

A Regional Approach Shows Differences Among Invasive Ants *Solenopsis geminata* and *Wasmannia auropunctata* (Hymenoptera: Formicidae) Within Its Native Range of Distribution

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Abstract

Worldwide, two of the most harmful invasive ants typical of disturbed sites are *Solenopsis geminata* (Fabricius) and *Wasmannia auropunctata* (Roger). Both are natives of the Neotropics and are widely distributed all over the tropics. Within its original geographic range, there are few data on its abundance and potential damage to natural ecosystems. In this study, we recorded their abundance and relationships to diversity and richness of soil ant communities in two localities with different amount of forested area (López Mateos, LM 77% and Venustiano Carranza, VC 27%), at Los Tuxtlas reserve. In each locality, four land use systems (LUS) were sampled: tropical rain forests, agroforestry plantations, annual crops, and pastures. Data were gathered from 360 ant samples obtained from litter squares, pitfall traps, and soil monoliths in 40 sampling points (20 per locality, and five per LUS). *Solenopsis geminata* was more abundant in LM than in VC; the opposite trend was observed for *W. auropunctata*. In LM, *S. geminata* was more abundant in crops than in the other LUS, whereas *W. auropunctata* tended to have higher abundances in less managed sites of both localities. Abundance and species richness of ant communities were higher in LM than in VC. At regional and local levels, we found negative relationships between the abundance of *S. geminata* and species richness; the inverse pattern was found for *W. auropunctata*. We conclude that at Los Tuxtlas, *W. auropunctata* can be considered as a typical dominant native species, whereas *S. geminata* is the common exotic invasive ant.

Key words: biological invasion, land use system, tropical forest, Los Tuxtlas

Resumen

A nivel mundial dos de las hormigas invasoras más dañinas son *Solenopsis geminata* (Fabricius) y *Wasmannia auropunctata* (Roger), ambas nativas del Neotrópico. Debido a que son especies típicas de ambientes perturbados, poco se sabe de su abundancia y potenciales efectos nocivos en los ecosistemas naturales dentro de su rango de distribución original. En este trabajo estudiamos sus patrones de abundancia y exploramos su relación con la riqueza total de hormigas del suelo en dos localidades con diferente cantidad de remanente de selva primaria (López Mateos, LM 77% y Venustiano Carranza, VC 27%) en la Reserva de la Biósfera Los Tuxtlas. En cada localidad se muestrearon cuatro sistemas de uso de suelo (LUS): selva tropical perennifolia, plantación agroforestal, cultivo de maíz y pastizal. Analizamos 360 muestras de hormigas obtenidas mediante cuadrantes de hojarasca, trampas de caída y monolitos de suelo en 40 puntos de muestreo (20 por localidad y cinco por LUS). La abundancia de *S. geminata* fue significativamente mayor en VC que en LM, mientras que la de *W. auropunctata* fue mayor en LM que en VC. En LM *S. geminata* fue más abundante en los cultivos de maíz que en los otros LUS, mientras que *W. auropunctata* tendió a ser más abundante en los sitios menos manejados en ambas localidades. La abundancia y la riqueza específica de hormigas fue mayor en LM que en VC. Un análisis de escalamiento multidimensional no métrico de las abundancias de todas las especies confirmó la relación de *S. geminata* y *W. auropunctata* con sitios perturbados y conservados, respectivamente. A nivel regional y local encontramos una correlación negativa entre la abundancia de *S. geminata* y la riqueza

total de hormigas; en contraste, la abundancia de *W. auropunctata* se correlacionó positivamente con la riqueza total de hormigas. Concluimos que *W. auropunctata* se comporta como una típica especie nativa dominante, mientras que *S. geminata* lo hace como una invasora exótica.

Palabras clave: Invasiones biológicas, hormigas invasoras, selva tropical perennifolia.

Ants play preponderant roles in terrestrial ecosystems and maintain interactions with many plants, arthropods, and fungus species (Hölldobler and Wilson 1990, Schultz and McGlynn 2000). In natural ecosystems, the natural or human mediated introduction of an invasive ant can produce important breakdowns in several functions, and also in the abundance and diversity of other animals and plants (Horvitz and Schemske 1986, Holway et al. 2002).

Nowadays there are more than 16,000 recognized ant species (AntWeb 2020), but only 19 are considered invasives, i.e., species that are capable of invade and disrupt natural ecosystems through several negative interactions with resident species of animals and plants (Suarez et al. 2010). Two of the most important invasive ant species are *Solenopsis geminata* (Fabricius 1804) and *Wasmannia auropunctata* (Roger 1863), both neotropical in origin and now widely dispersed in many tropical and subtropical zones of the world, mainly in islands (Wetterer and Porter 2003, Wetterer 2011).

Solenopsis geminata

Commonly known as the tropical fire ant, *S. geminata* belongs to a group of species originated in South America that naturally dispersed to the north (Trager 1991). It is considered one of the first trade-dispersed species, because of global trade networks developed during the 16th century. Molecular studies revealed that Indo-Pacific populations of this species are closely related to native populations from western Mexico, being highly probably that some Mexican *S. geminata* colonies were dispersed to Asia, within the ballast soil of Spanish ships (Gotsek et al. 2015). Nowadays this species is found all over the world, mainly in tropical zones, with records in Africa, Australia, Borneo, India, Indonesia, Malaysia, Madagascar, Hawaii, Polynesia, China, Japan, and many others (Hollway et al. 2002, AntWeb 2020).

A lot of evidence has been published about the damage this species produces to native biota wherever it has been introduced, being this impact worst in islands (butterflies, Nafus 1993; tortoises, Williams and Whelan 1991; sea birds, Plentovich et al. 2009). Regarding their impact over native ants, it has been reported that *S. geminata* has had devastating effects over native ant populations (Ness and Bronstein 2004). In contrast with all this information as invasive, there are few studies on the biology of *S. geminata* within its natural range of distribution. From these studies, we know that it is a disturbance specialist species typical of managed-disturbed sites like agroecosystems where it is often the dominant species (Risch and Carroll 1982, Perfecto 1991). It has also been found in several natural ecosystems, where it prefers sites with moderate vegetal cover (shrubs) over insolated (dunes) or dense covered vegetal (forests) sites (Rojas et al. 2014). Currently, there is a lack of information about the status of their populations in undisturbed tropical rain forests and on their effect over indigenous biota.

Wasmannia auropunctata

Commonly known as the little fire ant, this species originates from Central and South America, with a supposedly natural distribution ranging from northeast Mexico to Argentine, including most of the Caribbean islands (Wetterer and Porter 2003). Introduced in almost

all tropical and subtropical regions of the world, *W. auropunctata* represents in the many islands where it occurs a strong threaten to native ant communities and other animals (Le Breton et al. 2003). Recently, there were recorded populations of this species in Israel which at high densities, almost displaced local ant fauna (Vonshak et al. 2010). Some characteristics of *W. auropunctata* populations relate to the type and degree of habitat disturbance. For instance, in severely disturbed sites, ecological dominant populations are characterized by a single colony social structure (low intra-specific aggressiveness); conversely, in low disturbed sites predominate nondominant populations, with a multiple nests social structure (high intra-specific aggressiveness) (Orivel et al. 2009, Salguero et al. 2011). Considering that all dominant populations of this species have been found in human disturbed habitats, it has been suggested that its ecological dominance in these sites obeys to ecological factors modified by human activities (Foucaud et al. 2009).

Within its natural range of distribution *W. auropunctata* is a common species with typical generalist feeding and nesting habits (Tennant 1994). In agroecosystems, it can turn to be very abundant and promote the presence of agricultural pests (De Souza et al. 1998). Abundance of *W. auropunctata* is quite similar between nondisturbed forests, where it is a common species but not a dominant one (Armbrecht and Ulloa-Chacón 2003, Rojas et al. 2014). However, in disturbed natural forests, a negative correlation observed between the abundance of *W. auropunctata* and the species richness of native ants, suggests that it can be affecting native ant communities (Armbrecht and Ulloa-Chacón 2003, Orivel 2009).

Considering the potential damage that *S. geminata* and *W. auropunctata* can cause to ant communities in natural tropical forests, a priority should be to establish its status in protected areas. In Mexico, Los Tuxtlas Biosphere Reserve still contains areas with a significant amount of tropical rain forests, although in some sites is highly fragmented (Guevara et al. 2004). Rojas et al. (2009) recorded preliminary abundance patterns of these two species in this Reserve and found that both species appear as very good disturbance indicators at scales ranging from local to landscape level.

In this study, we firstly inquire about the patterns of abundance of *S. geminata* and *W. auropunctata* in the leaf-litter and soil of four land use systems (LUS) of Los Tuxtlas Biosphere Reserve, from two localities with different amount of forested area. Secondly, we explore the relation between the abundance of these two species and the species richness and abundance of soil ant assemblages. Land use systems included fragments of original tropical rain forests, agroforestry plantations, annual crops (maize), and pastures. Accordingly, we expect to find higher abundances of both species in managed ecosystems than in undisturbed tropical forests (Risch and Carroll 1982, Armbrecht and Ulloa-Chacón 2003). Other expected result relates to the landscape influence (i.e., percentage of forest cover) over these species; in this case, higher abundances of both *S. geminata* and *W. auropunctata* would be found in the locality with lower cover value (Prevedello and Vieira 2010). Both species act as invasive species outside its natural range of distribution, negatively influencing species richness of natural ant communities. If this also occurs within its natural range of distribution, we will

expect that the abundance of these species will negatively correlate with the amount of species of their own communities (Wetterer and Porter 2003, Wetterer 2011).

Materials and Methods

The study was carried out in the southern part of Los Tuxtlas Biosphere Reserve, Veracruz, Mexico in two localities that differed by the amount of forested surface at the landscape level, and by the land use system (conservation of tropical rain forest vs culture of grassland for cattle raising): 1) López Mateos (LM): 77% of forest surface and 2) Venustiano Carranza (VC): 27%. LM is a communal land of 572 ha located between 18°24'56" to 18°26'33"N and 94°56'53" to 94°58'18"W; VC, also a communal land has 970 ha of surface and is located between 18°19'09" to 18°21'50" N and 94°44'41" to 94°46'44" W. Climate in both localities is hot and humid, Am(f), with a mean annual temperature of 22°C and mean annual precipitation between 2,500 mm (LM) and 2,900 mm (VC). Altitude in both localities is around 230 masl. In each locality, 20 sampling points were selected, equally distributed into four main Land Use Systems (LUS): 1) five tropical rain forests (TRF), 2) five agroforestry plantations (AP), 3) five annual crops (C) and five pastures (P); each point was separated at least by 150 m. In total, 40 sampling points were obtained from the four LUS and the two localities.

Vegetation

1) Tropical rain forest. Characterized by the typical four strata, these forests are composed in the canopy stratum by >30 m trees as *Ocotea uxpanapana*, *Nectandra ambigens*, and *Brosimum alicastrum*. Second stratum include trees of 1–20 m height as *Cupania glabra*, *Dendropanax arboreus* and *Pseudolmedia oxyphyllaria*. Other important elements are palms (especially *Chamaedorea tepejilote*), epiphytes, and vines (López-Cano and Castillo-Campos 2009). 2) Agroforestry plantations. Species cultivated in these plantations are cedar (*Cedrela odorata*), pepper (*Pimenta dioica*), orange (*Citrus* spp.), guajava (*Psidium guajava*), and palms (*Chamaedorea tepejilote*) (López and Castillo 2009). 3) Pastures. Only grasses, mainly dominated by introduced species (*Cynodon dactylon* and *Panicum maximum*) over native ones (*Paspalum conjugatum*, *Axonopus compressus*) (López and Castillo 2009). 4) Annual crops. Main crop is self consumption native maize (*Zea mays*), associated with other crops like beans (*Phaseolus vulgaris*) and pumpkins (*Cucurbita* spp.) (López and Castillo 2009). More information about localities and sites can be found in García et al. (2009a).

Ant Sampling

Only soil ants were sampled. Along a one 40 m transect, five samples of 1 m² leaf litter were taken at intervals of 10 m; each sample was sieved (1 cm² aperture) and processed with mini-Winkler bags for 24 h (Agosti et al. 2000). In the same transect three pitfall traps filled with ethanol, 80% were placed at intervals of 10 m and left in the field during 24 h. Ants were also obtained in the vicinity of each transect, from one cubic soil monolith (25 × 25 × 30 cm) that was hand sorting for all soil macrofauna (García et al. 2009b). In total, 360 samples of ants (200 leaf litter quadrats, 120 pitfall traps, and 40 monoliths) were studied. A series of each ant species was mounted in entomological pins. The ants were identified to species level (or morphospecies) by the first author and deposited in the Formicidae collection of the Soil Invertebrate Laboratory of the Institute of Ecology (INECOL), in Xalapa, Ver. Mexico.

Community Parameters and Statistical Analysis

Abundance of each species was calculated as the number of samples (s) where each species was present relative to the total number of samples (S) (Frequency of occurrence, FO = s/S × 100). An 'occurrence' is any event in which an ant species (or morphospecies) is recorded in a sample, regardless the number of captured individuals. For both *S. geminata* and *W. auropunctata* abundance differences between LUS and localities were tested by One-way ANOVA; differences between mean values were obtained by Tuckey HSD test ($P < 0.05$). When data were not normally distributed and/or variance did not fulfill test of homogeneity (Levene test, $P < 0.05$) a non-parametric Kruskal–Wallis test was used, followed by a Wilcoxon matched-pairs signed rank test of differences among means. Simple linear regressions and Pearson correlation coefficients between percentage of samples of *W. auropunctata* and ant richness in each LUS were calculated. All these analyses were performed with STATISTICS '99 edition. Simpson (1–D) diversity index (Magurran 2004) was obtained for each LUS using the program EstimateS 6.0 (Colwell 2000). Ordination of the 40 sampling sites was conducted on the basis of ant similarities. A matrix of 40 sites by 120 ant species FO was analyzed with a Non-metric Multidimensional Scaling method (NMDS), using the program PAST3 (Hammer et al. 2001). We used Euclidean distance to build distance matrix; stress lowest value was obtained after eleven iterations. We considered *Solenopsis geminata* and *Wasmannia auronpunctata* as 'environmental variables' over a matrix of 40 sites × 118 ant species, in order to see its influence over site ordination. Direction and relative length of species vectors indicated its relationship with coordinates and site location.

Results

The effort sampling carried out in 40 sampling points of both LM and VC localities (10 points per each LUS) rendered 120 species of ants, placed in 46 genera of nine subfamilies (after Bolton 2020). The more diverse genera were *Strumigenys* (14 species), *Pheidole* (11), *Solenopsis* (8) and *Hypoponera* (7) (list of species in Rojas 2009). As expected, forests from both localities presented the highest total species richness (74) followed by agroforestry plantations (70); annual crops and pastures presented lesser species (50 and 42 species, respectively). *Wasmannia auronpunctata* was the more abundant species in LM, the locality with higher percentage of forest cover, whereas *S. geminata* dominated in the more deforested VC locality. In both localities, these species were ranked among the four more abundant species (Table 1).

Solenopsis geminata Abundance Patterns

Between localities

As expected, *S. geminata* was significantly more abundant in the lesser forested VC (mean FO = 38.8%, $n = 20$) than in LM (mean FO = 21.6%, $n = 20$), (ANOVA: $F = 5.35$, $df = 1, 38$, $P = 0.026$; Fig. 1A).

Among LUS, within each locality

After calculating average abundance (mean FO) in the four Land Use Systems, and considering that each LUS could differently influence this species, the following patterns emerged (Fig. 1B): 1) In both LM and VC, highest and lowest average abundances were respectively found in annual crops (FO_{LM} = 55.5%; FO_{VC} = 57.7%) and primary forests (FO_{LM} = 2.2%; FO_{VC} = 15.5%). 2) In LM, *S. geminata* abundances were higher in annual crops which significantly differed from the other three LUS (ANOVA: $F = 11.46$, $df = 3, 16$, $P = 0.00029$).

Table 1. Abundance of the seven more important ($FO \geq 15\%$) ant species in two localities of LosTuxtlas region (LM = López Mateos, VC = Venustiano Carranza)

Species	LM	VC
<i>Wasmania auropunctata</i>	30.6	14.4
<i>Hypoponera opacior</i>	24.4	8.3
<i>Octostruma balzani</i>	22.8	13.9
<i>Solenopsis geminata</i>	21.7	38.9
<i>Gnamptogenys strigata</i>	15.6	2.2
<i>Paratrechina longicornis</i>	15.6	–
<i>Solenopsis molesta</i>	10.0	21.7

FO = Frequency of occurrence expressed as percentage ($n = 180$ samples per locality).

A dash means absence of species.

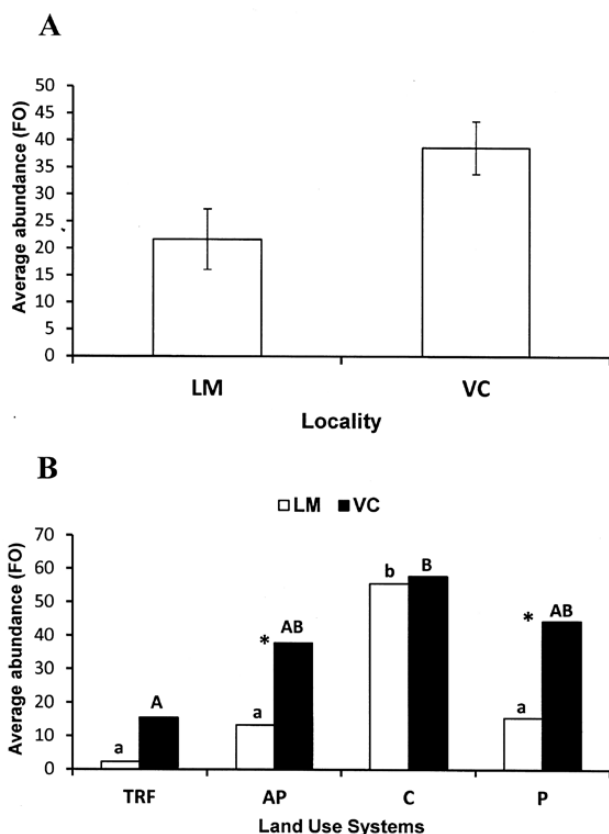


Fig. 1. Average abundance (FO) of *Solenopsis geminata* in LosTuxtlas tropical region. (A) Abundances (\pm SE) in López Mateos (LM) and Venustiano Carranza (VC) localities. (B) Abundances per each LUS in each locality. TRF = tropical rain forests, AP = agroforestry plantations, C = maize annual crops, P = pastures. Different lowercase letters indicate significantly differences among LM systems; different uppercase letters indicate significantly differences among VC systems. An asterisk indicates significantly differences among LM and VC (Tukey HSD test, $P < 0.05$).

3) In VC, in contrast, abundance values were similar in managed systems (agroforestry plantations, annual crops and pastures), with significantly differences observed only among crops and forests (ANOVA: $F = 5.71$, $df = 3, 16$, $P = 0.0074$); this result shows that this species has been very successful in all managed VC ecosystems.

Among LUS from different localities

Rational behind these comparisons is that LUS from each locality are immersed in a differently forested landscape; accordingly, the following patterns were observed: 1) even that average abundance of *S. geminata* in tropical rain forests was higher in VC than in LM, no significantly differences were observed. In annual crops, values from both localities were almost the same, being notably the high abundance values (Fig. 1B); 2) in the case of agroforestry plantations and pastures, abundance values of *S. geminata* were significantly higher in VC ($FO_{AgPI} = 37.7\%$, $FO_{Ps} = 44.4\%$) than in LM ($FO_{AgPI} = 13.32\%$, $FO_{Ps} = 15.5\%$) (ANOVA: Agroforestry plantations $F = 9.66$, $df = 1, 8$, $P = 0.014$; Pastures $F = 12.04$, $df = 1, 8$ $P = 0.0084$; Fig. 1B).

Wasmania auropunctata Abundance Patterns

Between localities

In contrast to the former species, *W. auropunctata* was significantly more abundant in the more forested locality LM (mean FO = 30.5%, $n = 20$) than in VC (FO = 14.4%, $n = 20$) (ANOVA $F = 5.04$, $df = 1, 38$, $P = 0.030$; Fig. 2A).

Among LUS within each locality

In both LM and VC, *W. auropunctata* was more abundant in forests and agroforestry plantations than in annual crops and pastures; however, no differences were observed in VC, and only in LM plantations values were higher than those of crops and pastures (ANOVA $F = 5.92$, $df = 3, 16$, $P = 0.0064$). Notably, in the less forested locality (VC), this species was particularly abundant in forests and very scarce in the sites with more intense management practices (crops and pastures) (Fig. 2B).

Among LUS from different localities

When comparing forests and annual crops between both localities, *W. auropunctata* presented the same pattern that *S. geminata*; conversely, an inverse pattern was observed in the case of agroforestry plantations and pastures. Accordingly: 1) No significantly differences were observed in the abundance of *W. auropunctata* (mean FO) in forests and annual crops between both localities (Kruskal-Wallis test, $P = 0.15$), even that crop values in VC (FO = 2.2%, $n = 5$) were considerably lower than in LM (FO = 15.5%, $n = 5$; Fig. 2B). 2) On the other hand, abundance of *W. auropunctata* was significantly greater in agroforestry plantations and pastures of LM compared to VC (ANOVA: Agroforestry plantations $F = 6.32$, $df = 1, 8$, $P = 0.036$; Pastures: $F = 9.8$, $df = 1, 8$, $P = 0.014$). Noteworthy, agroforestry plantations of LM presented the highest value of regional abundance for this species (mean FO = 48.9%, $n = 5$; Fig. 2B).

Ant Communities: Abundance, Species Richness, and Diversity

With the aim of determine possible relationships among the abundance of *S. geminata* and *W. auropunctata* and ant communities attributes, we evaluated the abundance, species richness and diversity of these communities in each Land Use System of each locality. Our results showed that ant communities clearly differed on several of these attributes at locality and LUS levels.

Abundance Patterns

As expected, average ant abundance was significantly higher in the more forested LM than in VC (ANOVA $F = 4.56$; $df = 1, 38$, $P = 0.039$; $n = 40$; Table 2). In the case of LUS, highest abundance values were recorded in the forests of both localities, whereas lowest

values corresponded to pastures of LM and VC. In both localities, pastures were significantly different from forests (Table 2). No significant differences were observed among the same LUS from different localities.

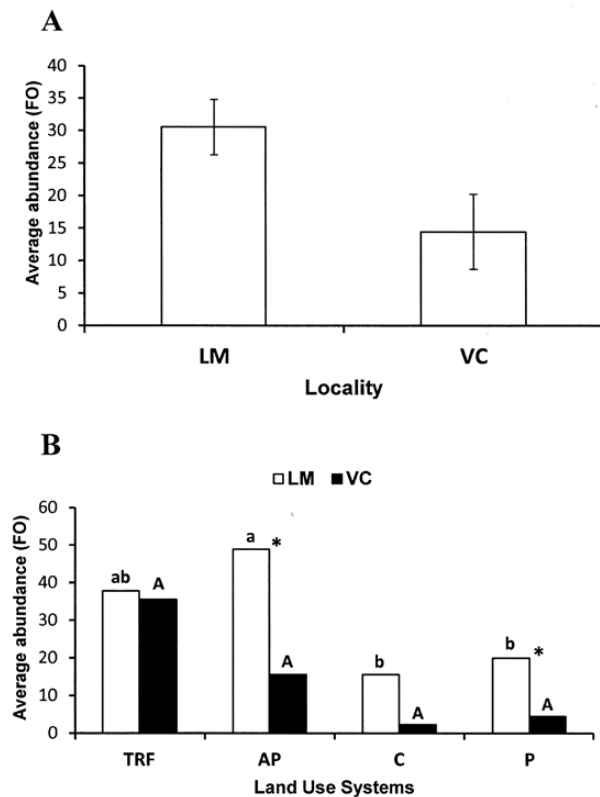


Fig. 2. Average abundance (FO) of *Wasmania auropunctata* in Los Tuxtlas tropical region. (A) Abundances (+/- SE) in López Mateos (LM) and Venustiano Carranza (VC) localities. (B) Abundances per each LUS in each locality. TRF = tropical rain forests, AP = agroforestry plantations, C = maize annual crops, P = pastures. Different lowercase letters indicate significant differences among LM systems; different uppercase letters indicate significant differences among VC systems. An asterisk indicates significant differences among LM and VC (Tukey HSD test, $P < 0.05$).

Table 2. Abundance, total and mean species richness, and mean Simpson Index (1-D) of ant communities in the four LUS of LM and VC localities at Los Tuxtlas region. In brackets \pm SD.

Locality	LUS	Abundance (FO mean)	Species richness (total)	Species richness (mean)	Simpson Index (1-D) mean
LM	TRF	37.4 (13.4) a	54	21 (7.3) A	0.92 (0.02) A
	AP	32.6 (6.2) a	53	19.6 (3.8) A	0.92 (0.01) A **
	C	34.2 (9.6) a	35	15.6 (4.1) A **	0.90 (0.02) A **
	P	18.6 (7.2) b	32	12.6 (3.4) A	0.71 (0.14) B
	Mean	30.7 (11.4)*	89	17.2 (5.6)*	0.86 (0.1)
VC	TRF	35.2 (8.9) a	46	20 (3.5) A	0.93 (0.01) A
	AP	23.2 (11.3) ab	38	13.4 (4.4) B	0.88 (0.03) B**
	C	19 (5.8) ab	33	12 (2.5) B**	0.86 (0.02) B**
	P	15.8 (1.5) b	25	9.4 (1.1) B	0.84 (0.02) B
	Mean	23.3 (10.4)*	81	13.7 (4.9)*	0.87 (0.04)

*One-way Anova significantly differences between localities ($P < 0.05$).

**Wilcoxon signed rank-test significantly differences between localities ($P < 0.05$).

Different letters indicate significant differences between LUS within the same locality. Lower case = Tukey HSD test, $P < 0.05$; Upper case = Wilcoxon signed rank-test, $P < 0.05$.

Ordination of sites by species abundances (NMDS analysis; Stress = 0.15), showed a clear separation of López Mateos sites from those of Venustiano Carranza (Fig. 3). On addition, *S. geminata* and *W. auropunctata* showed an opposite relationship with sites: whereas the first species correlates with VC crops, pastures, and agroforestry plantations, and LM crops, *W. auropunctata* relates to forests and agroforestry plantations of LM and VC forests (Fig. 3).

Species Richness and Diversity

Total and average (per sampling point) species richness followed the expected trend: higher values were observed in the more forested LM locality whereas in the less forested VC lower values were recorded. Average species richness was significantly higher in LM than in VC (ANOVA $F = 4.34$; $df = 1, 38$, $P = 0.043$; Table 2). Within both localities, the gradient of mean and total species richness followed the same trend: Forest > Agroforestry plantations > Crops > Pastures. However, whereas in LM, no significant differences of mean species richness were found among the four LUS (ANOVA $F = 3.02$, $df = 3, 16$, $P = 0.06$), forests of VC were significantly higher than extant LUS (ANOVA $F = 10.29$, $df = 3, 16$, $P = 0.0005$; Tukey HSD test $P < 0.02$). When comparing mean species richness of each LUS among LM and VC localities (Kruskal-Wallis test), no significant differences were observed in three (forests, agroforestry plantations, and pastures) of the four LUS; annual crops were the only LUS with higher values in LM than in VC (K-W $H = 21.3$, $df = 7$, $P = 0.003$; Wilcoxon test, $P = 0.043$). Average diversity (Simpson Index, 1-D) was not significantly different between LM and VC (Table 2). At LUS level, only agroforestry plantations and crops were significantly more diverse in LM than in VC (Wilcoxon test, $P = 0.043$) as far as no inter locality differences were observed in forests and pastures (Table 2). Within LM, pastures were significantly less diverse than the other LUS (Wilcoxon test, $P = 0.043$), whereas in VC forests were significantly more diverse than extant agroecosystems (Wilcoxon test, $P = 0.043$; Table 2).

Faunal Composition

Species composition between LM and VC was rather different. Firstly, these localities shared only 50 species of the regional pool of 120 species (Sorensen Index = 58.8%). Secondly, dominant species in each locality were also different, only sharing two of these species (with FO values $\geq 15\%$): *S. geminata* and *S. molesta* (Table 1).

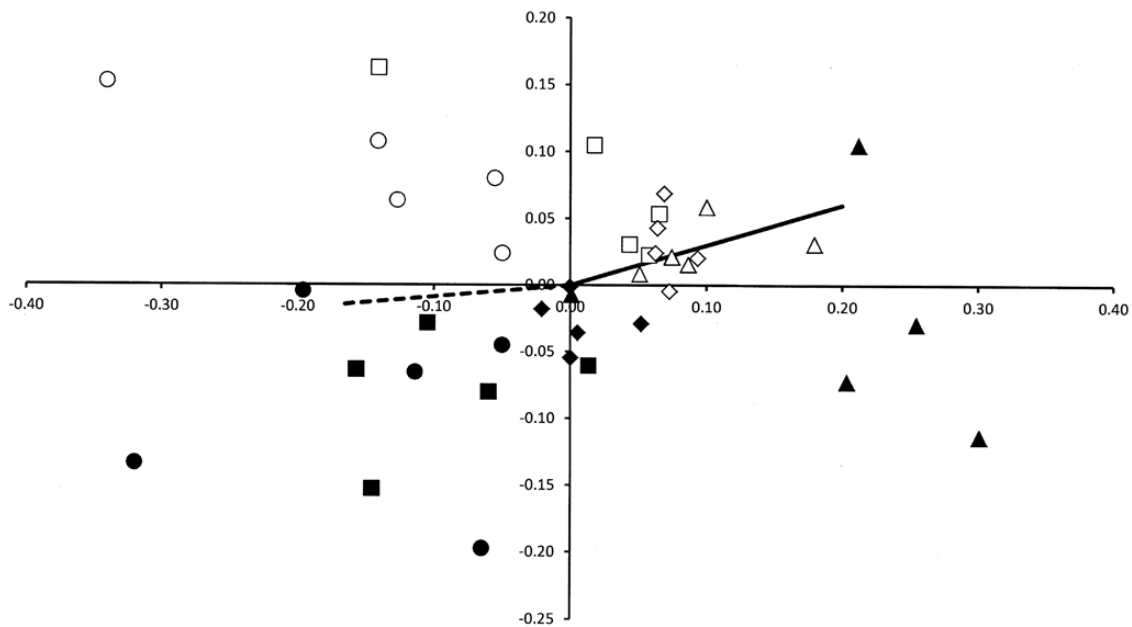


Fig. 3. Nonmetric multidimensional scaling ordination of the 40 studied sites in function of ant abundances (FO values, 120 species). Black symbols are from López Mateos; white symbols are from Venustiano Carranza. Circles = tropical forests; Squares = agroforestry plantations; Diamonds = pastures; Triangles = crops. Lines indicate the influence of the two main invasive ants over sites ordination. Solid line = *S. geminata*, dash line = *W. auropunctata*.

Relationship Between the Species Richness of Communities and the Abundance of *S. geminata* and *W. auropunctata*

Our results show that at the regional level, only in one case was the mean abundance negatively correlated to the number of species of the community. Accordingly, mean FO of *S. geminata* was negatively correlated with S (total species richness by point), both at the regional ($r = -0.54$, $P < 0.05$) and locality level ($r_{LM} = -0.45$, $P < 0.05$; $r_{VC} = -0.51$, $P < 0.05$). In contrast, mean FO of *W. auropunctata* was positively correlated to S, both at the regional ($r = 0.48$, $P < 0.05$) and locality level ($r_{VC} = 0.61$, $P < 0.05$); although in LM the low positive relation ($r_{LM} = 0.22$) was not significantly.

Discussion

Notwithstanding that *S. geminata* and *W. auropunctata* have been currently considered as disturbed specialist species (Majer and Delabie 1999), and even as indicators of low diversity communities (Armbrrecht and Ulloa-Chacón 2003), our results suggests that this can vary according to the kind of landscape forest matrix where they occur. At the regional scale both species were found among the most abundant; at the locality and site (LUS) level, however, their abundance patterns were very different. As expected, *S. geminata* dominated in the less forested locality VC, where changes have been intense as almost all the surface of forests has been converted to extensive, cattle raising pastures (García et al. 2009a). In contrast, and opposite to expected, *W. auropunctata* was very abundant in the highest forested locality LM, and low abundant in VC.

As observed in previous studies in the Mexican tropics (Risch and Carroll 1982, Chanatásig et al. 2011), *S. geminata* reached its highest abundance values in annual crops of both VC and LM localities; its success in this kind of managed environments has been related to its feeding behavior on annual plant seeds (Holway et al. 2002), hemiptera honeydew and other very abundant insects currently considered as cultivated fields pests (Taber 2000). *Solenopsis*

geminata lower abundances observed in forests of these localities, can be considered as positive from the point of view of Los Tuxtlas tropical forests conservation.

On the other hand, *W. auropunctata* tended to be more abundant in most conserved LUS (forests and agroforestry plantations) than in most disturbed ones (pastures and crops). The low abundance observed in all managed sites of VC (highest deforested locality), is against the statement made by other authors (Armbrrecht and Ulloa-Chacón 2003, Achury et al. 2008) about that disturbance favored the dominance of this species. Considering that in Los Tuxtlas *W. auropunctata* thrives in natural or low managed sites, we are reluctant to accept it as a typical 'disturbance specialist' species (Majer and Delabie 1999). Our results confirm our own previous observations carried out in a coastal gradient of natural ecosystems, where the abundance of this species diminishes as the amount of environmental stress increases (Rojas et al. 2014). A possible explanation for these contradictory observations could be that the populations of *W. auropunctata* from Los Tuxtlas have a different reproductive system in comparison to other studied populations. Within its native range, this species has two kinds of populations: those that live in natural habitats, characterized by sexual reproduction (classical sexual haplodiploid reproductive system) and with low densities; and others that inhabit anthropic places (South America populations of French Guiana, Brazil, and Argentine) with a clonal reproductive system and very high densities (Fournier et al. 2005; Orivel et al. 2009; Chifflet et al. 2016, 2018). As the reproductive system has not yet characterized in Mexican populations, we suspect that the populations of Los Tuxtlas present sexual reproduction. Future studies should test this hypothesis.

Quality of the Landscape Matrix

It seems that the different amount of forested area of LM (77%) and VC (27%) has influenced the inverse abundance pattern observed among *S. geminata* and *W. auropunctata* in the agroforestry plantations (AP) and pastures (P) of both localities: i.e., a higher

abundance of *S. geminata* in AP and P of VC than in LM and, conversely a higher abundance of *W. auropunctata* in AP and P of LM than in VC. It has been observed that a larger matrix quality (i.e., more forested) has positive effects in a variety of ecosystem functions (Ricketts 2001, Prevedello and Vieiria 2010); accordingly, we can infer that managed sites from LM present better ecological conditions than managed sites of VC. In VC, this low-quality matrix will emphasize the disturbed conditions of managed sites (see for example Perfecto and Vandermeer 2002), benefiting the spread of *S. geminata*. On the other hand, a LM high-quality matrix will benefit higher abundances of *W. auropunctata* in both pastures and agroforestry LUS. Interestingly, it seems that the matrix quality is not affecting the disturbance conditions of annual crops, as we observed again but independently of the locality an inverse abundance pattern among both species. As a typical disturbance ant specialist, *S. geminata* presented the higher abundances values in annual crops of both LM and VC; conversely, *W. auropunctata* presented their lower values in this land use system. Similar agricultural practices in annual crops all over the region, which will promote similar environmental conditions, could be the explanation behind this pattern.

Finally, the likely influence of forest matrix quality on ant community will explain three other observed results: 1) the similar species richness observed among tropical forests and managed systems of López Mateos (LM), 2) the significant lower species richness in managed systems of Venustiano Carranza (VC) in comparison to forest, 3) a significantly higher average amount of species in LM than in VC.

Relationship Among Species Richness and Abundance of *S. geminata* and *W. auropunctata*

The observed, and expected, relationship among abundance of *S. geminata* and the amount of species can be attributed to two well documented facts: 1) this species proliferates well in disturbed sites (Risch and Carroll 1982, Chanatásig et al. 2011), and 2) negative effects of human disturbance on species richness, both at local and regional scales (Gibb et al. 2015). In either LM and VC, highest abundances of *S. geminata* and lowest species richness were observed in those LUS with the higher human disturbance (annual crops and pastures). It has been suggested that this species better multiplies in poor species sites characterized by a lower competitive pressure from other ant species (Perfecto and Vandermeer 1996). However, a recent study indicates that few evidences support that competitive exclusion by native ant species (in this study *S. geminata*), can act as an important driver of local species richness patterns; instead this can be simply due to environmental disturbance (Arnán et al. 2018). Limitations of this study and the scarce amount of information available on this species, unable us to confer *S. geminata* a causal effect on the species poverty of the ant communities it inhabits. On the other hand, the positive correlation observed among ant species richness and the abundance of *W. auropunctata* was an unexpected result, as it is contrary to findings of Armbrecht and Ulloa-Chacón (2003) and Achury et al. (2012) in fragments of Colombian dry forests. These authors observed a negative correlation between the abundance of this species and ant community species richness, mentioning that sites with the lower species richness, and where *W. auropunctata* dominates, were those with the higher human and cattle disturbance. As mentioned before, differences among the reproductive system of the populations studied in Colombia and those from Los Tuxtlas, could explain these contrasting results (see Foucauld et al. 2009, Orivel et al. 2009, Chifflet et al. 2016). On addition, Brandao and

Silva (2006) did not observe in Brazil any correlation between the overall species richness in fragmented forest and the frequency of *W. auropunctata*.

Additionally, Arnán et al. (2018) found different effects of the presence and abundance of dominant species on ant community species richness, depending if these species were natives or exotics (invasives). After analyzing nearly 1,330 local ant assemblages, these authors found a positive relationship between the abundance of native dominant species and species richness, and a negative one with non-native dominants. Both species of this study are dominants and are found within its native range (i.e., natives); in spite of this, their LUS abundance patterns and its relationship to local species richness were strongly contrasting. In summary, whereas *W. auropunctata* behaves as a typical native dominant species, *S. geminata* behaves as an exotic-invasive dominant species.

Ant Communities Where *S. geminata* or *W. auropunctata* Prosper Have a Different Species Composition

With the exception of pastures, total species richness in all LUS of both LM and VC were similar; in spite of this, faunal composition in those assemblages dominated by *S. geminata* or *W. auropunctata* was very different, as they only share 50 species from the total regional pool of 120. We expect that future detailed analysis of faunal composition and trophic guilds will provide more insights about the different ecological patterns of these two species and its impact on ecosystem dynamics.

Considering that by now between 80 and 90% of Mexican tropical rain forests have been eliminated or severely disturbed (Guevara et al. 2004), the few well-preserved remnants of this type of forest in the region of Los Tuxtlas are a valuable reservoir of biodiversity. Notwithstanding that the Reserve of Los Tuxtlas is protected, it is not free of invasions, and should be periodically monitored to evaluate the populations of invasive ants and its potential negative impacts on native ant communities.

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Author Contributions

P.R.: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Validation; Visualization; Writing—original draft; Writing—review and editing. C.F.: Formal analysis; Validation; Writing—review and editing.

References Cited

- Achury, R., P. Chacón de Ulloa, and A. M. Arcila. 2008. Composición de hormigas e interacciones competitivas con *Wasmannia auropunctata* en fragmentos de bosque seco tropical. Revista Colombiana de Entomología. 34: 209–216.

- Achury, R., P. Chacón de Ulloa, and A. M. Arcila. 2012. Effects of the heterogeneity of the landscape and the abundance of *Wasmannia auropunctata* on ground ant assemblages in a Colombian tropical dry forest. *Psyche*. 10.1155: 1–12.
- Agosti, D., J. Majer, L. A. Alonso, and T. Schultz. 2000. *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution, Washington, DC.
- AntWeb. 2020. Version 8.56.3. California Academy of Science, online at <https://www.antweb.org>. Accessed 18 June 2020.
- Armbrecht, I., and P. Ulloa-Chacón. 2003. The little fire ant *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae) as a diversity indicator of ants in tropical dry forest fragments of Colombia. *Environ. Entomol.* 32: 542–547.
- Arnán, X., A. N. Andersen, H. Gibb, C. L. Parr, N. J. Sanders, R. R. Dunn, E. Angulo, F. B. Baccaro, T. R. Bishop, R. Boulay, et al. 2018. Dominance–diversity relationships in ant communities differ with invasion. *Glob. Change Biol.* 24: 4614–4625.
- Bolton, B. 2020. AntCat. An online catalog of the ants of the world. Available from <http://antcat.org>
- Brandao, C. R. F., and R. R. Silva. 2006. Synecology of *Wasmannia auropunctata*, an invasive ant species (Hymenoptera: Formicidae), in continuous and fragmented areas in the Brazilian Atlantic forest, pp. 141–151. In T. D. Paine (ed.), *Invasive forest insects, introduced forest trees, and altered ecosystems: ecological pest management in global forests of a changing world*. University of California, Riverside.
- Chanatásig, C. I., E. Huerta, P. Rojas, A. Ponce, J. Mendoza, A. Morón, H. Van der Wal, and B. B. Dzib–Castillo. 2011. Efecto del uso de suelo en las hormigas (Formicidae: Hymenoptera) de Tikinmul, Campeche, México. *Acta Zoológica Mexicana* (n. s.). 27: 441–461.
- Chifflet, L., N. V. Guzmán, O. Rey, V. A. Confalonieri, and L. A. Calcaterra. 2018. Southern expansion of the invasive ant *Wasmannia auropunctata* within its native range and its relation with clonality and human activity. *PLoS One*. 13: e0206602.
- Chifflet, L., M. S. Rodríguez, L. A. Calcaterra, O. Rey, P. A. Dinghi, F. B. Baccaro, J. L. Souza, P. Follett, and V. A. Confalonieri. 2016. Evolutionary history of the little fire ant *Wasmannia auropunctata* before global invasion: inferring dispersal patterns, niche requirements and past and present distribution within its native range. *J. Evol. Biol.* 29: 790–809.
- Colwell, R. K. 2000. *Estimates: statistical estimation of species richness and shared species from samples (software and user's guide)*, version 6.0. University of Connecticut, Storrs.
- De Souza, A. H., C. Delabie, and H. G. Fowler. 1998. *Wasmannia* spp. (Hym. Formicidae) and insect damages to cocoa in Brazilian farms. *J. Appl. Entomol.* 122: 339–341.
- Fabricius, J. C. 1804. *Systema piezatorum secundum, ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus*. C. Reichard, Brunswick.
- Foucaud, J., J. Orivel, D. Fournier, J. H. Delabie, A. Loiseau, J. Le Breton, P. Cerdan, and A. Estoup. 2009. Reproductive system, social organization, human disturbance and ecological dominance in native populations of the little fire ant, *Wasmannia auropunctata*. *Mol. Ecol.* 18: 5059–5073.
- Fournier, D., A. Estoup, J. Orivel, J. Foucaud, H. Jourdan, J. Le Breton, and L. Keller. 2005. Clonal reproduction by males and females in the little fire ant. *Nature*. 435: 1230–1234.
- García, J. A., I. Barois, M. Santos, P. Rojas, C. Fragoso, M. A. Morón, J. Bueno, and C. Sormani. 2009b. Land use and diversity of the soil macrofauna in Santa Marta, Los Tuxtlas, Veracruz, México, pp. 135–191. In I. Barois, E. J. Huising, P. Okoth, D. Trejo and M. Santos (eds.), *Below-ground biodiversity in sierra Santa Marta, Los Tuxtlas, Veracruz, México*. Instituto de Ecología A.C. Xalapa, México.
- García, J. A., T. Fuentes, V. Sosa, E. Meza, S. Negrete, I. Barois, D. Bennack, and P. Okoth. 2009a. Benchmark site description of the Los Tuxtlas, Veracruz, Mexico, pp. 21–39. In I. Barois, E. J. Huising, P. Okoth, D. Trejo and M. Santos (eds.), *Below-ground biodiversity in sierra Santa Marta, Los Tuxtlas, Veracruz, México*. Instituto de Ecología A.C. Xalapa, México.
- Gibb, H., N. J. Sanders, H. Gibb, R. R. Dunn, S. Watson, M. Photakis, S. Abril, A. N. Andersen, E. Angulo, I. Armbrecht, et al. 2015. Climate mediates the effects of disturbance on ant assemblage structure. *Proc. R. Soc. B.* 282:20150418.
- Gotzek, D., H. J. Axen, A. V. Suarez, S. Helms Cahan, and D. Shoemaker. 2015. Global invasion history of the tropical fire ant: a stowaway on the first global trade routes. *Mol. Ecol.* 24: 374–388.
- Guevara, S., J. Laborde, and G. Sánchez-Ríos. 2004. Los Tuxtlas: el paisaje de la sierra. Instituto de Ecología, A.C. and European Union. Xalapa, México.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 9.
- Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002. The causes and consequences of ant invasions. *Annu. Rev. Ecol. Syst.* 33: 181–233.
- Hölldobler, B., and E. O. Wilson. 1990. *The ants*. The Belknap Press, Harvard.
- Horvitz, C. C., and D. W. Schemske. 1986. Seed dispersal of a neotropical myrmecochore: variation in removal rates and dispersal distance. *Biotropica* 18: 319–23.
- Le Breton, J., J. Chazeau, and H. Jourdan. 2003. Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. *Austral Ecology* 28: 204–209.
- López–Cano, E. B., and G. Castillo–Campos. 2009. Report of the vascular flora characterization and α and β diversity index in three communities of Los Tuxtlas, Veracruz, Mexico, pp. 41–47. In I. Barois, E. J. Huising, P. Okoth, D. Trejo and M. Santos (eds.), *Below-ground biodiversity in sierra Santa Marta, Los Tuxtlas, Veracruz, México*. Instituto de Ecología A.C. Xalapa, México.
- Magurran, A. E. 2004. *Measuring biological diversity*. Blackwell Publishing, Oxford, UK.
- Majer, J. D., and J. H. C. Delabie. 1999. Impact of tree isolation on arboreal and ground ant communities in cleared pasture in the Atlantic rain forest region of Bahia, Brazil. *Ins. Soc.* 46: 281–290.
- Nafus, D. M. 1993. Movement of introduced biological control agents onto nontarget butterflies, *Hypolimnas* spp. (Lepidoptera: Nymphalidae). *Environ. Entomol.* 22: 265–272.
- Ness, J. H., and J. L. Bronstein. 2004. The effects of invasive ants on prospective ant mutualists. *Biol. Invasions* 6: 445–461.
- Orivel, J., J. Grangier, J. Foucad, J. le Breton, F. X. Andres, H. Jourdan, J. H. C. Delabie, D. Fournier, P. Cerdan, B. Facon, et al. 2009. Ecologically heterogeneous populations of the invasive ant *Wasmannia auropunctata* within its native and introduced ranges. *Ecol. Entomol.* 34: 504–512.
- Perfecto, I. 1991. Dynamics of *Solenopsis geminata* in a tropical fallow field after ploughing. *Oikos* 62: 139–144.
- Perfecto, I., and J. Vandermeer. 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. *Oecologia*. 108: 577–582.
- Perfecto, I., and J. Vandermeer. 2002. The quality of the agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conserv. Biol.* 16: 174–182.
- Plentovich, S., A. Hebshi, and S. Conant. 2009. Detrimental effects of two widespread invasive ant species on weight and survival of colonial nesting seabirds in the Hawaiian Islands. *Biol. Invasions*. 11: 289–298.
- Prevedello, J. A., and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodivers. Conserv.* 19: 1205–1223.
- Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 158: 87–99.
- Risch, S. J., and C. R. Carroll. 1982. Effect of a keystone predaceous ant, *Solenopsis geminata*, on arthropods in a tropical agroecosystem. *Ecology* 63: 1979–1983.
- Roger, J. 1863. Die neu aufgeführten gattungen und arten meines formiciden-verzeichnisses nebst Ergänzung einiger früher gegebenen Beschreibungen. *Berliner Entomologische Zeitschrift* 7:131–214.
- Rojas, P., A. Angeles, and L. Hernández. 2009. Diversity patterns of soil ants (Hymenoptera: Formicidae) related to land use in Los Tuxtlas, Veracruz, México, pp. 203–218. In I. Barois, E. J. Huising, P. Okoth, D. Trejo and M. Santos (eds.), *Below-ground biodiversity in sierra Santa Marta, Los Tuxtlas, Veracruz, México*. Instituto de Ecología A.C. Xalapa, México.

- Rojas, P., C. Fragoso, and W. P. Mackay. 2014. Ant communities along a gradient of plant succession in Mexican tropical coastal dunes. *Sociobiology* 61: 119–132.
- Salguero, B., I. Armbrecht, H. Hurtado, and A. M. Arcila. 2011. *Wasmannia auropunctata* (Hymenoptera: Formicidae): ¿unicolonial o multicolonial? en el valle geográfico del río Cauca. *Revista Colombiana de Entomología* 37: 279–288.
- Schultz, T. R., and T. P. McGlynn. 2000. The interactions of ants with other organisms, pp. 35–44. *In* D. Agosti, J. Majer, L. E. Alonso and T. Schultz (eds.), *Ants: standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington, DC.
- Suarez, A. V., T. McGlynn, and N. D. Tsutsui. 2010. Biogeographic patterns of the origins and spread of introduced ants, pp 233–244. *In* L. Lach, K. Parr and K. Abbot (eds.), *Ant ecology*. Oxford University Press, New York.
- Taber, S. W. 2000. *Fire ants*. Texas A & M. University Press, College Station.
- Tennant, L. E. 1994. The ecology of *Wasmannia auropunctata* in primary tropical rainforest in Costa Rica and Panamá, pp. 80–90. *In* D. F. Williams (ed.), *Exotic ants: biology, impact, and control of introduced species*. Westview Press, Boulder, CO.
- Trager, J. C. 1991. A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). *J. N. Y. Entomol. Soc.* 99:141–198.
- Vonshak, M., T. Dayan, A. Ionescu-Hirsh, A. Freidberg, and A. Hefetz 2010. The little fire ant *Wasmannia auropunctata*: a new invasive species in the Middle East and its impact on the local arthropod fauna. *Biol. Invasions* 12: 1825–1837.
- Williams, D. F., and P. Whelan. 1991. Polygynous colonies of *Solenopsis geminata* (Hymenoptera: Formicidae) in the Galapagos Islands. *Fla. Entomol.* 74: 368–371.
- Wetterer, J. K. 2011. Worldwide spread of the tropical fire ant, *Solenopsis geminata* (Hymenoptera: Formicidae). *Myrmecol. News* 14: 21–35.
- Wetterer, J. K., and S. D. Porter. 2003. The little fire ant, *Wasmannia auropunctata*: distribution, impact, and control. *Sociobiology* 42: 1–41.