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Article in *Journal of Integrative Agriculture* · April 2019

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REVIEW

## Impact of the red imported fire ant *Solenopsis invicta* Buren on biodiversity in South China: A review

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### Abstract

The red imported fire ant, *Solenopsis invicta*, is a problematic invasive species in China since at least 2003. Over the past 15 years, a numerous studies were published on the impacts of this species on flora, fauna, and ecosystem function in natural and agricultural systems. We reviewed the literature on *S. invicta* invasion biology and impacts on biodiversity in South China. Both monogyne and polygyne colonies of *S. invicta* were introduced to China and polygyne colony is the dominant type. The range expansion rate of *S. invicta* may reach 26.5–48.1 km yr<sup>-1</sup> in China. *S. invicta* forage activities occur year-round, peaking in the summer and fall in South China and show a preference for insects and plant seeds. We describe the ecological impacts of *S. invicta* on various habitats in South China, including arthropod community structure disruption and decreases in diversity and abundance of native ant species. *S. invicta* can replace the role of native ants in mutualisms between ants and honeydew-producing Hemiptera, which results in loss of important food resources for native ants and natural enemies of hemipterans. Further research is required to assess the complex ecosystem-level impacts of *S. invicta* in introduced areas.

**Keywords:** fire ant, biology, behavior, ecosystem function, non-native, invasion

### 1. Introduction

The red imported fire ant *Solenopsis invicta* Buren is native to South America and is a global invasive pest (Wetterer 2013). In non-native areas, it negatively impacts human health, public safety, ecosystems, and agriculture

(Vinson 2013). Distribution currently includes the United States, Mexico, Australia, New Zealand, China, Malaysia, Singapore, and the West Indies (Wetterer 2013; Wang and Lu 2017; GISD 2018). Although *S. invicta* was first recorded in Taiwan of China in 2003 (Lin *et al.* 2013) and then confirmed in Guangdong Province in 2004 (Zeng *et al.* 2005), it may have been present in China since the 1990s (Lu *et al.* 2008). At the end of 2016, *S. invicta* was found in Zhejiang, Fujian, Jiangxi, Hunan, Guangdong, Guangxi, Hainan, Chongqing, Sichuan, Guizhou, Yunnan, and Taiwan, occupying more than 280 counties across South China (Lu 2014; MARAC 2017). The range expansion rate of *S. invicta* may reach 26.5–48.1 km yr<sup>-1</sup> in China (Lu 2014). Both monogyne and polygyne colonies have been found in China, where the latter were predominantly the social form (Chen *et al.* 2006; Shao *et al.* 2008). In South China, *S. invicta* forages year-round, reaching peak activity in the summer

Received 29 November, 2017 Accepted 29 May, 2018  
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doi: 10.1016/S2095-3119(18)62014-3

and fall (Xi et al. 2010a; Zhou et al. 2011; Xu et al. 2014), and favoring insects and plant seeds (Zhang et al. 2015).

Where *S. invicta* has been introduced, it has had negative impacts on native biodiversity (Vinson 2013). Lin et al. (2006) predicted *S. invicta* invasions may potentially threaten 41 species on the China National List of Protected Wildlife, including 22 birds, one amphibian and 18 reptiles. Arthropods constitute the major food source for *S. invicta*, and invasions likely impacts on arthropod communities. For example, studies showed that *S. invicta* caused arthropod community instability (Jiang et al. 2010; Xi et al. 2010b), and reduced the number of species and other diversity indices including the spatial distribution of spiders in maize fields and lychee (*Litchi chinensis* Sonn) orchards (Xi et al. 2010b; Huang et al. 2012). Although *S. invicta* threatens arthropod community biodiversity, its negative impacts can be reversed by restoration (Chen 2008).

Numerous studies have been conducted on the biology, ethology, ecology, and management of *S. invicta* since it was first reported in China. Here, we review literature on the impacts of *S. invicta* on biodiversity in China.

## 2. Impact on diversity of native ants in South China

Porter and Savignano (1990) found that *S. invicta* invasions decimated indigenous ant fauna in Texas, United States, where species richness of native ants decreased by 70% in infested areas, while the total number of native individuals decreased by 90%. Camilo (1990) found that density of *S. invicta* was negatively correlated with species diversity and Porter and Savignano (1990) suggested that competitive replacement may be the primary mechanism. Similar food sources and habitat requirements between *S. invicta* and Chinese native ants is also a problem. Typical habitats of South China includes lychee (*L. chinensis*) and longan (*Dimocarpus longan*) orchards, lawns, abandoned land, and grassland. In each of these habitats, *S. invicta* has negatively impacted the structure and diversity of native ant communities across different regions of China including Taiwan, Guangdong, and Fujian provinces (Tsai et al. 2009; Song et al. 2010; Wu et al. 2010; Zhang 2010; Qi et al. 2015). For example, ant species richness was reduced by 33 and 46% as a result of *S. invicta* invasion in Beiliu, Guangxi, and Shenzhen, Guangdong, respectively (Shen et al. 2007; Wu et al. 2008). Fewer ant species were observed across habitats in *S. invicta*-infested plots compared to *S. invicta*-free plots (Table 1) (Shen et al. 2007; Wu et al. 2008, 2010; Song et al. 2010). Similarly, Porter and Savignano (1990) found that simple habitats appear to lose more native ant diversity than more complex

habitats. For example, the diversity and evenness of ant communities in wastelands and lawns decreased after *S. invicta* invasion, while *S. invicta* predominance increased significantly. Meanwhile, the opposite was found in lychee orchards, which have more complex habitats (Wu et al. 2008).

Resources competition appears to be a mechanism for species replacement. *S. invicta* is highly dispersive, aggressive, and competitive in securing territories and food resources, and these traits enable the displacement of native ants (Gao et al. 2011; Wu et al. 2014a, b). Investigations in Guangdong Province showed that *S. invicta* has the greatest influence on native ants within 5 m of the nest (Wu et al. 2009), and the impact increased with increasing population density (Song et al. 2010; Xi et al. 2010b). *S. invicta* can also suppress native Chinese ants by excluding mutual exploitation from the honeydew-producing mealybug (*Phenacoccus solenopsis*) (Zhou et al. 2017).

However, several ant species appear to coexist with *S. invicta* in China, including *Pheidole* spp., *Monomorium* spp., *Tapinoma melanocephalum*, and *Paratrechina longicornis* (Wu et al. 2008; Song et al. 2010; Qi et al. 2015), some of which changed behavior and food resources in response to *S. invicta* invasion. For example, *T. melanocephalum*, a dominant ant species in areas where *S. invicta* is present, has changed foraging behavior, food resource preferences, and also modified aggression levels to reduce confrontation with *S. invicta* workers (Huang 2016).

## 3. Honeydew-producing Hemipterans

The ant-Hemiptera mutualism is a common phenomenon in terrestrial ecosystems, where ants tend hemipteran insects and receive honeydew as food. This mutualism is important to the success of *S. invicta* invasions (Wilder et al. 2011), and native ants in native mutualistic relationships can be usurped in areas where *S. invicta* is present (Zhou A et al. 2014, 2017).

Mutualisms involving *S. invicta* and honeydew-producing hemipterans also have a negative impact on natural enemies and competitors of honeydew-producing hemipterans. For instance, *S. invicta* protects the *Aphis craccivora* aphid and *P. solenopsis* mealybug from natural enemies, such as lady beetles *Menochilus sexmaculatus*, *Propylaea japonica*, and *Scymnus (Neopullus) hoffmanni* (Huang et al. 2011; Cheng et al. 2013) and competitors such as *Echinothrips americanus* (Cheng et al. 2013). This leads to rapid populations increase of these pests (Huang et al. 2010; Zhou et al. 2012). The mutualistic relationship between *S. invicta* and honeydew-producing hemipterans indirectly impacts crop production because aphids enhance the occurrence of

**Table 1** Species composition of native ants in different habitats in *Solenopsis invicta*-infested plots compared to *S. invicta*-free plots in Guangdong and Guangxi, China<sup>1)</sup>

Family	Genus	Species	Wasteland		Orchard (lychee <i>Litchi chinensis</i> or longan <i>Dimocarpus longan</i> )		Lawn		
			Infected plot	Control plot	Infected plot	Control plot	Infected plot	Control plot	
Ponerinae	<i>Diacamma</i>	<i>D. rugosum</i>	+	+	+	+			
	<i>Odontoponera</i>	<i>O. transversa</i>	+	+	+	+	–	+	
	<i>Leptogenys</i>	<i>L. chinensis</i>	+	+	+	+	–	+	
	<i>Hypoponera</i>	<i>H. confinis</i>	–	+					
	<i>Pachycondyla</i>	<i>P. luteipes</i>	+/-	+	+	+	+	+	
		<i>P. sharpie</i>	+	+	–	+			
<i>P. rufipes</i>				+	–				
Dorylinae	<i>Dorylus</i>			–	+				
Myrmicinae	<i>Pheidole</i>	<i>P. piel</i>	+	+	+	+	+	+	
		<i>P. yeensi</i>	+	+	+	+	+/-	+	
		<i>P. aphраста</i>	–	+				+	
		<i>Pheidole</i> sp.	–	+					
		<i>P. fervens</i>	–	+			–	+	
	<i>Crematogaster</i>	<i>C. biroi</i>	+/-	+	–	+			
		<i>C. macaoensis</i>	+	+	+	+			
	<i>Tetramorium</i>	<i>T. smithi</i>	+	+	+	+	+	+	
		<i>T. bicarinatum</i>	+	+	–	+	–	+	
		<i>T. kraepelin</i>	–	+					
	<i>Pheidologeton</i>	<i>P. diversus</i>	+/-	+	+	+	+/-	+	
		<i>P. latinodus</i>	+	+	+	+			
	<i>Monomorium</i>	<i>M. concolor</i>	+	+	+	+	+	+	
		<i>M. orientale</i>	–	+	+	+	–	+	
		<i>M. floricola</i>	+	+			+	+	
		<i>M. mayri</i>	+	+			–	+	
		<i>Meranoplus</i>	<i>M. bicolor</i>	+/-	+	–	+	–	+
	Dolichoderinae	<i>Tapinoma</i>	<i>T. melanocephalum</i>	+	+	+	+	+	+
			<i>Technomyrmex</i>						
			<i>T. antennus</i>						
		<i>T. albipes</i>	+	–	+	–			
Formicinae	<i>Iridomyrmex</i>	<i>I. anceps</i>	+	–					
	<i>Plagiolepis</i>	<i>P. rothneyi</i>	+	+	+	+	–	+	
		<i>P. flavipes</i>	+	+	+	+	+	+	
	<i>Paratrechina</i>	<i>P. longicornis</i>	+	+	+	–	+	+	
		<i>P. bourbonica</i>	+	+	–	+			
		<i>P. picta</i>			+	+			
	<i>Polyrhachis</i>	<i>P. deves</i>			–	+			
	<i>Camponotus</i>	<i>C. dolendus</i>	+/-	+	+		+	+	
		<i>C. helvus</i>	+	–	–	+			
		<i>C. nicobaresis</i>	+	+					

<sup>1)</sup> + means ant species was found in the plot, – means ant species wasn't found in the plot, +/- means ant species was found in only one investigation.

Data were from Shen et al. (2007), Wu et al. (2008), Song et al. (2010) and Wu et al. (2010).

*S. invicta* on plants, which leads to increased crop damage by *S. invicta*.

*S. invicta* also forms a mutualism with *P. solenopsis* (Zhou et al. 2012a), a new invasive pest in southern China (Wu and Zhang 2009). *S. invicta* preys on natural enemies of *P. solenopsis* (Zhou et al. 2013), provides shelter for the pest (Zhou et al. 2012b), and excludes competitors of the pest (Cheng et al. 2013). Compared to native ant species, the higher rate of honeydew foraging and the associated

tending of *P. solenopsis* by *S. invicta* may provide more effective protection (Zhou et al. 2012b) and assistance with short-range (ca. 2–3 m) dispersal (Zhou A M et al. 2014) of the pest. *P. solenopsis* may adapt its behavior to retain and attract more tending workers ants, such as more frequent excretion of honeydew during tending and adjustments in carbohydrate metabolism to increase the preferred sugar content of *S. invicta*, melezitose, in honeydew (Zhou et al. 2015). Therefore, interactions between these two alien

species may facilitate the invasion success of both species.

#### 4. Flower-visiting insects

Aggressive ants presence is associated with decreased insect flower visitor number and diversity, visit duration, and total number of flowers visited (Vannette et al. 2017). For example, the Argentine ant, *Linepithema humile*, negatively affected diversity and abundance of flower-visiting insects, and thus the reproductive capacity of plants within the affected area (Visser et al. 1996; Blancafort and Gómez 2005). Field studies show that *S. invicta* also impacts the number and species richness of flower-visiting insects, including rapeseed (*Brassica napus*) where seed yield was reduced (Wu et al. 2015, 2016). In addition, the number of flea beetles (*Phyllotreta striolata*) was reduced by 59.4 and 43.5% in *S. invicta*-only plots and *S. invicta*-aphids plots, respectively. The interaction between *S. invicta* and aphids also decreased the abundance of two hoverflies, *Eristalinus quinquestriatus* and *E. quinquelineatus*, by 39.4% (Wu et al. 2016).

Studies have shown that *S. invicta* does not significantly impact the pollination efficiency of *Apis cerana*, a key pollinator of *B. napus*, where no changes in visit frequency or duration were observed (Wu 2014). However, visit duration of *Pieris rapae*, another key pollinator of *B. napus*, was reduced by 29.5 and 22.4% in *S. invicta*-only plots and *S. invicta*-aphid plots, respectively. The interaction between *S. invicta* and aphids impacted flower-visiting behavior of *P. rapae*. Olfaction may play a role in interactions between *P. rapae* and *S. invicta*. Gas chromatography-electroantennograms showed that male *P. rapae* can detect *S. invicta* odors, particularly the cuticular hydrocarbon heptacosane. This further suggests that *S. invicta* may mediate flower-visiting behavior of *P. rapae* (Wu 2014). Further, bioassays in lab and field are required to elucidate cause and effect of these behavioral responses to bioactive compounds.

#### 5. Crop seed and soil

Plant seeds are important food resources for *S. invicta* which can damage sown seeds before germination (Ready and Vinson 1995; Morrison et al. 1997). Morrison et al. (1997) reported that 15–95% damage can occur in wheat, corn, and sorghum sown seed due to presence of *S. invicta*. Huang et al. (2010) tested the selective feeding behavior of *S. invicta* on seeds across a range of crops in China including *Zea mays*, *Vigna radiate*, *B. alboglabra*, *Sesamum indicum*, *Lycopersicon esculentum*, *Oryza saliva*, *Ageratum conyzoides*, and *Pennisetum purpureum*. Results showed that *S. invicta* preferred *S. indicum* seeds, where

100, 82.4, and 86.4% of seeds were removed, scarified and discarded, respectively. Furthermore, over 50% of *S. indicum*, *A. conyzoides*, and *P. purpureum* exposed to *S. invicta* did not germinate (Huang et al. 2010). Similarly, the germination rate of *Z. mays* and *V. radiate* decreased by 14 and 7.4%, respectively, under high *S. invicta* density (5 mounds 100 m<sup>-2</sup>) (Huang et al. 2014). The impact of *S. invicta* on seeds of *Raphanus sativus*, *B. alboglabra*, *B. rapa pekinensis*, *B. oleracea*, *B. juncea*, and *B. campestris* was also tested, and it was found that *S. invicta* preferred seeds containing high levels of fat and protein (Ma 2011). The removal and scarification rates of *B. alboglabra* seeds were higher than others; however, no impact on germination rate of any seeds was found (Ma 2011). Since these studies were performed under laboratory conditions, further research is needed under field conditions to evaluate the economic loss of farmers due to damage to *S. invicta* on sown crop seeds.

Negative impacts of *S. invicta* on seed production in self-pollinating mungbean have also been reported, where daily pod counts, kernel number and weight, final pod number, and yield per plant were reduced (Wu et al. 2014). In cross-pollinating rapeseed, an *S. invicta*-only treatment had no impact on thousand-kernel weight, malformation rate, kernel weight, yield per plant, pod number, and kernel number. However, an *S. invicta*-aphid treatment negatively affected these parameters (Wu et al. 2014). Similarly, yield per plant of mungbean control plots was 3.65 g, compared to 2.50 and 2.40 g in *S. invicta*-only plots and *S. invicta*-aphid (including *A. spiraeicola*, *A. solanella*, and *A. craccivora*) mutualism plots, respectively. The results were approximately 35% yield loss in mungbean due to *S. invicta*. In mungbean, no significant difference was observed in yield per plant between control and *S. invicta* only plots (3.11 and 3.07 g, respectively). However, in *S. invicta*-aphid (including *A. gossypii* and *Rhopalosiphum maidis*) mutualism plots, yield per plant of mungbean was only 1.69 g resulting in roughly 45% yield loss due to *S. invicta*-aphid mutualism. In Texas, United States, production loss in crops and livestock exceeded 38 million USD in 1999 due to *S. invicta* invasion (Lard et al. 2002). In China, Sichuan, Hunan, and Chongqing are currently infected with *S. invicta*. Based on mungbean production of these three provinces in 2010 (Liu 2012) and data from Wu et al. (2015), the total economic loss of mungbean would be 4.75 billion CNY (approximately 67 million USD) per year (calculated to be 0.135 million tons×35% yield loss×10 CNY kg<sup>-1</sup>) if *S. invicta* occupy most of regions of these three provinces. Further investigations should be conducted to assess the total agricultural economic loss in China caused by *S. invicta*.

There is evidence to suggest that ants including the western harvester (*Pogonomyrmex occidentalis*) and

imported fire ants (*Solenopsis* spp.) alter physical properties of soil at nesting sites (Carlson and Whiteford 1991; Green et al. 1998). Carlson and Whiteford (1991) showed that concentrations of  $\text{NO}_3$ , P, and K were elevated in mound soil of *P. occidentalis*. It was also found that *S. invicta* incorporates ant-derived organic compounds into mound soil (Chen 2005, 2007). *S. invicta* also impacted physical and chemical properties of soil in lychee orchards (Xi et al. 2010c). Increased *S. invicta* density reduced soil particle size and increased soil plasticity and acidity, as well as decreased organic matter content and alkali-hydrolyzable N in lightly and heavily *S. invicta* infested soils by 29.0 and 42.1%, and 39.9 and 53.6%, respectively. In the same study, available P decreased by 43.3 and 52.6% in lightly and heavily *S. invicta* infested lychee orchards soil, respectively, but available K increased by 8.5 and 34.0%, respectively. Chen (2007) reported that *S. invicta* excretes phosphoric acid, resulting in elevated concentrations of P in mound soil. More research is needed on physical and chemical property changes in soil caused by *S. invicta* to better understand how these changes impact the ecological system.

## 6. Native arthropod communities

Previous studies in the United States show that *S. invicta* displaces native ant and arthropod species, having a negative impact on vertebrate populations and disrupting mutualisms in the introduced regions (Porter and Savignano 1990; Wojcik et al. 2001; Holway et al. 2002; Tschinkel 2006). However, some studies claim that *S. invicta* may negatively impact co-occurring ants but the effect is minor (King and Tschinkel 2006, 2013). Hill et al. (2013) suggest that more research is needed to assess the complex impacts of *S. invicta*.

Several studies were conducted in South China on the impact of *S. invicta* on native arthropod communities in manmade habitats. *S. invicta* affected soil, ground, and epigeal arthropod communities in lychee orchards (Xi et al. 2010b), with greater impacts on ground and soil communities than in the lower and canopy levels of vegetation. While *S. invicta* negatively impacted arthropod community structure in these orchards (e.g., reduced diversity and abundance of functional groups including insect pests and natural enemies), there were also population increases in other groups, including *Xylotrupes gideon* (Xi et al. 2010b).

Huang (2010) studied the effect of *S. invicta* on arthropods in maize fields in Guangdong Province and found the number of arthropods species decreased by 65.3%. The number of Hemiptera, Lepidoptera, and Araneae species were reduced by 88.9, 71.4, and 68.8%, respectively, and Hymenoptera species represented by Formicidae decreased from 58.6 to 31.0%. There was also a negative correlation

between *S. invicta* density and species richness (Huang 2010).

The impact of *S. invicta* invasion on arthropod community characteristics and structure varied spatially in banana plantations in Guangdong Province (Wang 2009). *S. invicta* had a slight impact on arthropod communities in mid to canopy weeds, and a significant negative impact in lower and ground level vegetation (Wang 2009). Arthropod species diversity and abundance in banana plantation weeds decreased by more than 30 and 50%, respectively, in various weed coverage types following *S. invicta* invasion (Wang et al. 2016). At the same time, the arthropod community dominance index in weeds increased by 25.0, 37.5 and 62.5% in high, medium, and low weed coverage types, respectively. Following invasion, diversity and abundance of ground-dwelling arthropods also decreased by 30 and 34%, respectively, and the dominance index increased by 46.2, 61.5, and 38.5% in high, medium, and low weed coverage types banana plantations, respectively (Wang et al. 2016).

Another investigation in Guangdong Province showed that *S. invicta* negatively impacted arthropods of vegetable farms, where the Berger-Parker dominance index increased and the richness index decreased in response to *S. invicta* invasion (Ma 2011). Arthropod abundance, especially of spiders and lepidopteran caterpillars, decreased by approximately 30% (Ma 2011).

All of the above investigations in China show that *S. invicta* drives biodiversity loss in manmade habitats, but some native species also coexist with *S. invicta*. Some research suggests that invader species will eventually decrease to tolerable levels after an initial period of high impact (Strayer 2012). However, since the above investigations were short-term observational studies, long-term observational studies and large-scale addition and removal experiments should be performed to better understand the broader impact of *S. invicta* invasion on native biodiversity. This will improve understanding of invaders impacts on biodiversity, and also assess whether these impacts moderate over time.

## 7. Perspective

*S. invicta* is a major invasive species. Since it was first recorded in China, much research has been conducted on *S. invicta* invasion, biology, and control. Current, studies focus on direct impacts of *S. invicta* on ecosystems. Several arthropod species have disappeared in *S. invicta* infected areas. *S. invicta* also interferes with the flower-visiting behavior of insects and has a negative impact on crop reproduction. Indirect effects of invasion by *S. invicta* on ecosystem function and dynamics remain unclear. For example, some native ant species adapt to incursions of

*S. invicta* by changing their behavior and dietary components, which results in trophic cascades within the ecosystem. Thus, understanding the range of direct and indirect ecosystem effects of *S. invicta* remains challenging.

Korzukhin et al. (2001) predicted the range of *S. invicta* in the eastern United States will expand over the next century due to climate change. A significant warming trend also occurred throughout China over the past 20 years (Yu et al. 2011). Therefore, in addition to direct anthropogenic-mediated activities, the range of *S. invicta* will continue to expand, and more habitats will be infected in China. Thus, the evolutionary biology and evolutionary ecology of *S. invicta* remains an important issue, especially *S. invicta* adaptation to new habitats and impacts on ecosystem function. At the same time, dynamics of *S. invicta* in new habitats also need to be investigated to improve understanding of *S. invicta* invasion biology, which are very important in managing these population and habitat expansion.

Traditional *S. invicta* management methods take time and manpower, especially in large areas with high *S. invicta* density. Development of rapid detection of nests is important to assessing control efforts and monitoring dispersal. Satellite aerial imagery is used to assess *S. invicta* mound distributions on a large scale (Vogt 2004a, b), and trained dogs and spectrum analysis technology were used to inspect and count *S. invicta* mounds (Lin et al. 2011; Wu et al. 2016). Other new technologies are needed to explore rapid and accurate detection methods of *S. invicta* mounds to facilitate targeted precise insecticide treatments. Meanwhile, to reduce both environmental and economic losses related to chemical control, new management strategies and environmentally friendly insecticides are needed, especially for use in aquafarm, drinking water source areas, organic farms, and natural reserves.

## Acknowledgements

This work was supported by the National Key Research and Development Program of China (2016YFC1201204) and the Key Project for Science and Technology Development of Guangdong Province, China (2017B020202009).

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