Rapid Communication

First record of the red imported fire ant, *Solenopsis invicta* Buren, from Hispaniola

Dietrich Gotzek[1,2,*] and Santiago Martinez[3]

[1]*Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington DC, USA*
[2]*Laboratories of Analytical Biology, National Museum of Natural History, Smithsonian Institution, Washington DC, USA*
[3]*Department of Clinical Sciences, Florida State University, Orlando, Florida, USA*

Author e-mails: *gotzekd@si.edu (DG), smartinez@doctor.com (SM)*

*Corresponding author

Abstract

The red imported fire ant, *Solenopsis invicta* Buren, is one of the most damaging pest species in the world. A native to the floodplains of subtropical South America, it has been spread to North America and more recently to Australia and Asia. In order to effectively control, manage, and mitigate its impact and spread, it is critical to understand its current distribution. While *S. invicta* has long been known from the smaller Caribbean islands, it has not been documented from the two largest islands (Hispaniola and Cuba). We present the first record of *S. invicta* from Hispaniola and discuss its presence in relation to its native congener, *S. geminata*.

Key words: invasive species, *Formicidae*, Dominican Republic, Caribbean

Introduction

Invasive pests are a major threat to human health, environment, and biodiversity (Mazza et al. 2014; Bellard et al. 2016). Early detection and immediate control and management of invasive species are the most efficient, effective, and cost-effective prevention measures (Mehta et al. 2007; Ujiyama and Tsuji 2018; Polasky 2010). The red imported fire ant, *Solenopsis invicta* Buren, 1972, is one of the most invasive and damaging pests in the world (Lowe et al. 2004). Native to periodically flooded grasslands of subtropical South America (Ascunce et al. 2011), it has been introduced to the USA in the mid to late 1930's (Tschinkel 2006). From its initial entry point in Mobile, Alabama, it has spread throughout the entire Southeast, covering a total of over 148 million hectares in 14 states and Puerto Rico (USDA APHIS 2020). Negative impacts of *S. invicta* infestation are wide-ranging and severe: they damage electrical equipment, damage crops by feeding on seeds, seedlings, and developing fruit, and are medically relevant pests of people, pets, livestock, and wildlife (Tschinkel 2006). Although there is some debate over the exact nature and degree of the ecological impact in undisturbed ecosystems (King and Tschinkel

2013a, b; Stuble et al. 2011, 2013), the negative impact in human-dominated environments is uncontroversial. Estimates of the exact economic costs of fire ant damage and control for the southeastern USA alone vary from more than half a billion to several billion dollars per year (Williams et al. 2001).

More recently, *S. invicta* has also spread far beyond the invasive range in North America. Earlier this century, it has been reported from mainland China, Taiwan, India, Philippines, Australia, and New Zealand (from where it was subsequently successfully eradicated) (Wetterer 2013). Interestingly, most of these populations all seem to have derived from the invasive US population (Ascunce et al. 2011), but China now appears to serve as a bridgehead for its further spread in Asia (Wylie et al. 2020) and a few incursions in Australia derived from the native range in Argentina (Wylie et al. 2016). *Solenopsis invicta* has been known from the Caribbean since the 1980's (Wetterer and Davis 2010; Wetterer 2013; Wetterer et al. 2014). To date, *S. invicta* has been reported from the Lucayan Archipelago, the Lesser Antilles, and most islands of the Greater Antilles (Puerto Rico, Jamaica, the Cayman Islands, and the Virgin Islands).

Interestingly, *S. invicta* has not yet been described from the Hispaniola, the second largest of the Caribbean islands with the longest history of European settlement, despite active entomological biodiversity research being conducted in the Dominican Republic (Lubertazzi 2019). The reasons for this could be manifold. Although unlikely, the species may not (yet) be established on the island for simple stochastic reasons, since unintended transport and establishment are probabilistic processes. If the introduction was recent, *S. invicta* may still be rare and highly localized, making detection unlikely. Further, a sampling bias of general biodiversity collections towards pristine habitats would also bias against the discovery of *S. invicta*, since this species prefers heavily disturbed habitats (Tschinkel 2006). Finally, *S. invicta* is easily confused with the native tropical fire ant, *S. geminata* (Fabricius, 1804), and can readily be mistaken for its congener if one does not utilize taxonomic keys including the South American native.

Recently, Dr. Santiago Martinez was presented with a medical case of a Santo Domingo patient displaying recurrent episodes of angioedema with skin lesions consisting of pustules typical of *S. invicta* stings, leading us to investigate its presence on Hispaniola.

Materials and methods

Sample collection: We searched for fire ants from August 26–31, 2019 in urban and agricultural areas of National Province, Puerto Plata Province, and Hato Mayor Province (Figure 1). A total of 18 fire ant nest series were collected from nests or foraging trails (Table 1). When possible, we always collected major workers to aid in morphological species identification (Trager 1991; Pitts et al. 2018). Vouchers are deposited in the entomological collection of the National Museum of Natural History (USNM), Smithsonian
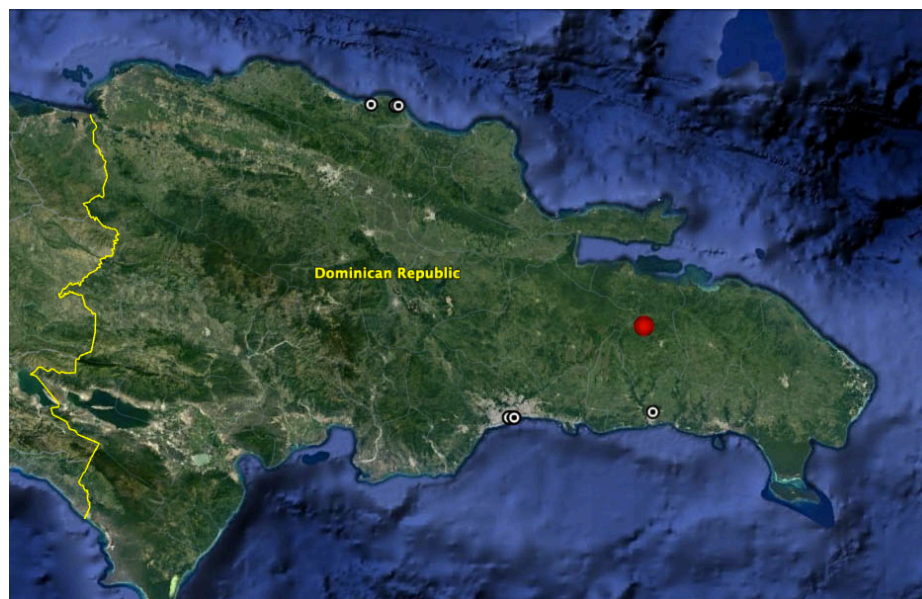
Figure 1. Satellite image of the Dominican Republic with collection sites indicated with circles. The invasive *Solenopsis invicta* collection site is marked by a red circle, native *S. geminata* collection sites are indicated by white circles. Image source: Google Earth 7.3.3 (13 December 2015). Dominican Republic, Hispaniola. http://www.google.com/earth (accessed 21 August 2020).

Table 1. Fire ant samples collected in the Dominican Republic in August 2019 and pertinent collection information. Voucher numbers are for the MNHNSD (top) and USNM (bottom), respectively.

Sample	Species	Province	Site	Latitude	Longitude	Voucher Number
DR19-01	*S. geminata*	Distrito Nacional	Santo Domingo, Paseo Presidente Billini	18.4680	−69.8893	USNMENT01126782 USNMENT01129693
DR19-02	*S. geminata*	Puerto Plata	Cabarete	19.7486	−70.3989	USNMENT01126783 USNMENT01129694
DR19-03	*S. geminata*	Puerto Plata	Cabarete	19.7496	−70.4094	USNMENT01126784 USNMENT01129695
DR19-04	*S. geminata*	Puerto Plata	Cabarete	19.7495	−70.4099	USNMENT01126785 USNMENT01129696
DR19-05	*S. geminata*	Puerto Plata	Cabarete	19.7488	−70.4101	USNMENT01126786 USNMENT01129697
DR19-06	*S. geminata*	Puerto Plata	Sosúa	19.7528	−70.5188	USNMENT01126787 USNMENT01129698
DR19-07	*S. geminata*	Distrito Nacional	Santo Domingo, 10A Ave. Máximo Gómez	18.4677	−69.9115	USNMENT01126788 USNMENT01129699
DR19-08	*S. geminata*	Distrito Nacional	Santo Domingo, 10A Ave. Máximo Gómez	18.4683	−69.9115	USNMENT01126789 USNMENT01129700
DR19-09	*S. geminata*	Hato Mayor	Coffee plantation	18.8416	−69.3293	USNMENT01126790 USNMENT01129701
DR19-10	*S. geminata*	Hato Mayor	Coffee plantation	18.835	−69.3323	USNMENT01126791 USNMENT01129702
DR19-11	*S. geminata*	Hato Mayor	Coffee plantation	18.8339	−69.3356	USNMENT01126792 USNMENT01129703
DR19-12	*S. invicta*	Hato Mayor	Coffee plantation	18.8425	−69.3288	USNMENT01126793 USNMENT01129704
DR19-13	*S. invicta*	Hato Mayor	Coffee plantation	18.8427	−69.3289	USNMENT01126794 USNMENT01129705
DR19-14	*S. invicta*	Hato Mayor	Coffee plantation	18.8427	−69.3289	USNMENT01126795 USNMENT01129706
DR19-15	*S. invicta*	Hato Mayor	Coffee plantation	18.8427	−69.3292	USNMENT01126796 USNMENT01129707
DR19-16	*S. geminata*	Hato Mayor	Coffee plantation	18.8418	−69.3292	USNMENT01126797 USNMENT01129708
DR19-17	*S. geminata*	San Pedro de Macoris	Coffee plantation	18.4915	−69.2886	USNMENT01126798 USNMENT01129709
DR19-18	*S. geminata*	Distrito Nacional	along Rt.3	18.4678	−69.8894	USNMENT01126799 USNMENT01129710

Institution, Washington DC, USA (USNMENT01129693–USNMENT01129710) and at the Museo Nacional de Historia Natural (MNHNSD), Santo Domingo, Dominican Republic (USNMENT01126782–USNMENT01126799).

Species identification: We used the keys in Pitts et al. (2018) and Trager (1991) to identify samples to species. For each nest series, we used the three largest workers (ideally majors) to work through the taxonomic keys. We further compared our samples to extensive fire ant collections at the NMNH.

Since species identification of fire ants based solely on morphology is error prone even for experienced systematists due to the paucity of fixed character differences between species and rampant intra- and interspecific variability, we also conducted molecular genetic-based species identification using DNA barcoding (Hebert et al. 2003) of specimens hypothesized to be *S. invicta.*

DNA barcoding: Genomic DNA was successfully isolated from the four samples provisionally identified as *S. invicta* at the Smithsonian Laboratory of Analytical Biology (LAB) using the Autogen Mouse Tail Tissue Prep. Only a single ant was extracted per collection event to avoid subsampling the same colony. Amplification and sequencing of the DNA barcode followed the standard protocol for this locus as applied to ants (Smith et al. 2005). Briefly, the barcoding fragment of the *cytochrome c oxidase subunit I* (*COI*) gene were amplified using the Folmer and jg primer pairs (Folmer et al. 1994; Geller et al. 2013) using the protocol of Smith et al. (2005). Amplification success was verified on an agarose gel. PCR products were purified using ExoSAP-IT (ThermoFisher Scientific, USA) and Sanger sequenced in both directions with the PCR primers (with BigDye Terminator v3.1 (Applied Biosystems, USA)) and run out on an ABI 3730xl DNA Analyzer.

After automated quality control and manual inspection of sequencing traces using *Geneious Prime 2019.2.3* (Biomatters 2019), all reads from a specimen were assembled to generate full length *COI* barcodes (GenBank accession number MT909544). Barcodes were used for species identification by searching NCBI GenBank nr database (National Center for Biotechnology Information 2020) using *megablast* (Morgulis et al. 2008) in the *BLAST+ 2.10.0* package (Zhang et al. 2000; Camacho et al. 2008). We also downloaded the top 100 *COI* sequences returned from the blast search and constructed a maximum likelihood tree using automated partition selection scheme (greedy strategy, Lanfear et al. 2012) and model selection (*Modelfinder*, Kalyaanamoorthy et al. 2017) implemented in *IQ-TREE* 1.16.10 (Nguyen et al. 2015). We implemented ten independent runs and estimated branch support using ultrafast bootstraps (1,000 replicates, Minh et al. 2013; Hoang et al. 2018) and two approximate likelihood-based measures (aLRT) (Shimodaira-Hasegawa-aLRT [SH-aLRT] with 1,000 replicates and the Bayesian-like transformation aLRT [aBayes] of Anisimova et al. 2011, which is particularly robust for branch-support of very short branches).

Figure 2. Images of head and side aspects of minor workers of *Solenopsis geminata* (top) and *S. invicta* (bottom). The two species are readily distinguished by the huge, cordate head in major workers in *S. geminata* (not shown). However, even without access to major workers, the two species can readily be differentiated using minor workers (shown here). Further characters are the presence of a medial tooth in *S. invicta* and a biphasic coloration of the head and legs in *S. geminata*.

Results

Of the 18 fire ant samples collected, we identified 14 as the Tropical Fire Ant, *Solenopsis geminata*, a wide-spread fire ant from Central and South America and also presumably native to the Caribbean (Wetterer 2011; Gotzek et al. 2015). The remaining four samples we identified as the red imported fire ant, *S. invicta* Buren. These four samples were all collected from nests at a single site, a coffee plantation in central Hato Mayor Province (Figure 1). The plantation itself was established in the mid 1980s and is surrounded by other types crop agriculture (e.g., cacao). Key features we used to differentiate *S. invicta* from its congener were lack of megacephaly in even the largest workers, presence of a median tooth on the clypeal margin, and homogeneous reddish-brown color of the head, thorax, and legs (see Figure 2). While not all nest series of *S. geminata* contained majors, all lacked the distinguishing median clypeal tooth. Additionally, in our samples all *S. geminata* were the bi-color morphs typical of the Caribbean cluster (Gotzek et al. 2015), a color pattern never seen in *S. invicta* (D. Gotzek *pers. observation*).
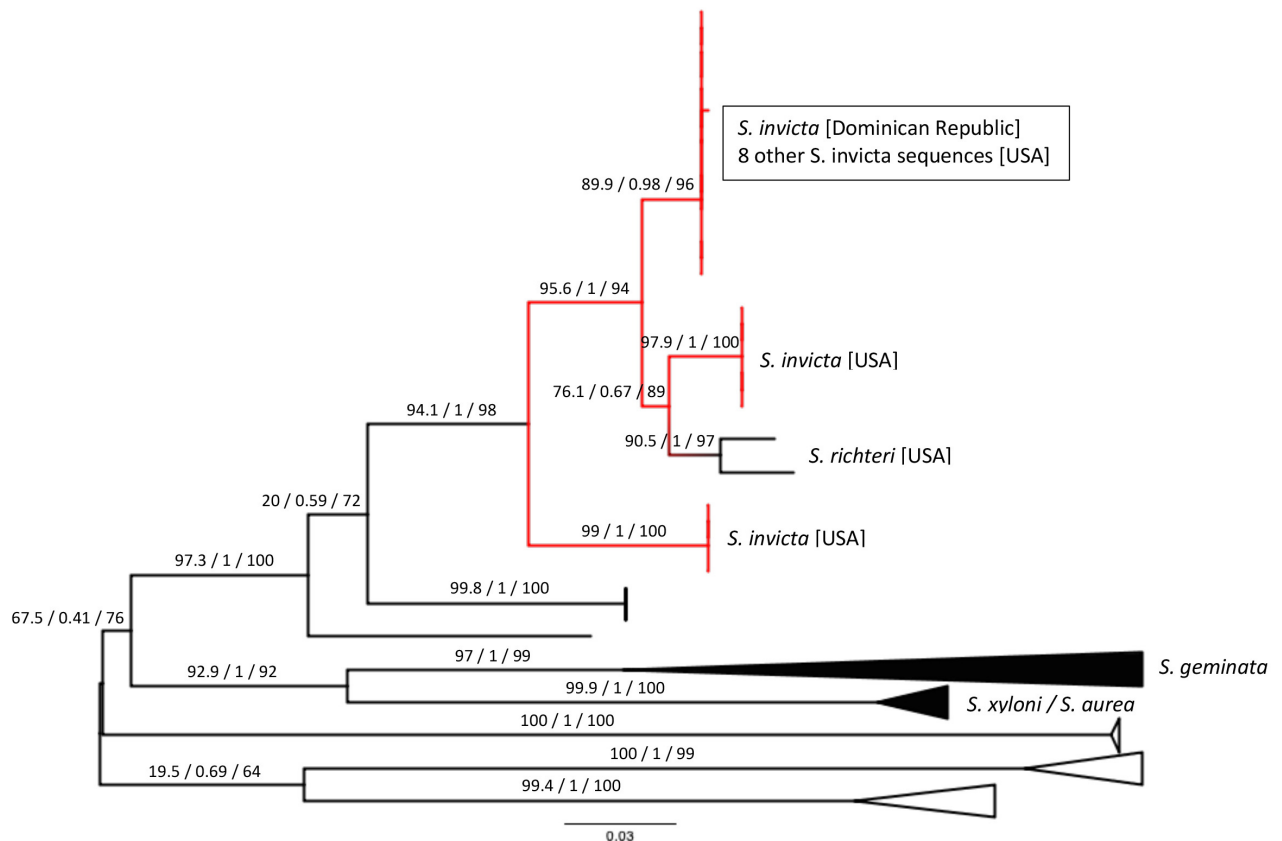
Figure 3. Mid-point rooted maximum likelihood tree of top 100 COI sequences returned by BLAST searches of GenBank and the new Dominican sequences. All sequences are derived from ants of the genus *Solenopsis*. The *Solenopsis invicta* clade is red. It is rendered paraphyletic by *S. richteri*, a well-known observation (Shoemaker et al. 2006). Solid triangles are other fire ant species, open triangles represent distantly related *Solenopsis* species. Clades of unidentified samples are not labelled. The scale bar represents average number of nucleotide substitutions per site. For ease of viewing, branch support is only given for the longer branches (SH-aLRT / aBayes / ultrafast bootstrap).

The DNA barcodes confirmed our morphological species identification. All four ostensible *S. invicta* samples shared a single *COI* haplotype. BLAST searches using this haplotype of the NCBI nucleotide collection database returned a *S. invicta* sequence from the USA as their top hit (Genbank accession number HQ215538) with very high support (E values = 0.0, percent identity > 99.2%, coverage 100%). Further, a maximum likelihood tree of the top 100 *COI* blast results not only placed our newly generated *S. invicta* sequence in the midst of their conspecific sequences with very high support, but shows it is identical to other *S. invicta* COI sequences from the USA (Figure 3).

Discussion

We present evidence documenting the highly invasive pest species, *Solenopsis invicta*, on the Hispaniola for the first time. *Solenopsis invicta* has been continually expanding its invasive range since first discovered around Mobile, AL in 1942 (Wilson and Eads 1949; Tschinkel 2006). From the USA, this species has been moved to Australia and Asia (Ascunce et al. 2011) and is also well known from other Caribbean islands, especially the Lesser Antilles (Davis et al. 2001; Wetterer 2013). Since the Dominican

Republic has the largest economy in the Caribbean and its most important trading partner is the USA (Central Intelligence Agency 2020), it is not surprising to also find *S. invicta* on Hispaniola. It is a little bit more difficult to explain why the species has not been detected earlier. Either it is a recent arrival, rare, only found in disturbed habitats (its discovery would be biased against during biodiversity assessments, which often focus on undisturbed habitats), or simply misidentified.

We note that based on our admittedly brief observation, *S. invicta* is not very widespread, nor common or dominant, especially not compared to its congener, the Tropical Fire Ant. The latter species is widespread, common, and dominant, especially in urban centers. Dominicans attest that this is one of the most common species on the island (D. Gotzek *pers. comm.*), although it is likely that the two species are conflated in local folk taxonomy. *Solenopsis geminata* is a well-known element of the Caribbean fauna since the mid-19th century (Wetterer 2011). Creighton (1930) describes it as very abundant in the Antilles and it readily occupies urban and agro-ecosystems (Perfecto 1991; Holway et al. 2002; Perfecto and Vandermeer 2011) and is often ecologically dominant (George and Narendran 1987). Wilson (2005) argued it being one of the infamous Hispaniolan plague ants of the early 16th century.

Two not mutually exclusive reasons can explain the scarcity of *S. invicta* in the Dominican Republic. First, it is possible that *S. invicta* is a recent arrival to Hispaniola and is not yet widespread enough, nor has yet built up sufficient population density to be common enough to be readily collected. This is possible, but not likely. The Dominican Republic has the largest GDP of Caribbean economies and has strong trading relationships in the Caribbean and further abroad. The USA in particular is its primary trade partner (41.4% imports from USA in 2017), from where it imports food and fabrics (Central Intelligence Agency 2020), giving ample opportunity for *S. invicta* to invade. Other Caribbean countries, especially the West Indies, with much smaller economies, have been known to have *S. invicta* since the 1980's (Wetterer 2013; Wetterer et al. 2014). Since trade is a major conduit for fire ants (Ascunce et al. 2011; Gotzek et al. 2015), it is unlikely that the *S. invicta* is a late arrival to the Dominican Republic.

Second, *S. invicta* may not be able to outcompete *S. geminata* in the tropics, as it has done along the Gulf Coast in the USA (Porter et al. 1997). Even though Morrison et al. (2004) predict the potential range of *S. invicta* to encompass much of the tropics (including the Caribbean), their model is based exclusively on rainfall, an environmental factor well known to restrict *S. invicta* in the USA. However, other climactic and especially biological factors are likely to limit its range elsewhere, effectively limiting its ecological dominance to the subtropics. In this scenario, it may well behave more like a tramp ant than an invasive pest species in the Caribbean.

Now that *S. invicta* has been documented on Hispaniola, researchers and biosecurity officers need to be careful to distinguish between the native *S. geminata* and invasive *S. invicta*. While the bi-color morphs are typical of the Caribbean cluster *S. geminata* (Gotzek et al. 2015) and are never seen in *S. invicta* (D. Gotzek *pers. observation*), we strongly advise against using coloration as a sole or primary discriminatory character during specimen identification. This is especially true since *S. geminata* also has a red phase (*S. geminata rufa*), which is well documented from the Caribbean (Creighton 1930) and thus renders them easily confused with *S. invicta*. Megacephaly in the largest workers is also a character never seen in *S. invicta* (Trager 1991; Pitts et al. 2018), but like coloration it is also an unreliable character since major workers or not always collected. Our recommendation is thus using the median tooth on the clypeal margin (present in *S. invicta*, absent in *S. geminata*) as the key character to differentiate *S. invicta* from its congener. To guard against mis-identifications due to possible wearing down of the median tooth in some individuals, we consider it prudent to always inspect a series of workers from a given collection / nest series (which is a general best practices recommendation when identifying taxonomically challenging taxa).

While further studies are required to determine *S. invicta*'s exact distribution and population densities on Hispaniola, its ecological dominance (especially in relation to *S. geminata*), and whether it poses an ecological, agricultural, medical, or economic threat, our findings warrant an immediate Risk Assessment and an Emergency Response Plan. Multiple case studies in New Zealand and Australia have shown that with early discovery and quick decisive action, eradication of *S. invicta* incursions are possible (Hoffmann et al. 2016).

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Ethics and Permits

Samples were collected with permission of Ministerio de Medio Ambiente y Recursos Naturales, Republica Dominica.

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