Biol Invasions (2018) 20:3207–3226
https://doi.org/10.1007/s10530-018-1769-1

ORIGINAL PAPER

Introduction history and genetic diversity of the invasive ant *Solenopsis geminata* in the Galápagos Islands

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Received: 29 December 2017 / Accepted: 26 May 2018 / Published online: 30 May 2018

Abstract The Galápagos Islands constitute one of the most pristine tropical systems on Earth. However, the complex and fragile equilibrium of native species is threatened by invasive species, among which is one of the most successful ants in the world, the tropical fire ant, *Solenopsis geminata*. We characterized the genetic structure and diversity of populations of *S. geminata* in the Galápagos Islands and unravelled the archipelago colonization by combining Bayesian clustering methods and coalescent-based scenario testing. Using 12 microsatellite markers and one mitochondrial DNA fragment (COI), we analysed individuals collected in all main invaded islands of the archipelago and from the native areas in Costa Rica and mainland Ecuador. We also used mitochondrial DNA to infer evolutionary relationships of samples collected in Galápagos Islands, Ecuador, Costa Rica and other Latin American countries. Our results showed that genetic diversity was significantly lower in Galápagos Islands and mainland Ecuador populations when compared to Costa Rican populations, and that samples from Galápagos Islands and mainland Ecuador (Guayaquil) clustered in a single group and all share a single mtDNA haplotype. Approximate Bayesian Computation favoured a scenario assuming that populations from Galápagos Islands diverged from mainland Ecuador. The city of Guyaquil, an obligatory hub for tourism and trade, could act as a bridgehead.

Keywords Approximate Bayesian Computation · Biological invasions · Founder effect · Island colonization · Microsatellites

Introduction

The Galápagos Islands are one of the most pristine large oceanic archipelagos on Earth, unique in its variety of species bearing many degrees of evolutionary changes within a particularly restricted area (Jackson 1994; Kricher 2006; Tye et al. 2002). However, like in other ocean archipelagos, the unique fauna and flora of the Galápagos Islands are particularly vulnerable to invasions, which now represent a primary threat to terrestrial ecosystems (e.g. Lockwood et al. 2007; Perrings et al. 2010; Sax et al. 2002;

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-018-1769-1) contains supplementary material, which is available to authorized users.

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Simberloff and Rejmanek 2011; Toral-Granda et al. 2017; Vitousek 1988; Walsh and Mena 2013).

Alien species have been traded and transported by humans for millennia (Mack et al. 2000; Simberloff and Rejmanek 2011; Vitousek et al. 1996). However, with the globalization and expansion of trade and transport, the world has entered a new phase in the magnitude and diversity of biological invasions (Hulme 2009; Richardson 2011). Ants constitute very damaging and ecologically destructive invasive species (Holway et al. 2002; Lach and Hooper-Bui 2010; Suarez and Tsutsui 2008). A subset of 150 species (out of more than 14,000 described to date; http://antbase.org/—May 2018) has been reported as "tramp species", i.e. groups of ants introduced into new environments by humans (McGlynn 1999; Passera 1994). Among tramp species, the tropical fire ant *Solenopsis geminata* is considered as one of the six most widespread, abundant and damaging (Holway et al. 2002; Tschinkel 2006). *Solenopsis geminata* is native to South and Central America, and has successfully colonized North America, Africa, Asia, Australia and the isles of Oceania, and many tropical oceanic islands (Gotzek et al. 2015; Wetterer 2011). This species is considered an economic and environmental pest with a major impact on ecological equilibrium (Plentovich et al. 2009; Risch and Carroll 1982), agriculture (Chang and Ota 1990; Perfecto 1994; Taber 2000) and human health (Knight and Bangs 2007). In the Galápagos Islands, *S. geminata* was first reported from San Cristóbal in 1891 (Brandão and Paiva 1994), in 1905 on the island of Floreana (Wheeler 1919) and in 1981 on the islands of Santa Cruz and Isabela (Linsley and Usinger 1966; Lubin 1984; Williams and Wilson 1986). To date, *S. geminata* is found on seven islands and 11 islets (Wauters et al. 2014). According to other areas to which it has been introduced, *S. geminata* is considered as a serious threat to Galápagos unique fauna: this species is a predator of arthropods and caused serious declines of vertebrates' clutches (Causton et al. 2006; Roque-Albelo and Causton 1999; Roque-Albelo et al. 2000; Wauters et al. 2016; Wetterer 2011). For instance, *S. geminata* reduces populations of native butterflies on Guam by predating eggs and larvae (Nafus and Schreiner 1988), preys on Hemiptera, Lepidoptera and eggs of snails in rice in the Philippines (Way et al. 1998), and is known to have the potential to eliminate other ants from areas where they are abundant. In Galápagos Islands, *S. geminata* displaces other ants (von Aesch and Cherix 2005) and its presence is associated with a low evenness of ant communities (Wauters et al. 2016). Moreover, Williams and Whelan (1991) reported that *S. geminata* workers caused problems in the rearing pens of young Galápagos tortoises and in tortoise holding pens, especially the egg-laying and feeding areas, and Roque-Albelo and Causton (1999) noted that the tropical fire ants may strongly impact nesting behaviour and youngs of the Galápagos penguin *Spheniscus mendiculus*. Finally, with the invasive ant *Wasmannia auropunctata*, *S. geminata* is engaged in an invasional meltdown process (O'Dowd et al. 2003; Simberloff and Von Holle 1999) by which these species facilitate each other, increasing their likelihood of establishment and expansion (Wauters et al. 2016).

Introduced populations usually experience bottlenecks and genetic drift, slow population growth due to low densities, and sometimes inbreeding depression (Lambrinos 2004; Sax and Brown 2000). In these respects, the success of invasive populations, despite low genetic diversity and low evolutionary potential, represents an evolutionary paradox (Estoup et al. 2016; Frankham 2005; Sax and Brown 2000). Several studies suggest that rapid and large population growth of established invasive species occur due to the right combination of recipient environment eco-evolutionary characteristics, characteristics inherent to the invader itself, and the demographic history of introduction (Davis 2009; Facon et al. 2006). Rapid demographic growth and/or range expansion following introduction can contribute to the retention of substantial levels of genetic diversity, diminishing the strength of population bottlenecks (Zenger et al. 2003). Genetic diversity loss can also be counterbalanced by a genetic admixture among introduced populations, originating from different sources in the case of multiple introduction events (Dlugosch and Parker 2008). Alternatively, maintenance of connectivity between the native and the introduced ranges can facilitate the spread of rare allelic variants (Facon et al. 2008; Kolbe et al. 2004; Lavergne and Molofsky 2007). In small invasive populations, bottlenecks of moderate intensity can purge deleterious alleles, decreasing costs associated with the inbreeding depression (Facon et al. 2011; Maderspacher 2011). Such ecological and evolutionary processes modulate the effects of invasive species over time by interfering the relation between the invasive species and the recipient ecosystem (Strayer et al. 2006).

Underlying evolutionary processes greatly impact the outcomes of biological invasions, and investigating these processes provides essential information to understand the dynamic nature of invasive processes. Moreover, retracing the routes of invasion and determining the origin of source populations can help to define prevention and eradication strategies, in the source region, along the pathways of invasions, or at the entry points of invaded areas (Hulme 2009). Inference of invasion history and migration routes of invasive species can be achieved through direct and indirect methods (Estoup and Guillemaud 2010). Direct methods rely on historical and observational field data, which are often sparse, incomplete and misleading, given that the records of interception do not necessarily result in successful invasions (Simberloff 2013; Suarez et al. 2005). Indirect methods are based on the molecular analysis of both source and introduced populations using highly polymorphic genetic markers. Although indirect methods might shed critical light on complex and sometimes counterintuitive stories of invasions, they are often limited by the stochasticity in the demographic and genetic history of introductions (i.e. genetic drift, multiple introductions and admixture events). These events can sometimes produce complex signals difficult to interpret for most indirect methods (Guillemaud et al. 2010). The development of Approximate Bayesian Computation (ABC; Beaumont 2010; Beaumont et al. 2002) for use with molecular data has allowed model-based inferences using complex scenarios, such as invasions-associated demographic and evolutionary scenarios (Estoup and Guillemaud 2010; Guillemaud et al. 2010). ABC has been successfully used to retrace the invasion routes of various invasive species by incorporating historical data and taking into account demographic and genetic stochasticity (e.g., Auger-Rozenberg et al. 2012; Barrès et al. 2012; Bermond et al. 2012; Boissin et al. 2012; Bolfíková et al. 2013; Brouat et al. 2014; Fountain et al. 2014; Gotzek et al. 2015; Keller et al. 2012; Lombaert et al. 2011; Rius et al. 2012). This method potentially allows the resolution of key issues concerning the life-history traits of the invasive species (i.e., dispersal and reproductive strategies and mechanisms underlying invasion success), their invasion routes, the population connectivity and their invasion history (Dutech et al. 2012; Estoup et al. 2010; Estoup and Guillemaud 2010; Lander et al. 2011).

In this study, we applied direct and indirect methods to unravel the invasion history of the ant *S. geminata* in the Galápagos Islands. More specifically, we used a combination of 12 highly polymorphic microsatellite markers to analyse individuals from each infested main island and from a portion of the native range in Costa Rica and mainland Ecuador. We combined genetic analyses, Bayesian clustering methods and Approximate Bayesian Computation to (1) analyse the genetic diversity and the reproductive and dispersal strategies of *S. geminata* in Galápagos populations and compare them to the samples collected in the native range; (2) determine the population structure of Galápagos and mainland populations; and (3) compare different colonization scenarios to unravel the routes of the introduction of the tropical fire ant to the Galápagos Islands.

Methods

Sample collection

Solenopsis geminata individuals were sampled from 58 sites (76 nests) covering the major islands of the Galápagos, 2 sites in Guayaquil (mainland Ecuador; 2 nests), and 4 sites in Costa Rica (18 nests) (Table S1 and Fig. 1). Ecuadorian samples were collected in March 2011, Costa Rican samples in June 2013. Costa Rica and mainland Ecuador were considered native areas whereas Galápagos Islands were considered the invaded range of *S. geminata* (Taber 2000; Tschinkel 2006; Wetterer 2011).

Microsatellites data analyses

Total genomic DNA was isolated from complete worker ants using Chelex beads (Bio-Rad, Hercules, CA) (Walsh et al. 1991). Genotyping was conducted at 12 statistically independent microsatellite loci previously developed for the genus *Solenopsis* (Ascunce et al. 2009) and arranged in two multiplex sets (Multiplex 1: *Sdag*-121_6FAM, *Sdag*-204_VIC, *Sdag*-234_PET, *Sdag*-264_VIC, *Sdag*-278_6FAM and *Sdag*-316_6FAM; Multiplex 2: *Sdag*-1_VIC, *Sdag*-367_PET, *Sdag*-368_VIC, *Sdag*-415_NED, *Sdag*-485_NED and *Sdag*-536_6FAM; forward

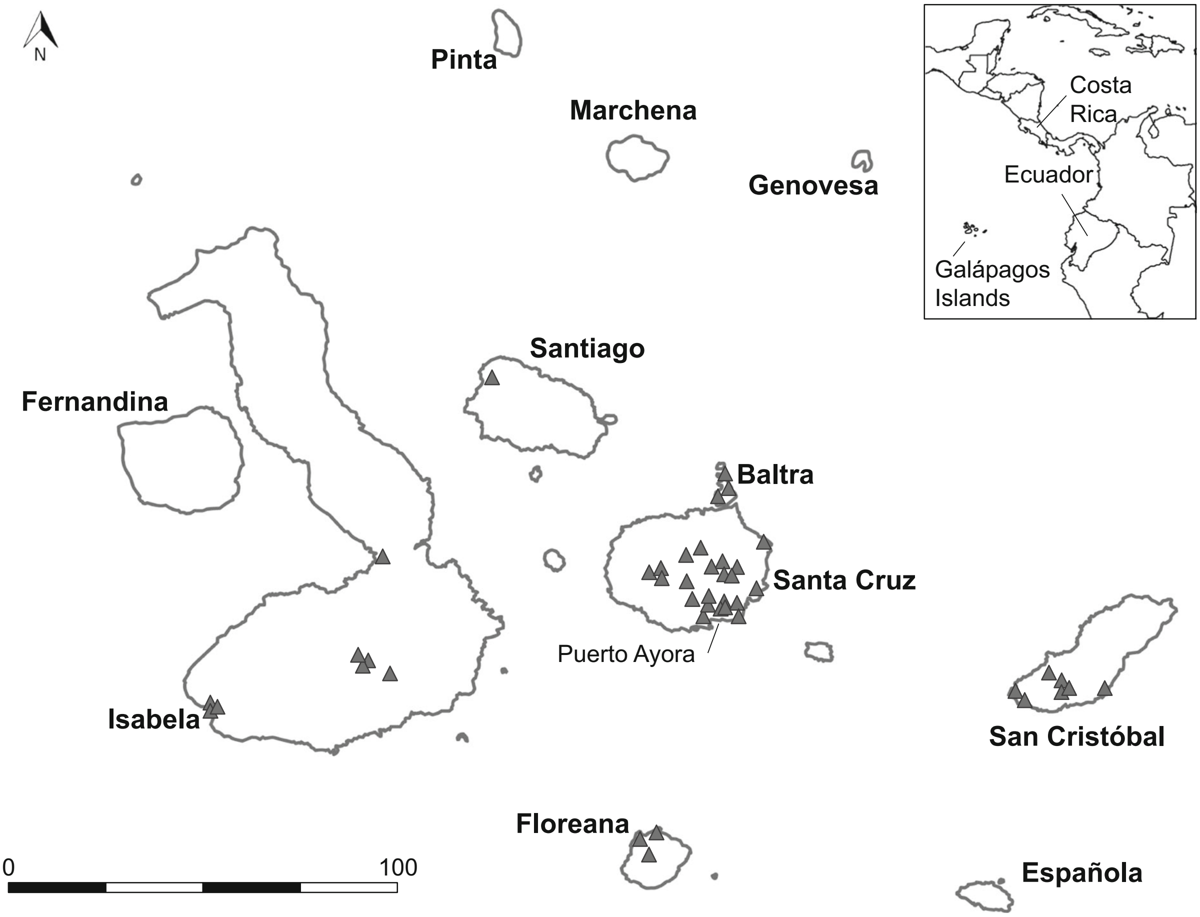


Fig. 1 Locations of studied sites of *Solenopsis geminata* in the Galápagos Islands

primers were 5′-fluorescently labelled 6FAM, VIC, PET or NED (Applied Biosystems)). PCR amplification was carried out in a total reaction volume of 12 µl containing Platinum Taq PCR SuperMix (Invitrogen, Carlsbad, CA), 0.2 µM of each primer, and 1 µl (~ 10–20 ng) of genomic DNA template. PCR amplifications were performed with a TProfessional thermocycler (Biometra, Göttingen, Germany) programmed as follows: an initial denaturation step of 94 °C for 2 min followed by 35 cycles of 94 °C for 30 s, 55 °C for 60 s and 72° C for 60 s, and a final extension step of 72 °C for 30 min after the last cycle. PCR products were separated on a 48-capillary 3730 DNA Analyzer (Applied Biosystems, Foster City, CA), and an internal size standard (GeneScan-500 LIZ, Applied Biosystems) was run in every sample. The lengths of the PCR products were determined using GeneMapper software (Applied Biosystems) and used to construct a multi-locus genotype for each individual. Stutter bands, large allele drop-out and null alleles were tested using the programme Micro-Checker (Van Oosterhout et al. 2004).

Genetic diversity

The genetic diversity at each site was estimated using Nei's unbiased genetic diversity *Hs* (Nei 1987) and the allelic richness *Ar* (i.e., a standardized measure of the number of alleles per locus independent of the sample size) with Fstat 2.9.3 (Goudet 1995). Significant differences in genetic diversity parameters between sites of introduced areas (the Galápagos Islands) and native areas (Costa Rica and mainland Ecuador) were tested using the "Comparison among groups of samples" option in Fstat 2.9.3 (permutation tests on sites).

Genetic variation between sites and spatial genetic structure

The overall level of genetic variation between sites sampled in Galápagos Islands (F_{ST}) and the level of genetic variation between each pair of sites (pairwise F_{ST}; Weir and Cockerham 1984) were estimated with FSTAT 2.9.3. Estimates were jackknifed over loci to give means and standards errors, and bootstrapped over loci (10,000 bootstrap replicates) to give 95% confidence intervals.

To visually assess genetic variation at the individual level in a multi-dimensional space, we performed a factorial correspondence analysis (FCA; calculated in GENETIX version 4.05; Belkhir et al. 1998) of multilocus genotypes.

For inferring Galápagos population structure and assigning individuals to populations, we used the Bayesian model-based clustering method implemented in STRUCTURE 2.3.4 (Pritchard et al. 2000). We assumed an admixture model with correlated allele frequencies (Falush et al. 2003) and included a priori sampling locations as prior information (LOCPRIOR) to detect weak population structure (Hubisz et al. 2009). We ran the software for 10^6 Markov chain Monte Carlo iterations with a prior burn-in of 10^4 chains. We tested a range of K from 1 to 20 (15 replicates for each K) for the complete data set. The estimate of the optimal number of clusters K was calculated as described by Evanno et al. (2005) using STRUCTURE HARVESTER WEB v0.6.94 July 2014 (Earl and vonHoldt 2012). Data from multiple replicates were summarized using the Greedy algorithm implemented in the software CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) and the means of the permuted results were visualized with DISTRUCT (Rosenberg 2004). For this Bayesian clustering analysis, we used only one individual per nest and per site (i.e. 64 sites) to avoid bias generated from sibling relatedness, and repeated this analysis five times with different individuals randomly chosen within each nest.

Inference of colonization pathways

To explore putative scenarios of invasion followed by the tropical fire ant *S. geminata* in Ecuador and into the Galápagos Islands, we used an Approximate Bayesian computation (ABC) approach as implemented in the software DIYABC 2.1.0 (Cornuet et al. 2014). According to the results of the spatial genetic structure emerging from our study, we defined three focal groups (i.e., Costa Rica, mainland Ecuador and Galápagos Islands), and all samples from each area were pooled to correspond to their group (see Results). We conducted our analysis in three steps. Step 1, we tested if Galápagos populations come from mainland Ecuador (Fig. 2, scenario 1), from an undetected and hence unsampled population, itself introduced from the source (Fig. 2, scenario 2), from Costa Rica (Fig. 2, scenario 3), or from the admixture between populations (Fig. 2, scenarios 4, 5 and 6). Step 2, we examined (1) whether mainland Ecuador is a native or an invasive population by testing if the population experienced a bottleneck (Fig. 2, scenarios 1 and 2, respectively), and (2) if mainland Ecuador is the result of an admixture between Costa Rica and an undetected, unsampled population. Step 3, we investigated whether Galápagos populations result or not from the admixture of multiple introductions from the same source (Fig. 2, scenarios 1 and 2).

All prior distributions of historical and demographic parameters are given in Table 1. Prior distributions of the different parameters for the mutation model of the microsatellites comply with the rates and modalities of mutation commonly used in ABC analyses (Brouat et al. 2014; Cornuet et al. 2010; Verdu et al. 2009), and correspond to the default parameter values in DIYABC 2.1.0: we assumed that each microsatellite locus follows a generalized stepwise mutation model (Estoup et al. 2002), with a uniform prior distribution for the mean mutation rate across loci ($10^{-4} < \mu < 10^{-3}$ per generation) and a uniform distribution for the parameters of the geometric distribution describing the number of repeat changes per mutation event ($0.1 < p < 0.3$).

We summarized the genetic variation within and between populations with four single-population (mean number of alleles, mean expected heterozygosity, mean allelic size variance and mean ratio of the number of alleles over the range of allele sizes (i.e. Garza-Williamson index)) and three pairwise-population (F_{ST} values, shared alleles distance and $d\mu^2$ distance) summary statistics that proved to be informative in previous population genetic studies (Boissin et al. 2012; Brouat et al. 2014; Estoup and Guillemaud 2010; Fountain et al. 2014; Lombaert et al. 2010, 2011). A million microsatellite datasets were simulated for each competing scenario.

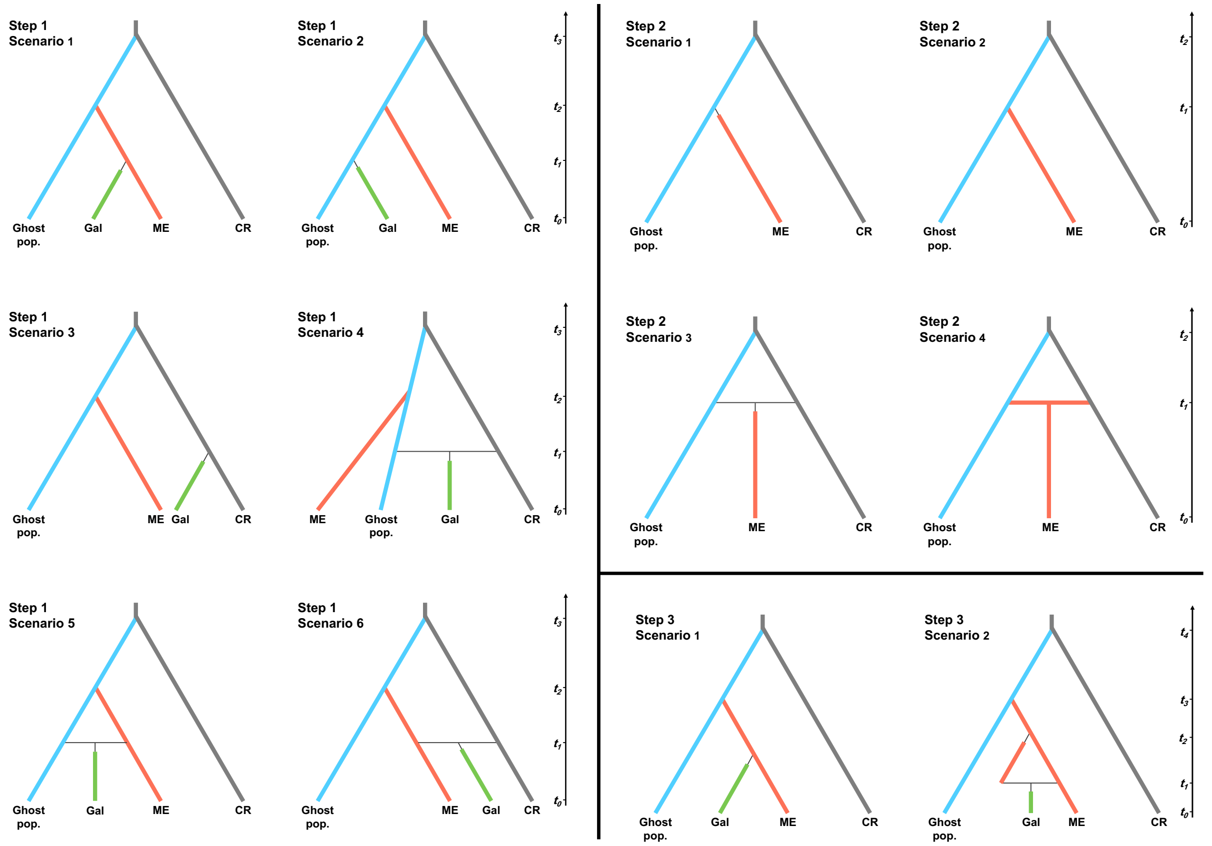


Fig. 2 Graphic representation of the competing introduction scenarios tested using DIYABC. Time 0 is the sampling date with time proceeding backwards into history as one follows branches up the tree to the most ancestral population. Bars represent stable effective population sizes, and thin grey lines represent bottleneck events. No migration was assumed. Details of the parameters priors are given in Table 1. Step 1, we tested if Galápagos populations come from the Costa Rica, from mainland Ecuador, or from an unsampled source ("ghost population"). Step 2, we examined whether mainland Ecuador is a native or an invasive population by testing if the population experienced a bottleneck. Step 3, we investigated whether Galápagos populations result or not from the admixture of multiple introductions from the same source. All samples from each area (i.e., Costa Rica, mainland Ecuador and Galápagos Islands) were pooled to correspond to their group

Posterior probabilities of the competing scenarios were estimated by performing a polychotomous weighted logistic regression on 1% of simulated data sets closest to the observed dataset. The selected scenario was the one with the highest probability value with a nonoverlapping 95% confidence interval. Confidence in each scenario was evaluated by computing type I and type II error rates. This was done by constructing 500 pseudo-observed datasets (pods) with the same number of loci and individuals as our dataset for each one of scenarios and generated from the prior distributions. Type I error rate was computed as the proportion of times that a given scenario did not have the highest posterior probability when it was the true scenario, and type II error rate was computed as the proportion of times that a scenario had the highest posterior probability when it was not the true scenario. We estimated the posterior distributions of parameters by using a local linear regression on the closest 1% simulated datasets (Beaumont et al. 2002). To assess precision of parameter estimation, we computed the relative median of the absolute error (RMAE; Cornuet et al. 2010) on 500 pseudo-observed datasets simulated under the best-fit scenario. Finally, we performed a model checking analysis for the selected scenario. Its goodness-of-fit was evaluated from a principal component analysis in the space of summary statistics, by assessing the location of 10,000 points simulated from the posterior predictive distribution relative to the one

Table 1 Prior and posterior distributions of the historical and demographic parameters used in ABC analyses (posterior distributions were obtained from the analysis of the chosen scenario: scenario 1 for step 1, scenario 2 and 4 for step 2, and scenario 1 for step 3)

Parameter	Prior distribution	Posterior distribution				
		Mean	Median	Mode	95% CI	RMAE
Step 1 Scenario 1						
CR	Uniform [10–10,000]	7340	7530	8150	4250–9720	0.178
NP	Uniform [10–10,000]	6490	7180	9950	1130–9840	0.397
ME	Uniform [10–10,000]	135	85.2	65.9	30.8–266	0.206
Gal	Uniform [10–10,000]	3650	3080	1870	994–8560	0.188
Galb	Uniform [2–1000]	440	397	111	51.3–934	0.412
t_1 (Gal)	Uniform [10–10,000]	107	86.3	60.9	26.9–260	0.288
db_1 (Gal)	Uniform [0–75]	45.5	49.3	75	7.7–73.1	0.432
t_2 (ME)	Uniform [10–10,000]	4280	4080	3030	997–8140	0.295
t_3 (NP)	Uniform [10–10,000]	7070	7340	9600	3450–9740	0.14
Step 2 Scenario 2						
CR	Uniform [10–10,000]	6960	7020	6230	3970–9650	0.197
NP	Uniform [10–10,000]	5990	6610	9920	684–9810	0.390
ME	Uniform [10–10,000]	154	71.3	50.5	29.3–258	0.253
t_1 (ME)	Uniform [10–10,000]	4720	4770	5350	650–8720	0.467
t_2 (NP)	Uniform [10–10,000]	7030	7300	8970	3370–9740	0.196
Step 2 Scenario 4						
CR	Uniform [10–10,000]	6790	6840	6480	3750–9580	0.191
NP	Uniform [10–10,000]	5460	5720	9690	606–9640	0.406
ME	Uniform [10–10,000]	136	117	82.2	52.9–252	0.247
t_1 (ME)	Uniform [10–10,000]	3760	3470	2790	960–7580	0.394
t_2 (NP)	Uniform [10–10,000]	7060	7320	9730	3400–9760	0.206
Admix. rate	Uniform [0.001–0.999]	0.517	0.528	0.807	0.0559–0.953	0.417
Step 3 Scenario 1						
CR	Uniform [10–10,000]	7240	7400	7680	4160–9700	0.194
NP	Uniform [10–10,000]	6040	6590	9910	854–9800	0.334
ME	Uniform [10–10,000]	141	89.2	56.2	31.7–280	0.217
Gal	Uniform [10–10,000]	3520	2890	2140	938–8330	0.213
Galb	Uniform [15–1000]	462	433	154	58.9–939	0.418
t_1 (Gal)	Uniform [10–10,000]	100	80.6	56.9	25.9–236	0.32
db_1 (Gal)	Uniform [0–75]	42.9	45.2	73.2	6.14–72.6	0.419
t_2 (ME)	Uniform [10–10,000]	4180	3920	2440	955–8200	0.303
t_3 (NP)	Uniform [10–10,000]	6960	7210	9470	3380–9720	0.132

N_i and Nb_i are respectively the effective stable size and the founding effective population size (in number of diploid individuals); $N_i > Nb_i$. *db* is the bottleneck duration (in number of generations). t_i is the time of founding (in number of generations going back to the past). When no information was available regarding their values, priors were deliberately defined broadly. The relative median of the absolute error (RMAE) was computed using 500 pseudo-observed datasets taking the median of posterior distributions as point estimates. CR, ME, Gal and NP refer to populations of Costa Rica, mainland Ecuador, the Galápagos Islands and to an undetected and unsampled population, respectively corresponding to the observed data (Brouat et al. 2014; Cornuet et al. 2010).

Reproductive and dispersal strategies

Population genetic structure at local scale (i.e., within and between nests within site) was investigated for two sites, El Ocidente in the island of Santa Cruz (19 nests, mean of individuals genotyped per nest ± SD = 8.89 ± 2.11 workers, $n = 169$) and Sabana in Costa Rica (15 nests, mean of individuals genotyped per nest ± SD = 7.89 ± 1.11 workers, $n = 118$). Estimation and tests of hierarchical F-statistics (F_{IS}, the inbreeding coefficient and F_{ST}, the fixation index; Weir and Cockerham 1984) and relatedness coefficients among nestmates workers (according to the statistic described by Queller and Goodnight (1989) were computed with FSTAT 2.9.3. Isolation-by-distance was investigated by plotting genetic distances (i.e., $F_{ST}/(1 - F_{ST})$) between pairs of nests against the logarithm of geographical distances (Rousset 1997; Slatkin 1993); significant correlations were tested applying Mantel tests in GenAlEx 6.5 (9999 permutations).

Significant differences in within-nest relatedness or F-statistics between introduced and native areas (Galápagos Islands and Costa Rica, respectively) were tested using permutation tests as implemented in FSTAT 2.9.3 (10,000 permutations).

Relatedness coefficients among nestmate workers were estimated using the program RELATEDNESS 5.08 (Goodnight and Queller 2000; Queller and Goodnight 1989). We determined the effective mean number of reproductive queens per nest, weighted by the respective contribution of each queen to the production of workers, from relatedness indices among workers (Ross 1993; Seppä 1994).

Mitochondrial DNA analyses

A 658 bp fragment of the mitochondrial cytochrome c oxidase subunit 1 was sequenced from a subset of 17 individuals from the Galápagos Islands (3 individuals each from Isabela, San Cristóbal and Santiago Islands, 2 individuals from Floreana Island and 6 individuals from Santa Cruz Island) and 3 individuals from Guayaquil. We also sequenced individuals originated from Brazil ($n = 6$ individuals), Colombia (4), Costa Rica (2), French Guiana (2), Guatemala (12), Honduras (4), Mexico (14), Peru (1), Trinidad (6) and Venezuela (2) (samples collected by D. Gotzek and D. Shoemaker; Table S2). The sequences of *Solenopsis globularia*, *S. gnoma* and *Pheidole williamsi* were used as outgroups. DNA extraction was performed on the full ant body using a NucleoSpin Tissue Kit (Macherey–Nagel, Düren, Germany). mtDNA PCR amplifications were carried out using the primers LCO1490 and HCO2198 (Folmer et al. 1994). DNA was amplified in 25 µl reactions (2 µl of DNA template, 0.03 U/µl of Platinum Taq DNA polymerase (Life Technologies, Carlsbad, CA), 1 × PCR buffer, 0.2 mM of each dNTP, 0.4 µM of each primer and 1.5 mM MgCl2) and amplified in a TProfessional thermocycler (Biometra) with the following PCR conditions: 3 min at 94 °C, 40 cycles of 94 °C for 40 s, 49.5 °C for 40 s and 72 °C for 60 s, then 72 °C for 7 min. mtDNA amplicons were gel-purified using a NucleoFast 96 PCR Plate (Macherey–Nagel), used in standard fluorescent cycle-sequencing PCR reactions (BigDye Terminators v1.1 chemistry; Life Technologies), and run on a 3130xl Genetic Analyzer (Applied Biosystems). Both forward and reverse strands were sequenced.

Sequence analyses

Sequences were aligned using MEGA version 7 (Tamura et al. 2013). No internal stop codons were detected. We used the same software to estimate the mtDNA sequence polymorphisms and the pairwise genetic distances between sequences, and to reconstruct and analyse phylogenetic relationships between mtDNA sequences. A phylogenetic tree was produced by using the maximum likelihood method; 1000 iterations of bootstrapping were used to test the robustness of the branches.

Results

Microsatellite genetic structure

Genetic diversity

We genotyped 12 microsatellite loci from 703 *S. geminata* workers sampled from 58 sites (mean of individuals genotyped per site ± SD = 12.12 ± 21.24) covering most of their range in the Galápagos

Islands, and 22 and 142 individuals from 2 (11.00 ± 4.24) and 4 (35.50 ± 55.00) sites in mainland Ecuador and Costa Rica, respectively (Table S1 and Fig. 1). Genetic diversity estimated for Galápagos nests (mean allelic richness based on the smallest sample size ($n = 7$) $Ar_{[7]} = 1.339 \pm 0.145$ and Nei's unbiased gene diversity $Hs = 0.137 \pm 0.058$) were all significantly lower than for native nests ($Ar_{[7]} = 2.891 \pm 1.207$, two-sided p values obtained after 10,000 permutations $p < 0.001$; $Hs = 0.499 \pm 0.233$, $p < 0.001$). However, genetic diversity was not different between Galápagos and Guayaquil nests ($p = 0.666$ and 0.478 for Ar and Hs, respectively).

Genetic variation between sites and spatial genetic structure

F_{ST} values computed across all sites sampled in Galápagos Islands were 0.448 (95% CI = 0.364–0.551). Pairwise F_{ST} values ranged from − 0.040 (Cerro Mesa vs. Puerto Ayora 5, both sites collected in Santa Cruz; Table S3) to 0.954 (a coffee plantation in Santa Cruz vs. Santa Monica in San Cristóbal; Table S3). Pairwise F_{ST} value was 0.045 (95% CI = 0.012–0.085) between Galápagos Islands and mainland Ecuador; it reached 0.508 (95% CI = 0.417–0.614) between Ecuador and Costa Rica.

The FCA clearly shows a genetic discontinuity between Costa Rican and Ecuadorian samples, and grouped samples from mainland Ecuador together with those of Galápagos Islands (Fig. 3a). Axis one explained 49.43% of the variation, and axis two an additional 14.93%. When Costa Rican populations were excluded, the distribution of samples tended to reflect their geographical distribution (Fig. 3b). The two first axes of the FCA explained 35.93 and 23.24% of total variance observed, respectively. Axis one suggested the differentiation of three groups, Floreana Island at the left, Santa Cruz Island at the right, and in between, the remaining sites; the second axis groups the islands of San Cristóbal and Isabela at the top of graph and Floreana Island at the bottom.

We found a similar pattern using STRUCTURE 2.3.4 software. Analysis of the entire data set shows that the ΔK parameter (i.e., the K value for which a further increase in K adds less likelihood than the previous increase in K) was maximum for $K = 2$ clusters (Fig. 4). The first group was composed of samples from Costa Rica. The second group is constituted of samples from mainland Ecuador together with those of the Galápagos Islands. Each increase in K (Fig. 4) split one of the clusters obtained with the previous value; it also shows that Costa Rica populations are clearly separated from Ecuadorian populations, while admixture occurs between populations from mainland Ecuador and Galápagos Islands.

Inference of colonization pathways

The first step of the ABC analysis aimed at defining the source of the populations established in the Galápagos Islands. Among the six scenarios tested (Fig. 2, Step 1), the scenario 1 gave the highest fit with the observed data set, with a posterior probability of 76.8% (95% CI [74.5–79.1]; Fig. S1, Step 1). This scenario assumes that populations from Galápagos Islands diverged from mainland Ecuador populations. The only other scenario receiving significant support, though much lower than the scenario 1, was the scenario 5 (posterior probability of 18.8%; 95% CI [16.6–21.0]; Fig. S1). The scenario 5 assumes that Galápagos populations derived from an admixture event between populations from mainland Ecuador and an undetected, unsampled population introduced from the source. All the other scenarios had a posterior probability of less than 4%. Therefore, confidence in the scenario 1 choice was strong. The evaluation of type I error rate showed that 43.9% of the datasets simulated with the scenario 1 were correctly identified as being produced by the scenario 1. Estimation of the type II error rate was low (mean value ± SD = 11.6% ± 12.1). Type I error rates and type II error rates for all scenarios are given in Table 2.

Posterior distributions for the parameters of interest were inferred for the scenario 1. Table 1 provides the mean, median and mode estimated for these distributions. Figure S2 shows the priors and posteriors for all parameters. For some parameters, the posterior differs from the prior (e.g. for the effective population sizes of Costa Rica CR, Mainland Ecuador ME and Galápagos Gal and Galb (Galb had undergone an initial size reduction), and the times t_1 and t_2 of divergence events), suggesting that the genetic data contain substantial information to estimate these demographic parameters. However, for other parameters (e.g. NP), little information seems to be provided beyond that present in the prior, or distributions are too wide to clearly assess and summarize our results.

The second step of the ABC analysis aimed to determine if the population of mainland Ecuador, from which diverged the populations of the Galápagos Islands, underwent a bottleneck event (Fig. 2, Step 2). Scenarios introducing an event that drastically reduces the size of the population (scenarios 1 and 3) have the lowest likelihood (posterior probability less than 5;5%). Scenarios 2 and 4 had equal posterior probabilities (Fig. 2 and Fig. S1, Step 2). One showed that mainland Ecuador populations derived from an unsampled population (43.6%; 95% CI [40.6–46.6]). The other defined mainland Ecuador populations as an admixture between Costa Rica population and an unsampled population (46.2%; 95% CI [43.3–49.2]), with a rate of approximately 50% (see Fig. S1, Step 2). Type I (the probability with which the chosen scenario is rejected although it is the true scenario) and II (the probability of deciding for the chosen scenario when it is not the true scenario) errors are respectively for scenarios 2 and 4 81.7 and 43.5% and 12.5% ± 4.4 and 22.1% ± 11.5.

Finally, step 3 aimed to assess the plausibility of an admixture event giving birth to Galápagos populations. ABC analysis discard this hypothesis and confirms that populations from the Galápagos Islands directly come from those of mainland Ecuador (posterior probabilities of 65.3% (95% CI [60.8–69.7]) and 34.7% (95% CI [30.3–39.2]), respectively; Fig. S1, Step 3). Type I and II errors for chosen scenario were estimated at 37.8 and 48.8, respectively.

Fig. 4 Estimated *Solenopsis geminata* population structure ▶ from Bayesian STRUCTURE analyses for $K = 2$ to $K = 10$. Each individual is represented by a vertical bar partitioned into K coloured segments that represent the individual's estimated membership fractions in K clusters. Each plot is based on the highest-probability run (among 11) at that value of K. Individuals are arranged based on their origins. Geographic areas are labelled at the bottom of the plots

Reproductive and dispersal strategies

We observed a significant genotypic differentiation between pairs of nests for all pairwise comparisons (Costa Rica, site Sabana: mean F_{ST} ± SE = 0.249 ± 0.019 [95% CI 0.217–0.289]; Ecuador, Santa Cruz Island, site El Ocidente: 0.223 ± 0.071 [95% CI 0.100–0.353]), and a positive relatedness among nestmate workers (Sabana: 0.437 ± 0.019 [95% CI 0.402–0.475]; El Ocidente:

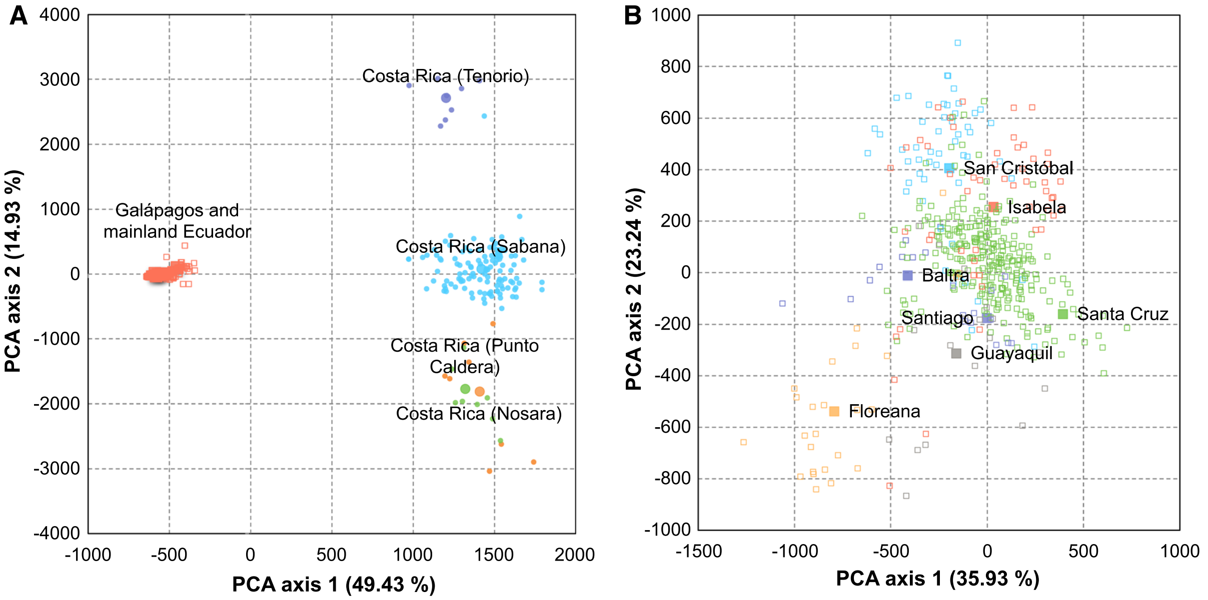


Fig. 3 Factorial correspondence analysis of all individual multilocus genotypes, based on allelic variation at 12 microsatellite loci. Multilocus scores are computed in the bivariate space defined by the first two factorial components. Separate analyses were performed on the whole data set (i.e., Costa Rica and Ecuador, **a**) and for Ecuadorian samples (**b**). Cluster centers are represented by a filled, larger mark

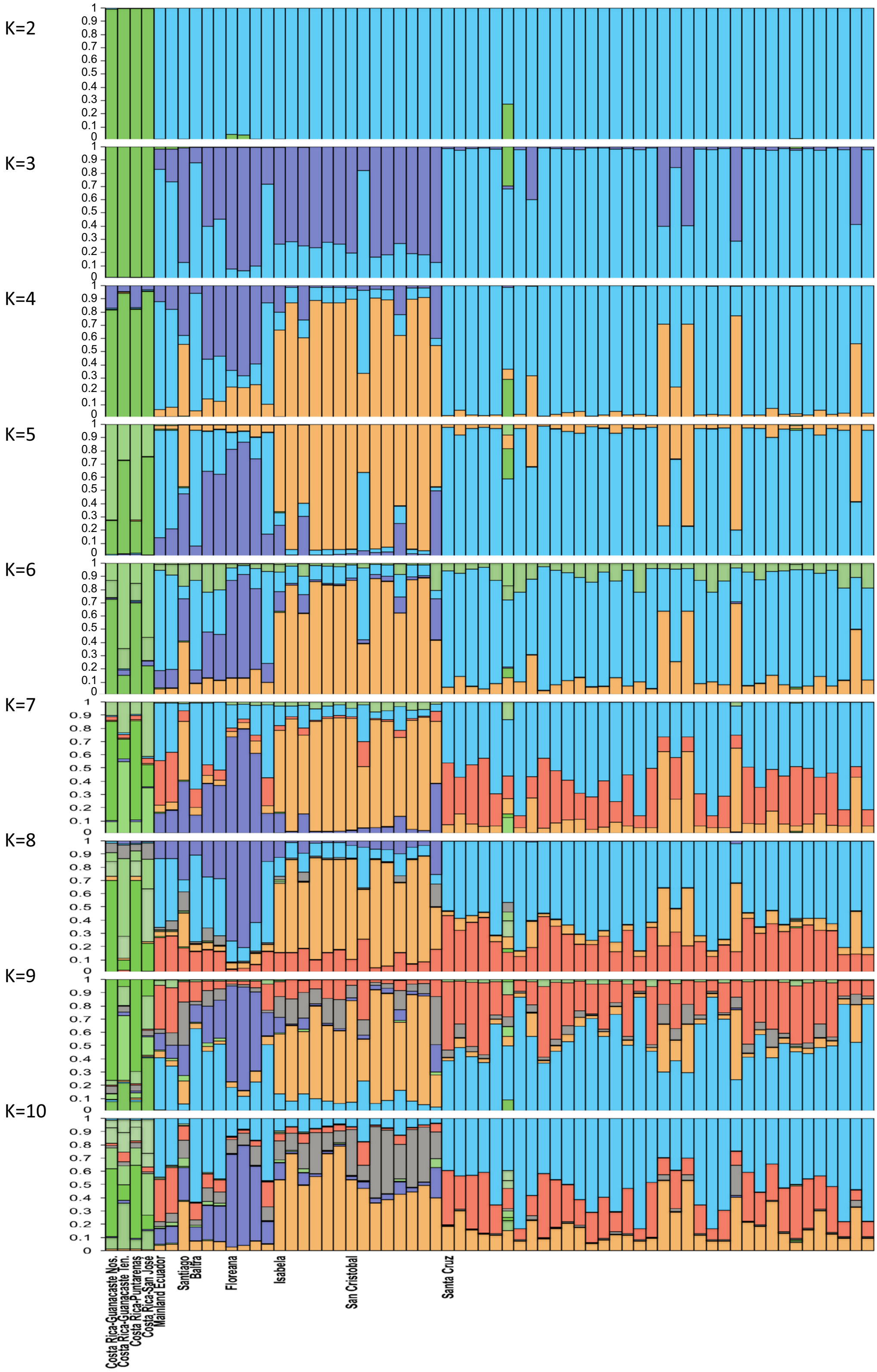

K=2
K=3
K=4
K=5
K=6
K=7
K=8
K=9
K=10
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Costa Rica-Guanacaste Nos.
Costa Rica-Guanacaste Ten.
Costa Rica-Puntarenas
Costa Rica-San José
Mainland Ecuador
Santiago
Baltra
Floreana
Isabela
San Cristobal
Santa Cruz

Table 2 Type I and Type II error rates and posterior probabilities calculated from diyABC for each scenario at steps 1 and 2 (error rates for step 3 are given in the text as step 3 consists of only two competing scenarios)

True scenario used for simulation	Type II error						Type I error	Post. Prob. [95% CI]
	Sc. 1	Sc. 2	Sc. 3	Sc. 4	Sc. 5	Sc. 6		
Step 1								
Scenario 1	–	0.181	0.015	0.026	0.151	0.066	0.439	0.7681 [0.7448,0.7914]
Scenario 2	0.162	–	0.064	0.101	0.129	0.085	0.541	0.0083 [0.0032,0.0133]
Scenario 3	0.003	0.087	–	0.148	0.008	0.055	0.301	0 [0.0000,0.0000]
Scenario 4	0.025	0.177	0.259	–	0.053	0.196	0.710	0.0002 [0.0000,0.0053]
Scenario 5	0.301	0.267	0.021	0.059	–	0.109	0.757	0.1883 [0.1666,0.2100]
Scenario 6	0.088	0.133	0.142	0.165	0.081	–	0.681	0.0352 [0.0277,0.0427]
Mean	0.116	0.169	0.100	0.100	0.084	0.102		
SD	0.121	0.067	0.102	0.058	0.058	0.056		
Step 2								
Scenario 1	–	0.165	0.253	0.270			0.688	0.0546 [0.0110,0.0983]
Scenario 2	0.300	–	0.213	0.304			0.817	0.4359 [0.4063,0.4655]
Scenario 3	0.169	0.077	–	0.090			0.336	0.0471 [0.0000,0.0965]
Scenario 4	0.175	0.132	0.128	–			0.435	0.4624 [0.4329,0.4920]
Mean	0.215	0.125	0.198	0.221				
SD	0.074	0.044	0.064	0.115				

0.361 ± 0.098 [95% CI 0.171–0.505]). Values were not different between Sabana and El Ocidente populations (two-sided p values obtained after 10,000 permutations; F_{ST}: $p = 0.454$; within-nest relatedness: $p = 0.079$). The mean numbers of queens estimated from within-nest relatedness were 3.66 (min–max: 0.97–20.83) and 3.65 (1.05–16.52) for populations of Sabana and El Ocidente, respectively. Calculations of inbreeding coefficients showed contrasting patterns; $F$is values from Costa Rica indicate that individuals are less related than expected under a model of random mating. F_{IS} values were negative and significantly lower in Costa Rica (Sabana: -0.143 ± 0.030 [95% CI -0.190–-0.077]) than in Galápagos Islands (El Ocidente: 0.042 ± 0.040 [95% CI -0.021–0.127]; $p = 0.039$).

Correlation analyses showed that the genetic and geographical distances between the nests were significantly associated in population Sabana (Mantel test, $r = 0.218$, $p = 0.002$), but not for the population El Ocidente ($r = 0.133$, $p = 0.087$).

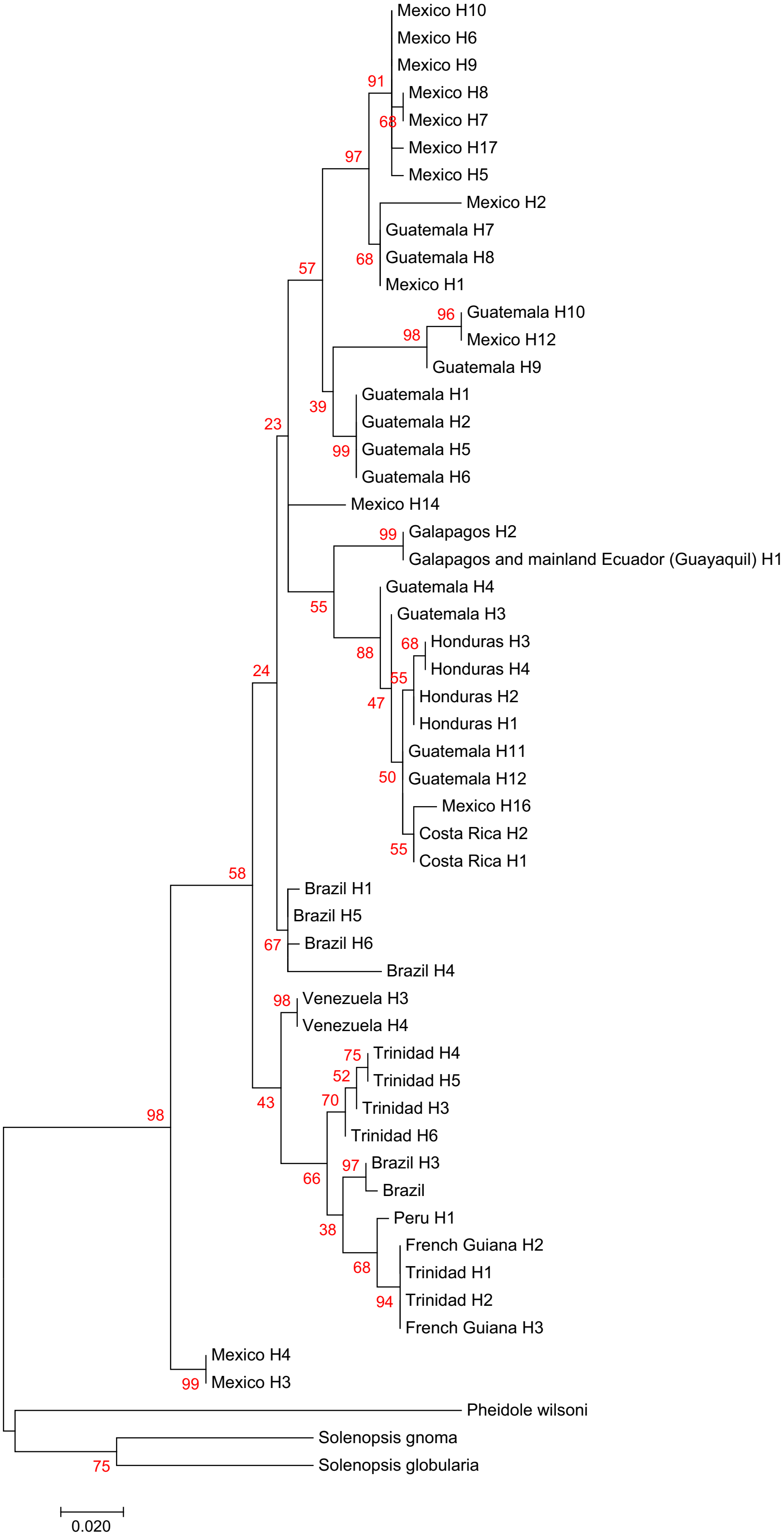
Mitochondrial sequence analysis

DNA sequence analysis from Ecuadorian specimens (3 from Guayaquil and 17 from Galápagos) revealed two different haplotypes of 658 base pairs, separated by a single site change (a C instead of a G at position 32) (Genbank accession numbers KT200421 and KT200422). One haplotype was represented in 19 out of 20 individuals; the second was found in one individual collected on Isabela Island. The phylogenetic tree (Fig. 5) shows that the sequences of the Ecuadorian specimens of *S. geminata* are very close to those isolated from samples collected in Guatemala and Honduras (BLAST above 94% identity).

Discussion

By analysing samples collected in different sites of the Galápagos Islands, and comparing them with populations collected in native areas (Costa Rica and mainland Ecuador), we showed that mainland Ecuador and Galápagos *S. geminata* sites displayed a lower genetic diversity compared to Costa Rica sites, and

Fig. 5 Molecular phylogenetic analysis by maximum likelihood method summarizing mtDNA relationships among 51 haplotypes of South American *Solenopsis geminata*, and 3 outgroup haplotypes (*S. gnoma* Genbank accession numbers KT200423, *S. globularia* KT200424 and *Pheidole williamsi* KT200425). Numbers at the nodes represent the number of times each node was represented in a bootstrap analysis (1000 replicates). Scale bar indicates number of nucleotide substitutions per site. South American samples, except those from Ecuador, were collected by D. Gotzek and D. Shoemaker. GPS positions are given in Table S2



that almost all individuals from Galápagos Islands and mainland Ecuador share the same COI haplotype. Galápagos Islands populations likely derived from populations established in mainland Ecuador. Our study also provides information on reproduction and dispersal strategies of *S. geminata* in the Galápagos Islands that can be important for management practices.

Reconstruction of invasion history

The worldwide invasion history of the tropical fire ant *S. geminata* is strongly linked to the development of the global trade of the sixteenth century (Gotzek et al. 2015). Ascunce et al. (2011) demonstrated that the worldwide populations of the fire ant originated from nine independent introductions from one introduced area in the Southern United States. Our reconstruction of the invasion history suggests that the populations of the Galápagos Islands diverged from mainland Ecuador populations. Furthermore, our mtDNA analysis showed a strong similarity between nucleotide sequences of the Galápagos Islands and mainland Ecuador populations. Altogether, these results favour the hypothesis of a single source that played a bridgehead role in the introduction and invasion of *S. geminata* in the archipelago of the Galápagos Islands. As compared to multiple introductions occurring independently from native populations, bridgehead processes are evolutionary more parsimonious since only one evolutionary shift towards invasiveness has to occur in the bridgehead population (Bolfíková et al. 2013; Estoup and Guillemaud 2010; Foucaud et al. 2010; Guillemaud et al. 2010, 2011; Keller et al. 2012; Lombaert et al. 2010; Yang et al. 2012).

As suggest the placement of mainland Ecuadorian samples in the midst of the Galápagos samples (Fig. 3a), the presence of the same single haplotype in the Galápagos and the Ecuadorian samples, and since the Ecuadorian mainland is an obligatory hub for tourism and trade (Bigue et al. 2012; Toral-Granda et al. 2017), it is likely that the sources of *S. geminata* in the Galápagos Islands are located in Guayaquil. This result should however be interpreted by bearing in mind that the number of samples from Costa Rica and mainland Ecuador is limited. Moreover, there appears to be other source populations for the invasive populations, the Bayesian clustering approach suggesting that the invasion of the Galápagos Islands is not unique. As a matter of fact, a recent work identified southwestern Mexico as the most likely source for all invasive populations of *S. geminata* around the world (Gotzek et al. 2015), but showed that introduced Galápagos populations are not derived from the same source as the other invasive populations in the world. Our work suggests that Galápagos populations are derived from mainland Ecuador or at least from a greater cluster that Ecuador belongs to what Gotzek et al. (2015) termed the Caribbean cluster. The relationships between the original source, the potential steps, and the Galápagos Islands merit further analyses.

Reproductive and dispersal strategies of *S. geminata*

Our results show that the numbers of functional queens per nest reach up to 17 and 21 in the Galápagos Islands and in Costa Rica populations, respectively. These values are relatively low compared to a native area where the number of queens per nest was estimated to be about 30, with a range of 3–90 (Vargo 1993). A high number of reproductive queens usually involves a higher productivity and higher population densities (Goodisman et al. 2007; Holway et al. 2002; Ross 2001), and successful invasive ant species are often highly polygynous (Holway et al. 2002; Rabitsch 2011; Suarez and Tsutsui 2008). However, the most notorious and globally distributed fire ant, *S. invicta*, contains both monogyne and polygyne forms in introduced areas (Glancey et al. 1987; Valles and Porter 2003), suggesting that, at least for this group, a high level of polygyny is not a key factor for its invasive success. Moreover, in the Galápagos Islands, relaxed selective pressures, e.g. due to the lack of competitors, predators or pathogens, could also explain such differences in reproductive strategies with native areas.

At local scale (i.e., between nests within the site of El Ocidente in the island of Santa Cruz), we have observed no isolation by distance, which suggests that dispersal occurs, at least to some extent, by nuptial flights (Taber 2000; Wauters et al. 2014). This implies that *S. geminata* disperse on short and medium distances within the archipelago, sometimes facilitated by human transportation of infested material or by climatic events such as El Niño (Roque-Albelo and Causton 1999). Dispersal by nuptial flights is rare in invasive populations of ants: *Anoplolepis gracilipes*, *Linepithema humile*, *Pheidole megacephala* and *Wasmannia auropunctata* all reproduce by budding (Holway et al. 2002). Their rates of spread are between 10 and 400 m per year. *Solenopsis geminata*, along with the monogyne form of *S. invicta*, constitutes an exception (Holway et al. 2002). Its patterns of spreading on a regional scale may therefore be driven by both winged dispersal (up to a few kilometres) and human-mediated transportation (Everett 2000; Holway et al. 2002). As for reproductive strategies, relaxed selective pressures in the archipelago may explain why founding by budding, and so beginning with a large worker force, is not a fundamental prerequisite of the colonisation success of *S. geminata*.

Evolutionary processes underlying the invasion of *S. geminata* in the Galápagos Islands

Introduction of a species to a new area often results in the sampling of only a small portion of the source population's total genetic diversity (i.e., founder event). Furthermore, the small size of the newly introduced populations can cause strong genetic drift for several generations and population must not succumb to the deleterious consequences associated with low genetic variation (Dlugosch and Parker 2008). Our results highlight a reduced genetic diversity of populations from the Galápagos Islands and mainland Ecuador populations compared to Costa Rican populations (Table S1). Theoretically, low genetic diversity should negatively impact the invasion of *S. geminata* in the Galápagos Islands, but instead the species is very common all over the archipelago and its distribution is expanding (Wauters et al. 2014, 2016).

Some invasive species, such as the Argentine ant, *Linepithema humile*, the big-headed ant, *Pheidole megacephala*, or the little fire ant, *Wasmannia auropunctata*, might be able to take advantage of reduced genetic diversity (Foucaud et al. 2009; Fournier et al. 2009, 2012; Giraud et al. 2002; Tsutsui et al. 2000). A loss of genetic diversity might result in a loss of genetic variation at genes involved in chemical recognition cues, which in turn might lead to a loss of the ability to discriminate nestmates from non-nestmates (Giraud et al. 2002; Tsutsui et al. 2000). This is followed by the formation of networks of interconnected nests (i.e., supercolonies) that exchange individuals and share territory peacefully over extensive areas. These supercolonies can collide to form an unicolonial population with high workers densities. Such a huge cooperative unit allows interspecific dominance and habitat saturation by competitive exclusion of interspecific competitors (Holway et al. 1998, 2002). Our preliminary observations of *S. geminata* social structure suggest a lack of agonistic relationships between workers.

Alternatively, the success of invasive species, even after a founding effect, can also depend on ecological factors, such as the presence of predators, competitors or parasites in the new environment, resources availabilities and life-history traits of the invader (Facon et al. 2006; Lau and terHorst 2015). Known parasites of *S. geminata* (Plowes et al. 2009; Williams et al. 2003), such as the phorid fly *Pseudacteon*, the strepsipteran *Caenocholax fenyesi*, or the protozoa *Mattesia geminata* are lacking in the archipelago. In the case of *S. geminata* in the Galápagos Islands, a combination of low intra- and interspecific competition, omnivory, association with human transportation and dispersal by nuptial flights (Adams et al. 1976; Causton et al. 2006; Herrera 2011; Taber 2000) can provide partial answers to the invasive success of this species.

Implications for control and conservation

Our study provides information on reproduction and dispersal strategies, genetic diversity and introduction history of *S. geminata* in the Galápagos Islands that can be important for management practices. Many invasive insects have colonized the archipelago from mainland Ecuador. The parasitic fly *Philornis downsi* has been accidentally introduced to the Galápagos Islands in the 1960s. Its larvae feed on the blood and flesh of nestling and adult birds, and the presence of this species is associated with a high morbidity and mortality in almost all Galápagos hosts (McNew and Clayton 2018). Genetic analyses revealed low levels of genetic variation and were consistent with a small founding population or few introduction events (Dudaniec et al. 2008). Similarly, the paper wasps *Polistes versicolor* and *Brachygastra lecheguana* were introduced in the archipelago in 1988 and 1994, respectively, probably associated with economic and touristic activities to and within the archipelago (Roque-Albelo and Causton 1999). These species strongly impact Galápagos fauna by commonly preying on lepidopteran larvae, larvae that constitute main food sources for reptiles and birds. Another evidence for regular introductions into the Galápagos Islands comes from the mosquito *Culex quinquefasciatus*, a vector for diseases such as West Nile fever and avian malaria (an avian malaria parasite has been detected consistently in the Galápagos Penguin *Spheniscus mendiculus* and, less frequently, in some passerines; Asigau et al. 2017). Bataille et al. (2009) demonstrate that mosquitoes breed with already-established populations of *C. quinquefasciatus*, and that tourist and inter-island boats are the most likely mechanism for transporting mosquitoes between islands. They also suggest that *C. quinquefasciatus* has been introduced frequently to the Galápagos Islands by air transportation. All these cases evidence the role of maritime and airplane traffic in the establishment and spread of alien species in isolated oceanic islands. In the archipelago, traffic originates in mainland Ecuador, further suggesting it as the original source of invasions (Causton et al. 2006; Toral-Granda et al. 2017). Such understanding of evolutionary processes and pathways of introduction underlying successful invasions is therefore crucial for designing efficient prevention and control strategies of invasive species (Simberloff et al. 2013; Toral-Granda et al. 2017). Invasion management requires an understanding of life-history traits of the invader to predict invasiveness, as well as knowledge about the resistance ability of native communities (Carroll 2011), and a diversity of evolutionary factors influences the ecological outcome of biological invasions, including phylogenetic history, population structure and genetic constraints and facilitation under altered selection (Carroll 2011).

Acknowledgements We are grateful to M. Martin Cerezo for her help in genotyping, J. Kwasigroch for his assisting during the process of data simulation, J. Parikka for his reading of the first draft of this manuscript and H.J. Axen, J. Foucaud, D. Gotzek, T. Guillemaud, F. Hendrickx, E. Lombaert and anonymous referees for their useful comments on a previous version of this paper. This work was supported by several grants from the Belgian FRS-FNRS (Fonds National pour la Recherche Scientifique) (DF), the Fonds Defay (DF), the Royal Belgian Institute of Natural Sciences (WD) and the King Léopold III Fund (WD). We are also grateful to Gontran Sonet (RBINS) for his help preparing and calibrating the sequencer. The molecular research was funded by the FWO project (G0D2915N)—Poneroid Ants of Ecuador (Formicidae: Agroecomyrmicinae, Amblyoponinae, Ponerinae, Proceratiinae, Paraponerinae). All administration on legislation and permits was done with the help of Henri Herrera and Sonia Cisneros of the Charles Darwin Foundation in collaboration with the Galapagos National Park Directorate (GNPD). This publication is contribution number 2195 of the Charles Darwin Foundation for the Galápagos Islands.

Author contributions D.F. designed the study. All authors collected samples. N.W. performed the molecular work. N.W. and D.F. analysed the data. N.W. and D.F. wrote the manuscript with input from W.D.

Data accessibility Sampling information can be found in Table S1 and Table S2 (Supporting information). DNA sequences are deposited in GenBank (accessions nos KT200372-KT200425).

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