Invasions of four South American tramp ants: a systematic review

Inversiones de cuatro hormigas vagabundas suramericanas: una revisión sistemática

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ABSTRACT

The invasion and spread of four native South American ants (Hymenoptera: Formicidae) Linepithema humile, Solenopsis invicta, Wasmannia auropunctata and Paratrechina (Nylanderia) fulva all over the world, their environmental and economic impact, and intended control tactics are documented. Displacement of these invasive species is triggered by human international movement of goods, and in one case, P. fulva, a deliberately introduction as a candidate for biological control of Atta spp. and snakes. These tramp ants displace native ants, attack native birds and reptiles, protect and transport sap sucking insects, cause damage to human commodities, and are able to cause health problems to men and domestic animals. Chemical control, producing negative environmental side effects, has shown poor success and short residual effect. Current tendencies use biological control agents, the natural enemies, parasites, predators and diseases of their original range. Quarantine and eradication programs have been implemented. The success of the tramp ants involves a small size that permits hiding in all types of packing materials, their organization in societies, varied diets, and in many cases to their late detection and initial control.

Keywords: invasion biology; insect invaders; exotic species; Formicidae; pests.

RESUMEN

La invasión y la diseminación en todo el mundo, de cuatro hormigas sudamericanas nativas (Hymenoptera: Formicidae) Linepithema humile, Solenopsis invicta, Wasmannia auropunctata y Paratrechina (Nylanderia) fulva, su impacto ambiental y económico y las medidas de control empleadas, es documentado. El desplazamiento involuntario, se desencadena por el transporte internacional de bienes por los humanos y, en un caso, P. fulva, incluso, se introdujo deliberadamente, como posible agente de control biológico de Atta spp. y culebras. Estas hormigas vagabundas desplazan, principalmente, a las hormigas nativas, atacan a algunos vertebrados, aves, reptiles, entre otros, protegen y transportan insectos chupadores, dañan los productos humanos y pueden causar problemas de salud a hombres y animales domésticos. El control químico, además de sus efectos secundarios negativos ambientalmente, ha tenido poco éxito y un efecto residual corto y la tendencia actual es el uso de agentes de control biológico, teniendo en cuenta, que las hormigas traídas a su nuevo ecosistema han dejado atrás a sus enemigos naturales, parásitos, depredadores y enfermedades. También, para evitar nuevas invasiones o nuevas infestaciones, se han implementado medidas especiales de cuarentena y programas de erradicación. El éxito de las hormigas vagabundas, se debe, en parte, a su pequeño tamaño, que permite que se escondan en todo tipo de productos utilizados como material de embalaje, para el movimiento de productos, a su
luggage of passengers, mainly with seeds and stakes, were introduced (Forel, 1911). Many inclusions of small insects, such as ants in the accidentally or deliberately to other continents or other latitudes. Among the invasive insect species, the most destructive ones are considered to be the ants (Van Wilgenburg et al. 2010) and among them those of South American origin, which have been introduced accidentally or deliberately to other continents or other latitudes. The increase of commercial activities since the beginning of the XX century has facilitate the transport of many not desirable invaders, such as weeds, arthropods, diseases, to name only few groups (Forel, 1911). Many inclusions of small insects, such as ants in the luggage of passengers, mainly with seeds and stakes, were introduced undetected. The original migration of tramp ants has however not been documented and can only be imagined. Tramp ants are defined by Hölldobers & Wilson’s (1990) as formicids that are distributed around the world, mainly through human commercial activities and live in close connection with men. These authors mention as notorious tramp species the pharaoh ant, Monomorium pharaonis (Linnaeus, 1758) (Myrmicinae), the big-headed ant, Pheidole megacephala (Fabricius, 1793) (Myrmicinae), the Argentine Ant, Iridomyrmex humilis, sinónimo de Linepithema humile (Mayr, 1868) (Dolichoderinae) and the little fire ant, Wasmannia auropunctata (Roger, 1863) (Myrmicinae). Passera (1994) added, among others, the pavement ant, Tetramorium caespitum (Linnaeus, 1758) (Myrmicinae), a crazy ant, Paratrechina longicornis (Latreille, 1802) (Formicinae) and two species of the genus Cardiocondyla (Myrmicinae). For the purpose of this study, the crazy ant, Paratrechina (Nylanderia) fulva (Mayr, 1862) (Formicinae) and the red imported fire ant Solenopsis invicta Buren, 1972 (Myrmicinae) are included.

Invasion biology, a relatively “new” scientific discipline, which has gained special importance, focusses and has as main research objectives all the relevant aspects related with the migration and transport of living entities from its original habitat to other places, with the consequent impact on the existing biodiversity (Kegel, 2001). As part of this discipline as special study objective it includes the tramp ants, cosmopolitans and generalists, which normally prefer disturbed habitats, and live in close proximity with humans. Kegel (2001) cites as the most important tramp ants W. auropunctata, L. humile, M. pharaonis, Ph. megacephala, Anoplolepis longipes and Tapinoma melanocephalum.

The importance of this branch of the biology is also reflected in the creation, since March 1999, in a series of publications, the journal Biological Invasions, publishing monthly research and synthesis papers on patterns and processes of biological invasions in terrestrial, freshwater, and marine (including brackish) ecosystems, also includes conservation programs, global enhancement and management of invasions.

This review documents the invasive behavior, through time, of four South American tramp ants, which actually are present in North America, Central America, Galapagos Island, Australia, New Zealand, Africa, Oceania, Europe, China, Japan, among other conquered regions, causing economic and environmental damage and are considered pests.

### MATERIALS AND METHODS

For this systematic review, four recognized treaties which the main component “myrmecology”, we reviewed Hölldober & Wilson’s (1990) The ants; Exotic Ants Biology, Impact, and Control of Introduced species, edited by D.E. Williams (1994); Vander Meer et al. (1990). Applied Myrmecology. A World Perspective and “Die Ameise als Tramp”, Kegel (2001). Additionally, publications of the Entomological Society of America, SciELO - Scientific electronic library online, the “Revista Colombiana de Entomología” y other Colombian journals, using the terms: Linepithema humile, Wasmannia auropunctata, Paratrechina (Nylanderia) fulva and Solenopsis invicta, alone or combined with words such as, biology, invasion, impact, control.

### RESULTS AND DISCUSSION

**Origin, migration, internal movement:** Both L. humile and S. invicta are considered native to Argentina; the imported fire ants also from Mato Grosso, Brazil (Buren, 1972). The first one, believed to be the world most successful invasive species, with its native range around the Paraná River Drainage, (Wild, 2004), seems to have reached the United States in coffee shipments from Brazil to New Orleans around 1891 (Titus, 1905). Since its invasion in the United States, it has conquered the Carolinas and Southern Florida and has reached Texas and California (Wetterer et al. 2009). Suarez et al. (2001) define as poor its dispersal ability and attribute its worldwide movement to human-mediated diffusion. Linepithema humile has established in the North Carolina, but has not invaded regions farther north. Brightwell et al. (2010) found that the foraging activity of the workers stops below 5°C and concluded that winter soil temperatures could impede foraging long enough to cause colony death. Although climatic changes are occurring all over the world, it can be assumed that in the near future the ant, were it has established in temperate zones, would not spread farther north.

The Argentine ant has been established on six continents and on many oceanic islands. Men-mediated jump dispersal has also been the primary means of distribution at a continental scale within the United States, South America, and New Zealand (Suarez et al. 2001).

In South and Central America, the Argentine ant occupies temperate and tropical regions, but apparently not as a dominant species.
Similar routes of dispersion around the word have been documented for the red imported fire ant *Solenopsis invicta* Buren, judged to be one of the most important ant tramp species. Native to South America, Mato Grosso, Brazil (Williams et al. 1975), Uruguay and Argentina it has invaded the United States (Callcott & Collins, 1996), Mainland China, Taiwan, Australia, Mexico (Sánchez Peña et al. 2009) and the Caribbean (Wetterer et al. 2014; Wetterer & Davis, 2010; Wetterer & Snelling 2006; Davis et al. 2001; Lofgren, 1986) and recently the news (NHK channel) has reported several detections, in Japan.

According to Davis et al. (2001), *S. invicta* widespread in the West Indies, apparently is still not present in Jamaica, Hispaniola, and Cuba. Its absence in Cuba is mentioned in 2011, by Fontenla Rizo & Matienzo Brito.

The date of introduction of the red imported fire ant into the United States is placed sometimes between 1933 and 1945, at Mobile, AL, coming possibly in ships’ ballast from Brazil. *Solenopsis invicta* has occupied a wide range in the southern United States and already by 1985 it had been detected in over 9.3 million km² (USDA-APHIS, Gov., 2018; Jemal & Hugh-Jones, 1993).

In contrast to *L. humile*, ant up to now apparently not detected in China, *S. invicta* has been mentioned in China, since 2003, identification confirmed by mitochondrial DNA and assumedly introduced from the United States (Zhang & Hou, 2013). Zhang et al. (2007) mention its presence in Taiwan in 2003 and indicate that in South China it has rapidly invaded many provinces such as Guangdong, Guangxi, Hunan, Fujian and Jiangxi. In Mainland China, Zeng et al. (2005) date its introduction to 2004. In 2012, *S. invicta* has been reported from five provinces in South China and is considered to have the capacity to invade regions further north, by means of both natural dispersal and human transportation; it has been found that its population increases greatly in spring and autumn (Wang et al. 2012).

The Argentine ant is registered in Europe, while according to Ascunce et al. (2011), the red imported fire ant has not yet invaded this continent. An exhaustive literature review confirms this. *Solenopsis invicta* has been detected in various commodities imported from the United States, however it has not been established, or invaded Spain, Italy, or other Mediterranean countries.

In Australia *S. invicta* is considered the worst invasive ant species to arrive at the eastern shores, contrary to *L. humile* which started the invasion at the western regions of the continent. This contrasting arrival can be attributed to the importance of the east coast ports for imports of goods. *Solenopsis invicta* was first reported in 2001, at the Port of Brisbane and in some south western suburbs of this city (Moloney & Vanderwoude, 2002). Additional invasions were discovered in the following years, 2006, 2013, 2015 and the Port of Brisbane, in 2016. Red imported fire ants were detected at the Port Botany, Sydney in 2014 (National pest & disease outbreaks, 2018; Wylie & Janssen-May, 2016).

Up to 2009 three different invasions of the red fire ant have been reported in New Zealand; the first two occurred in 2001, at
Auckland Airport and the second at Port of Napier, 2004, both successfully managed and eradicated. At that moment north of Napier, an eradication program was undertaken, (Ward, 2009). Apparently, no new invasions to New Zealand occurred during the following years, due to strict airport measures and detection procedures.

The most recent report of an invasion by *Solenopsis invicta* comes as news report from Japan, where the Red Imported fire ant was discovered in 2017, in shipping containers coming from China; consequently, Japan’s Ministry of Transportation ordered detection and extermination measures at more than 60 ports with regular cargo shipments from China (Globalvoices Org, 2017).

The third tramp ant, the little fire ant, *Wasmannia auropunctata*, possibly would not have gained so much attention and research, if it had not been brought accidentally to the Galápagos Islands. Foucaud et al. (2010) mention that it is still one of the least studied invasive species. Lubin (1984) documented the invasion in five islands in the Galápagos archipelago and De La Vega (1994) mentions its probable introduction between 1930 and 1940, while Brandão & Paiva (1994) analyzed the Galápagos ant fauna, with emphasis on the little fire ant and other introduced ant species.

Native to the tropics and subtropics of America, *W. auropunctata* shows a distribution range from central Argentina and Uruguay, through eastern Mexico, to the southernmost area of Texas (Wetterer, 2013; Kusneko, 1951). Invasions to Europe, Africa, Australia, Oceana and the West Indies are well documented (Wetterer, 2013; Foucaud et al. 2010; Jucker et al. 2008; Walsh et al. 2004; Wetterer & Porter, 2003). Special attention is given to several introductions, for example to Israel where its establishment has recently been recorded raising alarm about potential further distribution to the Mediterranean region (Vonshak et al. 2010).

The ant’s ecology and interaction with other native ants has been studied in Colombia (Salguero et al. 2011; Achury et al. 2008; Armbracht et al. 2001). Observations in the department of Cundinamarca indicate that it is very common in the coffee growing area, from 1000 to 1550 m.a.s.l., and feared for its painful sting by coffee pickers. Tennant (1994) studied its ecology in a tropical rainforest of Costa Rica and Panama and Delabie et al. (1994) documented the serious problems the ant causes in Brazilian’s cocoa plantations for its symbiosis with homopterans and the painful sting they inflict to pod pickers.

Ulloa-Chacón & Cherix (1990) highlight the following characteristics that allow *W. auropunctata* to become an effective invader: “its adaptability to a wide range of habitats; polyphagous feeding habits; high interspecific aggression; and lack of intraspecific aggression which leads to unicoloniality”.

Of the four tramp ants, only *Paratrechina (Nylanderia) fulva* has been deliberately introduced, at least into Colombia, for biological control purposes. This ant has been recorded from Brazil, where it is a house pest, and a control agent of snakes and leaf cutting ants (*Atta* spp.), controlling efficiently the ant colonies (Mariconi, 1970; Soares-Brandão, 1941). These observations triggered several confirmed importations to Colombia during 1960s into the coffee growing area of the department of Cundinamarca, in 1971 to grassland of Puerto Boyaca, and in 1985 to sawmills in the region of Carare-Opon (Santander), always for the purpose of either control *Atta* spp., or poisonous snakes (Zener de Polanía, 1990a; 1990b; 1994).

In 1986, the ant was detected in a sugarcane plantation in the Cauca Valley, presumably “imported” due to the rumor of its control of the sugarcane borer *Diatraea saccharalis*, from where it spread to the “Reserva Natural Laguna de Sonso”, causing a serious ecological impact (Aldana et al. 1995). *Paratrechina (Nylanderia) fulva* was also introduced by farmers to the unrefined brown sugar production area of Barbosa (Santander), for the control of the sugarcane borer; in 1999, large areas of sugarcane plantations had been invaded, causing crop loss, mainly because of its association with the scale insect *Pulvinaria pos. elongata* (Zener de Polanía et al. 2001).

Wetterer et al. (2014) recognizes the crazy ant as *Nylanderia fulva* Mayr, formerly *Paratrechina fulva*; in this review *P. fulva* is the accepted scientific name and used as such.

*Paratrechina fulva* is not only known and has been studied in Brazil and Colombia, but recently also in the United States, where it was reported already in 1983 from Brownsville, Texas (Trager, 1984). According to LeBrun et al. (2013), this ecologically dominant and exotic ant species is spreading through the Southeastern United States and Texas. This ant is able to displace *Solenopsis invicta*.

*Paratrechina fulva* is also reported from St. Croix, the U.S. Virgin Islands, suggesting an on-going population explosion (Wetterer et al. 2014). Fontenla Rizo & Matienzo Brito (2011) as well as Fontenla et al. (1995) registered the presence of *P. fulva* in Cuba.

This tramp ant has not crossed the border of South and North America, or to invade other continents, but taking into account the trade relations of the United States, Brazil and Colombia with Mainland China, Australia, Mediterranean regions of Europe and Africa, it is suggested to put *Paratrechina (Nylanderia) fulva* on the list of exotic tramp ants, since it represents high risks to native vertebrate species, due also to its protections and transport of homopterans, causing damage to human commodities, and is able to cause health problems to men and domestic animals. Strict port inspection measurements, quarantine and detection procedures should be implemented in all regions not invaded by the crazy ant.

**Impact:** The negative impact of the four tramp ants such as displacement of other ants; symbiosis with homopteran pests protecting and transporting mainly immatures; the raid of native vertebrate species such as birds and reptiles; the damage to human commodities and health problems to men and domestic animals, has been well documented. Here some of the most prominent research will be presented and discussed.

In 1971, Erickson documented the displacement of three harvester ant species in California by the Argentine ant, indicated three competitive advantages of *I. humilis* over the displaced native
ants: “its aggressive nature; the large number of queens and the establishment of new colonies in a very short time; raiding columns of workers clear the way and pioneer groups of workers and queens follow into freshly opened nest areas.

Ward (1987) indicated that the species richness of native ants is markedly reduced in the lower Sacramento Valley of California at riparian woodland sites occupied by the Argentine ant. Apparently, the native epigaeic ants, aboveground foraging species are more susceptible to displacement than hypogaeic species.

During an invasion by the Argentine ant in northern California, its occurrence meant a disassembly of the native ant populations. Without *L. humile*, native ant communities exhibit significant species segregation, while in the presence of the Argentine ant, they act randomly or weakly-aggregated (Sanders et al. 2003).

Similar results had been obtained by Porter & Savignano (1990), studying over several years a *S. invicta* invasion in Texas. The red fire ant produced major changes in the abundance and diversity of other ant communities, reducing the native species richness, which declined by 70%.

In Mainland China, native ant abundance was clearly reduced by *S. invicta* invasion, and the richness of ant species was reduced up to 46%. The influence of *S. invicta* was found to be greatest within 5m of its mound (Wang et al. 2012).

Wetterer & Porter (2003), in their review of the distribution, impact and control of *W. auropunctata*, mention its relevant invasion in the Galapagos, causing the disappearance of native ants, and terrestrial invertebrates. According to Clark et al. (1982), the little fire ant, either eliminates or lessens, to very low numbers all sympatric ant species, while Lubin (1984) detected that the presence of *W. auropunctata* not only originated lower diversity and density of other ants, but also decreased densities of other insects, as well as scorpions and spiders.

The impact of *Paratrechina fulva* on other ant species has been studied, mainly in Colombia. Zenné de Polanía (1994) documented the displacement of at least fourteen ant species, when comparing three areas: invaded by the crazy ant, free of the invader; and one at the border of the infestation. The species diversity index of 0.763318 in the *P. fulva* free area dropped to 0.008795 in the completely *P. fulva*-infested area. Zenné de Polanía & Ruiz Bolaños (1985) determined that the diet of *P. fulva* is constituted by a liquid component, obtained from sugary substances secreted by the sap sucking Homoptera, which in turn affect all types of vegetation, and another solid one, protein, from its predatory activity on some insects, arachnids and other animals, among them birds and reptiles. This ant has been found associated with 28 species of Homoptera, of 7 families (Zenné de Polanía & Ruiz Bolaños, 1985). In Cuba, the crazy ant at high densities is capable of causing serious problems to chicken and pig production, as well as in apiaries (Fontenla et al. 1995). The association of *P. fulva* with the cottony grass scale *Pulvinaria pos. elongata* is another example of the negative impact of the deliberately introduced ant (Zenné de Polanía et al. 2001). In the Cauca Valley, the colonization of the crazy ant of the Laguna de Sonso Natural Reserve, has caused an important ecological impact. Comparing the ant fauna between an area free of the invader and one with a high population of *P. fulva* registered a reduction in ant species richness by 74% (Aldana et al. 1995). Even in its country of origin, Brazil, Campos-Farinha & Zorzenon (2005) observed *P. fulva* interacting with the aphid *Cerataphis brasilienis* and pseudococcids, transporting first instars nymphs from infested to uninfested palm plants.

In the U.S., *P. fulva* at high density has been found to eliminate *S. invicta* reducing also the abundance and species richness of other ants (LeBrun et al. 2013).

Not only the crazy ant uses honeydew produced by phloem-sucking hemipterans, considered a common behavior of many ant species. Mutualism is a wide spread and relevant ecological phenomenon illustrated by beneficial interaction between two species, ants and homopterans. In China, *S. invicta* has a close symbiosis with another introduced pest: *Phenacoccus solenopsis*. Defending the mealybug against its natural enemies, and significantly decreasing the survival of lady beetle larvae (Zhou et al. 2013).

**Control, eradication:** Toxic baits, chemical control and the use of biological control agents are the tools used to mitigate ant invasions, avoid their spread, and occasionally eradicate incipient arrivals. Whatever program is implemented for control purposes still further research is needed in order to produce an integrated management package.

However, prevention is the most effective instrument, to avoid the use of chemical control measurements, which will always affect negatively other non-target species. Therefore, an adequate and timely effective detection schedule in all ports of commodities entrance of the countries were tramp ants have not been introduced, is imperative. Training of the personal in charge of sanitary inspections in ant identification has to be procured, together with the correct information of world ant dispersal and the origin of the imported product and its package.

Equally public education, explaining and forewarning the general danger of introducing whatever biological element, specially ants as pets is fundamental.

Also, agricultural and food commodities shipped to markets abroad have to meet the importing countries’ entry requirements, related to sanitary aspects, such as being free of pests, being this condition already the law in many countries around the world.

The most promising management measures of the tramp ants seem to be the use of parasites; being the classical biological control the most appropriate one. Survey of natural enemies in the sites of origin, extensive studies, mass rearing and supervised liberations is imperative. However, a complete control can never be guaranteed. Biological control will only be part of a management program.
In the U.S. Phorid flies have been the main study target for biocontrol of *Solenopsis invicta* (Porter et al. 2003). Lately several of *Pseudacteon* spp. (Diptera: Phoridae) have been released throughout the southern United States; a decrease in its foraging intensity is expected having as result a decreased colony success (Puckett & Harris, 2010), but not a complete control.

_Cannobola foyesi* (Strepsiptera: Myrmecolacidae), is known as a Texas native endoparasite of males of *S. invicta* and found in regions invaded by the ant (Cook et al. 1997). It seems to have adapted to the imported host, however, apparently, no intend of using it as biological control agent have been made.

Another biological control approach is the incorporation of entomopathogenic fungi, such as *Beauveria bassiana* into baits. *B. bassiana* alginate pellets, coated with peanut oil produced significant decrease in *S. invicta* population indices and could be recommended as control measurement in the field (Bextine & Thorvilson, 2002). A survey of the presence of key pathogens and parasites of *S. invicta* in the West Indies, undertaken by Valles et al. (2015), revealed as the most promising pathogen the microsporidian *Kneallhazia solenopsae*, also, *Vairimorpha invicta*, was detected in St. Croix, as well as the Solenops invicta densovirus (SiDNV). Two species of *Pseudacteon* decapitating flies were found to have dispersed into the Bahamas. The authors discuss these islands “for release, establishment, and impact assessment of *S. invicta* natural enemies.”

Eradication programs of *Solenopsis invicta* have been implemented mainly in New Zealand and Australia. Wylie & Janssen-May (2016) mentioned several successful eradications of the insect has since 2001, when the red fire ant was first reported in Brisbane, Queensland. However, the main Brisbane population remains. The authors insist in an eradication program since it “remains technically feasible, cost beneficial and in the national interest to eradicate”. Actually, Australia has given up on this effort. A successful eradication of the red imported fire ant has been reported for northern Taiwan, using pyriproxyfen; after one year, *S. invicta* had been eradicated (Hwang, 2009).

An eradication program of *Wasmannia auropunctata* at the Marchena Island in the Galapagos Archipelago employing Amdro® (hydramethylnon) manually up to three times in the area at three month intervals between March and October 2001, was realized; the consequent surveys revealed the absence of *W. auropunctata* in May 2003 and April 2004, assuming a successful eradication (Causton et al. 2009).

Finally, a small infestation of *Wasmannia auropunctata* was discovered on the island of Maui, Hawaii; for an eradication purpose, during a year on twelve occasions, granular baits and a paste bait containing indoxacarb (0.18% a.i.) were used. One year after initiation of treatments, no new detections have been made, suggesting the eradication of the little fire ant from Maui (Vanderwoude et al. 2010).

Apparently, no other documented efficacious eradication program of the four tramp ants has been reported, but should be in mind as soon as new invasions of these or other invasive ants are reported.

**Conflicts of interest:** The manuscript was prepared and revised by the author, who declares the absence of any conflict which can put the validity of the presented information in risk.

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