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ORIGINAL PAPER

Lack of genetic structuring, low effective population sizes and major bottlenecks characterise common and German wasps in New Zealand

Julia M. Schmack · Evan C. Brenton-Rule · Ruan Veldtman · Tom Wenseleers · Jacqueline R. Beggs · Philip J. Lester · Mariana Bulgarella

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Abstract Invasive species cause severe ecological and economic impacts in their introduced ranges. *Vespula* wasps, native to Eurasia, are a major threat to New Zealand native ecosystems. Understanding factors that influence the success of wasp invasion is pivotal for the development of control strategies. Here, we compare genetic diversity and structure of *Vespula germanica* and *Vespula vulgaris* between regions of their native and introduced ranges using microsatellite markers. Our study found lower diversity and lack of genetic structure for both invasive *Vespula* species within New Zealand. The significant reduction in allelic richness, gene diversity and effective population size illustrate a major bottleneck in New Zealand *V. germanica* and *V. vulgaris* populations. Strong signatures of population structure were found for both *Vespula* species with two clusters being identified as optimal *k*, approximately corresponding to the native and the invaded ranges. Our results highlight the fact that the lack of genetic diversity does not impede successful invasions in *V. germanica* and *V. vulgaris* and encourage further research into mechanisms that promote the success of invasive social insects. Overall, this study provides insights into the genetics of invasive *Vespula* wasps that can be useful for the development of efficient management strategies.

Keywords Biological invasions · Hymenoptera · New Zealand · Social wasps · *Vespula*

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J. M. Schmack · J. R. Beggs
Centre for Biodiversity and Biosecurity, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

E. C. Brenton-Rule · P. J. Lester · M. Bulgarella (✉)
School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand
e-mail: Mariana.Bulgarella@vuw.ac.nz

R. Veldtman
South African National Biodiversity Institute, Private Bag X7, Newlands, Cape Town 7735, South Africa

R. Veldtman
Department of Conservation Ecology and Entomology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

T. Wenseleers
KU Leuven Lab of Socioecology and Social Evolution, Naamsestraat 59, 3000 Leuven, Belgium

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Introduction

Biological invasions result in severe impacts on ecosystems, the economy and human health (Clavero and García-Berthou 2005; Pimentel et al. 2005; Pyšek and Richardson 2010). Social insects like wasps, ants and termites are a particularly harmful group of invaders; their social lifestyle, high dispersal and reproduction rates as well as strong competitive abilities and the potential of rapid spread throughout the invaded range facilitate the invasion process (Moller 1996; Chapman and Bourke 2001; Suarez et al. 2002; Kenis et al. 2009).

Reduced genetic diversity through founder events, measured through reduced heterozygosity and number of alleles, is expected to result in decreased fitness in the invaded range (Nei et al. 1975; Allendorf and Lundquist 2003; Reed and Frankham 2003). Yet, the majority of studies demonstrates high invasion success despite severe bottlenecks (Golani et al. 2007; Dlugosch and Parker 2008; Puillandre et al. 2008; Burne et al. 2017; Zhang and Evans 2017). In contrast, some studies found high levels of genetic diversity in invasive populations, suggesting that a large founding population and/or multiple introductions lead to invasion success (Kolbe et al. 2004). Examples for elevated genetic diversity within the invaded range include the invasive brown anole, *Anolis sagrei*, and the European paper wasp, *Polistes dominula*, both introduced to the United States (Johnson and Starks 2004; Kolbe et al. 2004) and the mosquitofish, *Gambusia affinis*, invasive in New Zealand (Purcell et al. 2012). A recent study on the mosquito *Aedes albopictus*, invasive in several islands in the Indian Ocean, indicates that genetic diversity is likely to increase with increasing time since establishment (Sherpa et al. 2018).

The effective population size (N_e) is a powerful parameter to determine the rate of change in the composition of a population caused by genetic drift, the level of variability in a population, and the effectiveness of selection relative to drift (Wright 1931; Charlesworth 2009). N_e describes the amount of the gene pool that is passed on to the next generation; it determines within-species diversity and potential degree of inbreeding (Charlesworth 2009; Wang et al. 2016) and thus, is key for assessing the viability of invasive populations (Zayed 2004; Zayed et al. 2007; Luikart et al. 2010; Laugier et al. 2016). Reduced genetic diversity through founder effects during the invasion process can result in low N_e which leads to high levels of genetic drift and reduces the population's ability to adapt to changing environments (Reed and Frankham 2003; Zayed et al. 2007). Departures from the ideal of random mating alter N_e (Sugg and Chesser 1994). For example, multiple mating or polyandry increases N_e in reptiles (Davis et al. 2001; Pearse and Avise 2001; Moore et al. 2008), mammals (Shurtliff et al. 2005) and land snails (Murray 1964; but see also Karl 2008), while complementary sex determination leads to the production of infertile diploid males (Whiting 1933; Beye et al. 2003), which is expected to result in even lower N_e than predicted under haplodiploidy only (Zayed 2004). Exceptions to this theory are the invasive Asian honey bee, *Apis cerana*, which overcame the genetic depletion during the invasion of Australia due to natural selection of rare *csd* alleles (Gloag et al. 2017) and the solitary bee, *Lasioglossum leucozonium*, which successfully invaded North America despite extremely reduced levels of genetic variation, a significant bottleneck and lack of population structure (Zayed and Packer 2007). Thus, genetic variability may be conserved through mechanisms of natural selection, which compensates even for severe bottlenecks in hymenopterans (Gloag et al. 2017).

Vespula wasps, native to Eurasia, are highly efficient invaders and the economic and ecological impacts in their invaded ranges are numerous. Social behaviour, a polyphagous diet and the initiation of colonies by a single mated queen are considered the reasons for their exceptional global invasion success (Moller 1996; Hanna et al. 2014; Lester and Beggs 2019). *Vespula* wasps have become invasive in Argentina, Oceania, South Africa and the United States including all major islands of Hawaii (Visscher and Vetter 2003; Beggs et al. 2011) and recent studies show that climate change is likely to increase the invasion pressure by *Vespula* wasps on a global scale (Parmesan 2006; Hulme 2009).

The highest densities of *Vespula* wasps in the world are found in New Zealand South Island's honeydew-beech forests (*Nothofagus* spp.) (Moller et al. 1991; Beggs et al. 1998). Invaded ecosystems undergo numerous negative shifts including the decline of native taxa (Beggs et al. 2011; Gardner-Gee and Beggs 2013; Lester et al. 2013; Burne et al. 2017). As social wasps use invertebrate prey to rear their larvae, high

densities of *Vespula* wasps restructure insect communities (Toft and Rees 1998; Beggs and Rees 1999).

Two *Vespula* species invaded New Zealand. The German wasp (*Vespula germanica*) established on the North Island of New Zealand around 1945 (Clapperton et al. 1989). The common wasp (*Vespula vulgaris*) was first recorded in New Zealand in 1921 (Donovan 1984) becoming widespread and very abundant since the 1970s. Mitochondrial DNA (mtDNA) suggests that England and Scotland were the most likely sources of *V. germanica* wasps into New Zealand (Brenton-Rule et al. 2018) whereas the New Zealand population of *V. vulgaris* seem to have originated from England and Ireland (Lester et al. 2014). An assessment of the effective population size of *V. germanica* and *V. vulgaris* within New Zealand and a comparison with those in their native ranges are lacking.

We hypothesised that genetic bottlenecks during the introduction of *V. germanica* and *V. vulgaris* into New Zealand reduced the effective population size, heterozygosity and number of alleles considerably when compared to those in the native range (Dlugosch and Parker 2008). If we find evidence of a bottleneck, then higher levels of overall genetic diversity in the native range are expected when compared to the New Zealand introduced range of both *Vespula* species. We genotyped 10 and 14 microsatellite loci for *V. germanica* and *V. vulgaris*, respectively, to determine whether: (1) New Zealand populations were founded by a small number of individuals; (2) genetic diversity reflects a population bottleneck, and (3) these wasp populations are genetically structured within their invaded and native ranges.

Materials and methods

Wasp collection

Foraging wasps, *V. germanica* ($n = 44$) and *V. vulgaris* ($n = 40$) were collected throughout their native range in Europe and invaded ranges. Samples for *V. germanica* from the native range included specimens from Austria ($n = 2$), Belgium ($n = 2$), England ($n = 2$), France ($n = 3$), Germany ($n = 1$), Italy ($n = 1$), Portugal ($n = 2$), Scotland ($n = 3$), Spain ($n = 2$), Sweden ($n = 1$) and Switzerland ($n = 1$). The invasive range was represented by *V. germanica* individuals from Australia ($n = 1$), New Zealand ($n = 20$) and South Africa ($n = 3$). *Vespula vulgaris* samples from the native range included specimens from Belgium ($n = 10$) and Germany ($n = 10$) and from the invasive range in New Zealand ($n = 20$). Sampling in New Zealand for both species includes six offshore islands on the northern east coast of the North Island (Fig. 1). Specimen collection information is presented in Supplemental Table S1. Individuals were collected and immediately placed in 99% ethanol, and frozen upon arrival to the laboratory until DNA extraction. Following the criteria of Brenton-Rule et al. (2018), we considered the United Kingdom (UK) samples (England and Scotland) separated from mainland Europe. First, because the UK is geographically separated from the mainland. Secondly, it is the known source of the *Vespula* spp. invasions into New Zealand (Lester et al. 2014; Brenton-Rule et al. 2018).

Genetics

We extracted DNA from whole wasps using a modified chloroform protocol (GENEzol reagent, Geneaid Biotech, Taiwan was used in combination with β-mercaptoethanol, Sigma Aldrich, St Louis, MI, USA). We tested microsatellite primers previously developed for other vespine wasps in *V. germanica* and *V. vulgaris* (Thorén et al. 1995; Foster et al. 2001; Daly et al. 2002; Hasegawa and Takahashi 2002; Arca et al. 2012). Primer pairs were initially tried on six *V. germanica* individuals (30 loci assayed of which 24 amplified) and seven *V. vulgaris* individuals (31 loci assayed of which 27 amplified) from New Zealand. We finally assayed the multilocus genotype of 44 *V. germanica* individuals for 10 variable loci (of the 24 loci that amplified, 6 were non-variable and 8 presented excessive stuttering therefore these 14 loci were discarded) and of 40 *V. vulgaris* individuals at 14 variable loci (of the 27 loci that amplified successfully, 8 were non-variable and 5 loci presented excessive stuttering and were discarded; Supplemental Table S2). We screened one worker per nest as nestmates are related and not independent from one another (Goodisman et al. 2001). A M13 tag (TGTAAAACGACGGCCAGT) was added to the 5′-end of the forward primer of each locus. Each locus was amplified in 10 µL PCRs that contained 1 µL of template DNA, 0.2 µM forward primer, 0.8 µM reverse primer, 0.8 µM M13 primer (labelled with FAM, NED, PET or HEX), 0.8 uL Bovine Serum

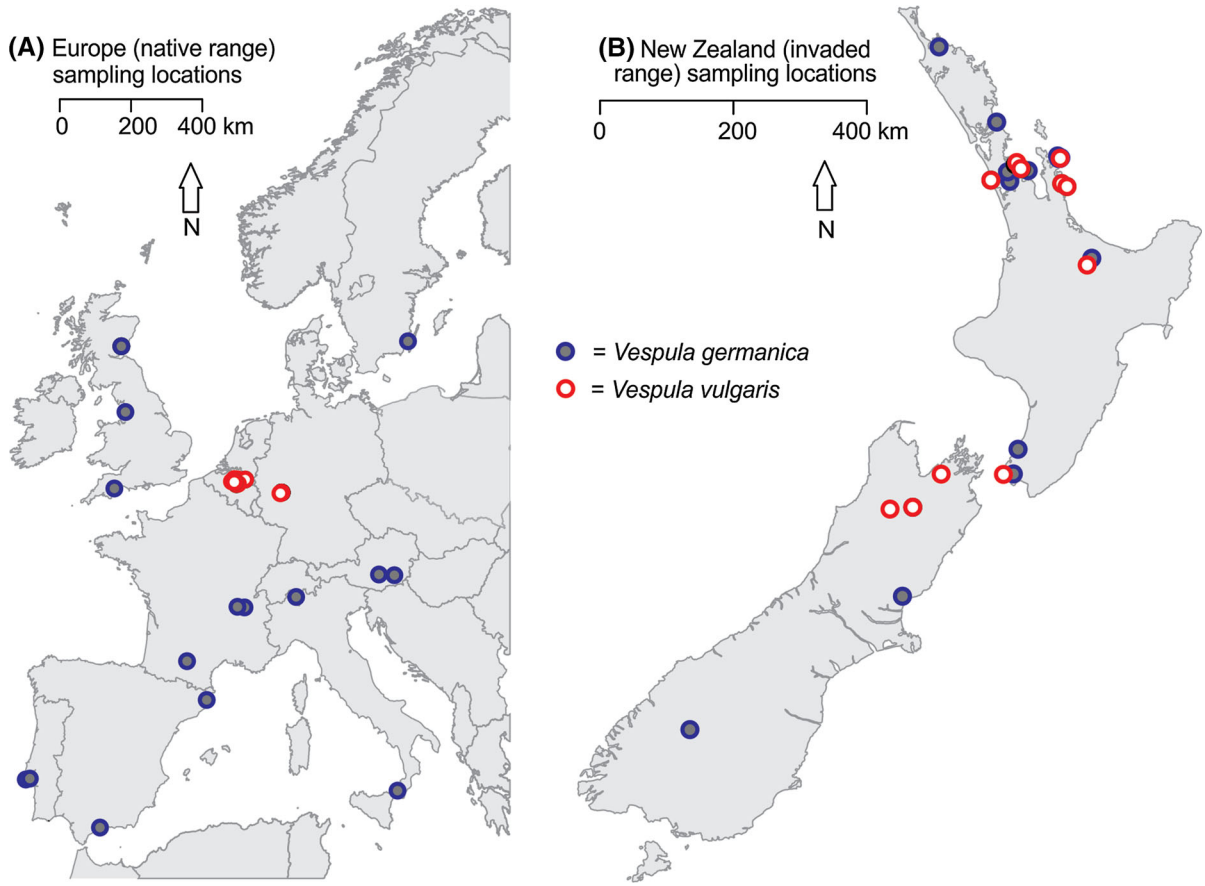


Fig. 1 Sampling locations of *Vespula germanica* and *V. vulgaris* in the native European range (left) and the introduced range in New Zealand (right). The *V. germanica* samples collected from Australia and South Africa are not shown

Albumin (Sigma Aldrich), ultra-pure water and 1 × MyTaq Mix (Bioline, London, UK). Multiplex PCR thermocycling conditions and primer annealing temperatures are reported in Supplemental Tables S2 and S3. Genotyping was performed on an ABI 3130x1 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) at Massey Genome Service (Massey University, Palmerston North, New Zealand). Alleles were sized using the internal size standard GeneScan 500 LIZ (Applied Biosystems) and scored by hand using Geneious v.10.2.3 (Kearse et al. 2012). To avoid dye shifts (Sutton et al. 2011) we assigned one dye per locus (FAM, NED, PET or HEX) and whenever possible genotyped all individuals for one locus in the same run. Possible scoring errors caused by null alleles, stutter and allelic dropout were assessed with Microchecker v2.2.3 (van Oosterhout et al. 2004). To estimate genotyping errors, 10% of the samples were re-amplified and genotyped at least once for quality control. We found no inconsistencies between replicates. Allelic scores for *V. germanica* are presented in Supplemental Table S4 and for *V. vulgaris* in Supplemental Table S5.

Analysis of genetic diversity

Allele frequencies, observed (H_o) and expected (H_e) heterozygosities at the assayed microsatellite loci within the native or introduced *V. germanica* and *V. vulgaris* populations were estimated using GenAlEx v.6.5 (Peakall and Smouse 2012). Allelic richness per locus and population as an unbiased measure of the number of alleles adjusted by sample size was estimated using FSTAT v.2.9.3 (Goudet 1995). Gene diversity was also calculated with FSTAT for both species. We used Wilcoxon signed-rank test to compare allelic richness and gene diversity between the invaded and native ranges for both species.

Possible deviation from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD) between all locus pairs and by population (1000 dememorisations, 1000 batches, and 10,000 iterations per batch) were analysed using Genepop v.4.2 (Rousset 2008). Significance levels ($p = 0.05$) for departure from HWE and LD were corrected for multiple comparisons.

Analysis of genetic structure

We estimated the degree of population differentiation within *V. germanica* and *V. vulgaris* by calculating F_{ST} and R_{ST} in Arlequin v.3.5.2.2 (Excoffier and Lischer 2010). A Bayesian clustering approach was used to assign individuals to admixture proportions based solely on allele frequencies without including a priori information as implemented in the program STRUCTURE v.2.3.4 (Pritchard et al. 2000; Hubisz et al. 2009). Data were analysed using the admixture model assuming correlated frequencies with a 100,000 burn-in period and a million Markov Chain Monte Carlo iterations, the possible number of populations (k) ranged from 1 to 10 for *V. germanica* and from 1 to 12 for *V. vulgaris*; analyses were repeated 10 times to ensure consistency across runs. We used the Evanno et al. (2005) method to determine the optimal number of genetic clusters (k) given the data as implemented in STRUCTURE HARVESTER web v0.6.94 (Earl and vonHoldt 2012).

We performed a factorial correspondence analysis (FCA) of multilocus genotypes to visualise the genetic variation at the individual level as implemented in GENETIX v.4.05 (Belkhir et al. 1998).

We estimated contemporary effective population sizes (*Ne*) for *V. germanica* and *V. vulgaris* populations with the software NeESTIMATOR v.2 (Do et al. 2014) using the linkage disequilibrium method. This method evaluates non-random associations formed among alleles at different loci that occur when *Ne* is low and thus genetic drift influences allelic frequencies (Luikart et al. 2010). We used the random mating model and 95% confidence limits were obtained by jackknifing over loci. To test the effects that low-frequency alleles have on effective population size estimates, rare alleles (alleles with frequency $<$ Pcrit) were excluded (Sonsthagen et al. 2017). We estimated *Ne* with Pcrit values from the lowest frequency of 0.01–0.09 and without frequency restriction. If *Ne* estimates vary across a range of Pcrit values, this suggests a history of gene flow and/or the presence of first-generation dispersers. If *Ne* remains stable across a range of Pcrit values, this indicates isolated populations (Waples and England 2011; Sonsthagen et al. 2017).

Results

Genetic diversity

Vespula germanica

All loci in the native population were in Hardy–Weinberg equilibrium (HWE) although five loci in the introduced population deviated significantly from HWE after sequential Bonferroni correction (Holm 1979). All loci pairs were in linkage disequilibrium (LD) for *V. germanica* in the native and the invasive populations following Bonferroni correction. Microchecker found no evidence of scoring errors or large alleles dropout. However, there is evidence of null alleles for the native population at locus List-2007 (estimated frequency of 0.1388). For the introduced population, null alleles were detected for six loci (Rufa-5 with an estimated frequency of 0.2307, List-2007: 0.1204, List-2011: 0.1841, List-2019: 0.1325, VMA-6: 0.15 and R4-114: 0.159); which might explain the deviation from HWE. The null allele frequencies at these loci was estimated to be low (< 0.25) and previous research demonstrated that low frequency null alleles have little influence on the detection of genetic differentiation (Carlsson 2008; Rico et al. 2017), therefore, we decided to retain these seven loci.

Observed (*Ho*) and expected (*He*) heterozygosities ranged from 0.108 to 0.536 in the native range and 0.071–0.347 in the invaded range, respectively. Alleles per locus ranged from 1 to 12 in *V. germanica* (mean = 4.1, Table 1). The native population presented a larger number of alleles (mean = 5.1) when compared to the introduced population (mean = 3.2, Table 2). The number of private alleles was also larger for the native population with a total of 24 private alleles from 7 loci (mean = 2.4) while for the introduced *V. germanica* population, only 5 private alleles were found each corresponding to a different locus (mean = 0.5, Table 1).

Table 1 Indices of genetic diversity for native and invasive populations of *Vespula germanica* and *V. vulgaris*

	Vespula germanica		*Vespula vulgaris*	
	Native	Invasive	Native	Invasive
No. alleles	5.100 (1.1)	3.200 (0.4)	5.714 (0.8)	3.500 (0.5)
Private alleles	2.400 (0.7)	0.500 (0.1)	2.786 (0.6)	0.571 (0.2)
H_o	0.536 (0.1)	0.325 (0.1)	0.593 (0.07)	0.442 (0.09)
H_e	0.498 (0.1)	0.347 (0.07)	0.563 (0.06)	0.383 (0.07)
Ne	3.398 (0.8)	1.731 (0.2)	3.174 (0.5)	1.987 (0.2)
n	20	24	20	20

Values correspond to mean (standard error)

Table 2 Number of alleles sampled, gene diversity and allelic richness (A_R) per locus and population (native versus introduced) of *Vespula germanica* (top) and *V. vulgaris* (bottom)

Locus	# alleles sampled		Gene diversity		Allelic richness (A_R^a)	
	Native	Introduced	Native	Introduced	Native	Introduced
Vespula germanica						
Rufa-5	5	4	0.687	0.404	4.692	3.638
Rufa-19	8	3	0.844	0.538	7.703	2.923
List-2004	9	4	0.866	0.657	8.618	3.864
List-2011	1	2	0.000	0.166	1.000	1.989
VMA-6	12	6	0.909	0.586	11.273	5.426
R4-114	3	2	0.303	0.093	2.750	1.923
List-2007	5	4	0.675	0.268	4.749	3.245
List-2019	3	2	0.099	0.159	2.500	1.984
VMA-7	2	2	0.097	0.085	1.942	1.884
Rufa-15	3	3	0.629	0.607	3.000	3.000
Average	5.1	3.2	0.511	0.356	4.823	2.987
Vespula vulgaris						
Rufa-5	5	1	0.276	0.000	3.385	1.000
Rufa-19	10	3	0.877	0.493	8.823	2.884
List-2003	10	6	0.833	0.501	10.000	4.844
List-2004	7	5	0.658	0.551	5.485	4.013
List-2011	3	1	0.521	0.000	2.500	1.000
VMA-6	10	7	0.887	0.800	8.550	6.151
R4-114	2	1	0.295	0.000	1.996	1.000
List-2012	5	4	0.662	0.579	4.269	3.309
List-2013	6	3	0.748	0.305	5.014	2.490
List-2014	4	4	0.601	0.507	3.447	3.472
List-2017	3	2	0.188	0.053	2.385	1.526
List-2018	9	6	0.831	0.744	7.682	5.205
R1-169	4	3	0.247	0.417	3.091	2.588
VMA-3	2	3	0.503	0.529	2.000	2.526
Average	5.7	3.5	0.581	0.391	4.902	3.000

[a]For *V. germanica*, A_R estimates are based on a corrected sample size of 15 diploid individuals and for *V. vulgaris*, A_R estimates are based on a corrected sample size of 10 diploid individuals

Introduced populations of *V. germanica* show extremely low levels of genetic diversity. Allelic richness was significantly reduced in the introduced population when compared to the native population (Table 2; Wilcoxon sign-rank test, $n = 10$, $p = 0.028$). The same pattern was observed for gene diversity (Table 2; Wilcoxon sign-rank test, $n = 10$, $p = 0.037$).

Vespula vulgaris

No significant LD was detected among paired loci comparisons by population and no deviations from HWE were observed after Bonferroni correction. The *V. vulgaris* data shows no evidence of scoring errors, large allele dropout or null alleles for either population. *Ho* and *He* ranged from 0.184 to 1.000 in the European native range. In the New Zealand invaded range, *Ho* and *He* varied from 0.000 to 0.895. Alleles per locus ranged from 2 to 10 in the native population (mean = 5.7) and from 1 to 7 in the invaded population (mean = 3.5, Tables 1, 2). As expected, the number of alleles was larger in the native than in the invasive population of *V. vulgaris* with the native population having a larger number of private alleles (mean = 2.786) than the invasive population (mean = 0.571, Table 1).

As found for the congener species, *V. vulgaris* showed significantly reduced allelic richness in the introduced range when compared to the native range wasps (Table 2; Wilcoxon sign-rank test, $n = 14$, $p = 0.001$). Gene diversity was also significantly lower in the invaded range than in the native range (Table 2; Wilcoxon sign-rank test, $n = 14$, $p = 0.006$).

Genetic structure

Vespula germanica

A strong signature of population structure was found for *V. germanica* with frequency differences detected among microsatellite loci ($F_{ST} = 0.166$, $p < 0.0001$; $R_{ST} = 0.101$, $p = 0.017$). The STRUCTURE HARVESTER analysis of Δk indicated that the optimal k was 2, $\Delta k = 371.678$ (Fig. 2; Suppl. Fig. S1) corresponding roughly to the native European population and the invasive localities. Secondary optima were detected at $k = 5$, $\Delta k = 9.074$ and at $k = 7$, $\Delta k = 2.255$.

At $k = 2$, samples collected in the introduced ranges of New Zealand and Australia clustered with the five samples collected from the United Kingdom (3 from Scotland, 2 from England) confirming that the United Kingdom is the origin of the New Zealand and Australian introductions. However, the samples collected in the introduced range in South Africa grouped with samples from European countries (Austria, Belgium, France, Germany, Italy, Spain, Portugal, and Sweden) suggesting that continental Europe is the most likely origin for the South African *V. germanica* introduction (Fig. 2).

At $k = 5$, wasps were assigned to five admixture proportions. Samples from mainland Europe were mostly assigned with equal probability to two proportions. The five samples from the United Kingdom grouped into a third proportion with high probability as did four of the New Zealand wasps and the only Australian wasp. The remaining 16 New Zealand wasps grouped on a fourth proportion and the three South African samples clustered together in the fifth admixture proportion (Fig. 2).

At $k = 7$, additional population structuring was evident. Samples from mainland Europe were assigned with equal probability to four admixture proportions. The five samples from the United Kingdom grouped into a fifth proportion together with one Australian and four New Zealand wasps. Sixteen New Zealand wasps grouped on a sixth proportion and the three South African samples clustered together in one of the four admixture proportions identified for the European samples (Fig. 2).

The first two axes of FCA for *V. germanica* explained 16.56% and 10.70% of the total variance observed (Fig. 4a) with the three South African samples grouping apart from the rest of the individuals. When excluding the South African samples, axis 1 explained 13.09% and axis 2 9.22% of the variance, with the introduced population clustering tightly together (Fig. 4b).

Vespula vulgaris

Population differentiation was high among microsatellite loci for this species as well ($F_{ST} = 0.108$, $p < 0.0001$; $R_{ST} = 0.109$, $p = 0.002$). STRUCTURE HARVESTER uncovered an optimal k at 2, $\Delta k = 198.902$. These two admixture proportions represented the native population (proportion 1: Belgium and Germany, Fig. 3) and the New Zealand invasion (proportion 2, Fig. 3) with the exception of one sample collected in the Karori suburb of Wellington that seemed to have originated from either Belgium or Germany. These results suggest that the main *V. vulgaris* invasion into New Zealand has not occurred from Belgium or Germany but from a population not sampled for this study. Suboptimal k were detected at $k = 3$, $\Delta k = 21.153$ and $k = 5$, $\Delta k = 4.444$.

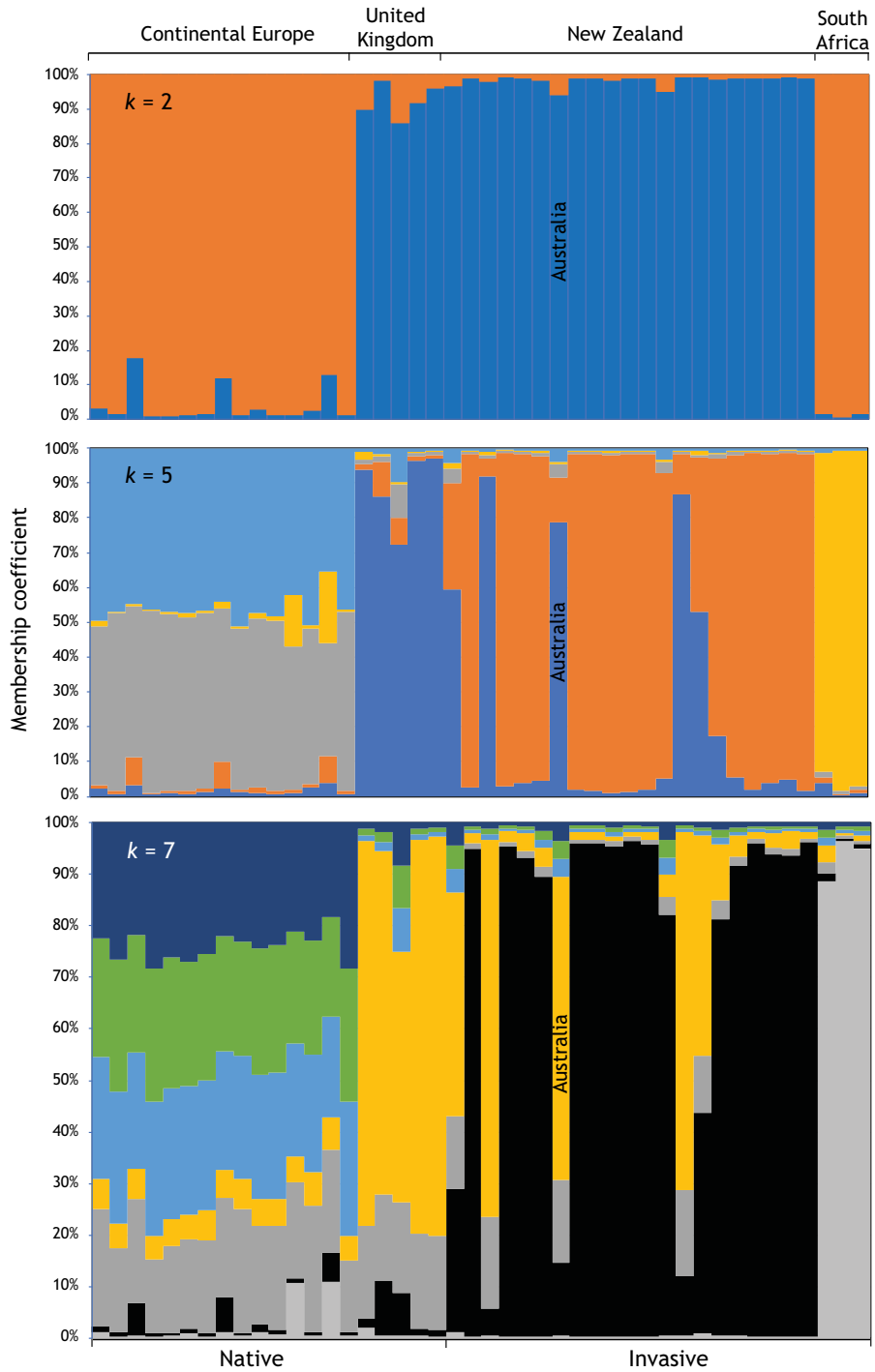


Fig. 2 STRUCTURE outputs for *Vespula germanica* inferred from 10 microsatellite loci. $k = 2$ was selected as the most likely k value by Structure Harvester but higher levels of k revealed further population subdivision. Secondary optima identified at $k = 5$ and $k = 7$ are also shown

At $k = 3$, the samples from Belgium and Germany and one sample from the Karori suburb of Wellington grouped with approximately equal probability into two admixture proportions whereas the New Zealand samples clustered in a third independent group (Fig. 3).

At $k = 5$, the European samples, plus the Karori sample, were assigned equally to four admixture

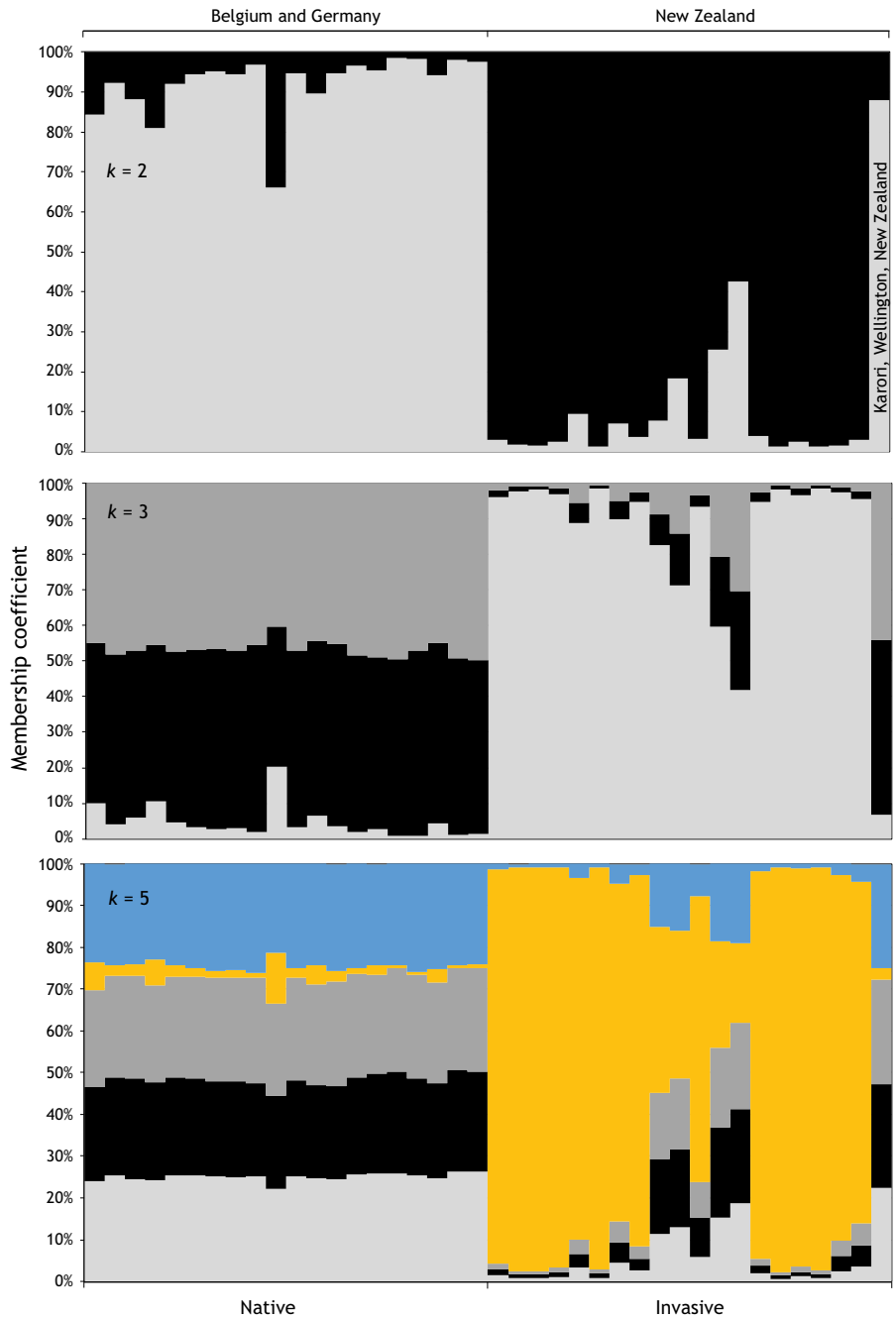
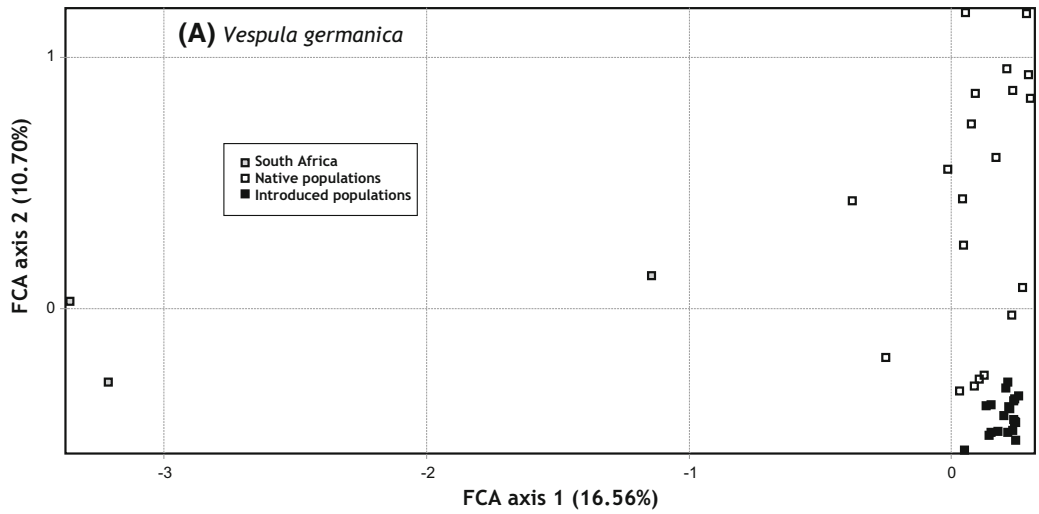
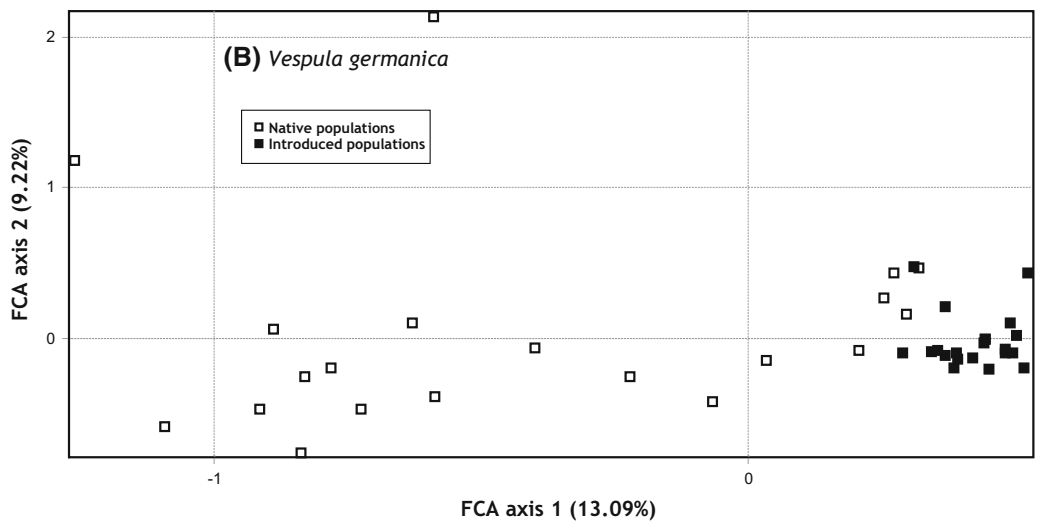


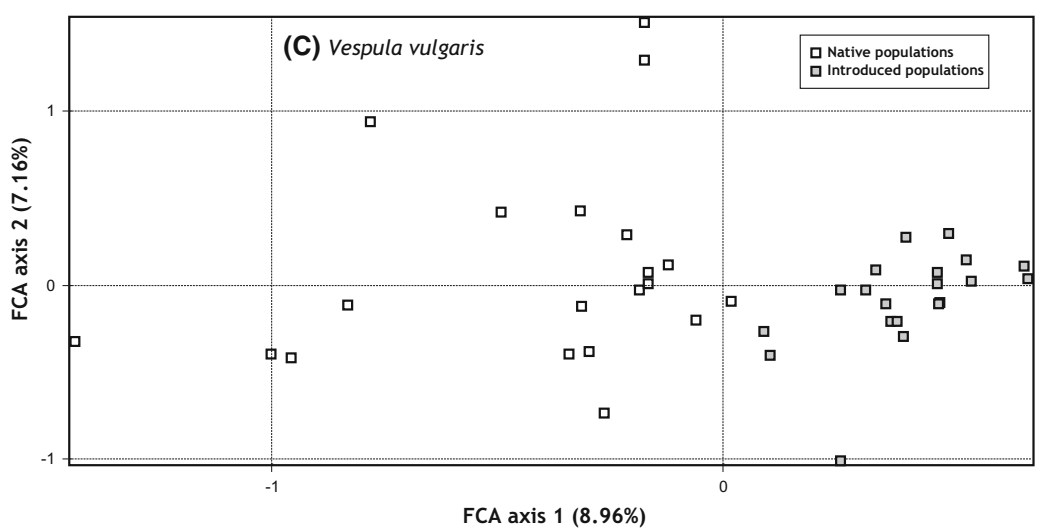
Fig. 3 STRUCTURE outputs for *Vespula vulgaris* inferred from 14 microsatellite loci. $k = 2$ was selected as the most likely k value by Structure Harvester. Secondary optima identified at $k = 3$ and $k = 5$ are also shown

proportions. Fifteen New Zealand wasps collected from offshore islands and other northern localities of the North Island grouped together in a fifth proportion while four other New Zealand samples: three collected from Nelson Lakes in the South Island and one collected in Rotokakahi Lake, Rotorua, North Island were assigned to the five proportions previously identified (Fig. 3).

The FCA shows higher genetic diversity in samples from the native range than in the introduced populations, with the first two axes explaining 8.96% and 7.16% of the observed variance, respectively (Fig. 4c).


(A) Vespula germanica
South Africa
Native populations
Introduced populations
FCA axis 2 (10.70%)
FCA axis 1 (16.56%)
1
0
-3
-2
-1
0


(B) Vespula germanica
Native populations
Introduced populations
FCA axis 2 (9.22%)
FCA axis 1 (13.09%)
2
1
0
-1
0


(C) Vespula vulgaris
Native populations
Introduced populations
FCA axis 2 (7.16%)
FCA axis 1 (8.96%)
1
0
-1
-1
0

◀**Fig. 4** Factorial correspondence analysis of individual multilocus genotypes. Multilocus scores are computed in the bivariate space defined by the first two factorial components. **a** FCA performed on all 44 *V. germanica* individuals based on 10 microsatellite loci, **b** same analyses for *V. germanica* excluding the 3 South African samples, and **c** results for all *Vespula vulgaris* individuals (n = 40) based on 14 microsatellite loci

Effective population sizes (*Ne*)

A signature of a reduced effective population size for the invasive population of *V. germanica* was observed based on the linkage disequilibrium method (Fig. 5a). Both native and introduced populations presented relatively stable values of *Ne* across Pcrit values, with the introduced population presenting narrow confidence limits. The native population upper bound confidence interval was infinity.

Native *V. vulgaris* represent a large and stable population across Pcrit, suggestive of a panmictic population with substantial levels of gene flow across its natural range. The introduced *V. vulgaris* population however, presents small estimates of effective population size with very narrow confidence intervals (Fig. 5b).

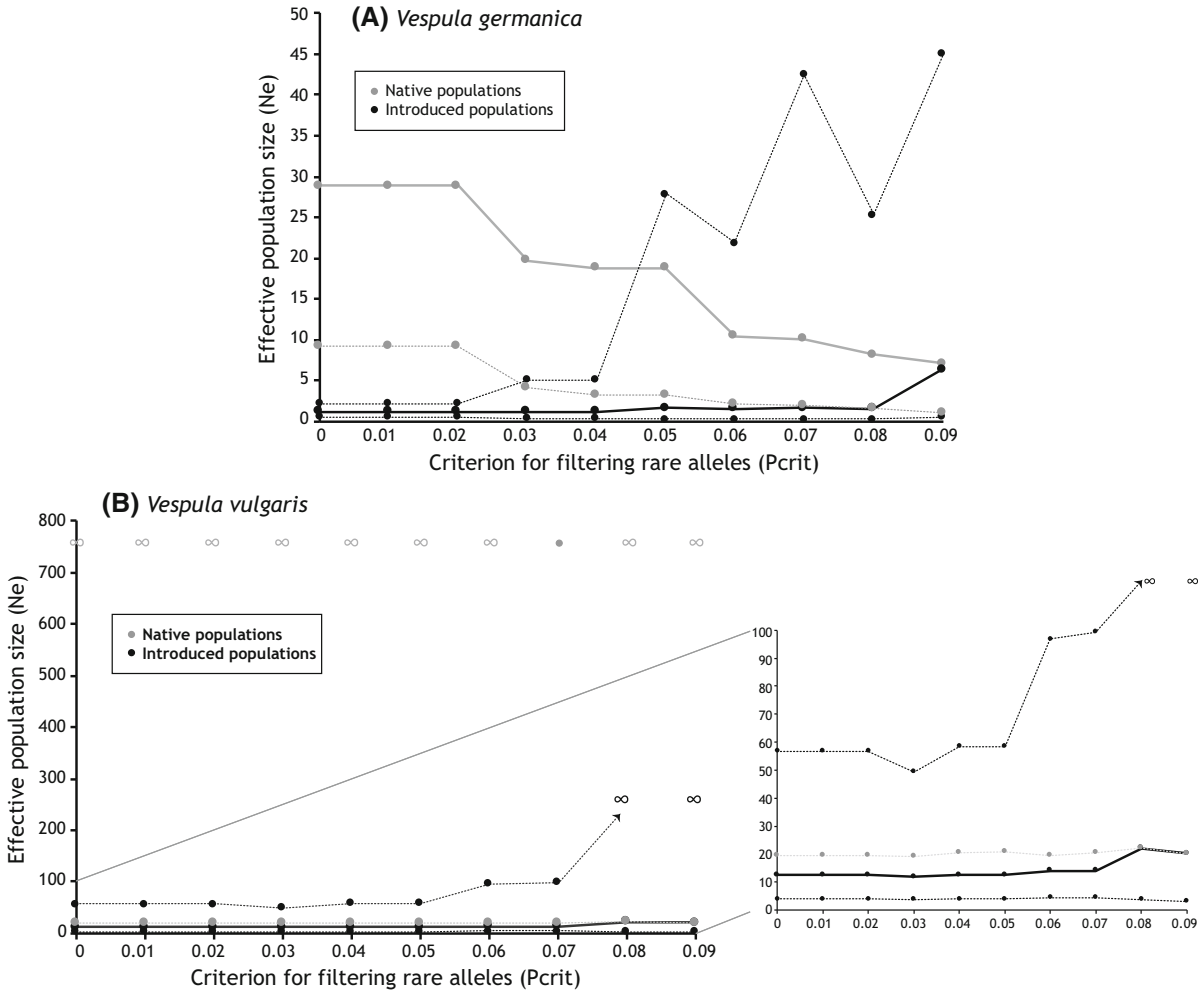


Fig. 5 Changes in contemporary effective population sizes (*Ne*) estimates for *V. germanica* (top) and *V. vulgaris* (bottom) as a function of excluding rare alleles (Pcrit). The solid lines represent the point estimate of *Ne*, and dashed lines are the associated 5% and 95% confidence limits. Upper 95% confidence limits for the native population of *V. germanica* was ∞ for all estimates. The native population of *V. vulgaris* presented values of *Ne* = ∞ for all values of Pcrit except 0.07, with upper 95% confidence limits = ∞ for all estimates

Discussion

We compared levels of genetic diversity within the native and the invaded range of *V. germanica* and *V. vulgaris* and found a strong reduction in genetic diversity in the invaded range of New Zealand for both species, as predicted. *Vespula germanica* in the invaded range showed 70% of the expected heterozygosity and 63% of the allelic richness found in the native range. *Vespula vulgaris* in the invaded range had 68% of the expected heterozygosity and 61% of the allelic richness found in the European samples. For both species, only 20–21% of private alleles present in the native range were found in the invaded range, a reduction of 80%. Our findings indicate a strong genetic bottleneck for *V. germanica* and *V. vulgaris* in their invaded range of New Zealand and suggest that New Zealand populations were founded by a small number of individuals. The reduction of genetic diversity through bottleneck effects in invasive *Vespula* wasps is in line with studies on other invasive social wasps (Goodisman et al. 2001; Husseneder et al. 2012; Tsuchida et al. 2014; Arca et al. 2015; Chau et al. 2015; Cheng et al. 2016; Takeuchi et al. 2017).

A similar relation between reduced genetic diversity, particularly allelic richness, and invasion success has been observed in other invasive social insects, such as ants and termites. There are well-known examples of bottleneck effects in populations of the Formosan subterranean termite, *Coptotermes formosanus*, which is invasive in the United States (Vargo and Husseneder 2009; Husseneder et al. 2012). The Argentine ant, *Linepithema humile,* successfully invaded parts of Europe, South Africa, the United States, and New Zealand despite displaying low levels of genetic diversity (Tsutsui et al. 2000; Giraud et al. 2002; Suarez et al. 2008; Cheng et al. 2016). Allelic richness in Argentine ant colonies was reduced by 55.5% in Hawaii (Tsutsui and Case 2001) and 40% in New Zealand (Corin et al. 2007).

There is a possible link between low genetic diversity and changes in social phenotypes which leads to invasion success in invasive social hymenopteran (Chapman and Bourke 2001). Some invasive *Vespula* species develop perennial, polygynous nests in their invaded ranges (Spradbery 1973; Akre and Reed 1981; Plunkett et al. 1989; Donovan et al. 1992; Leathwick and Godfrey 1996; Visscher and Vetter 2003). The mechanisms underlying the occurrence of multi-year *Vespula* colonies with multiple queens are poorly understood, yet the lack of thermal constraints has been considered to be a major factor (Visscher and Vetter 2003). Additionally, recent studies on *Vespula pensylvanica* suggest that ancestral weak nestmate discrimination may facilitate the adaptation of polygyny in the invaded range (Loope et al. 2018). Another change in social phenotype that might facilitate the invasion success of *Vespula* wasps is gene flow induced by queen movement and resulting in an increased exchange of genetic information between meta-populations. Colonies in the introduced ranges have been found to contain more workers that have been produced by multiple, foreign queens (Goodisman et al. 2001; Hanna et al. 2014). In addition, polyandry is likely to have helped *Vespula* wasp invasion in New Zealand; only a single multi-mated queen might have successfully established a whole new population (Goodisman et al. 2007; Schmid-Hempel et al. 2007; Arca et al. 2015; Dobelmann et al. 2017). Further, *V. germanica* and *V. vulgaris* might be successful invaders despite drastic genetic bottlenecks due to their haplodiploid sex determination system, which exposes recessive, deleterious mutations to selection (Schmid-Hempel et al. 2007). Thus, offspring of such purged lines might be able to tolerate high levels of genetic load and inbreeding (Schmid-Hempel et al. 2007; Zayed et al. 2007; Gloag et al. 2017).

While genetic structure of *V. germanica* and *V. vulgaris* populations differed between the native and the invaded ranges, genetic differentiation of New Zealand wasps was low. In both species, the genetic variation within New Zealand was not sufficient to distinguish between meta-populations. Low levels of genetic structure found in our study contrast with studies on invasive *Vespula* wasp populations in Australia (Goodisman et al. 2001) and Hawaii (Chau et al. 2015) but are in line with work on invasive paper wasp populations, *Polistes* spp., in New Zealand (Tsuchida et al. 2014). The difference between our results and the findings from the Hawaiian Islands and Australia might be due to weaker dispersal barriers among sample sites in New Zealand. Low levels of genetic structure in New Zealand may indicate ongoing gene flow within New Zealand wasps or underline strong founder effects during the introduction of *Vespula* wasps.

Contrary to other studies on genetic structure in invasive social wasps (Hoffman et al. 2008; Chau et al. 2015), *V. germanica* showed some genetic structure within its native range, with populations from mainland Europe being genetically different from the United Kingdom wasps. However, because we could not secure *V. vulgaris* specimens from the United Kingdom, we were not able to detect if there is the same differentiation in its native range as observed for *V. germanica*. Previous studies found that in its native range, *V. pensylvanica* seem to be panmictic with large populations and unrestricted gene flow (Chau et al. 2015), in agreement with our estimates of effective population size for *V. vulgaris* in its native range.

Our study confirms that *V. germanica* populations in New Zealand originated from a source population in the United Kingdom (England and Scotland) in agreement with mitochondrial DNA data (Brenton-Rule et al. 2018). The South African *V. germanica* introduction, however, seems to have its origin somewhere in mainland Europe; suggesting an introduction that was independent from the New Zealand invasion and not introduced into South Africa from the New Zealand stock. Further research with increased samples from both, South Africa and Northern European countries is necessary to determine the country of origin of the South African introduction.

A study using mitochondrial DNA data showed that the *V. vulgaris* populations found in New Zealand likely originated in England and Ireland (Lester et al. 2014). We could not secure samples from these countries for our current study. We can confirm that neither Belgium nor Germany are the source populations. However, one sample collected in a suburb of Wellington seems to have originated from either Belgium or Germany, suggesting an independent invasion event in the Wellington region, likely through maritime traffic as the Wellington harbour is a busy transport hub.

We found a reduction of effective population sizes (*Ne*) for both, *V. germanica* and *V. vulgaris*, in their invaded ranges in agreement with allelic richness and other population differentiation estimates.

This is the first study to compare both *Vespula* wasp species from their native and introduced ranges as well as six offshore islands on the east coast of New Zealand. The population structure analyses did not identify these islands as discrete from mainland New Zealand wasp populations therefore we have little evidence for considering them as genetically isolated from the mainland. Further research to understand the colonisation patterns of *Vespula* wasps into offshore islands and to gain insights into the effect of geographic factors on dispersal patterns of invasive wasps would be beneficial. It is a key question for conservation management whether each island invasion is an independent colonisation process or if invasive species establish in an area by 'hopping' from island to island (Parkes et al. 2017; Russell et al. 2017). For example, a recent point of discussion for conservation management in New Zealand is if establishing marine reserves around islands could prevent introductions or reintroductions of invasive species into unique island ecosystems (Department of Conservation and Ministry of the Environment 2000; Secretariat of the Convention on Biological Diversity 2004; Edgar et al. 2017; Sala and Giakoumi 2018).

Studies on the population genetic patterns of invasive populations are key for developing a sound understanding of the evolutionary mechanisms underpinning invasion success and the development of control strategies including novel techniques such as gene editing. Overall, insights into the invasion of *V. germanica* and *V. vulgaris* across New Zealand's mainland and offshore islands may provide essential knowledge on invasion processes and help manage invasions by social wasps.

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Author contributions JMS collected the New Zealand samples and together with JPL and JRB conceived the project. ECBR, RV and TW collected or provided samples. MB and JMS led the genetic work, analysed and interpreted the data. JMS and MB led the writing with input from all authors.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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