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ORIGINAL PAPER

The little fire ant *Wasmannia auropunctata*: a new invasive species in the Middle East and its impact on the local arthropod fauna

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Abstract The little fire ant, *Wasmannia auropunctata,* probably arrived in Israel in ca. 1998 and was identified in 2005; this is the first record of this species from open areas outside the tropics and subtropics. It survives harsher conditions than in its native habitats, with minimal annual temperatures as low as 6°C, and 5–12 consecutive rainless months (under 15 mm rainfall per month). It is now known from 26 localities in Israel, mostly in irrigated gardens. As in other regions where they have invaded, these ants pose a serious threat to local biodiversity. At high densities they displaced almost all the local ant species sampled, affecting population abundances, species richness, and community structure. *W. auropunctata* seems to have a detrimental effect also on other ground arthropods, judging from the observed decline in spider and beetle abundances. We show here that this tropical species can pose a critical threat to local arthropods at a wider range of climatic conditions than was previously known.

Keywords Ants · Invasive species · Israel · Invasive ants · *Wasmannia auropunctata*

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Introduction

Invasive species are regarded as one of the greatest threats to biodiversity worldwide, second only to habitat destruction (Schmitz and Simberloff 1997). Among these, social insects, and in particular invasive ants, are especially destructive (Holway et al. 2002). Invasive ants have a complex negative impact on their new ecosystems, affecting mainly but not only other ant species; they are agricultural pests and also pose a danger to human health (Passera 1994; Williams 1994). In addition they were found to affect soil properties and mutualistic interactions of other ant species with plants and other arthropods (Holway et al. 2002).

The most devastating impact of invasive ants on their new environment is their ability to displace local ant species (Holway et al. 2002), in some cases not only by reducing their numbers, but also by changing community organization (Sanders et al. 2003). Ants are an important component of natural ecosystems; they are numerically dominant and represent a large proportion of the animal biomass in almost every terrestrial habitat worldwide (Alonso and Agosti 2000). Therefore, the decline in ant diversity may have substantial consequences for many other organisms (e.g. Christian 2001; Ness and Bronstein 2004).

The little fire ant, *Wasmannia auropunctata*, is a widespread and abundant invasive ant (Holway et al. 2002). Native to South and Central America, it has been introduced to other localities in these regions as well as to West Africa, Australia, and several Caribbean and Pacific islands (Department of Primary Industries and Fisheries [DPI&F] 2006; McGlynn 1999; Holway et al. 2002; Wetterer and Porter 2003). It is listed among the "one hundred of the world's worst invasive alien species" tabulated by the Invasive Species Specialist Group (ISSG) of the International Union for Conservation of Nature (IUCN) (Lowe et al. 2000) owing to its particularly severe environmental impact. It devastates local ant species, which it outcompetes and displaces, mainly on oceanic islands (Clark et al. 1982; Jourdan 1997; Holway et al. 2002; Armbrecht and Ulloa-Chacon 2003; Wetterer and Porter 2003). It also causes population declines of local invertebrates through extensive predation (Clark et al. 1982; Lubin 1984; Romanski 2001) and is renowned for harming domestic and possibly also wild vertebrates (Jourdan et al. 2001; Romanski 2001; Holway et al. 2002; Wetterer and Porter 2003). It is an agricultural pest in 35 countries. *W. auropunctata* is also infamous for its unpleasant sting (Wetterer and Porter 2003).

This species reproduces mostly or entirely by nest budding rather than nuptial flights (Hölldobler and Wilson 1977), and its natural long-range dispersal is limited (Lubin 1984). Therefore, *W. auropunctata* spreads in its non-native range primarily through human activities (Holway et al. 2002), such as transfer of plants, soil, food packaging, logs, and wood products (Lubin 1984; Roque-Albelo and Causton 1999; Romanski 2001; Wetterer and Porter 2003). *W. auropunctata*'s success as an invader is attributed to its ability to form supercolonies, its polyphagous habits, and its ability to use a wide range of habitats (Ulloa-Chacon and Cherix 1990; Le Breton et al. 2004; Errard et al. 2005). Insight into this species' social behavior, ecology, and modes of spread can ultimately help control or at least contain it.

Wasmannia auropunctata was first identified in Israel in 2005. The Israeli population reflects a single introduction of one queen and one male genotypes, that reproduce clonally (Vonshak et al. 2009). In Israel *W. auropunctata* forms one supercolony with no intraspecific aggression in its entire invasive range; however, the ants exhibit high interspecific aggression in experimental laboratory settings (Vonshak et al. 2009).

Invasion trajectory models, based on bioclimatic envelopes of species' known distribution range, are commonly used in order to predict invasive species' potential spread (e.g. Welk et al. 2002). These as well as empirical studies have suggested that the climate in invaded ranges of invasive ants approximately matches that of their native range (e.g. *Linepithema humile* in Mediterranean climate [Holway 1998] and *Pheidole megacephala* in tropical climate [Hoffmann et al. 1999]). It was therefore surprising to find a successful invasion of the tropical ant *W. auropunctata* in Mediterranean and even desert regions of Israel.

Our objectives were: (a) to assess the introduction pathways and invasion trajectories of *W. auropunctata* in Israel; (b) to characterize the climatic conditions of the *W. auropunctata* population in Israel and to assess whether it is confined to irrigated gardens inside villages or found in native habitats as well; (c) to study the impact of *W. auropunctata* on the local arthropod fauna. Specifically we addressed its effect on population abundances, species richness, and community structure of ants, spiders, and beetles; and we test whether *W. auropunctata*'s impact on the local fauna in a Mediterranean climate conforms to the impact known from tropical habitats.

Methods

The preliminary survey

We conducted a preliminary survey of *W. auropunctata*'s distribution in Israel between January and March 2006 in several villages and their surroundings in the Jordan Valley, where the ant was first detected. These included gardens in villages, open and agricultural lands, and undisturbed river banks.

Three main methods were used for the preliminary survey: peanut butter baits, active search, and pitfall traps: (a) flat wooden sticks smeared with peanut butter were positioned as baits in every sampling point for at least 1 h. The 20–40 (proportional to sampled area) evenly distributed sampling points were selected by setting grids on aerial photos of each investigated area; (b) active search for ants under stones, logs, potted plants, etc.; (c) In order to study the ants' distribution in cultivated lands, we set 47 pitfall traps (7.5 cm diameter, filled with detergent) and 47 peanut butter baits placed at 20 m intervals along the outskirts of an infested village (Kibbutz

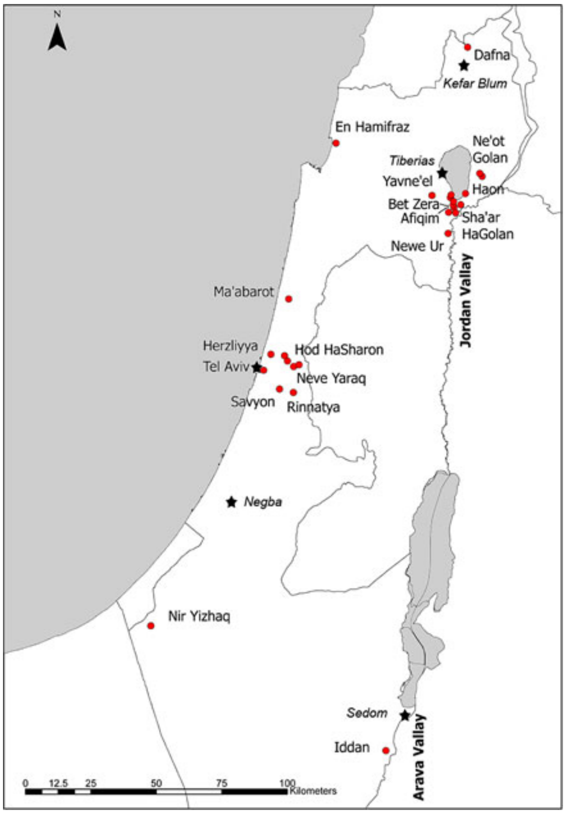

Fig. 1 A map of Israel (excluding the south) showing the villages infested with *Wasmannia auropunctata* so far (*circles*) and meteorological stations, corresponding to Table 2 (*asterisks*)

Afiqim; Fig. 1; Table 1). Another transect of 47 baits was set 5 m into the cultivated lands. The peanut butter baits were checked twice: in the afternoon, 2 h after they were set, and on the following morning; the pitfall traps were collected after 24 h and sorted immediately. *W. auropunctata* was identified in situ whereas other ant species were preserved in 80% ethanol for later identification. All specimens collected were deposited in the National Entomological Collections (Museum of Natural History) at Tel-Aviv University. Each collecting site was recorded either by GPS or directly on the aerial photo and digitized using ArcView 8.2.

Impact on the arthropod fauna

We studied *W. auropunctata*'s impact on three major local arthropod groups: ants, beetles, and spiders. The study was conducted during February–March 2006. The impact on species richness and abundance of these groups was investigated using pitfall traps. Ant populations were studied by using both baits and pitfall traps. The study area included three adjacent villages in the Jordan Valley: Afiqim, Bet Zera, and Sha'ar HaGolan (Fig. 1; Table 1), that share a similar climate (Jaffe 1988), soil (Dan 1988) and irrigation. All plots were located in disturbed habitats comprising irrigated public gardens comprising mainly lawns and perennial plants. Prior to setting the plots, we conducted preliminary sampling using active search to assess *W. auropunctata* densities. High density plots ("high") were characterized by very high foraging activity of *W. auropunctata* and abundant nests. Low density plots ("low") were typified by low foraging activity and scarce nests. Plots in which we could not find any *W. auropunctata* were considered clear of this species ("none"). There were a total of six plots per village, two plots for each density, except for Sha'ar HaGolan where only one low density plot was located. Eight 7.5 cm diameter pitfall traps containing 85% propylene glycol and 15% ethanol as preservatives were set in every plot for 5 days. The traps were placed in two rows set at least 10 m apart, each row comprised four traps placed at 10 m intervals. The contents of all pitfall traps were sorted in the laboratory, and ants, spiders, and beetles were identified to the species level.

In addition, four baits containing honey, peanut butter, and cracked cookies on a Petri dish were placed at both ends of each row of traps on the last day, several hours before the pitfall traps were collected. The baits were checked after 30 and 60 min and after about 4 h, just before the pitfall traps were collected. Ants on the baits were identified to species on the spot, except for *Monomorium*, *Pheidole* and *Tetramorium*, which were identified only to the genus level. Owing to unresolved taxonomic status, *Plagiolepis ancyrensis* was combined with *Plagiolepis* sp., and *Tetramorium simillimum* was combined with *Tetramorium* sp. of the *simillimum* group for all analyses.

Statistical analyses

All analyses were made excluding *W. auropunctata* from the data set. Because few ants were attracted to the baits, the three time intervals were pooled and analyzed similarly to the pitfall traps. Because ants

Table 1 Infested localities in Israel, including year of discovery, detection method and coordinates

Locality	Year discovered	Detection method	*X*	*Y*
Afiqim	2005	Sample sent to TAU	32.67966432	35.5779148
Bet Zera'	2005	Report	32.68890887	35.5741244
Kinneret Qevuza	2005	Report	32.71401729	35.5629409
Ashdot Ya'aqov (meuchad)	2006	Preliminary survey	32.66156719	35.5839385
Menahamya	2006	Preliminary survey	32.66348845	35.5552386
Kinneret Moshava	2006	Preliminary survey	32.72293491	35.5662507
Sha'ar HaGolan	2006	Preliminary survey	32.6891048	35.6049098
Yavne'el	2006	Report	32.72173373	35.4880667
Dafna	2006	Report	33.23063065	35.6356041
Ne'ot Golan	2006	Report	32.78651794	35.6923475
En Hamifraz	2006	Report	32.90161284	35.0968511
Ma'barot	2007	Report	32.36538663	34.9056578
Tel Aviv	2007	Report	32.11971133	34.8052321
Newe Yaraq	2007	Florida Keratopathy	32.13266879	34.9268182
Hod HaSharon	2007	Report	32.15184479	34.9016254
Giv'at Yo'av	2007	Report	32.79686004	35.6829335
Haon	2008	Report	32.7276089	35.6242379
Deganya B	2008	Report	32.70077059	35.5757933
Ramot HaShavim	2008	Report	32.169969	34.8900816
Herzliyya	2008	Report	32.17457667	34.8344642
Savyon	2008	Florida Keratopathy	32.05510765	34.8696983
Nir Yizhaq	2008	Report	31.23840221	34.3571982
Newe Ur	2008	Report	32.59063441	35.5533097
Iddan	2009	Report	30.81182028	35.298499
Rinnatya	2009	Florida Keratopathy	32.04372145	34.9257074
Hagor	2009	Report	32.13892918	34.9485049

Most of the localities were detected following a report by villagers; note that three of the infested localities were detected following the discovery of the eye disease Florida Keratopathy in cats by DVM Havi Sarfaty. The disease is presumably caused by *Wasmannia auropunctata*

are spatially clumped (Longino 2000) we analyzed the pitfall traps and baits data as follows: (a) we pooled the number of individuals and species by site in order to asses the impact of *W. auropunctata* on overall ant abundance (number of individuals) and species richness (number of species). These analyses were conducted by ANOVA (on square root transformed counts) for factor density (high, low, none) followed by Tukey HSD post-hoc test; (b) we counted the number of traps occupied by each species in areas of differing *W. auropunctata* density ("none" and "low") in order to asses differences in relative species abundance. We compared each species frequency between "none" and "low" densities to that expected by chance using a *G*-test for homogeneity of replicates followed by a post-hoc test for heterogeneous groups (Sokal and Rohlf 1981, p. 728). Since most species were represented by few individuals, we analyzed only species that were trapped in at least ten traps and within three or more plots.

For beetles and spiders overall comparisons of number of individuals per trap (abundances) and number of species per trap (species richness) were conducted by ANOVA (on square root transformed counts) for factor density (high, low, none), separately for Afiqim, Bet Zera, and Sha'ar HaGolan (species richness was studied only for Bet Zera and Sha'ar HaGolan owing to a problem with the preservative used for specimens collected in Afiqim). The probabilities of the individual ANOVA results were combined following Sokal and Rohlf (1981, p. 779). Redundancy analysis (RDA) was used to test the relationship between the communities of spiders and beetles and the explanatory variables: *W. auropunctata* density (high, low, none), and locality (Bet Zera and Sha'ar HaGolan), with data pooled by site. The significance of each variable was tested using a Monte-Carlo permutation test (4999 permutations, main effects: design-based permutation; interactions: model-based permutation [ter Braak and Šmilauer 2002]). For spiders, a partial analysis was carried out in order to study the partial effects of *W. auropunctata* as the explanatory variable, with locality as a covariable (similarly to the effects of partial regression coefficients in a multiple regression; Leps and Šmilauer 1999).

All ordination analyses were performed using CANOCO FOR WINDOWS 4.5 (ter Braak and Šmilauer 2002). Other statistical analyses were performed using Statistica 7.1 (StatSoft Inc., Oklahoma, USA).

Results

The preliminary survey

In the 2006 preliminary survey we found *W. auropunctata* in eight localities, and since then in 18 additional localities (Fig. 1; Table 1). This is the first record of *W. auropunctata* in the Middle East; it is the northernmost point (33°13′) where this ant nests outdoors. Table 2 presents climatic data of *W. auropunctata*'s native range in Brazil, and introduced range worldwide, as well as of five sampling sites in Israel adjacent to infested localities (asterisks in Fig. 1). In Israel the ant survives in Mediterranean and even desert climatic conditions with temperature extremes in winter and in summer that are considerably greater than those of their native range, and of other invaded regions. More importantly, in Israel there are several consecutive dry months in summer (5–12 months with less than 15 mm rainfall compared to 0–2 months in the rest of the invasive range; Table 2), creating a significantly drier habitat than in the native range or other regions invaded by this species.

Table 2 Climatic data of *Wasmannia auropunctata*'s native (Brazil) and invasive ranges (Israel in bold and worldwide): minimum and maximum daily average temperatures throughout the year (°C) and the number of months with precipitation below 15 mm (Kefar Blum, Tel Aviv, Negba, and Sedom according to the Israel Meteorological Service; the rest according to the World Meteorological Organization)

Place	Country	Continent	Minimum temperature (°C)	Maximum temperature (°C)	# of months with less than 15 mm precipitation
Manaus	Brazil	South America	22.7	32.9	0
Honolulu	Hawaii	Oceania	18.6	31.5	2
Tahiti	French Polynesia	Oceania	20.5	30.8	0
Noumea	New Caledonia	Oceania	17.2	29	0
Port Vila	Vanuatu	Oceania	19.3	30.3	0
Auki	Solomon Islands	Oceania	22.3	30.7	0
Miami	Florida	North America	15.1	31.7	0
Nassau	Bahamas	North America	17.3	32.1	0
Hamilton	Bermuda	North America	15.5	29.8	0
Libreville	Gabon	Africa	21.8	30.2	2
Yaounde	Cameroon	Africa	13.9	30.9	1
Kefar Blum	**Israel**	**Asia**	**5.8**	**34.5**	**5**
Tiberias	**Israel**	**Asia**	**8.1**	**36.3**	**5**
Tel Aviv	**Israel**	**Asia**	**9.6**	**30.2**	**5**
Negba	**Israel**	**Asia**	**8**	**31.1**	**5**
Sedom	**Israel**	**Asia**	**12.7**	**39.7**	**12**

Of the 94 pitfall traps set in the preliminary survey at the edges of cultivated crops and around abandoned greenhouses *W. auropunctata* was found in 11 traps. Only a few workers were found at all sites (1.7 ± 6.14 per trap), except for the greenhouse site, in which there were 20.3 ± 16.7 workers per trap. Manual search for this species' nests and activity revealed their presence in low densities in additional sites, all with frequent human activity (fishponds, cemeteries, etc.). Finally, these ants were also found in an undisturbed habitat along the Jordan River.

Impact on the arthropod fauna

Results obtained from the pitfall traps corroborated our a priori assessments of *W. auropunctata* densities in the different plots (Table 3). Ant abundance, species richness, and community composition were all significantly affected by *W. auropunctata* density (Fig. 2; statistical analyses in Table 3). We found a significant impact of *W. auropunctata* density on other ant abundance and species richness per plot, with significant differences between "high" and "none", and between "high" and "low" in both

Table 3 Analyses of abundances and species richness of ants collected by pitfall traps and baits in three villages: Afiqim, Bet Zera, and Sha'ar HaGolan

Analysis		*Wasmannia auropunctata*'s density			One-way ANOVA		Significant comparisons ($P < 0.05$)
		High (a)	Low (b)	None (c)	F	P	
Pitfall traps	*W. auropunctata*						
	No. of individuals	1142.83 ± 0.21	47.2 ± 13.25	0.33 ± 280.37			
	Other ant species						
	No. of individuals	15.5 ± 10.36	148.6 ± 32.06	187.33 ± 55.25	14.41	0.0004	a × b; a × c
	No. of species	3.5 ± 0.76	10.2 ± 1.07	9.5 ± 1.18	16.57	0.0002	a × b; a × c
Baits	*W. auropunctata*						
	No. of individuals	43 ± 18.16	1.6 ± 1.17	0			
	Other ant species						
	No. of individuals	10.83 ± 5.22	333 ± 103.31	339 ± 84.97	12.8	0.0007	a × b; a × c
	No. of species	0.83 ± 0.4	4.2 ± 0.37	3.17 ± 0.6	11.47	0.001	a × b

Data pooled and analyzed by site (Data presented–average no. of individuals/species per site ± SE)

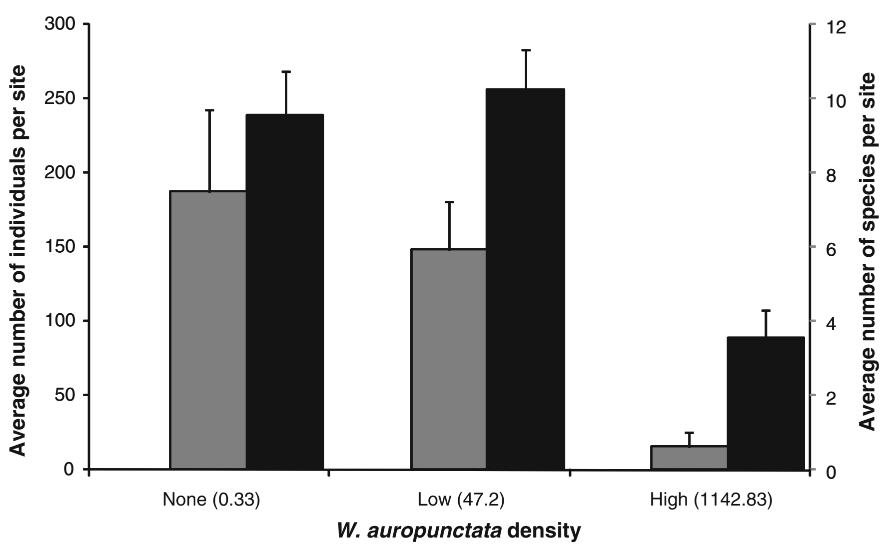

Fig. 2 The impact of *Wasmannia auropunctata* density on other ant abundance (*light columns*) and species richness (*dark columns*). The data represent mean (± SE) number of ants per site (eight pitfall traps) excluding *W. auropunctata* (The average number of *W. auropunctata* per site is indicated in parenthesis)

Table 4 Species of ants identified in the sampled villages in the Jordan Valley region, Israel, during the survey (§); and using pitfall traps for the assessment of the impact of *W. auropunctata* on local arthropod fauna (*); most species collected by baits were identified only to Genus level (see text)

Subfamily	Species	Zoogeographic element
PONERINAE	*Hypoponera ragusai* (Emery, 1894)§	M
DORYLINAE	*Dorylus fulvus* (Westwood, 1839)§	M
MYRMICINAE	*Aphaenogaster syriaca schmitzi* Forel, 1910§*	Endemic
	Cardiocondyla emeryi Forel, 1881§*	Tramp
	Crematogaster auberti Emery, 1869§	M
	C. jehovae Forel, 1907§	M
	Messor dentatus Santschi, 1927§*	M + IT
	M. hebraeus Santschi, 1927§	Endemic
	M. minor (André, 1883)§	M
	M. intermedius Santschi, 1927§	Endemic
	M. orientalis (Emery, 1898)§	M + IT
	M. semirufus (André, 1883)§	M + IT
	Monomorium clavicorne André, 1881§*	M
	M. pallidum Donisthorpe, 1918§*	M + IT
	M. phoenicum Santschi, 1927§*	M
	M. sahlbergi Emery, 1898§*	Endemic
	M. subopacum ebraicum Menozzi, 1933§*	Endemic
	Pheidole pallidula (Nylander, 1849)§	M + IT
	P. teneriffana Forel, 1893§*	Tramp
	Solenopsis orbula Emery, 1875*	M
	Temnothorax semiruber (André, 1881)§	M
	Tetramorium davidi Forel, 1911§*	M + IT
	T. lanuginosum Mayr, 1870§*	Tramp
	T. lucidulum Menozzi, 1933§*	M
	T. sahlbergi Finzi, 1936§*	M
	T. simillimum (Smith, 1851)§*	Tramp
	Wasmannia auropunctata (Roger, 1863)§*	Tramp
DOLICHODERINAE	*Tapinoma israele* Forel, 1904§*	Endemic
	T. simrothi phoeniceum Emery, 1925§	M
FORMICINAE	*Camponotus rebeccae* Forel, 1913§	Endemic
	C. sanctus Forel, 1904§*	M + IT
	C. truncatus (Spinola, 1808)*	P
	Cataglyphis lividus (André, 1881)§	M + IT
	C. savignyi (Dufour, 1862)§*	M
	Cataglyphis sp. near *nodus* (Brullé, 1832)§	Endemic
	Lepisiota bipartita (Smith, 1861)§*	M + IT
	L. dolabellae (Forel, 1911)§	M + IT
	L. syriaca (André, 1881)§	M
	Paratrechina jaegerskioeldi (Mayr, 1904)§*	Tramp
	P. longicornis (Latreille, 1802)§*	Tramp
	P. sindbadi Pisarski, 1960§*	M + IT
	Plagiolepis ancyrensis Santschi, 1920§*	M

Zoogeographic elements following Kugler (1988): *P* Palaearctic, *M* Mediterranean, *IT* Irano-Turanian

pitfall traps and baits, but no differences between the "none" and "low" plots. A total of 42 ant species were recorded from the Jordan Valley region during the research period, 25 of which were represented in pitfall trap catches; ten taxa were represented at baits (Table 4). Although there were no significant

Table 5 Analyses of relative abundance of the eight most abundant ant species in pitfall traps: number of traps in which a species was found; number of occupied sites in parentheses

Species	*W. auropunctata*'s density			Total	Status
	None	Low	High		
P. longicornis	4 (3)	8 (3)	0	12	No change
M. subopacum ebraicum	8 (3)	5 (3)	0	13	No change
P. jaegerskioeldi	12 (4)	4 (2)	0	16	Decrease
T. davidi	6 (3)	16 (5)	1	23	Increase
C. emeryi	18 (5)	6 (3)	1	25	Decrease
P. ancyrensis	26 (5)	18 (5)	3 (2)	46	No change
M. clavicorne	20 (5)	14 (4)	14 (6)	48	No change
T. simillimum group	34 (6)	21 (5)	2 (1)	57	No change

Status refers to the difference between sites with no *W. auropunctata* and those with low densities

differences in ant species diversity between the "none" and "low" plots (Fig. 2), a more detailed inspection revealed nonetheless important differences. The proportion of traps occupied by ants in "none" vs. "low" sites differed significantly from homogeneity (for the ant species found in more than ten traps in at least 3 plots. Table 5, $G_H = 18.57$, $df = 7$, $P < 0.05$), with two heterogeneous groups (critical value $X^2_{.05[7]} = 14.07$), *Paratrechina jaegerskioeldi* and *Cardiocondyla emeryi* ($G = 12.33$) were found in fewer traps in "low" compared to "none" sites, and *Tetramorium davidi* ($G = 7.46$) was found in more traps in "low" sites. As only few taxa were identified from the baits, and even fewer were represented in three on more sites, we did not perform a *G*-test analysis for the bait data.

Population density of *W. auropunctata* also affected the two other ground arthropod groups, spiders, and beetles. Spider abundances were significantly lower at high densities of *W. auropunctata*, but the reduction in species richness was only marginally significant (Fig. 3; Table 6). A partial redundancy analysis showed that 48% of the variance was explained by high densities of *W. auropunctata* when locality served as covariable ($F = 11.78$, $P = 0.006$), and locality explained 23% of the variance when *W. auropunctata*'s density served as a covariable ($F = 4.95$, $P = 0.048$). In addition, the RDA analysis also showed that high densities of *W. auropunctata* had different impacts on different spider families in that the dominant spider family, Linyphiidae (67.85% of the individuals), was highly affected by high densities of the ant, compared to other families.

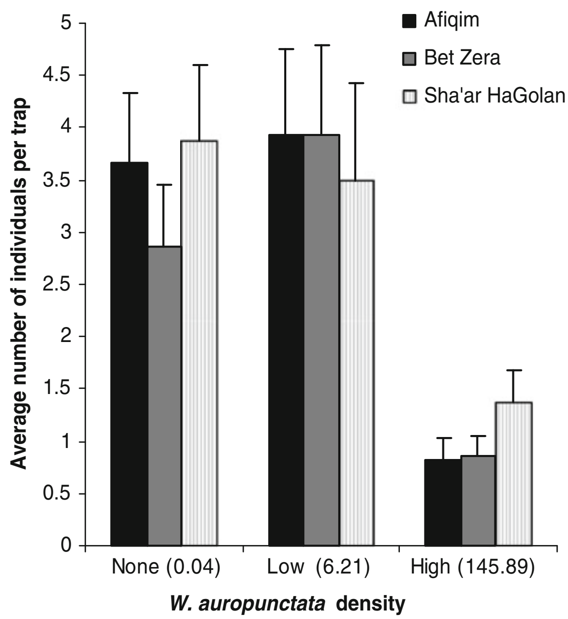

Fig. 3 Average (± SE) number of spider individuals caught in pitfall traps at different densities of *Wasmannia auropunctata* (the average number of *W. auropunctata* per trap is indicated in parenthesis)

Similar significant reductions in beetle abundances and species richness (Fig. 4; Table 7) were noted at high *W. auropunctata* densities, but the redundancy analysis (RDA) did not reveal any significant factors.

Discussion

Wasmannia auropunctata is a globally known invasive species that generally occupies tropical and

Table 6 Analyses of abundances and species richness of spiders collected by pitfall traps in three villages: Afiqim, Bet Zera, and Sha'ar HaGolan

Treatment	*W. auropunctata*'s density			ANOVA		χ^2 tests		
	None	Low	High	*F*	*P*	χ^2	*df*	*P*
Abundance								
Afiqim	3.67 ± 0.66	3.94 ± 0.81	0.81 ± 0.22	9.39	<0.001			
Bet Zera	2.87 ± 0.6	3.93 ± 0.86	0.87 ± 0.19	5.84	0.006			
Sha'ar HaGolan	3.88 ± 0.73	3.5 ± 0.92	1.38 ± 0.3	4.17	0.023	33.49	6	<0.0001
Species richness								
Bet Zera	2 ± 0.34	2.14 ± 0.41	0.87 ± 0.19	3.65	0.034			
Sha'ar HaGolan	1.81 ± 0.25	1.5 ± 0.35	1.25 ± 0.29	1.2	0.31	9.11	4	0.059

The counts data were square root transformed and analyzed by one-way ANOVA. The significance of the combined probabilities of two or three villages was tested by χ^2 (Data presented–average per trap ± SE)

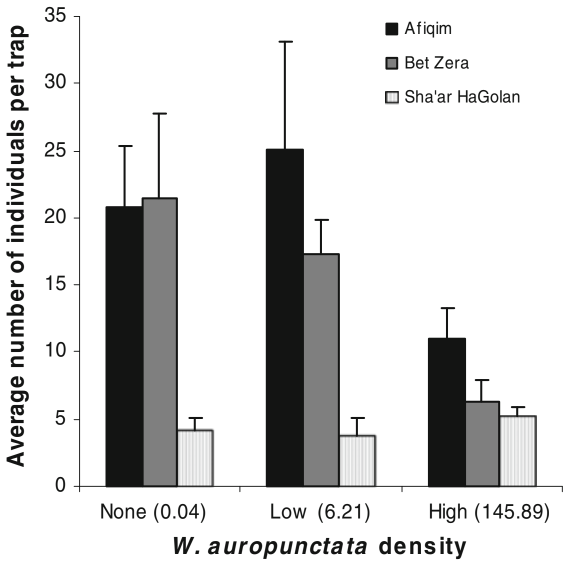

Fig. 4 Average (± SE) number of beetle individuals caught in pitfall traps at different densities of *Wasmannia auropunctata* (the average number of *W. auropunctata* per trap is indicated in parenthesis)

subtropical habitats (McGlynn 1999) climatically similar to those of its native range in South and Central America. In contrast to the prediction that invasive ants will establish only in habitats similar to those in their native range (Holway 1998; Hoffmann et al. 1999), in Israel *W. auropunctata* is established in climatic conditions that are very different from those found in their native and other introduced habitats worldwide (see below). Israel's climate is typified by dry summers and greater temperature extremes. It is possible that in Israel *W. auropunctata* was first established in irrigated gardens in the warm climate of the Jordan Valley, and only afterwards spread into less favorable habitats (the Golan Heights, Arava Valley, etc.). Bytinski-Salz (1966) claimed that irrigation in the Mediterranean climate of Israel simulates a subtropical or tropical climate, facilitating the dispersal of pests of tropical origin. Indeed, the ants seem to be confined almost entirely to irrigated habitats, most frequently inside villages, or at most in open and undisturbed areas adjacent to irrigated land or natural water sources. It is likely that the ants enter houses during summer in search of moisture, since most stinging appears to have occurred in kitchens and bathrooms during that season. The significance of wet conditions to the ant's spread was emphasized by Meier (1994), who demonstrated that following an extraordinary El Ninõ year, *W. auropunctata* expanded its distribution in the Galapagos Islands to arid habitats. A similar trend was shown in studies on the distribution of the red imported fire ant (*Solenopsis invicta*) in the US, where at first the ants were established in habitats with similar climate to their native range, but later they expanded their distribution into climatically dissimilar habitats (Fitzpatrick et al. 2007).

Despite the climatic differences between Israel and the ant's tropical and subtropical range, its ecology seems to be quite uniform throughout its range. *W. auropunctata* was found to nest in superficial nests in the ground under stones and inside hollow parts of plant material such as tree bark, similar to the species behavior in tropical habitats (Wetterer and Porter 2003). Nest size is diverse–from dozens of workers to

Table 7 Analyses of abundances and species richness of beetles collected by pitfall traps in three villages: Afiqim, Bet Zera, and Sha'ar HaGolan

Treatment	*W. auropunctata*'s density			ANOVA		χ^2 tests		
	None	Low	High	*F*	*P*	χ^2	*df*	*P*
Abundance								
Afiqim	20.73 ± 4.63	25.06 ± 8	10.94 ± 2.38	1.32	0.27			
Bet zera	21.4 ± 6.39	17.29 ± 2.6	6.27 ± 1.6	4.45	0.017			
Sha'ar HaGolan	4.13 ± 0.93	3.75 ± 1.33	5.19 ± 0.77	1.06	0.36	12.81	6	0.046
Species richness								
Bet zera	3.8 ± 0.41	5.21 ± 0.56	2.87 ± 0.35	6.71	0.003			
Sha'ar HaGolan	2.25 ± 0.4	1.88 ± 0.37	3.13 ± 0.33	2.65	0.084	16.57	4	0.002

The counts data were square root transformed and analyzed by one-way ANOVA. The significance of the combined probabilities of two or three villages was tested by χ^2 (Data presented–average per trap ± SE)

thousands, with or without brood, and with 0–100 queens per nest (Vonshak, unpublished data). The studied colonies probably comprise satellite nests of larger colonies, as no aggression was found between them (Vonshak et al. 2009).

Introduction pathways and spread inside Israel

Wasmannia auropunctata was introduced into Israel as early as 1998, judging from reports of stinging made by residents of the infested areas. Definite identification of the species was made in 2005 after specimens were received through the Ministry of Agriculture and Rural Development.

Genetic analysis at 12 microsatellite loci points to a single introduction of one queen and one male genotype in Israel (Vonshak et al. 2009). Most alleles observed in Israel were not found in any of the invasive populations, including a population from Gabon (J. Foucaud and A. Estoup, personal communication), refuting an early hypothesis based on historical records of wood imports that the ant was introduced from Gabon. We therefore assume that *W. auropunctata* may have arrived from sites located in its native range. Since wood was also imported from Brazil to the plywood factory in Afiqim, this country may have been the origin of the Israeli population. *W. auropunctata*'s distribution in Israel indicates that human activities account for its dispersal in this area, as it was found outside villages only in places visited regularly by people (e.g., cemeteries). In addition we found at least two human-mediated dispersal pathways–potted plants and logs.

Impact on the arthropod fauna

We found a remarkable impact of the little fire ant on abundance, species richness, and community composition of the local ant species. Most ant species sampled were highly affected by *W. auropunctata,* but only at high densities of this invasive ant. However, a closer inspection of species diversity revealed that a few tramp species, living near human residences, were also found in lower frequencies in low-density plots compared to control plots, whereas other species were either unaffected or even found at higher frequencies in low-density plots. Most species nevertheless were absent at high densities. For example, while *Tetramorium davidi* is a native species that might get an advantage from the decrease in the incidence of other species, *Paratrechina longicornis* is a tramp species that could be more tolerant of low densities of *W. auropunctata* compared to other species as it is opportunistic; opportunist ants can continue foraging in the presence of dominant species (Hölldobler and Wilson 1990). Another species, *Monomorium clavicorne*, seemed to be unaffected by *W. auropunctata*'s presence, even at high densities. This tiny ant (1.2 mm) is distributed in tropical Africa and the Middle East (Collingwood 1985), and it is widespread in Israel. It is ecologically similar to *W. auropunctata*, nests under stones and recruits to bait in large numbers. It is possible that this species can tolerate *W. auropunctata*'s presence to some extent, possibly owing to the passivity of the workers, which were observed feeding from the same bait as *W. auropunctata* (similar to the reports of Grangier et al. 2007, dealing with ants of the genus *Cyphomyrmex*). The endemic species sampled in this study are widely distributed in Israel, and therefore are not threatened by *W. auropunctata* to date. Nevertheless, as *W. auropunctata* has also been established in natural habitats, its future spread may threaten other species, especially those with very localized distribution.

King and Tschinkel (2006) suggested that *Solenopsis invicta* ants do not affect ant community structure in their invaded habitats, and that the observed reduction in local ant species is a result of habitat disturbance rather than competition. This is definitely not the case for *W. auropunctata* in Israel. As all research plots with different *W. auropunctata* densities were located at similarly disturbed habitats (irrigated public gardens in three adjacent villages), the significant impact found on local ant species cannot be explained by habitat disturbance but rather by *W. auropunctata* presence and density.

We found a negative impact of the little fire ant on spider abundance, richness, and community composition and structure. Spiders could be affected either directly through predation by *W. auropunctata* or indirectly, because of the reduction in general arthropod abundance. Different spider families were affected differently, with the strongest impact on the most abundant family, the sheet-web spider family (Linyphiidae). Members of this family have agricultural importance as they reduce agricultural crop pest abundances (Symondson et al. 2002). Thus their reduction could lead to an indirect negative impact of *W. auropunctata* on agriculture. Beetle abundances and species richness were also negatively affected by *W. auropunctata*, but not their community structure. The observed decline in ground arthropod populations conforms to observations in previous studies from this ant species' invasive range in the tropics (Clark et al. 1982; Lubin 1984; Le Breton et al. 2003). Conversely, in its native range, *W. auropunctata* is not a dominant species (Tennant 1994), except in disturbed habitats (e.g. Armbrecht and Ulloa-Chacon 2003; Orivel et al. 2009). Wetterer and Porter (2003) suggested that *W. auropunctata* is a less serious pest in more temperate areas such as Florida, the Bahamas, and Bermuda, compared to its serious impact in the Solomon Islands, Vanuatu, and Gabon. However, based upon our study we conclude that *W. auropunctata* also has a dramatic impact on the local arthropod fauna in a more temperate area.

In sum, it appears that *W. auropunctata* arrived at Kibbutz Afiqim in northern Israel on logs imported from Brazil to the local plywood factory and later dispersed in Israel through commercial transport of chopped wood, logs, and potted plants. The ants have a substantial negative impact on the local myrmecofauna in heavily infested villages as well as on the abundance of other arthropods. This study revealed the possible consequences of the continued spread of *W. auropunctata* in a Mediterranean climate. So far there is no indication of impact on agriculture, although we found the ants near fish ponds and on the border of agricultural fields. Although ants were found in open landscapes and in natural habitats, their distribution appears to be limited at present by their need for water. Water availability could be key to the spread of *W. auropunctata* in our region. The ability of *W. auropunctata* to thrive in a Mediterranean climate suggests that we should re-evaluate its potential for spread in broader climatic regions than considered so far.

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