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**Biological Invasions**

ISSN 1387-3547

Biol Invasions  
DOI 10.1007/s10530-014-0690-5



 Springer

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# Habitat degradation and introduction of exotic plants favor persistence of invasive species and population growth of native polyphagous fruit fly pests in a Northwestern Argentinean mosaic

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Received: 9 April 2013 / Accepted: 25 March 2014  
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**Abstract** Expansion of agricultural land is one of the most significant human alterations to the global environment because it entails not only native habitat loss but also introduction of exotic species. These alterations affect habitat structure and arthropod dynamics, such as those among host plants, tephritid fruit flies, and their natural enemies. We compared abundance and dynamics of pest and non-pest tephritids and their natural enemies over a mosaic of habitats differing in structure, diversity and disturbance history on the Sierra de San Javier in Tucuman, Argentina. Our prediction was that conserved habitats would be more resistant to the establishment and spread of invasive tephritid species due in part to a greater abundance of natural enemies, a greater diversity of

native species in the same family and trophic level, and a greater wealth of biotic interactions. We further predicted that native species with broad host ranges should be more sensitive to habitat loss yet more competitive in less disturbed habitats than generalist native and exotic species. We found that environmental degradation, and introduction and spread of exotic host plants strongly affected distribution patterns, abundance, and phenology of native and exotic tephritids. Monophagous tephritid species and several specialized parasitoids were more sensitive to habitat loss than polyphagous species and parasitoids exhibiting a wide host range. In contrast, native monophagous species and native parasitoids appeared to exclude the invasive Mediterranean fruit fly from conserved patches of native vegetation. Nevertheless, the Mediterranean fruit fly persisted in uncontested exotic host plants and thrived in highly degraded urban landscapes.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10530-014-0690-5) contains supplementary material, which is available to authorized users.

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**Keywords** *Ceratitidis capitata* · *Anastrepha* spp. · Parasitoids · Fragmentation · Yungas

## Introduction

Habitat loss, landscape fragmentation, and invasion of non-native species have been recognized as the most important threats to global diversity (Didham et al. 2007). The establishment and spread of invasive species in the environment depends upon factors such

as escape from natural enemies, competitive displacement of native species, or the invader ability to occupy empty niches (Kolar and Lodge 2001; Reitz and Trumble 2002; Duyck et al. 2004, 2007). Such factors in turn are closely linked to environmental resistance (biotic forces that hinder the establishment of species in a new location) and evolutionary history (Simberloff and Von Holle 1999) and can be severely affected by environmental degradation (Reitz and Trumble 2002).

Expansion of agricultural land is widely recognized as one of the most significant human alterations to the global environment (Matson et al. 1997) because it entails not only native habitat loss but also introduction of exotic species. Agricultural alteration results in severe ecosystem simplification with shortened trophic chains and reduced species diversity (Landis et al. 2000). Simplification in turn has a profound influence on the abundance and composition of associated biota. Whose interactions can also produce new forms of environmental degradation (Simberloff 2003).

Habitat structure has been shown to play an important role in pest species dynamics. A good example of habitat driven pest dynamics are Tephritid fruit flies and their natural enemies. Host plant distribution and abundance, vegetation surrounding crops, and distribution of essential resources (food, shelter, oviposition substrates) strongly influences behavior, distribution, and abundance of these insects (Aluja and Birke 1993; Aluja et al. 2012).

In general, distribution and abundance of pest tephritids have been studied in strict relation to agricultural production and import and export of fruit commodities (Virgilio et al. 2011). However, it has become evident that environmental degradation, climatic change, and increased international trade are modifying distribution patterns of many insect species, with tephritids expanding their range to regions that were previously un-accessible or inadequate (Duyck et al. 2004, 2006a, 2007 De Meyer et al. 2008, 2010; Aluja et al. 2011). Upon invasion, the establishment and spread of exotic species depends on complex interactions between natural and man regulated processes (Virgilio et al. 2011), of these interactions several instances of competitive displacement have been documented (Duyck et al. 2004) but their relationship to habitat fragmentation, introduction and spread of exotic plant species and interactions with natural enemies and competitors, with few exceptions,

have not been studied in detail (Duyck et al. 2006b, 2007).

In Argentina *Ceratitis capitata* (Wiedemann) (exotic) and *Anastrepha fraterculus* (Wiedemann) (native) are two highly polyphagous tephritid species that cause significant annual damage to fruit production (Spinetta 2004; Ovruski et al. 2003; Oroño et al. 2005). In contrast, *Anastrepha schultzi* Blanchard (Blanchard) is a native oligophagous species of no economic importance whose larvae develop almost exclusively in fruit of the native *Juglans australis* Grisebach, and to a lesser degree in the exotic *Psidium guajava* L. (Schliserman et al. 2004). According to a model proposed by Duyck et al. (2004), *C. capitata* has been able to displace several species of *Anastrepha* in the Americas after its introduction and spread early in the twentieth century. However a careful look at distribution records suggests that *C. capitata* populations only thrive in introduced host plants that are not recognized and locally exploited by native species of *Anastrepha* (e.g. Coffee in Central America; citrus in South America)(Niklaus-Ruiz Borge and Basedow 1997; Ovruski et al. 2003) and that such populations are not abundant in pristine environments where native hosts prevail (Da Silva et al. 1996). Such patterns could be due to the fact that *C. capitata* has a shorter life cycle and much wider host range than *Anastrepha*, which in ecological terms would define this species as an r strategist, with low competitive ability but high environmental plasticity.

Northeastern Argentina has a thriving citrus, sugar cane, and soybean production. Agricultural development and the growth of human settlements in the region have produced deforestation of native vegetation and transformation and degradation of natural ecosystems. As a consequence, the landscape has acquired a mosaic aspect as defined by Forman (1997). It is common to find in the surroundings of crops in the western sector of the Tucumán province, areas of tropical forest with different degrees of disturbance and different histories of use and abandonment. These wild vegetation areas correspond to the austral sector of the forest known as “Yungas” which covers de foothills of the oriental slope of the Sierra de San Javier in Tucumán (Grau et al. 1997).

Studies on the interaction between fruit flies and their habitat are scarce and mostly focused on quantifying distribution of adult pestiferous species, and behavioral patterns such as feeding, mating, egg-

laying and resting (Prokopy 1976; Smith and Prokopy 1981; Malavasi et al. 1983; Hendrichs et al. 1991; Aluja et al. 1993; Aluja and Birke 1993). Studies such as those of Bateman (1972), Aluja (1993), Kovaleski et al. (1999), and Sugayama and Malavasi (2000) refer to the type of dispersive (within the habitat) and non-dispersive (across habitats) movements of fruit flies. The majority of studies have been performed in agroecosystems while information on natural and urban environments is scarce. More recently, Virgilio et al. (2011) report a quantitative comparison of tephritid species in tropical forests and rural areas of the Democratic Republic of Congo, yet studies analyzing species interactions and their effects on population dynamics, abundance and distribution are yet to come. Given the magnitude of the threat of biological invasions to global biodiversity, agricultural production and the economy in general (Pimentel et al. 2005) it becomes highly relevant not only to identify distinctive properties of invasive species, but also to characterize the degree of invasiveness susceptibility of potential habitats (Richardson and Pysek 2006).

Habitat destruction and replacement of native vegetation with agricultural crops drastically influences diversity, abundance, and behavior of fruit fly parasitoids. In particular because wild plant species play an important role as reservoirs during periods of commercial host scarcity (López et al. 1999; Sivinski et al. 1997; Aluja et al. 2003b; Ovruski et al. 2004). Habitat degradation, can be coupled with persistence and population growth of invasive species such as *C. capitata*, which are not controlled by guilds of native parasitoids (Ovruski et al. 2000). Ovruski (1995), Canal and Zucchi (2000), and Ovruski et al. (2004) report that the majority of native braconid species in South America are unable to parasitize *C. capitata* larvae, or when they do, defensive physiological mechanisms hindering development may result in low percentages of parasitism.

Studying fruit fly population dynamics and inter-specific interactions in different types of environments can also yield useful information for area-wide management and conservation purposes. It is necessary to focus on the fruit fly problem from a broader perspective paying more attention to the ecology of these organisms in natural and altered environments that could be acting as a source or sink. Such studies can facilitate development and application of

environmentally friendly control methods (Aluja and Rull 2009), that have little negative impact on the environment such as biological control, cultural control and the sterile insect technique.

To increase the breadth of our understanding on fruit fly and parasitoid dynamics and document exotic and native species interactions in continental South America, we compared abundance and dynamics of pest and non-pest tephritids and their natural enemies (parasitoids) on a mosaic of habitats differing in structure, diversity and disturbance history on the western slopes of the Sierra de San Javier. Our prediction was that less disturbed habitats would be more resistant to invasive species due in part to a greater abundance of natural enemies, a greater diversity of native species in the same family, and their interaction. We further predicted that native species with broad host ranges should be more sensitive to habitat loss yet better able to exclude generalist native and exotic species from less disturbed habitats.

## Materials and methods

Field work lasted for 26 months, and was carried out during two periods, the first from December 2001 to December 2002 and the second from January 2003 to January 2004. Meteorological data (minimum and maximum temperatures and precipitation) were obtained during both periods from the Sierra de San Javier Park using a thermograph and a pluviometer located at 700 masl.

### Study area

The study area belongs within a region known as the Yungas, a cloud or mountain forest on the oriental slopes of the Sierra de San Javier, between 26°48'02,3" and 26°53'05,7" of Southern latitude and 65°18'22,5" and 65°20'17,1" of Western longitude, and between 400 and 700 masl. The area encompasses the departments of Yerba Buena and Lules, 9 km West of the city of San Miguel de Tucumán and covers a total surface of 42 km<sup>2</sup> (10,5 km long 4 km wide). According to Koppeñs classification, the climate in the region is moderate-temperate and rainy with a humid summer and dry winter (Cwa) (Torres-Bruchmann 1976). As a

consequence of logging, human settlement, permanent and transitional agriculture, and to a lesser degree cattle raising, during the past few decades the cloud forest landscape became heterogeneous (Brown et al. 2001) with three different environments varying in disturbance degree.

The sites were selected for each of the three types of environment using maps and satellite images from LANSAD TM República Argentina, San Miguel de Tucumán 2766-17 (1:100.000 scale) and aerial photographs (1:5,000 scale) taken during 2001 on a flight sponsored by the Instituto de Geografía of the Facultad de Filosofía y Letras of the Universidad Nacional de Tucumán (UNT).

#### Habitat characterization

To characterize vegetation within sites a sample was performed by establishing five 100 m long  $\times$  10 m wide transects spaced by 100 m from each other at each location. Within transects, every individual bush or tree with more than 10 cm of diameter at breast height (DBH) was identified measured. The number of plant families and species represented at each site was recorded.

#### Secondary forest

Composed of native forest, altered by agriculture and cattle raising and then gradually abandoned from 1970 due to urbanization of the human population, loss of soil fertility in áreas with steep slopes (Grau et al. 2007), and the creation of the Sierra de San Javier Park, a protected area under the Universidad Nacional de Tucumán. The area was subsequently recolonized by native plant species from the Yungas, resulting in a combination of native [*Alophylus edulis* (st. Hill.) Radlkofer, *Cupania vernalis* Cambess., *Heliocarpus popayanensis* H.B.K., *Juglans australis* Griseb., *Solanum riparium* L., *Tecoma stans* (L.), etc.], exotic Invasive vegetation (*Gleditsia amorphoides* (Griseb.) Taub. *Ligustrum lucidum* Ait. *Morus Nigra* L., etc. (Grau et al. 1997) and exotic non invasive vegetation (*Citrus aurantium* L., *Eriobotrya japonica* Lind., *Prunus persica* (L.) and *Psidium guajava* L.

This environment yielded abundance values of  $65.70 \pm 10.2$  of trees and shrubs, with DBH greater than 10 cm, every 2,000 m<sup>2</sup>; of which  $44.27 \pm 9.88$  %, were exotic species and was represented by two

collection sites, one located in the Lules department (between 26°47'6,4" and 26°47'42,4" southern latitude and 65°19'44,4" and 65°20'4,8" western longitude) and the other one in the Yerba Buena department (between 26°51'00,4" and 26°51'07,4" southern latitude and between 65°19'21,8" and 65°20'17,1" western longitude).

#### Organic orchards

Areas with crop management practices that do not include pesticide application. The main crop is citrus and to a lesser degree other fruit species such as peaches, mangos, avocados, etc. Exotic plant species predominate. This environment yielded abundance values of  $48.70 \pm 10.47$  of trees and shrubs with a DBH greater than 10 cm, every 2,000 m<sup>2</sup>; of which  $83.08 \pm 5.91$  %, were exotic species. One of the collection sites was located in the in the Yerba Buena department (between 26°48'52,5" and 26°48'57,3" southern latitude and 65°18'51,6" and 65°20'17,1" western longitude) and the other one in Lules (between 26°49'53" and 26°50'21,8" southern latitude and between 65°18'22,5" and 65°18'50,5" western longitude).

#### Urban

An environment characterized by the establishment of households. Existing vegetation is that found on paths and gardens with a strong preponderance of exotic species. Abundance values for this environment were  $18.40 \pm 1.35$  for trees and shrubs with a DBH greater than 10 cm, every 2,000 m<sup>2</sup>; of which ( $73.74 \pm 5.91$ ) %, were exotic species. This environment was represented by a site in the Lules department (between 26°53'00,8" and 26°53'05,7" southern latitude and 65°18'23" and 65°19'3,9 western longitude) and the other one in the Yerba Buena department (between 26°48'02,3" and 26°48'44,5" southern latitude and between 65°17'54,3" and 65°18'28,8" western longitude).

#### Fruit collection, and fly trapping

Ripe fruit was collected every 15 days from December 2001 to January 2004, to record variation in fruit fly infestation levels, proportion of adult emergence, and emergence of fruit fly parasitoids. Collections consisted

in 1 kg-sample per host plant species at each study site. The following ten plant species in seven plant families were recovered across sites: *Mangifera indica* L. (mango) (Anacardiaceae), *Diospyros kaki* L. (persimmon) (Ebenaceae), *Juglans australis* Griseb. (walnut) (Juglandaceae), *Persea americana* Mill. (avocado) var. Americana, cv. Collinson y cv. Tonnage (Lauraceae), *Psidium guajava* L. (guava) (Myrtaceae), *Prunus persica* (L.) Batsh (peach), *Eriobotrya japonica* Lind. (loquat) (Rosaceae), *Citrus aurantium* L. (sour orange), *C. sinensis* L. (Osbeck) (sweet orange) y *C. paradisi* Macfadyen (grapefruit) (Rutaceae).

Adult fly trapping was carried out from January 2002 to January 2004 with trap services spaced every 15 days. To monitor *Anastrepha* spp. and *C. capitata* adults of both sexes, Multilure<sup>®</sup> traps were baited with three 3, 3 gr pellets of hydrolyzed protein + borax, diluted in 400 ml of water. A total of 29 Multilure<sup>®</sup> traps were deployed across the 6 sites. Traps were positioned in the upper half of tree canopies well within tree foliage following guidelines established in the IAEA (2003) fruit fly trapping manual. At each site, traps were spaced within a linear transect separated by distances of 100 m. Traps were rotated on fruiting host trees following the maturation phenology of the main fruit hosts. By rotating the traps in such manner it is possible to follow more accurately fruit fly populations throughout the year (IAEA 2003).

#### Fruit processing/pupal recovery and trap captures

Field collected fruit were washed with a 20 % sodium benzoate solution, counted, weighted and individually placed in plastic containers with a thin layer of sand and covered with a piece of Voile cloth. Individually held fruit was kept under ambient environmental conditions for a month, except during winter when containers were held at  $26 \pm 1$  °C and  $70 \pm 5$  % R.H. Fruit was checked on a weekly basis to recover pupae which were identified at the fruit fly genus level. After a month from collection, all fruit were dissected to recover remaining larvae (dead or alive). Pupae were kept in plastic containers, with sand and a Voile cover until emergence of adults (fruit fly and parasitoids) for taxonomic identification at the species level. Adults recovered from traps were counted sexed and identified in the laboratory. All identified material (insects and plants) were deposited in the Fundación Miguel Lillo permanent collection as voucher specimens.

#### Data analysis

Paired *t* tests were used to compare results from the two study periods, and meteorological conditions.

Mixed effect linear models were used to evaluate the effect of environmental variables on abundance of *C. capitata*, *A. fraterculus* and *A. Schultzi* (trap captures), infestation levels (larvae per Kg of fruit), and percent parasitism ([parasitoid number/(parasitoid number + fly number)] \* 100). These models are appropriate for analysis of autocorrelated data, in this case by sampling period (time). We choose to use a mixed model with random intercepts corresponding to collection/sampling month and fixed effects corresponding to the following independent variables within each month: host fruit (loquat, peach, walnut, guava and grapefruit), type of environment (secondary forest, organic orchards and urban) and the two periods of collections (I = December 2001 to December 2002 and II = January 2003 to January 2004).

Mixed effect linear models were also used to analyze variation of *C. capitata*, *A. fraterculus* and *A. Schultzi* captures, standardized through calculation of the FTD (Flies/trap/day) index, as a function of the same environmental variables described above.

Model selection was based on Akaike's Information Criterion (AIC) values. R and Statistica V7 software were used to run analyses.

## Results

#### Temperature and rainfall fluctuation

There were significant statistical differences between temperatures from the two study periods (I = 2001–2002; II = 2003–2004). Average maximum temperature was for period I:  $27.32 \pm 7.37$  °C and for period II  $28.56 \pm 7.56$  °C [n = 365, d.f. = 364,  $t = -3.25$ ,  $p = 0.001$ ]. Average minimum temperature for period I was  $12.73 \pm 5.4$  °C and for period II  $13.68 \pm 5.70$  °C [n = 365, d.f. = 364,  $t = -3.05$ ,  $p = 0.001$ ]. The coldest months were June and July, with an average temperature of 6 °C, while the warmest month was January with temperatures reaching 37.5 °C. No statistical differences in annual cumulative rainfall (n = 365, d.f. = 364,  $t = 1.48$ ,  $p = 0.14$ ) were observed between the two study periods. Cumulative rainfall during the entire study

was 2,280.12 mm with 1,419.76 mm recorded during the first period and 860.36 mm during the second. Ninety one percent of precipitation occurred from October to April, with March being the rainiest month.

### Host plant phenology

Fruit from a total of 305 trees belonging to 10 different host species were sampled. Twelve thousand two hundred and ninety-two individual fruits were collected, totalling 648.79 kg. Of these sampled plant species loquat, peach, walnut, guava, avocado and grapefruit were represented in the three environments, while mango, kaki and sweet orange were found in the urban landscape and organic orchards only and sour orange in the secondary forest and organic orchards only. During sampling, hosts exhibited different fruiting phenology, with some degree of overlap (Fig. 1).

### Tephritid species and associated parasitoids

Three species of Tephritidae were recovered during fruit sampling: *C. capitata*, *A. fraterculus* and *A. schultzi*. All host species except *Persea americana* were infested with *C. capitata* and *A. fraterculus*, while *A. schultzi* was only found infesting *Juglans australis* and *Psidium guajava*.

A total of 30,006 tephritid larvae were recovered from collected fruit, 50.84 % (15,255 larvae) of which corresponded to *C. capitata* and 49.16 % (14,751 larvae) to *Anastrepha* spp. Infestation levels for *C. capitata* reached an average of 28.16 larvae/kg and 27.23 larvae/kg for *Anastrepha* spp ( $n = 26$ , d.f. = 50  $T = 0.44$ ,  $p = 0.66$ ). Of a total of 18,292 adults emerged in the laboratory 63.40 % corresponded to *C. capitata*, 30.44 % to *A. fraterculus* and 6.16 % to *A. schultzi* (Supplemental Table 1).

Trapping yielded a total of 14,558 *C. capitata* adults, and 3,338 *A. fraterculus* adults, while only 193 *A. schultzi* adults were recovered.

Out of the 10 host plants sampled, five recorded parasitism by hymenopterans. From the total pupae recovered 786 parasitoids from four species emerged. These were: *Doryctobracon areolatus* (Szépligeti), *Doryctobracon brasiliensis* (Szépligeti), *Opius* (*Bellopius*) *bellus* (Gahan) (all belonging to Braconidae, Opiinae subfamily); and *Aganaspis pelleranoi* (Bréthes) (Figitidae, subfamily Eucoilinae). *A. pelleranoi*,

was the most abundant, totaling 54 % of all identified parasitoids. Braconidae, despite the fact of including three species, only amounted to 46 %. Among Braconidae *D. brasiliensis* was the most abundant followed by *D. areolatus* and *O. bellus*. The host plant yielding the greatest parasitoid abundance was peach with 402 individuals, followed by walnut with 331, guava with 43, loquat with 9, and sour orange with 1, the remaining host species failed to yield parasitoids (Supplemental table 2). *A. pelleranoi* was the only species exploiting both *C. capitata* and *Anastrepha* spp., while the remaining species only parasitized *Anastrepha* spp.

### Host plant—fruit flies—parasitoids and environment interaction

Only those host plants present in the three environments were considered for analysis, and in the case of *A. schultzi*, only walnut and guava were considered due to the fact that these two plants are the only hosts for this species.

Model selection (based on AIC) indicated that the greatest number of *C. capitata*, emerging from collected fruit depended on the interaction between urban environment and peach availability (coefficient = 16.09, SE = 56.51,  $t$  value = 2.87,  $p$  value = 0.01) and on the interaction between urban environment and walnut (coefficient = 177.52, SE = 59.32,  $t$  value = 2.99,  $p$  value = 0.003). Additionally, an increase in walnut infestation was recorded during the second (II) period (coefficient = 148.81, SE = 50.58,  $t$  value = 2.94,  $p$  value = 0.0004) (Fig. 2a).

*Ceratitis capitata* infestation levels (larvae/kg of fruit) were positively related with the interaction between the urban environment and both peach (coefficient = 92.71, SE = 34.90,  $t$  value = 2.66,  $p$  value = 0.01), and walnut (coefficient = 116.37, SE = 36.56,  $t$  value = 3.18,  $p$  value = 0.002). Besides, infestation was greater during period II, both for peach (coefficient = 73.04, SE = 29.29,  $t$  value = 2.49,  $p$  value = 0.01) and walnut (coefficient = 82.33, SE = 31.39,  $t$  value = 2.62,  $p$  value = 0.01) (Fig. 2b).

The greatest abundance of *A. fraterculus*, emerging from collected host fruit, was related to the presence of walnut (coefficient = 37.70, SE = 15.64,  $t$  value = 2.41,  $p$  value = 0.02), and the interaction between organic orchards and guava (coefficient = 39.63,



**Fig. 1** Fruiting phenology in a landscape mosaic of altered Yungas forest, organic orchards, and urban landscape patches. In *black* available, in *gray* highly available, in *white* absent

Fruit Species	Period		December 2001 – January 2004																							
	Month		J		F		M		A		M		J		J		A		S		O		N		D	
	Fortnight		1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
<i>Eriobotrya japonica</i>																										
<i>Citrus aurantium</i>																										
<i>Citrus sinensis</i>																										
<i>Prunus persica</i>																										
<i>Juglans australis</i>																										
<i>Manguifera indica</i>																										
<i>Diospyros kaki</i>																										
<i>Psidium guajava</i>																										
<i>Persea americana</i>																										
<i>Citrus paradisi</i>																										

SE = 14.62, *t* value = 2.71, *p* value = 0.01). By contrast, when peach could be found in organic orchards, there was a reduction in the number of recovered *A. fraterculus* (coefficient = -36.10, SE = 15.22, *t* value = -2.37, *p* value = 0.02) (Fig. 2a).

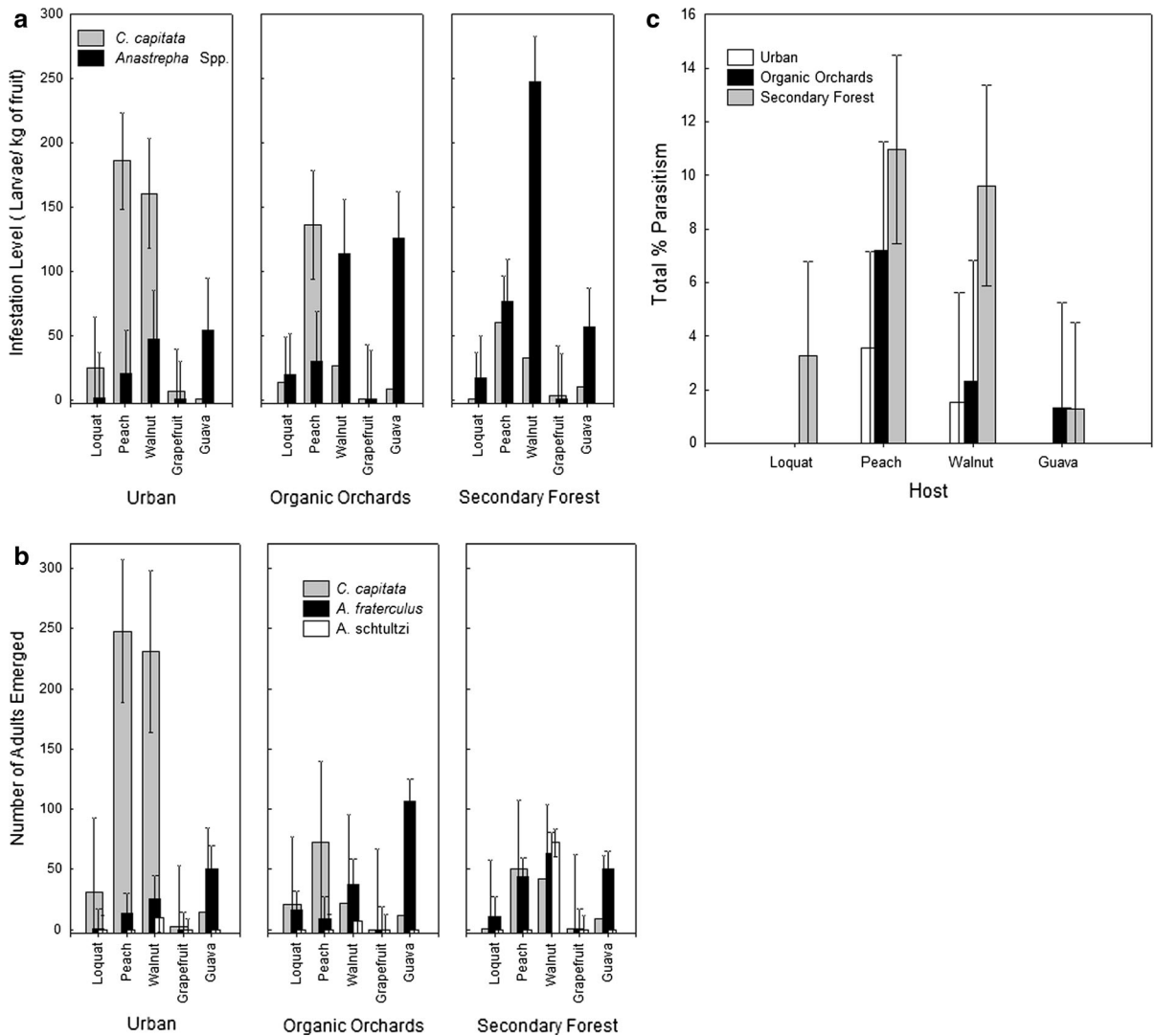
Abundance of *A. schultzi* emerging from collected fruit, was positively related to secondary forest, and walnut availability in any of the three environments (coefficient = 39.43, SE = 20.93, *t* value = 1.88, *p* value = 0.05). There was a general trend for *A. schultzi* numbers to decrease in the urban environment (coefficient = -60.42, SE = 14.05, *t* value = -4.30, *p* value = 0.0001) and organic orchards (coefficient = -60.81, SE = 15.04, *t* value = -4.04, *p* value = 0.0002). The presence of this fly species in the urban environment (coefficient = 60.22, SE = 19.51, *t* value = 3.08, *p* value = 0.0003) and organic orchards (coefficient 60.59, SE = 19.72, *t* value = 3.07, *p* value = 0.003) was dependent on their interaction with guava availability (Fig. 2a).

Greatest *Anastrepha spp.* infestation levels (larvae/kg) were related with peach (coefficient = 73.29, SE = 27.60, *t* value = 2.65, *p* value = 0.01), walnut (coefficient = 213.86, SE = 29.44, *t* value = 7.26, *p* value = 0.001), and guava (coefficient = 52.58, SE = 27.03, *t* value = 1.99, *p* value = 0.05)

availability and with the interaction between organic orchards and guava (coefficient = 65.58, SE = 33.50, *t* value = 1.96, *p* value = 0.05). By contrast, infestation levels were low for walnuts in organic orchards (coefficient = -129.56, SE = 36.74, *t* value = -3.53, *p* value = 0.0005) and in the urban environment in general (coefficient = -181.62, SE = 36.29, *t* value = -5.00, *p* value = 0.05) (Fig. 2b).

Regarding % parasitism, the later was positiveley related to secondary forest, loquat, and period I (coefficient = 4.64, SE = 1.59, *t* value = 2.91, *p* value = 0.004). It was also positively related to peach (coefficient = 7.62, SE = 2.23, *t* value = 3.41, *p* value = 0.0008), and walnut (coefficient = 7.27, SE = 2.37, *t* value = 3.06, *p* value = 0.003) availability. Percentages experienced a significant decrease in urban environments (coefficient = -5.55, SE = 2.87, *t* value = -1.93, *p* value = 0.05) (Fig. 2c).

Because the remaining host plants were not represented in the three environments and yielded a low number of replicates, it was not possible to perform statistical analyses to explain variation of response variables depending on their availability. However, it can be observed in general lines that sour orange, sweet orange, Mango and Persimmon, tended to yield greater infestations by *C. capitata* than by *A. fraterculus*. Additionally, on these hosts, infestations by *C.*



**Fig. 2** Interactions among host fruit, fruit flies, and parasitoids with three different types of landscape elements (secondary forest, organic orchards, and urban landscape) **a** Total number

( $\pm$ SE) of adults fruit flies emerged from kg of collected fruit, **b** Fruit fly Infestation level (larvae/kg of fruit ( $\pm$ SE)) and **c** Total % ( $\pm$ SE) parasitism

*capitata* were greater in the urban environment (Table 1).

Seasonality and environment

A Generalized Linear Mixed Model (LMM) run to evaluate the influence of season according to environment revealed that *C. capitata* FTDs were positively related (coefficient = 0.23, SE = 0.06, *t* value = 3.78, *p* value = 0.0002) to the interaction between urban environments and the last months of the year (December and January) (Fig. 3a).

The greatest *A. fraterculus* FTDs were significantly associated to secondary forest (coefficient = 0.40, SE = 0.11, *t* value = 3.80, *p* value = 0.0002), first months of the year (March and April mostly) (coefficient = -0.04, SE = 0.01, *t* value = -2.75, *p* value = 0.02) and to samplig period II (coefficient = 0.06, SE = 0.03, *t* value = 2.35, *p* value = 0.02). A significant decrease of FTDs was observed for the urban environment (coefficient = -0.20, SE = 0.07, *t* value = -2.93, *p* value = 0.004), with captures related to the months of November and

December (coefficient = 0.02, SE = 0.01,  $t$  value = 2.22,  $p$  value = 0.03) (Fig. 3b).

Increases in *A. schultzi* FTD values were positively related to secondary forest and period I (coefficient = 0.12, SE = 0.01,  $t$  value = 8.94,  $p$  value = 0.0001) and greatest captures occurred during the beginning of the year (January, February, and March). Captures in the other environments were significantly lower (coefficient =  $-0.09$ , SE = 0.02,  $t$  value =  $-5.32$ ,  $p$  value = 0.0001) (Fig. 3c).

## Discussion

Structurally speaking, the environments under study were different in terms of plant diversity, evenness, density, and number of fruit fly host species with different fruiting periods. Together, these habitat factors influenced the dynamics of three tephritid species (*C. capitata*, *A. fraterculus* and *A. schultzi*) and that of their natural enemies. According to Virgilio et al. (2011) the main source of variability affecting tephritid distribution is related to differences in environmental characteristics partly because, differences in structure across the landscape produce different microclimates (Barbosa and Benrey 1998), but also because these differences can influence oviposition site selection and dispersal patterns which in turn affect foraging patterns of their natural enemies.

The structure of the urban landscape produces an environment where high temperatures and low humidity prevail, due to direct solar radiation on large surfaces without or with little cover (Thaha 1997). Such conditions appear to have favored the more plastic and polyphagous *C. capitata* by suppressing competition for oviposition sites and to a lesser degree the effect of natural enemies. Such findings concur with those of Putruele (1998), Segura et al. (2004; 2006) and Ovruski et al. (2003) for urbanized areas of Argentina and those of Kovaleski et al. (2000) and Malavasi et al. (2000) in highly disturbed urban areas and in association with exotic hosts in Brazil. Analysis of competitive interactions among three species of invasive tephritids (including *C. capitata*) and a native species in the island of la Reunion revealed that climatic niche partitioning allowed coexistence of successive invaders in this ecosystem (Duyck et al. 2006a), apparently such a mechanism is produced or

accentuated in continental South America through disturbance of native habitats.

Previous studies in Tucumán, focused on trapping in citrus farms, highlighted dominance of *C. capitata* (Domato and Aramayo 1947; Turica and Mallo 1961; Nasca et al. 1981). Nevertheless, results from this study revealed that variation in the predominance of this tephritid species is tightly linked to some habitat types and particularly to the presence of uncontested introduced host plants. In the secondary forest *Anastrepha* spp. larval infestation levels and FTD values, were significantly higher than those recorded for *C. capitata*. Ovruski et al. (2003, 2004) and Ovruski and Schliserman (2003) report similar results during native and exotic fruit collections in secondary forest patches, while in Brazil, *A. fraterculus* is also abundant in areas with slightly disturbed vegetation with predominance of different species of native Myrtaceae and Anacardiaceae that offer different oviposition opportunities over the year (Malavasi and Morgante 1981; Sugayama et al. 1998; Kovaleski et al. 1999; Santos Veloso et al. 2000). Altogether, we believe that considering *C. capitata* as the dominant species in continental South America is a misconception based on host sampling strongly biased towards exotic commercial species of plants (mainly citrus) and on the species quarantine importance.

The observed differences in Tephritid species distribution patterns could be explained either by a preference for dryer, warmer habitats by *C. capitata*, or alternatively because *Anastrepha* excludes this species from more suitable habitats. The later hypothesis gains support from the fact that *C. capitata* thrives in Central America in warm humid environments as the sole tephritid species exploiting coffee (Niklaus-Ruiz Borge and Basedow 1997), and that it was displaced from Hawaiian coastal lowlands by *Bactrocera dorsalis* to higher and cooler coffee growing areas (Duyck et al. 2004). Apparently, *C. capitata* compensates for poor competitive abilities with a high environmental plasticity that allows it to exploit and persist in empty niches. By contrast, conserved habitats where native species and their natural enemies are found are resistant to invasion by this species and yet under risk if disturbance upsets the existing ecological balance.

Variation in fruiting of different host species across space and time allows tephritids to access resources for reproduction across the mosaic in a continuous manner, the presence or absence of particular hosts as well as the

**Table 1** Infestation levels (larvae/kg of fruit  $\pm$  SE) for fruit species found in only two environments

Host fruit	Environments	Infestation level	
		<i>C. capitata</i>	<i>A. fraterculus</i>
Sweet orange	O. orchards	(2.38 $\pm$ 0.94)	(0.07 $\pm$ 0.04)
	Urban	(4.55 $\pm$ 1.35)	(0.05 $\pm$ 0.05)
Sour orange	O.orchards	(14.48 $\pm$ 4.88)	(0.37 $\pm$ 0.23)
	S. forest	(12.85 $\pm$ 7.18)	(0.10 $\pm$ 0.10)
Mango	O. orchards	(12.02 $\pm$ 3.65)	(0.50 $\pm$ 0.29)
	Urban	(23.10 $\pm$ 8.51)	0.00
Persimmon	O. orchards	(26.51 $\pm$ 6.52)	(0.85 $\pm$ 0.60)
	Urban	(137.87 $\pm$ 99.87)	0.00

composition of surrounding vegetation influences abundance of tephritids and their parasitoids (Aluja and Birke 1993) and as pointed out by Duyck et al. (2004) it can influence the outcome of competitive interactions.

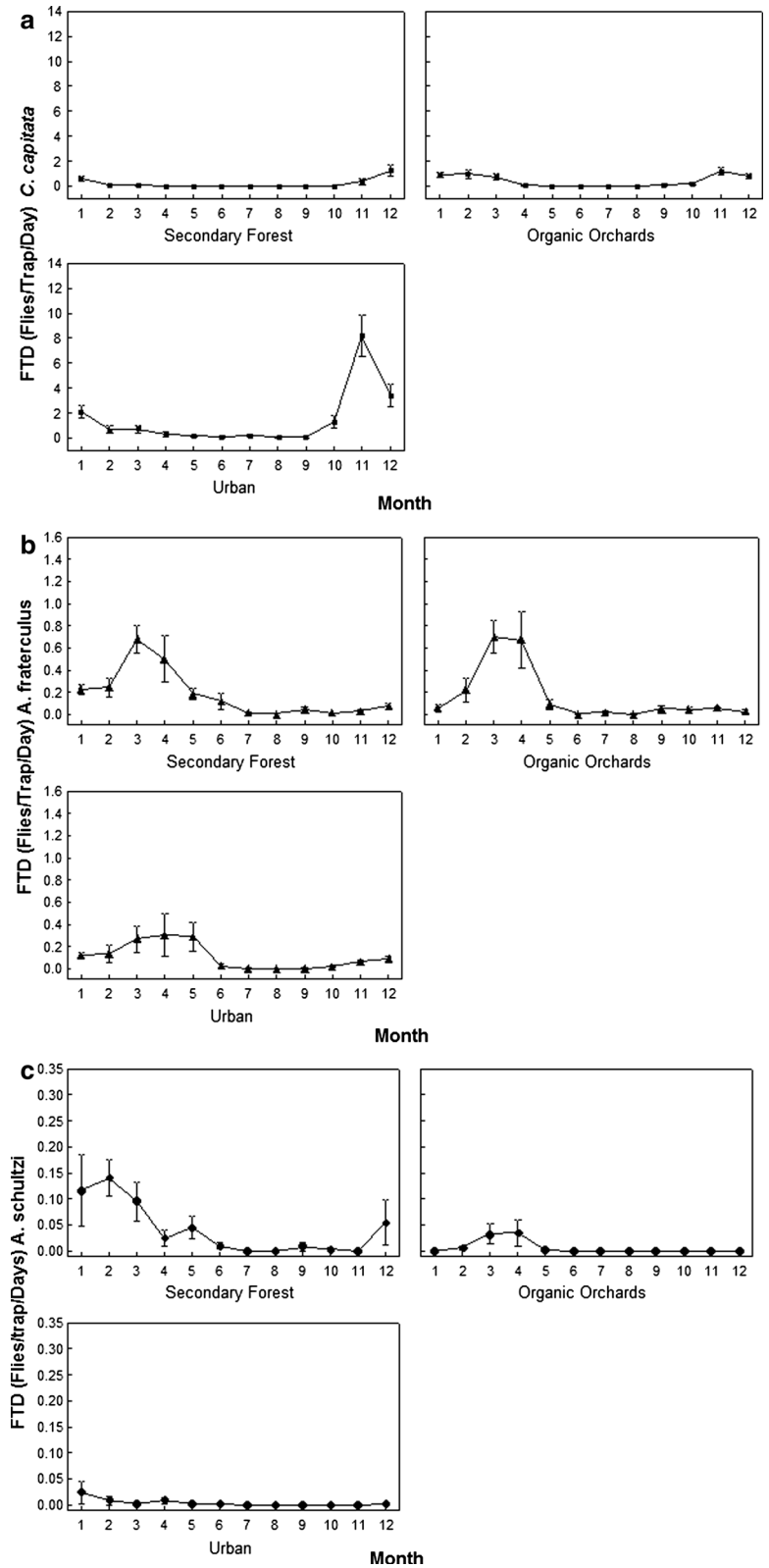
In a study encompassing several Argentinian regions, Segura et al. (2006) found marked differences in *C. capitata* and *A. fraterculus* infesting similar hosts at different localities. Here, analyzing different environments within a mosaic, we also detected variability in abundance and predominance of both species in the same host. Loquat (*E. japonica*) and peaches (*P. persica*) are clear examples of the influence of disturbance on infestation levels and abundance of different fruit fly species. These exotic introduced host plants were present and infested in the three environments. However, in secondary forest patches and organic orchards they were mainly exploited by the native polyphagous *A. fraterculus*, while in urban settings they were attacked by *C. capitata*. The fruiting period of these hosts coincides with the end of the cold-dry season and beginning of the warm-humid season, which allows for progressive population growth. Loquat and peach have been recorded by Ovruski et al. (2003) and Santos Veloso et al. (2000) as good hosts for both species in Argentina and Brazil and as the multiplication host for *A. fraterculus* in R o Grande do Sul (Brazil) (Kovaleski et al. 2000). Here, the introduction and spread of exotic plant species not only favors persistence of exotic pests, but also favors population growth of native polyphagous herbivores that become pests of commercial crops.

In sharp contrast, in the native *J. australis*, *A. schultzi*, a specialized oligophagous native species, predominated in the secondary forest, *A. fraterculus*

did so in organic orchards, and *C. capitata* in urban settings. *A. schultzi* is only known so far from the Yungas region in close association with *J. australis*, although it has also been found sporadically, infesting *P. guajava* at low levels (Schliserman et al. 2004). *Anastrepha fraterculus* by contrast is one of the most polyphagous and widely distributed species in the genus (Norrbom 2004) prevailing in different hosts and diverse environments. Walnuts, nonetheless, along with the myrtaceous *Eugenia uniflora* and *Myrcianthes pungens*, had previously been recorded for Tucum n as the main native hosts where *A. fraterculus* populations grow (Ovruski et al. 2003; 2004). When exploiting this host in undisturbed environments the competitive hierarchy seems to be that monophagous native species dominate polyphagous native species which in turn displace the exotic invader. This pattern would be consistent with conclusions reached by Duyck et al. (2007) in island ecosystems, where K selected species possess advantageous traits under competitive scenarios.

Exotic citrus species in the mosaic (*C. aurantium*, *C. sinensis* and *C. paradisi*) served mainly for *C. capitata* multiplication regardless of the environment where they were found. Although several Citrus species have been listed as *A. fraterculus* hosts in South American countries such as Brazil, Peru and Venezuela, some of these records are questionable or represent occasional infestations (Norrbom 2004). In M xico, Aluja et al. (2003a) demonstrated that citrus are not suitable for *A. fraterculus* larval development, perhaps because *Anastrepha* are not capable to circumvent the existence of toxic compounds in the peel (Aluja et al. 2000). Here, we found the three citrus species we collected, to be poor hosts of *Anastrepha*,

**Fig. 3** Influence of season on adult fly trap captures in three different types of landscape elements (secondary forest, organic orchards, and urban landscape) **a** *C. capitata* trap captures. **b** *A. fraterculus* trap captures and **c** *A. schultzi* trap captures. (FTD ( $\pm$ SE) index values)



allowing in this case *C. capitata* to exploit these hosts in all environments. Such findings provide further support for the hypothesis that *C. capitata* is excluded from conserved habitats by native species exploiting the same niche, because the invasive species is perfectly capable of exploiting uncontested exotic host plants in conserved habitats. Additionally, the three species of Citrus provide ripe fruit during the whole cold-dry season providing a bridge between periods of host availability of other hosts such as loquat.

Habitat structure has been found to exert a profound influence on diversity and abundance of natural enemies (Marino and Landis 1996). Certain elements of the landscape can favor predator and parasitoid survival and have been manipulated for control purposes (Barbosa and Benrey 1998). More recently it has been proven for some cropping systems that proximity to undisturbed habitats can favor natural enemy dispersal and provide pest control to adjacent fields (Tscharntke et al. 2007). The contrast among environments in our study was remarkable in the case of parasitoids, secondary forest patches generated 2–3 times more individuals than organic orchards and urban settings, and the highest levels of parasitism and greatest diversity were also detected in forest patches. López et al. (1999) and Aluja et al. (2003a) found greater abundance and diversity of *Anastrepha* parasitoids in natural and semi conserved areas than in agricultural and urban settings in Mexico. In general, diversity of parasitoid species associated to phytophagous insects is very sensitive to disturbance of the ecosystem (LaSalle and Gould 1992, 1993; Barbosa and Benrey 1998).

Additionally, in the case of parasitoids of tephritid eggs and larvae, presence/absence can be tightly linked to diversity and abundance and type of host fruit in a particular environment. Each fruit species has particular physical and chemical properties which can foster or not parasitoid foraging and infestation within fruit (Sivinski et al. 1997; Ovruski et al. 2000) this was highlighted by the fact that exotic plants such as citrus harbored very few parasitoids, while peach (also introduced) was the most important host for natural enemy reproduction. In the case of native plants guava was a poor host for parasitoid reproduction but walnut yielded many individuals. Finally, it is worth noting that only one species of native parasitoid was able to exploit the exotic *C. capitata*, in part for its preference

for citrus, which enables escape from short ovipositors, but also due to the fact that *C. capitata* prevails in highly disturbed areas where most parasitoid species are not found.

In sum we found that environmental degradation strongly affected distribution patterns of native tephritids. Monophagous species and several specialized parasitoids appear to be more sensitive to habitat loss than polyphagous species and parasitoids exhibiting a wide host range. Altered patterns of species distribution, along with the introduction and spread of exotic host plant species have created a wide array of empty niches that opportunistic invasive species can exploit. We also produced compelling evidence dispelling the notion that *C. capitata* is a dominant species when interacting with flies of the genus *Anastrepha*. Despite the fact that K-specialist invasive Tephritid species are more likely to displace native species, because agricultural and forest ecosystems, and human settlements, currently account for 95 % of the terrestrial environment (Pimentel et al. 1992), there is ample opportunity for invasive r-specialists to colonize and persist in novel environments through microclimatic niche partitioning, a fact that should be taken into account when analyzing tephritid invasion risk.

**Acknowledgments** We are grateful to Luis Oroño, Nury Ovruski, Segundo Nuñez Campero, Patricia Albornoz Medina, Omar Ulises Chaya, (PROIMI) for valuable technical and field assistance. We are grateful to the authorities of the “Parque Sierra de San Javier” (Universidad Nacional de Tucumán) for allowing us to collect fruits and providing local weather data. We also thank all the families who allowed us to sample fruit in their homes. We also express our gratitude to the organic orchards owners. We sincerely thank two anonymous reviewers and the subject editor for their constructive input. Special Thanks to Mariela Alderete for statistical advice. This study was supported by Agencia Nacional de Promoción Científica y Tecnológica de Argentina through Fondo Nacional de Ciencia y Tecnología (FONCyT) (grants PICT/2007 No. 01970 and PICT/2010 No. 0393), by Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET) (Grant PIP/2009-2011, No. 1353).

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