*, 86, 139–148. <https://doi.org/10.1017/S001667230500772X>
- Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: A flexible trimmer for Illumina sequence data. *Bioinformatics*, 30, 2114–2120. <https://doi.org/10.1093/bioinformatics/btu170>
- Bolton, B. (2007). Taxonomy of the dolichoderine ant genus *Technomyrmex* Mayr (Hymenoptera: Formicidae) based on the worker caste. *Contributions of the American Entomological Institute*, 35, 1–149.
- Boomsma, J. J. (2009). Lifetime monogamy and the evolution of eusociality. *Proceedings of the Royal Society B*, 364, 3191–3207.
- Boomsma, J. J., Huszár, D. B., & Pedersen, J. S. (2014). The evolution of multiqueen breeding in eusocial lineages with permanent physically differentiated castes. *Animal Behaviour*, 92, 241–252. <https://doi.org/10.1016/j.anbehav.2014.03.005>
- Boulay, R., Arnan, X., Cerdá, X., & Retana, J. (2014). The ecological benefits of larger colony size may promote polygyny in ants. *Journal of Evolutionary Biology*, 27, 2856–2863. <https://doi.org/10.1111/jeb.12515>
- Boutin-Ganache, I., Raposo, M., Raymond, M., & Deschepper, C. (2001). M13-tailed primers improve the readability and usability of microsatellite analyses performed with two different allele-sizing methods. *BioTechniques*, 28, 6–24.
- Buchli, H. (1958). L'origine des castes et les potentialités ontogénétiques des termites européennes du genre *Reticulitermes* Holmgren. *Annales des Sciences Naturelles, Zoologie*, 11, 261–429.
- Charlesworth, D. (2006). Evolution of plant breeding systems. *Current Biology*, 16, R726–R735. <https://doi.org/10.1016/j.cub.2006.07.068>
- Charlesworth, D., & Charlesworth, B. (1987). Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics*, 18, 237–268. <https://doi.org/10.1146/annurev.es.18.110187.001321>
- Charlesworth, D., & Willis, J. H. (2009). The genetics of inbreeding depression. *Nature Reviews Genetics*, 10, 783–796. <https://doi.org/10.1038/nrg2664>
- Cole, B. J., & Wiernasz, D. C. (1997). Inbreeding in a lek-mating ant species, *Pogonomyrmex occidentalis*. *Behavioral Ecology and Sociobiology*, 40, 79–86. <https://doi.org/10.1007/s002650050318>
- Cook, J. M., & Crozier, R. (1995). Sex determination and population biology in the Hymenoptera. *Trends in Ecology & Evolution*, 10, 281–286. [https://doi.org/10.1016/0169-5347\(95\)90011-X](https://doi.org/10.1016/0169-5347(95)90011-X)
- Cornell, S. J., & Tregenza, T. (2007). A new theory for the evolution of polyandry as a means of inbreeding avoidance. *Proceedings of the Royal Society B*, 274, 2873–2879. <https://doi.org/10.1098/rspb.2007.0926>
- Cornuet, J. M., & Luikart, G. (1996). Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics*, 144, 2001–2014.
- Cremer, S., Ugelvig, L. V., Drijfhout, F. P., Schlick-Steiner, B. C., Steiner, F. M., Seifert, B., ... Boomsma, J. J. (2008). The evolution of invasiveness in garden ants. *PLoS ONE*, 3, e3838. <https://doi.org/10.1371/journal.pone.0003838>
- Crnokrak, P., & Spencer, C. H. B. (2002). Perspective: Purging the genetic load: A review of the experimental evidence. *Evolution*, 56, 2347–2358. <https://doi.org/10.1111/j.0014-3820.2002.tb00160.x>
- Day, S. B., Bryant, E. H., & Meffert, L. M. (2003). The influence of variable rates of inbreeding on fitness, environmental responsiveness, and evolutionary potential. *Evolution*, 57, 1314–1324. <https://doi.org/10.1111/j.0014-3820.2003.tb00339.x>
- Dronnet, S., Chapuisat, M., Vargo, E. L., Lohou, C., & Bagnères, A.-G. (2005). Genetic analysis of the breeding system of an invasive subterranean termite, *Reticulitermes santonensis*, in urban and natural habitats. *Molecular Ecology*, 14, 1311–1320. <https://doi.org/10.1111/j.1365-294X.2005.02508.x>
- Duthie, A. B., Bocedi, G., & Reid, J. M. (2016). When does female multiple mating evolve to adjust inbreeding? Effects of inbreeding depression, direct costs, mating constraints, and polyandry as a threshold trait. *Evolution*, 70, 1927–1943. <https://doi.org/10.1111/evo.13005>
- Earl, D. A., & vonHoldt, B. M. (2012). STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, 4, 359–361. <https://doi.org/10.1007/s12686-011-9548-7>
- Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software structure: A simulation study. *Molecular Ecology*, 14, 2611–2620. <https://doi.org/10.1111/j.1365-294X.2005.02553.x>
- Facon, B., Hufbauer, R., Tayeh, A., Loiseau, A., Lombaert, E., Vitalis, R., ... Estoup, A. (2011). Inbreeding depression is purged in the invasive insect *Harmonia axyridis*. *Current Biology*, 21, 424–427. <https://doi.org/10.1016/j.cub.2011.01.068>
- Faircloth, B. C. (2008). msatcommander: Detection of microsatellite repeat arrays and automated, locus-specific primer design. *Molecular Ecology Resources*, 8, 92–94. <https://doi.org/10.1111/j.1471-8286.2007.01884.x>
- Fauvergue, X., Vercken, E., Malausa, T., & Hufbauer, R. A. (2012). The biology of small, introduced populations, with special reference to biological control. *Evolutionary Applications*, 5, 424–443. <https://doi.org/10.1111/j.1752-4571.2012.00272.x>
- Foitzik, S., Kureck, I. M., Rüger, M. H., & Metzler, D. (2010). Alternative reproductive tactics and the impact of local competition on sex ratios in the ant *Hypoponera opacior*. *Behavioral Ecology and Sociobiology*, 64, 1641–1654. <https://doi.org/10.1007/s00265-010-0977-1>
- Foitzik, S., Rüger, M. H., Kureck, I. M., & Metzler, D. (2011). Macro- and microgeographic genetic structure in an ant species with alternative reproductive tactics in sexuals. *Journal of Evolutionary Biology*, 24, 2721–2730. <https://doi.org/10.1111/j.1420-9101.2011.02397.x>
- Foucaud, J., Estoup, A., Loiseau, A., Rey, O., & Orivel, J. (2010). Thelytokous parthenogenesis, male clonality and genetic caste determination in the little fire ant: New evidence and insights from the lab. *Heredity*, 105, 205–212. <https://doi.org/10.1038/hdy.2009.169>
- Fournier, D., De Biseau, J. C., & Aron, S. (2009). Genetics, behaviour and chemical recognition of the invading ant *Pheidole megacephala*. *Molecular Ecology*, 18, 186–199. <https://doi.org/10.1111/j.1365-294X.2008.04018.x>
- Fournier, D., Estoup, A., Orivel, J., Foucaud, J., Jourdan, H., Le Breton, J., & Kelle, L. (2005). Clonal reproduction by males and females in the little fire ant. *Nature*, 435, 1230–1234. <https://doi.org/10.1038/nature03705>
- Frankham, R. (2004). Resolving the genetic paradox in invasive species. *Heredity*, 94, 385–385.
- Giraud, T., Pedersen, J. S., & Keller, L. (2002). Evolution of supercolonies: The Argentine ants of southern Europe. *Proceedings of the National Academy of Sciences*, 99, 6075–6079. <https://doi.org/10.1073/pnas.092694199>
- Glémin, S. (2003). How are deleterious mutations purged? Drift versus nonrandom mating. *Evolution*, 57, 2678–2687. <https://doi.org/10.1111/j.0014-3820.2003.tb01512.x>
- Goudet, J. (1995). FSTAT (Version 1.2): A computer program to calculate F-Statistics. *Journal of Heredity*, 86, 485–486. <https://doi.org/10.1093/oxfordjournals.jhered.a111627>
- Guénard, B., & Dunn, R. R. (2010). A New (Old), invasive ant in the hardwood forests of eastern north America and its potentially widespread impacts. *PLoS ONE*, 5, e11614. <https://doi.org/10.1371/journal.pone.0011614>

- Haag-Liautard, C., Vitikainen, E., Keller, L., & Sundstrom, L. (2009). Fitness and the level of homozygosity in a social insect. *Journal of Evolutionary Biology*, 22, 134–142. <https://doi.org/10.1111/j.1420-9101.2008.01635.x>
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, 7, 1–16. [https://doi.org/10.1016/0022-5193\(64\)90038-4](https://doi.org/10.1016/0022-5193(64)90038-4)
- Harpur, B. A., Sobhani, M., & Zayed, A. (2013). A review of the consequences of complementary sex determination and diploid male production on mating failures in the Hymenoptera. *Entomologia Experimentalis et Applicata*, 146, 156–164. <https://doi.org/10.1111/j.1570-7458.2012.01306.x>
- Hedrick, P. W. (1994). Purging inbreeding depression and the probability of extinction: Full-sib mating. *Heredity*, 73, 363. <https://doi.org/10.1038/hdy.1994.183>
- Heinze, J. (2017). Life-history evolution in ants: The case of *Cardiocondyla*. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20161406. <https://doi.org/10.1098/rspb.2016.1406>
- Heinze, J., Schrempf, A., Rakotondrazafy, H., & Fisher, B. L. (2014). Polygyny, Inbreeding, and Wingless Males in the Malagasy Ant *Cardiocondyla shuckardi* Forel (Hymenoptera, Formicidae). *Sociobiology* 61, 300–306.
- Helanterä, H., Strassmann, J. E., Carrillo, J., & Queller, D. C. (2009). Unicolonial ants: Where do they come from, what are they and where are they going? *Trends in Ecology & Evolution*, 24, 341–349. <https://doi.org/10.1016/j.tree.2009.01.013>
- Henter, H. J., & Fenster, C. (2003). Inbreeding depression and haplodiploidy: Experimental measures in a parasitoid and comparisons across diploid and haplodiploid insecta taxa. *Evolution*, 57, 1793–1803. <https://doi.org/10.1111/j.0014-3820.2003.tb00587.x>
- Hill, W. G., & Weir, B. S. (2007). Prediction of multi-locus inbreeding coefficients and relation to linkage disequilibrium in random mating populations. *Theoretical Population Biology*, 72, 179–185. <https://doi.org/10.1016/j.tpb.2006.05.006>
- Holland, M. M., & Parson, W. (2011). GeneMarker® HID: A reliable software tool for the analysis of forensic STR data. *Journal of Forensic Sciences*, 56, 29–35. <https://doi.org/10.1111/j.1556-4029.2010.01565.x>
- Hölldobler, B., & Wilson, E. O. (1990). *The Ants*. The Belknap Press of Harvard University. Cambridge: Mass.
- Holway, D. A., Lach, L., Suarez, A. V., Tsutsui, N. D., & Case, T. J. (2002). The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics*, 33, 181–233. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150444>
- Holway, D. A., & Suarez, A. V. (2004). Colony-structure variation and interspecific competitive ability in the invasive Argentine ant. *Oecologia*, 138, 216–222. <https://doi.org/10.1007/s00442-003-1414-1>
- Ingram, K. K. (2002). Plasticity in queen number and social structure in the invasive Argentine ant (*Linepithema humile*). *Evolution*, 56, 2008–2016. <https://doi.org/10.1111/j.0014-3820.2002.tb00127.x>
- Jaquière, J., Vogel, V., & Keller, L. (2005). Multilevel genetic analyses of two European supercolonies of the Argentine ant, *Linepithema humile*. *Molecular Ecology*, 14, 589–598. <https://doi.org/10.1111/j.1365-294X.2005.02433.x>
- Kaufmann, B., Boomsma, J. J., Passera, L., & Petersen, K. N. (1992). Relatedness and inbreeding in a French population of the unicolonial ant *Iridomyrmex humilis* (Mayr). *Insectes Sociaux*, 39, 195–200. <https://doi.org/10.1007/BF01249294>
- Keller, L. (1995). Social life: The paradox of multiple-queen colonies. *Trends in Ecology & Evolution*, 10, 355–360. [https://doi.org/10.1016/S0169-5347\(00\)89133-8](https://doi.org/10.1016/S0169-5347(00)89133-8)
- Keller, L., & Passera, L. (1993). Incest avoidance, fluctuating asymmetry, and the consequences of inbreeding in *Iridomyrmex humilis*, an ant with multiple queen colonies. *Behavioral Ecology and Sociobiology*, 33, 191–199. <https://doi.org/10.1007/BF00216600>
- Keller, L. F., & Waller, D. M. (2002). Inbreeding effects in wild populations. *Trends in Ecology & Evolution*, 17, 230–241. [https://doi.org/10.1016/S0169-5347\(02\)02489-8](https://doi.org/10.1016/S0169-5347(02)02489-8)
- Kirkpatrick, M., & Jarne, P. (2000). The effects of a bottleneck on inbreeding depression and the genetic load. *The American Naturalist*, 155, 154–167. <https://doi.org/10.1086/303312>
- Kobayashi, K., Hasegawa, E., & Ohkawara, K. (2008). Clonal reproduction by males of the ant *Vollenhovia emeryi* (Wheeler). *Entomological Science*, 11, 167–172. <https://doi.org/10.1111/j.1479-8298.2008.00272.x>
- Kokko, H., Ots, I., & Tregenza, T. (2006). When not to avoid inbreeding. *Evolution*, 60, 467–475. <https://doi.org/10.1111/j.0014-3820.2006.tb01128.x>
- Krieger, M. J. B., & Keller, L. (2000). Mating frequency and genetic structure of the Argentine ant *Linepithema humile*. *Molecular Ecology*, 9, 119–126. <https://doi.org/10.1046/j.1365-294x.2000.00837.x>
- Krieger, M. J. B., Ross, K. G., Chang, C. W. Y., & Keller, L. (1999). Frequency and origin of triploidy in the fire ant *Solenopsis invicta*. *Heredity*, 82, 142–150. <https://doi.org/10.1038/sj.hdy.6884600>
- Kukuk, P. F., & May, B. (1990). Diploid males in a primitively eusocial bee, *Lasiglossus (dialictus) zephyrum* (Hymenoptera: Halictidae). *Evolution*, 44, 1522–1528.
- Kureck, I. M., Jongepier, E., Nicolai, B., & Foitzik, S. (2012). No inbreeding depression but increased sexual investment in highly inbred ant colonies. *Molecular Ecology*, 21, 5613–5623. <https://doi.org/10.1111/mec.12060>
- Lacy, R. C., & Ballou, J. D. (1998). Effectiveness of selection in reducing the genetic load in populations of *Peromyscus polionotus* during generations of inbreeding. *Evolution*, 52, 900–909. <https://doi.org/10.1111/j.1558-5646.1998.tb03715.x>
- Le Breton, J., Jourdan, H., Chazeau, J., Orivel, J., & Dejean, A. (2005). Niche opportunity and ant invasion: The case of *Wasmannia auropunctata* in a New Caledonian rain forest. *Journal of Tropical Ecology*, 21, 93–98. <https://doi.org/10.1017/S0266467404002019>
- Lee, C. E. (2002). Evolutionary genetics of invasive species. *Trends in Ecology & Evolution*, 17, 386–391. [https://doi.org/10.1016/S0169-5347\(02\)02554-5](https://doi.org/10.1016/S0169-5347(02)02554-5)
- Lehmann, L., & Perrin, N. (2003). Inbreeding avoidance through kin recognition: Choosy females boost male dispersal. *The American Naturalist*, 162, 638–652. <https://doi.org/10.1086/378823>
- Leniaud, L., Dedeine, F., Pichon, A., Dupont, S., & Bagnères, A.-G. (2010). Geographical distribution, genetic diversity and social organization of a new European termite, *Reticulitermes urbis* (Isoptera: Rhinotermitidae). *Biological Invasions*, 12, 1389–1402. <https://doi.org/10.1007/s10530-009-9555-8>
- Luikart, G., Allendorf, F. W., Cornuet, J. M., & Sherwin, W. B. (1998). Distortion of allele frequency distributions provides a test for recent population bottlenecks. *Journal of Heredity*, 89, 238–247. <https://doi.org/10.1093/jhered/89.3.238>
- Michalczyk, A., Millard, A. L., Martin, O. Y., Lumley, A. J., Emerson, B. C., Chapman, T., & Gage, M. J. G. (2011). Inbreeding promotes female promiscuity. *Science*, 333, 1739–1742. <https://doi.org/10.1126/science.1207314>
- Miller, P. S., & Hedrick, P. W. (2001). Purging of inbreeding depression and fitness decline in bottlenecked populations of *Drosophila melanogaster*. *Journal of Evolutionary Biology*, 14, 595–601. <https://doi.org/10.1046/j.1420-9101.2001.00303.x>
- Moller, H. (1996). Lessons for invasion theory from social insects. *Biological Conservation*, 78, 125–142. [https://doi.org/10.1016/0006-3207\(96\)00022-5](https://doi.org/10.1016/0006-3207(96)00022-5)
- Murata, N., Tsuji, K., & Kikuchi, T. (2017). Social structure and nestmate discrimination in two species of *Brachyponera* ants distributed in Japan. *Entomological Science*, 20, 86–95. <https://doi.org/10.1111/ens.12232>
- Nei, M. (1973). Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences USA*, 70, 3321–3323. <https://doi.org/10.1073/pnas.70.12.3321>

- Nei, M., Maruyama, T., & Chakraborty, R. (1975). The bottleneck effect and genetic variability in populations. *Evolution*, 29, 1–10. <https://doi.org/10.1111/j.1558-5646.1975.tb00807.x>
- Ohkawara, K., Nakayama, M., Satoh, A., Trindl, A., & Heinze, J. (2006). Clonal reproduction and genetic caste differences in a queen-polymorphic ant, *Vollenhovia emeryi*. *Biology Letters*, 2, 359–363. <https://doi.org/10.1098/rsbl.2006.0491>
- Parker, G. A. (2006). Sexual conflict over mating and fertilization: An overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361, 235–259. <https://doi.org/10.1098/rstb.2005.1785>
- Passera, L., & Keller, L. (1994). Mate availability and male dispersal in the Argentine ant *Linepithema humile* (Mayr) (*Iridomyrmex humilis*). *Animal Behaviour*, 48, 361–369. <https://doi.org/10.1006/anbe.1994.1249>
- Pearcy, M., & Aron, S. (2006). Thelytokous parthenogenesis and its consequences on inbreeding in an ant. *Heredity*, 96, 377–382. <https://doi.org/10.1038/sj.hdy.6800813>
- Pearcy, M., Goodisman, M. A., & Keller, L. (2011). Sib mating without inbreeding in the longhorn crazy ant. *Proceedings of the Royal Society B*, 278, 2677–2681. <https://doi.org/10.1098/rspb.2010.2562>
- Pedersen, J. S., Krieger, M. J. B., Vogel, V., Giraud, T., & Keller, L. (2006). Native supercolonies of unrelated individuals in the invasive Argentine ant. *Evolution*, 60, 782–791. <https://doi.org/10.1111/j.0014-3820.2006.tb01156.x>
- Perdereau, E., Bagnères, A. G., Vargo, E. L., Baudouin, G., Xu, Y., Labadie, P., ... Dedie, F. (2015). Relationship between invasion success and colony breeding structure in a subterranean termite. *Molecular Ecology*, 24, 2125–2142. <https://doi.org/10.1111/mec.13094>
- Pérez, J. E., Nirchio, M., Alfonsi, C., & Muñoz, C. (2006). The biology of invasions: The genetic adaptation paradox. *Biological Invasions*, 8, 1115–1121. <https://doi.org/10.1007/s10530-005-8281-0>
- Piry, S., Luikart, G., & Cornuet, J. M. (1999). Computer note. BOTTLENECK: A computer program for detecting recent reductions in the effective size using allele frequency data. *Journal of Heredity*, 90, 502–503. <https://doi.org/10.1093/jhered/90.4.502>
- Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, 155, 945–959.
- Queller, D. C., & Goodnight, K. F. (1989). Estimating relatedness using genetic markers. *Evolution*, 43, 258–275. <https://doi.org/10.1111/j.1558-5646.1989.tb04226.x>
- Rodriguez-Cabal, M. A., Stuble, K. L., Guénard, B., Dunn, R. R., & Sanders, N. J. (2012). Disruption of ant-seed dispersal mutualisms by the invasive Asian needle ant (*Pachycondyla chinensis*). *Biological Invasions*, 14, 557–565. <https://doi.org/10.1007/s10530-011-0097-5>
- Roman, J., & Darling, J. A. (2007). Paradox lost: Genetic diversity and the success of aquatic invasions. *Trends in Ecology & Evolution*, 22, 454–464. <https://doi.org/10.1016/j.tree.2007.07.002>
- Ross, K. G., Vargo, E. L., Keller, L., & Trager, J. C. (1993). Effect of a founder event on variation in the genetic sex-determining system of the fire ant *Solenopsis invicta*. *Genetics*, 135, 843–854.
- Rousset, F. (2008). genepop'007: A complete re-implementation of the genepop software for Windows and Linux. *Molecular Ecology Resources*, 8, 103–106. <https://doi.org/10.1111/j.1471-8286.2007.01931.x>
- Schrempf, A., Reber, C., Tinaut, A., & Heinze, J. (2005). Inbreeding and local mate competition in the ant *Cardiocondyla batesii*. *Behavioral Ecology and Sociobiology*, 57, 502–510. <https://doi.org/10.1007/s00265-004-0869-3>
- Schrieber, K., & Lachmuth, S. (2017). The genetic paradox of invasions revisited: The potential role of inbreeding × environment interactions in invasion success. *Biological Reviews*, 92, 939–952. <https://doi.org/10.1111/brv.12263>
- Simberloff, D. (2009). The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, 40, 81–102. <https://doi.org/10.1146/annurev.ecolsys.110308.120304>
- Simpson, J. T., Wong, K., Jackman, S. D., Schein, J. E., Jones, S. J., & Birol, I. (2009). ABySS: A parallel assembler for short read sequence data. *Genome Research*, 19, 1117–1123. <https://doi.org/10.1101/gr.089532.108>
- Slatkin, M. (1993). Isolation by distance in Equilibrium and Non-Equilibrium populations. *Evolution*, 47, 264–279. <https://doi.org/10.1111/j.1558-5646.1993.tb01215.x>
- Suarez, A. V., Holway, D. A., & Tsutsui, N. D. (2008). Genetics and behavior of a colonizing species: The invasive Argentine ant. *The American Naturalist*, 172, S72–S84. <https://doi.org/10.1086/588638>
- Sundstrom, L., Keller, L., & Chapuisat, M. (2003). Inbreeding and sex biased gene flow in the ant *Formica exsecta*. *Evolution*, 57, 1552–1561. <https://doi.org/10.1111/j.0014-3820.2003.tb00363.x>
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., & Kumar, S. (2011). MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, 28, 2731–2739. <https://doi.org/10.1093/molbev/msr121>
- Tarpy, D. R., & Page, R. E. (2002). Sex determination and the evolution of polyandry in honey bees (*Apis mellifera*). *Behavioral Ecology and Sociobiology*, 52, 143–150. <https://doi.org/10.1007/s00265-002-0498-7>
- Templeton, A. R., & Read, B. (1994). Inbreeding: One word, several meanings, much confusion. In: V. Loeschke, S. K. Jain & J. Tomiuk (Ed.), *Conservation genetics* (pp. 91–105). Basel: Birkhäuser Basel. <https://doi.org/10.1007/978-3-0348-8510-2>
- Thünken, T., Bakker, T. C. M., Baldauf, S. A., & Kullmann, H. (2007). Active inbreeding in a Cichlid fish and its adaptive significance. *Current Biology*, 17, 225–229. <https://doi.org/10.1016/j.cub.2006.11.053>
- Thurin, N., & Aron, S. (2009). Sib-mating in the ant *Plagiolepis pygmaea*: Adaptive inbreeding. *Journal of Evolutionary Biology*, 22, 2481–2487. <https://doi.org/10.1111/j.1420-9101.2009.01864.x>
- Thurin, N., Sery, N., Guimbretiere, R., & Aron, S. (2011). Colony kin structure and breeding system in the ant genus *Plagiolepis*. *Molecular Ecology*, 20, 3251–3260. <https://doi.org/10.1111/j.1365-294X.2011.05161.x>
- Tregenza, T., & Wedell, N. (2002). Polyandrous females avoid costs of inbreeding. *Nature*, 415, 71–73. <https://doi.org/10.1038/415071a>
- Trontti, K., Thurin, N., Sundström, L., & Aron, S. (2007). Mating for convenience or genetic diversity? Mating patterns in the polygynous ant *Plagiolepis pygmaea*. *Behavioral Ecology*, 18, 298–303. <https://doi.org/10.1093/beheco/arl083>
- Tsutsui, N. D., Suarez, A. V., Holway, D. A., & Case, T. J. (2000). Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences USA*, 97, 5948–5953. <https://doi.org/10.1073/pnas.100110397>
- Vargo, E. L., & Hunseneder, C. (2009). Biology of subterranean termites: Insights from molecular studies of *Reticulitermes* and *Coptotermes*. *Annual Review of Entomology*, 54, 379–403. <https://doi.org/10.1146/annurev.ento.54.110807.090443>
- Vargo, E. L., Leniaud, L., Swoboda, L. E., Weiser, M. D., Miller, D. M., & Bagnères, A. G. (2013). Clinal variation in colony breeding structure and level of inbreeding in the subterranean termites *Reticulitermes flavipes* and *R. grassei*. *Molecular Ecology*, 22, 1447–1462. <https://doi.org/10.1111/mec.12166>
- Vitikainen, E., & Sundström, L. (2011). Inbreeding and caste-specific variation in immune defence in the ant *Formica exsecta*. *Behavioral Ecology and Sociobiology*, 65, 899–907. <https://doi.org/10.1007/s00265-010-1090-1>
- Wang, J. (2004). Sibship reconstruction from genetic data with typing errors. *Genetics*, 166, 1963–1979. <https://doi.org/10.1534/genetics.166.4.1963>
- Wang, J. (2011). coancestry: A program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Molecular Ecology Resources*, 11, 141–145. <https://doi.org/10.1111/j.1755-0998.2010.02885.x>
- Waser, P. M., Austad, S. N., & Keane, B. (1986). When should animals tolerate inbreeding? *The American Naturalist*, 128, 529–537. <https://doi.org/10.1086/284585>

- Whiting, P. W. (1943). Multiple alleles complementary sex determination of *Habrobracon*. *Genetics*, 28, 365–382.
- van Wilgenburg, E., Driessen, G., & Beukeboom, L. W. (2006). Single locus complementary sex determination in Hymenoptera: An "unintelligent" design? *Frontiers in Zoology*, 3, 1. <https://doi.org/10.1186/1742-9994-3-1>
- Yamauchi, K., Furukawa, T., Kinomura, K., Takamine, H., & Tsuji, K. (1991). Secondary polygyny by inbred wingless sexuals in the dolichoderine ant *Technomyrmex albipes*. *Behavioral Ecology and Sociobiology*, 29, 313–319. <https://doi.org/10.1007/BF00165955>
- Yashiro, T., Matsuura, K., Guénard, B. S., Terayama, M., & Dunn, R. R. (2010). On the evolution of the species complex *Pachycondyla chinensis* (Hymenoptera: Formicidae: Ponerinae), including the origin of its invasive form and description of a new species. *Zootaxa*, 2685, 39–50.
- Zayed, A., & Packer, L. (2005). Complementary sex determination substantially increases extinction proneness of haplodiploid populations.

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