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Habitat-Specific Occupancy and a Metapopulation Model of *Triatoma sordida* (Hemiptera: Reduviidae), a Secondary Vector of Chagas Disease, in Northeastern Argentina

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Abstract

Triatoma sordida Stål (Hemiptera: Reduviidae), a secondary vector of *Trypanosoma cruzi* Chagas (Kinetoplastida: Trypanosomatidae), occasionally colonizes human sleeping quarters in Paraguay, Bolivia, and Brazil, whereas only sylvatic and peridomestic populations are found in Argentina. We carried out a cross-sectional survey of house infestation in a well-defined rural area of northeastern Argentina to identify the key habitats of *T. sordida*; describe its spatial distribution in an apparently undisturbed setting under no recent insecticide treatment and use metapopulation theory to investigate these spatially structured populations. Timed-manual searches in 2,177 georeferenced sites from 368 houses yielded *T. sordida* in 78 sites (house infestation prevalence, 19.9%). Most triatomines occurred in chicken nests, chicken coops, and trees where chickens roosted (prime habitats). Goat or sheep corrals and pig corrals had a lower fraction of occupied sites (occupancies) and abundance. Both occupancy and catch increased with increasing refuge availability according to multimodel inference with model averaging. The majority of suitable habitats were unoccupied despite their proximity to occupied sites. The site-specific occurrence of *T. sordida* and *Triatoma infestans* Klug (Hemiptera: Reduviidae) was positively and homogeneously associated over ecotopes, showing no evidence of interspecific interference. An incidence function metapopulation model (including intersite distances and vector carrying capacity) predicted a fivefold greater occupancy relative to the observed pattern, suggesting the latter represented a transient state. *T. sordida* failed to colonize human sleeping quarters, thrived in peridomestic habitats occupied by chickens, and had a limited occupancy likely related to a poor colonizing ability and the relative instability of its prime habitats

Key words: chagas disease, ecology and population dynamics, vector ecology

Environmental changes affect the dynamics of vector-borne pathogens and vector invasion of human-made or -modified habitats (Patz et al. 2008). Sylvatic triatomine species adapted to thrive in both domestic and sylvatic habitats become relevant for the transmission to humans of *Trypanosoma cruzi* Chagas (Kinetoplastida: Trypanosomatidae), the causal agent of Chagas disease, which affects 6–10 million people (Gottdenker et al. 2011, WHO 2015). Domestic and peridomestic habitats offer numerous refuges and abundant hosts throughout the year, allowing triatomine populations to reach much higher densities than in sylvatic habitats (WHO Expert Committee 2002, Gürtler et al. 2014). Henceforth (peri) domestic refers to domestic or peridomestic structures. Limited research efforts on sylvatic triatomine species that establish breeding foci in (peri)domestic habitats impair our ability to understand the domestication process (Schofield and Dias 1999, Guhl et al. 2009).

Triatoma sordida Stål (Hemiptera: Reduviidae) is a secondary vector of *T. cruzi* with a broad range extending from central Argentina, Bolivia, Paraguay, up to northeastern Brazil (Carcavallo et al. 1999, Gurgel-Gonçalves et al. 2015). It is frequently found in trees associated with birds, bromeliads, small mammals' burrows, and peridomestic chicken coops or nests (Diotaiuti et al. 1994), and inside human sleeping quarters in Paraguay (Rojas de Arias et al. 2012, Sánchez et al. 2016), Bolivia (Noireau et al. 1995), and Brazil (Rocha e Silva et al. 1977, Falavigna Guilherme et al. 2001, Gurgel-Gonçalves et al. 2010, Maeda et al. 2012), where it was classified as a semidomestic species (Pessoa et al. 2015). Surveys conducted

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in Argentina frequently found colonies of *T. sordida* in sylvatic and peridomestic habitats (e.g., Damborsky et al. 2001, Bar et al. 2002, Alvarado-Otegui et al. 2012), very few adult specimens in human sleeping quarters (Gurevitz et al. 2011), and *T. cruzi* overall infection rates averaging 6% (Macchiaverna et al. 2015). *T. sordida* feeds on a wide variety of mammals and birds (Rabinovich et al. 2011), with no apparent preference for any of them (Crocco and Catalá 1997).

Recent findings show *T. sordida* includes at least two sibling species or subspecies as determined by chromosomal markers (Panzera et al. 2015) and cuticular hydrocarbons (Calderón-Fernández and Juárez 2013). *T. sordida sensu stricto*, the most widespread across the species' geographic range, appeared to be genetically distinct from specimens collected in northern Argentina (Chaco, Formosa, Santiago del Estero, and Corrientes), Paraguay, and Bolivia (Cochabamba) as determined by isoenzymatic analysis and chromosomal characteristics; the latter group was considered compatible with a new species or chromosomal taxon designated as *T. sordida Argentina* (Gonzalez-Britez et al. 2014, Panzera et al. 2015). Both taxa apparently displayed relevant ecological differences linked to their vectorial capacity: *T. sordida sensu stricto* was frequently collected in human sleeping quarters, peridomestic, and sylvatic habitats in Bolivia, Paraguay, and Brazil, whereas *T. sordida Argentina* apparently was restricted to sylvatic and peridomestic ecotopes, where it was closely associated with chickens. The population dynamics of *T. sordida Argentina* and its role as a secondary vector of *T. cruzi* remain ill-defined.

The occurrence of sylvatic triatomines in the (peri)domestic space has been linked to the type of construction and materials used in outbuildings for storage or housing animals, the presence of mammalian or avian hosts and lights in human sleeping quarters, and proximity to sylvatic areas (Andrade et al. 1995, Gajate et al. 1996, Walter et al. 2005, Dumonteil et al. 2013, Rossi et al. 2015). In general, triatomine population size is positively related to the number of available local hosts (Gorla and Schofield 1989, Cecere et al. 1997, Enger et al. 2004). Little is known about the habitat- and site-specific occupancy of *T. sordida* in Argentina and whether its presence and abundance is affected by the type and number of available hosts, refuge availability, and the spatial configuration of potentially suitable habitats.

Triatomine habitats are expected to occur in a network of discrete habitat patches linked by dispersal across an unsuitable matrix. Suitable habitats may sustain a set of potentially ephemeral local populations (subject to extinction) connected by colonization, i.e., a metapopulation (Levins 1969, Hanski 1999). Metapopulation structure can arise from the patchy distribution of resources or habitats and from anthropogenic habitat loss (Sjögren-Gulve and Hanski 2000). Unsynchronized events of local extinction and colonization ensure metapopulation persistence depending on patch characteristics that allow local populations to grow or drive them to extinction (e.g., patch quality or carrying capacity) and the capacity to disperse and reach empty (unoccupied) or low-density patches (i.e., rescue effect) as a function of interpatch distance. The parameters obtained by model fitting (x, protection against the severity of environmental stochasticity; and $e * y^2$, constants for the relations between extinction and patch area, and between colonization ability and migration, respectively) may be used to simulate metapopulation dynamics and predict transient states and the proportion of occupied patches at equilibrium (Hanski and Thomas 1994). This theoretical framework was useful to assess the viability of spatially structured populations with incomplete occupancy, mainly for conservation purposes (Sjögren-Gulve 1994). Metapopulation theory proved versatile to address the issues of time of persistence, proportion of occupied

patches at equilibrium, relative importance of individual patches for global persistence, and comparative forecasts of the spatial configuration of the network for management purposes. The metapopulation perspective has rarely been applied to Triatominae and is appropriate to assess population persistence and expansion. Zu Dohna et al. (2007) modeled the status and turnover rate of patch occupancy with *T. infestans* in the dry Argentine Chaco.

As part of a research program on the eco-epidemiology and control of Chagas disease in a well-defined rural area in the humid Argentine Chaco, we conducted a cross-sectional census survey of house infestation to identify the key (peri)domestic habitats of *T. sordida*; described its spatial distribution in an apparently undisturbed setting, and used metapopulation theory to investigate the spatially structured populations. In this area, the last insecticide campaign targeting the primary vector *Triatoma infestans* Klug (Hemiptera: Reduviidae) had been conducted 10–11 yr before our baseline survey. Therefore, we hypothesized that this long period would have allowed the spatial dynamics of triatomine populations to run its full course, with potential (re)colonization of unoccupied or newly created sites and further propagation throughout the area. Therefore, the baseline (preintervention) data collected immediately before a new area-wide insecticidal intervention were taken to represent the equilibrium habitat occupancy of *T. sordida*. These pieces of information (i.e., key (peri)domestic habitats, spatial distribution, and spatially structured population dynamics) are needed to define the population biology of *T. sordida* and its public health relevance.

Materials and Methods

Study area

Field studies were carried out in a rural section (Area I) of Pampa del Indio (25° 55′ S 56° 58′ W), San Martín Department in the Province of Chaco, Argentina, during September and November 2007. The study area encompassed 368 house compounds and 24 public buildings in 13 neighboring rural villages covering a 450-km² section. These numbers represent slight revisions of the data published (Gurevitz et al. 2011, 2013), which focused on occupied houses and excluded public buildings; here, we included the latter because they contained peridomestic habitats of *T. sordida*. Vector control activities in the area had historically been very sparse; the last community-wide insecticide spraying campaign conducted by vector control personnel was carried out in 1996–1997.

Study Design

A prospective cohort study of house infestation and triatomine abundance was conducted between late 2007 and 2010. Here, we report the results of the baseline (preintervention) survey conducted in September and November 2007 before an area-wide insecticide spraying campaign. Following an initial (exploratory) assessment of house infestation in September 2007 (including 51 houses), a full-coverage, cross-sectional survey was conducted in November 2007. All existing house compounds and public buildings were inspected at least once.

Each house compound encompassed a domestic area (including human habitations, although on rare occasions they were absent) and a peridomestic area including several types of ecotopes as defined by its characteristic physical structure and use: kitchens; mud ovens; storerooms; granaries; latrines; structures occupied by chickens (trees, nests, and coops); and corrals for goats or sheep, pigs, and cows or horses. Chicken nests ('nidero') usually consisted in an elevated platform made of wood or bricks where chickens, and

occasionally ducks or turkeys, roosted (Gurevitz et al. 2011). Other peridomestic structures difficult to classify included small chapels (which nearly always remained closed), piled materials (highly variable in location and persistence over time), and abandoned structures where chickens roosted (e.g., ruined vehicles). A site was defined as any individual structure which may provide shelter and host-feeding sources to triatomines. The geographic position of each site was registered with a GPS (GeoXM; Trimble Navigation Ltd, Sunnyvale, CA) with an error of 1–3 m. Distances between sites smaller than 3 m were corrected by field observations summarized in a sketch map showing the relative position of all sites within each house compound. Additionally, on April 2008 (first postspraying survey), householders were asked for the number and type of domestic animals that used each site.

All sites within each house compound were searched for triatomines by timed-manual collections conducted by two skilled bug collectors using 0.2% tetramethrin spray (Espacial, Argentina) as a dislodging agent. Domiciles were inspected by one person for 20 min, while each peridomestic site was searched by another person for 15 min. Most sites were inspected thoroughly before finishing the stipulated time period, and therefore, search efforts were roughly similar across sites. All triatomines collected were identified taxonomically and counted according to species, stage, and sex at the field laboratory. Vector surveys using the same protocol were repeated every 4–6 mo over 3 yr, totaling eight surveys (Gurevitz et al. 2013). For house compounds inspected both in September and November 2007, we computed the mean catch of triatomines per unit effort rounded to the nearest integer.

The building materials used in each structure were recorded. Refuge availability was categorized from 1 (no refuge) to 5 (maximum refuge) based on the type of construction materials and the existence of cracks and crevices where triatomine could hide as described in Gurevitz et al. (2011). Research team members who evaluated refuge availability had previously been trained to make consistent assessments.

Data Management

The complete database for the preintervention survey encompassed 2,547 sites from 368 house compounds and 24 public buildings. For habitat-specific occupancy with *T. sordida*, the database was restricted to 2,177 sites inspected by timed-manual searches. The spatial analysis and metapopulation fit described below were restricted to ecotopes that were likely to be occupied with *T. sordida* (i.e., suitable habitats, as revealed by this study) and had complete spatial data (total, 814 sites).

For a comprehensive assessment of habitat quality regardless of our categorization based on the main use of each site, we considered four different variables as proxies: total number of available hosts, type of host, refuge availability, and vector carrying capacity. We used the maximum catch of *T. sordida* recorded over the eight consecutive surveys at each individual site as a proxy of local vector carrying capacity, i.e., habitat quality at site level (Pellet et al. 2007). Local carrying capacity had complete data for 814 sites. The total number of available hosts encompassed only the farm animals (fowl, pigs, goats, and sheep) that occupied each site. Dogs and cats were not fully enumerated, and since they are not typical hosts of *T. sordida* (Rabinovich et al. 2011), they were excluded from consideration. Host type usually coincided with the main function of an ecotope ('typical ecotope', e.g., pig corrals were used by pigs; chicken-occupied ecotopes were typically used by fowl). On some occasions, host numbers were reported at the house-compound level;

therefore, to preserve the resolution at site level, these hosts were reassigned *a posteriori* to its typical ecotope at each house compound. When more than one possible typical ecotope existed (e.g., 20 goats in the house and two goat corrals in use), hosts were equally distributed among them (10 goats per corral). Refuge availability had complete data for 693 sites, which also have complete data for the three habitat-quality variables. The missing data occurred independently of any other site attribute, and thus, the subset of 693 sites may be considered a random sample of all sites.

Data Analysis

Global spatial statistics were used to assess the spatial distribution of sites potentially occupied with *T. sordida* (K-function, Ripley 1976) and the catch of triatomines per unit effort at each site (weighted K-function, Getis 1984). Given the aggregated nature of house compounds in rural areas (with villages including several houses separated from other villages by large stretches of productive land and secondary forest) and the proximity among peridomestic sites within the same compound, we were not able to consider the classical null hypothesis of no clustering. Instead, for each analysis we compared L (linearized K-function) and Lw (linearized weighted K-function) statistics across spatial scales against the point pattern locations of all sites. All spatial analyses were performed using the *spatstat* package (Baddeley and Turner 2005, version 1.46–1) on R platform (version 3.3.1).

The four variables representing habitat quality at site level were taken as explanatory variables of the presence and total catch of *T. sordida* per site for the 693 sites with complete data. We fitted generalized linear mixed models for binomial distributions (presence/absence, logistic regression) and negative binomial distributions (catch per standardized unit effort, overdispersed Poisson regression), taking the house compound as a random factor. We used a multimodel inference approach with model averaging run in R with MuMIn package (Barton 2016), for a global model with all habitat-quality variables and no interactions. Model selection was based on Akaike's information criterion corrected for small samples (AIC_c). The subset of models that were within 4 AIC_c units from the best-fitting model were considered top models (Burnham and Anderson 2004), and were averaged. This analysis was performed with the glmmADMB package (Fournier et al. 2012) on R platform, which estimates true maximum-likelihood standard errors using a Laplace approximation.

Incidence Function Models and simulation

A patch (site) was considered occupied when at least one *T. sordida* nymph or adult was found by timed-manual collections. Incidence function models (IFMs) were fitted to the patch occupancy data. We assumed that in the absence of any massive intervention against triatomines over the last 10–11 yr prior to the preintervention survey, the observed occupancy pattern would correspond to a quasi-stationary stochastic equilibrium characterized by a stationary distribution of turnover events per unit time, and would approximate the average long-term probability of patch occupancy (i.e., the incidence of patch occupancy).

The IFM is a discrete-time stochastic patch model used for studying metapopulation dynamics when only occupancy data for one or a few time steps (snapshot data) are available (Hanski and Thomas 1994, Hanski 1998) . The incidence of occupancy for each patch is fitted considering an extinction factor, which depends on patch quality and the possibility of being rescued by individuals from other occupied patches, and a colonization factor which depends on the

quality and distance to each occupied patch. The equation has the form of a logistic model:

$$\text{logit } J_i = \log\left(\frac{J_i}{1 - J_i}\right) = \beta_0 + \beta_1 * (\log A_i) + \beta_2 * \log(S_i)$$

(1)

where A_i is the carrying capacity of focal patch i, and $S_i = \sum p * e^{-\alpha * d_{ij}} * A_j^b$, in which p defines the occupied=1/empty=0 state of patch j, α denotes the inverse of dispersal capacity (constant), d_{ij} is the distance between patches i and j, and A_j the carrying capacity of patch j. The b exponent scales the colonization probability with the carrying capacity and is taken as 1. S_i summarizes the ability of the patch network (including j patches) to colonize each i-patch, based on vector carrying capacity and interpatch distances to occupied patches (as sources of propagules). S_i increases with increasing carrying capacity ($* A_j^b$) and decreases with increasing interpatch distance ($e^{-\alpha * d_{ij}}$).

A distance matrix was constructed based on the Euclidean distances among the 814 patches. Previous studies on *T. sordida* recovered flight-dispersing adults 100 m apart from the release point under adequate weather conditions for flight initiation (Schofield et al. 1991). We take this value as a first approximation to the dispersal capacity of *T. sordida* and set α to 10 (100 m). We also analyzed the sensitivity of the model to different α values.

Traditional occupancy models use the area of each patch as a proxy of local maximum population size (Sjögren-Gulve and Hanski 2000), which we represent by a 'local carrying capacity' following the rationale developed by Pellet et al. (2007). All maximum values were increased by one unit to work with logarithms.

The snapshot data was fitted to a logistic regression model with a binomial distribution. β_2 is constant and equals 2. β_1 (named x by Hanski [1994]) represents protection against the severity of environmental stochasticity, a measure of how unlikely is to register an extinction event even in good-quality patches. β_0 combines e and y^2 parameters, which are constants for the relations between extinction and patch area, and between colonization ability and migration, respectively. To tease apart e and y^2, we set a threshold for patch quality (A0) above which extinction is certain. We set

A0 = 2, because local carrying capacity (expressed as number of triatomines) does not allow values lower than 1 for occupied patches. Additionally, we performed simulations using other values of A0 and found that the qualitative conclusions were robust to variations of A0 between 0.5 and 10. In addition, parameter estimation was optimized with Simulated Annealing procedures (Moilanen 1995) with GenSA package (Xiang et al. 2013) on R platform.

Model fitting was not evaluated by traditional measures since the snapshot occupancy pattern represents an aggregate measure of metapopulation dynamics (Moilanen 2000) and a state of the process under study. The fit of the IFM was measured by comparing the incidence of occupancy fitted by patch against the incidence obtained by iteration of the metapopulation dynamics on the initial occupancy pattern (Moilanen et al. 1998). We simulated 500 time steps of stochastic metapopulation dynamics using the estimated parameters and obtained 500 sequential patterns of patch occupancy, each one based on the previous pattern. We took the last 100 patterns to compute the proportion of times in which each patch was occupied (i.e., a measure of the probability of occupancy). We replicated the 500 time-step simulations 10 times. The relationship between the fitted incidence and the simulated probability of occupancy is expected to be linear for a quasi-stationary stochastic equilibrium. The stochastic simulation of IFM dynamics was implemented on R platform as a Markov chain.

Results

Site-Specific Occupancy

Timed-manual searches yielded a total of 355 *T. sordida* from 78 (3.58%) of 2,177 sites inspected for triatomines (Table 1). *T. sordida* was closely associated with ecotopes used by chickens: taking together chicken nests, coops, and trees where chickens roosted, they encompassed 85.8% of all *T. sordida* collected and 60% (47 of 78) of the occupied sites. *T. sordida* nymphs and adults were rarely found in human sleeping quarters, storerooms, kitchens, and cow or horse corrals. Granaries had one adult specimen, and latrines, mud ovens, and public buildings were all negative. This set of habitats was considered unsuitable for *T. sordida*.

Table 1. Inspection coverage, prevalence, and abundance of *T. sordida* according to ecotope in Pampa del Indio, Chaco, 2007

Ecotopes	No. of sites inspected (%)	No. of sites positive (%)	No. of insects collected (nymphs, adults)	Mean catch per positive site (SD)	Maximum catch per site	Percent of triatomines collected
Chicken nest	118 (92.19)	19 (16.10)	102 (60, 42)	5.34 (6.07)	23	30.2
Chicken coop	186 (94.42)	16 (8.60)	107 (61, 46)	6.69 (7.21)	28	28.5
Chicken tree	198 (83.90)	12 (6.06)	96 (70, 26)	8.00 (19.88)	71	27.1
Goat or sheep corral	118 (88.72)	9 (7.63)	18 (12, 6)	2.00 (1.58)	5	5.08
Pig corral	200 (91.32)	8 (4.00)	15 (6, 9)	1.88 (2.10)	7	4.24
Storeroom	143 (89.94)	4 (2.80)	4 (1, 3)	1.00 (0.00)	1	1.13
Human sleeping quarters	370 (85.85)	4 (1.08)	4 (2, 2)	1.00 (0.00)	1	1.13
Other[a]	124 (79.49)	2 (1.61)	3 (2, 1)	1.50 (0.71)	2	0.85
Kitchen	199 (92.56)	2 (1.01)	2 (1, 1)	1.00 (0.00)	1	0.56
Cow or horse corral	96 (71.64)	1 (1.04)	3 (3, 0)	3.00 (NA)	3	0.85
Granary	39 (97.50)	1 (2.56)	1 (0, 1)	1.00 (NA)	1	0.28
Latrine	223 (81.68)	0	0	0	0	0
Mud oven	156 (81.68)	0	0	0	0	0
Public building[b]	7 (20.00)	0	0	0	0	0
Total	2177 (85.51)	78 (3.58)	355 (218, 137)	4.54 (9.08)	71	100

[a]Other peridomestic structures difficult to classify included small chapels, piles of materials, and abandoned structures where chickens roosted.

[b]Schools, churches, and primary healthcare posts without outbuildings.

The three ecotopes used by chickens, with maximal values of total and mean catch of triatomines (Table 1), were classified as prime habitats for *T. sordida* despite some differences between them: chicken nests displayed the maximal fraction of occupied sites and submaximal total catch, whereas chicken coops had extremely abundant bug colonies but were slightly less frequently occupied than chicken nests and trees where chickens roosted harbored abundant bug colonies though were less frequently occupied than chicken coops (Fig. 1). The largest population of *T. sordida* (including 71 individuals) occurred in a grape vine that had chickens resting on the canopy despite householders' reports on not allowing them in there. Goat or sheep corrals and pig corrals had similar occupancies (8–9%) and a lower total and mean number of triatomines per positive site than other ecotopes (Fig. 1), and thus were classified as secondary habitats.

In total, 2,018 *T. infestans* were collected by timed-manual searches in 193 inspected sites, as described in Gurevitz et al. (2011). The occurrence of *T. sordida* and *T. infestans* was homogeneously associated over ecotopes according to a Mantel–Haenszel test for stratified samples (χ^2 = 118.78, df = 1, $P < 0.01$) and a Woolf test for equality of odds ratios among ecotopes ($P = 0.31$). The relative odds of finding at least one *T. infestans* in sites simultaneously occupied with at least one *T. sordida* were always higher than 1, although the association was nonsignificant in habitats unsuitable for *T. sordida* (OR = 1.83; 95% CI, 0.76–2.90) and trees with chickens (OR = 2.91; 95% CI, 0.85–4.97). The association was marginally significant in chicken nests (OR = 2.09; 95% CI, 1.00–3.17) and significant in chicken coops (OR = 3.06; 95% CI 1.78–4.34) and secondary habitats (OR = 4.16; 95% CI, 1.84–6.49) (Table 2). This
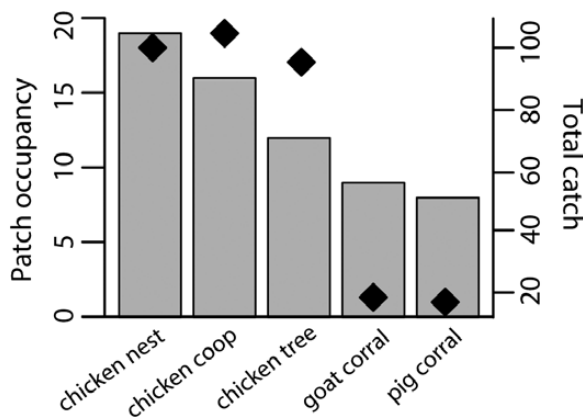
analysis shows no evidence of a negative association (interference) between *T. sordida* and *T. infestans,* and justifies focusing on the spatial habitat occupancy of *T. sordida* alone.

Spatial Analysis and Site Quality

The 78 sites occupied by *T. sordida* were scattered among almost 2,100 empty sites including every type of ecotope, despite the extensive occurrence of prime habitats and abundance of fowl (Fig. 2). All suitable sites (i.e., prime and secondary habitats) were aggregated over all the radii tested between 0.1 and 8 km according to global K Ripley analysis. Weighted global K analysis for total catch per site over all suitable sites showed a random pattern for radii <5 km and aggregation above that value (Supp. Fig. 1 [online only]). This indicates that empty and occupied suitable sites separated by <5 km had uncorrelated infestation values. Nonetheless, a contagious infestation pattern emerged globally when bigger radii were considered, which included sites from neighboring villages.

Sites with higher values of refuge availability and higher local carrying capacity were more frequently occupied with *T. sordida* populations including at least one nymph (i.e., colonies; Fig. 3), in agreement with the outcome for the averaged top models (Table 3). Patch occupancy was not modified by the number or type of available hosts. The total catch per unit effort increased significantly only with increasing refuge availability and was not associated with local carrying capacity, host availability, and host type.

IFM and Simulation

The IFM was fitted to the subset of data that included all suitable habitats (64 occupied patches and 750 empty patches). The fitted parameter x (Table 4) showed values higher than 1, suggesting the existence of habitat-quality thresholds that prevented the extinction of local populations and a relatively constant environment. The fitted value of x is independent of the threshold value for extinction (A0), which is set after fitting to tease apart parameters e and y^2. The fitted incidence of patch occupancy showed maximal values at central locations, which were separated from each other by short distances (Fig. 4). IFM fitted to only prime habitats (including 47 occupied patches and 450 empty patches) showed similar parameter estimates. The mean distance to the nearest neighbor differed between patterns including all suitable habitats (~40 m) and only prime habitats (>100 m, t-test = –4.94, df = 623, $P < 0.01$), which exceeded the maximum value set for dispersal capacity. A detailed analysis at site level revealed that high-incidence patches for prime habitats also had high-incidence values in the model including all suitable habitats. Nevertheless, the reverse was not valid: after excluding pig corrals and goat or sheep corrals in the model including all suitable habitats, some prime high-incidence patches had substantially reduced fitted

Fig. 1. Frequency of sites occupied with *Triatoma sordida* (bars, left axis) and total catch per unit effort by timed–manual collections (diamonds, right axis) according to ecotope in Pampa del Indio, Chaco, 2007.

Table 2. Relationship between current site infestation with *T. sordida* and *T. infestans* according to habitat (ecotope) suitability for *T. sordida* for 2,177 sites inspected before interventions, 2007, Pampa del Indio, Chaco

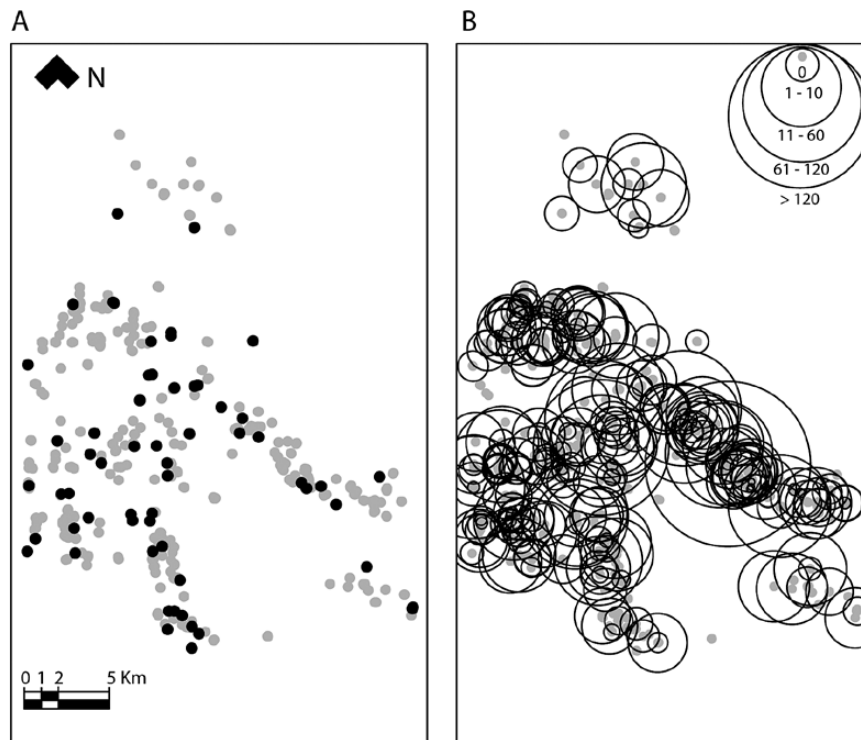| *T. sordida*	*T. infestans*	Prime			Secondary		Total
		Chicken nests	Chicken coops	Chicken trees	Goat and pig corral	Unsuitable habitats	
Presence	Presence	10	7	2	3	6	28
Presence	Absence	9	9	10	14	8	50
Absence	Presence	12	6	2	1	144	165
Absence	Absence	87	164	184	300	1,199	1,934
Total		118	186	198	318	1,357	2,177

Fig. 2. Map of 814 sites (patches) in Pampa del Indio, Chaco, 2007. (A) Empty (gray) and occupied (black) patches with *T. sordida*. (B) Number of fowl at site level (black circles) centered on each site (gray). Points near each other may overlap and cannot be distinguished at this scale.

values compared to the prime-habitat only model, suggesting inter-patch distances were of major relevance.

The metapopulation simulation based on fitted parameters (Table 4) showed a steep increase up to a mean equilibrium of 390 occupied patches when all suitable habitats were considered (Fig. 5A), which is over fivefold the observed occupancy. The fraction of occupied patches fluctuated relatively little once that value was reached. The simulated probabilities and fitted incidence rates did not agree (Fig. 5B), in line with the increase in the fraction of occupied patches relative to preintervention occupancy. These results are strongly dependent on the dispersal capacity assigned to *T. sordida*: when it was set to 10 m ($\alpha = 100$), the number of occupied patches remained around 60, but again the simulated probability did not agree with the fitted incidence rates. Simulations only including prime habitats revealed a slight increase in occupancy up to an equilibrium of 239 occupied patches, in which mean interpatch distances increased from ~40 to ~100 m. Despite this, the parameter *S* (which reflects the potential contributions of each patch as sources) displayed a 45% increase. Likewise, the simulated fraction of occupied patches did not agree with the incidence fitted by the model.

The sensitivity of model predictions to dispersal capacity (α^{-1}) showed that even after reducing α^{-1} to 10 m, the equilibrium occupancy reached a mean of 60 occupied patches, with less frequent local extinctions than expected. In agreement with this result, the protection against environmental stochasticity (*x*-value) was always higher than 1, indicating either a low risk of local extinction regardless of patch quality or low environmental stochasticity. The interpretation of the fitted coefficients for the relationship between extinction and vector carrying capacity (*e*) and between colonization ability and migration (*y*) depend on the A0 value chosen. However, the fitted *y*-values remained high with a maximum dispersal capacity of 1 km and A0 values varying between 0.5 and 10, reflecting the limited colonizing ability of *T. sordida*.

Discussion

Our study shows that *T. sordida* failed to colonize human sleeping quarters despite householders' reports of frequent house invasion (unpublished results) and the absence of insecticide spraying campaigns over a decade and was mainly restricted to peridomestic ecotopes used by chickens (prime habitats), where they reached maximal values of occupancy, total, and mean abundance. The highly unusual finding of the largest population of *T. sordida* occurring in a grape vine where chickens roosted highlights the well-known relevance of trees as suitable habitats for this species, and the occurrence of a super-productive source of propagules in an ecotope usually disregarded for triatomines and rather difficult to search in. The close relationship between *T. sordida* and peridomestic fowl suggested that keeping chickens enclosed in coops (rarely done so in the Chaco) would offer a continuous host supply that boost triatomine population size (Diotaiuti et al. 1994).

Goat or sheep corrals and pig corrals accounted for a small fraction of the total catch of *T. sordida* and had a lower mean abundance, supporting that they were secondary habitats. Thus, different peridomestic ecotopes may fulfill different roles in the population dynamics of *T. sordida*, as recorded for *T. infestans* elsewhere (Gurevitz et al. 2011, Gürtler et al. 2014). Human sleeping quarters and nearby peridomestic ecotopes built in a similar fashion (e.g., kitchens and storerooms) hardly ever harbored a few adult *T. sordida*. These findings coincide with views on *T. sordida* from Brazil, Argentina, western Bolivia and Paraguay as 'predominantly peridomestic, without significant colonisation inside dwellings' (Waleckx et al. 2015).

Variations in the occurrence and catch of *T. sordida* were not explained by host numbers and host type despite of the widespread occurrence of fowl and fowl habitats, contrary to expectations and results for the sibling species *Triatoma garciabesi* Carcavallo, Martinez, Cichero, Prosen &Ronderos (Hemiptera: Reduviidae) in
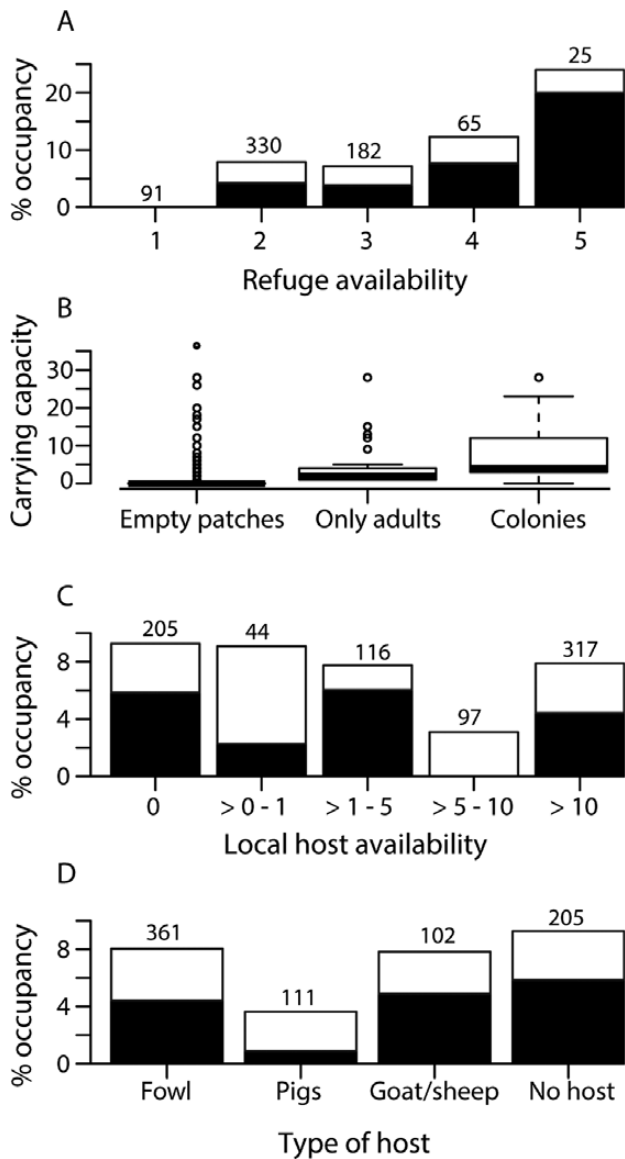
Fig. 3. *T. sordida* occupancy according to four habitat–quality variables among all suitable sites in Pampa del Indio, Chaco, 2007. Dark bars indicate triatomine populations and white bars the occurrence of only adult triatomines. The numbers over each bar indicate inspected sites for each category.

the dry Chaco (Rodríguez-Planes et al. 2015) . For example, domestic fowl numbers may vary widely over time depending on household inflow (birth and acquisition) and outflow (consumption, sales, and death), disease outbreaks (especially among chickens), and interannual variations set by family and regional economies. Thus, our point estimates of host numbers may not always adequately represent long-term habitat quality at site level. In addition, the disagreement between the fact that prime habitats were occupied with chickens and the inability of host-related variables to explain variations in site infestation suggest that host numbers per se are insufficient to define the probability of occurrence of *T. sordida*.

Refuge availability was strongly and positively associated with the fraction of sites occupied with *T. sordida* and total catch per unit effort. In agreement with these findings, in replicated experimental huts housing one chicken, the trajectory and final population size of *T. infestans* depended on structural characteristics of the site defining

refuge availability (Cecere et al. 2003). The structural characteristics of habitats (i.e., presence of wood and size) were considered a risk factor for the occurrence of *T. sordida* and other sylvatic species elsewhere (Walter et al. 2005, Rossi et al. 2015), reinforcing the links between triatomine occurrence and housing materials similar to those found in their sylvatic habitats (Gajate et al. 1996).

Local vector carrying capacity was closely associated with the fraction of sites occupied with *T. sordida* and not with preintervention total catch, suggesting that some populations which reached high numbers did not necessarily persist as such after intervention. These findings are consistent with the notions of peridomestic and sylvatic populations having a low threshold to disturbance and being liable to local extinctions triggered by unstable host occupancy and other factors (see stochasticity below).

Our results show no evidence of competitive interference between *T. sordida* and *T. infestans*. Conversely, both species were positively and significantly associated in some prime and secondary habitats, with a greater relative frequency of mixed populations rather than unmixed populations of *T. sordida*. In our study area, *T. infestans* was more abundant and mainly occupied human sleeping quarters and multiple peridomestic structures (Gurevitz et al. 2011), several of which were here categorized as unsuitable for *T. sordida*. The existing consensus is that *T. infestans* outcompetes *T. sordida* at a regional level in terms of survival, developmental times, and ability to obtain blood meals (Noireau et al. 1996, Oscherov et al. 2004). In experimental competition trials including three closed populations (two unmixed and one mixed) starting with 178 nymphs or adults and 116 eggs of each species and one chicken in 0.8 m³, *T. sordida* was excluded after a 6-mo period (Oscherov et al. 2004). However, such experimental population densities notably exceed site-level triatomine densities in our study area. Therefore, the observed limited occupancy of *T. sordida* is unlikely to be explained by competition with *T. infestans*.

The limited occupancy of *T. sordida* supports a stochastic metapopulation dynamics likely driven by habitat destruction or structural modification and host instability over time, despite of the availability and proximity of suitable habitats. Habitat and host instability would lead to less frequent, smaller blood meals, and increasing competition (Schofield 1994), local extinctions, and increased triatomine out-migration from occupied patches, eventually contributing to rescuing very small populations. In addition, *T. sordida* apparently has a limited dispersal and colonizing ability (Schofield et al. 1991, Noireau et al. 1999), likewise other sylvatic triatomines in the arid Chaco (Cavallo et al. 2016), as suggested by the nonsignificant relation between catches at local sites and those within a 5-km radius.

Our simulations were unable to recover the data fitted by the metapopulation model, suggesting that the observed occupancy pattern represented a transient state (not a quasistationary equilibrium) potentially driven by a deterministic climatic and regional trend acting on the metapopulation or by environmental stochasticity (which maintained patch occupancy in an early state en route towards the equilibrium), or a combination of both processes. While past disturbance dynamics is invisible to the occupancy snapshot data, the extended period without community-wide insecticide spraying may not have been sufficient to reach the stable occupancy of the patch network.

The fivefold greater occupancy obtained when all suitable habitats were included in the simulations indicates that *T. sordida* could potentially expand at this spatial scale, more so given the available sources in the surrounding forest (Alvarado-Otegui et al. 2012). Several factors may contribute to explain the gap between the observed and simulated patterns of occupancy, including dispersal

Table 3. Model-averaged ORs and coefficients of generalized linear mixed models for the presence (binomial distribution) and total catch per unit effort (negative binomial distribution) of *T. sordida* with refuge availability, local vector carrying capacity over a 3-yr period, host availability and host type as explanatory fixed factors, and house compound as a random factor

Variable	Patch occupancy		Total catch per unit effort		
	OR	95% CI	β	SE	95% CI
Refuge availability	1.581	**1.154–2.165**	2.517	0.372	**1.212–5.226**
Carrying capacity[a]	1.061	**1.0273–1.095**	1.052	0.033	0.986–1.123
No. of total hosts available	1.007	0.995–1.018	1.007	0.013	0.982–1.033
Type of animal			not included		
Fowl	1		—	—	—
Goat	1.384	0.563–3.403	—	—	—
Pig	0.526	0.169–1.640	—	—	—
No host	1.050	0.487–2.265	—	—	—

Note: Confidence intervals excluding 1 are in bold.

[a]Preintervention values were included for analysis of patch occupancy and excluded for total catch per unit effort.

Table 4. Results of fitting the incidence function model (see Equation 1) to observed patch occupancy patterns of *T. sordida* in Pampa del Indio, Chaco, 2007, considering all suitable habitats and ecotopes occupied by chickens (prime habitats)

Parameter	All suitable habitats	Prime habitats
No. of patches	814	497
Occupancy proportion	0.079	0.095
Mean nearest neighbor distance: (SE) (m)	44.3 (4.4)	109.5 (12.4)
Mean A (carrying capacity)	1.62	2.23
Mean S[a]	4.73	6.87
α[b]	10	10
x[c]	1.88	2.29
$e*y^2$[d]	0.34	0.004

Note: Parameters x and $e*y^2$ were optimized by simulated annealing procedures.

[a]Mean ability of the patch network (excluding the *i*–patch) to colonize other patches.

[b]Inverse dispersal capacity.

[c]Protection against environmental stochasticity.

[d]Constants for the relation between extinction and carrying capacity (*e*), and colonization ability and migration (*y*).

capacity, habitats with different roles, population dynamics, stochasticity, and detectability, as described subsequently.

First, the dispersal capacity set for IFM simulations was based on results for *T. sordida* from southern Brazil (Forattini et al. 1973, 1979) and from central Argentina (Schofield et al. 1991). In both cases, marked triatomines were recaptured at distances exceeding 50 m from the release point, and the lost insects were taken to represent movements greater than 100 m. One marked specimen was recovered at 240 m from its release point (Forattini et al. 1973). These findings suggest that *T. sordida* has a limited flight dispersal capacity. No discernible orientation during dispersive flights was recorded in *T. sordida* and *T. infestans* (Schofield et al. 1991, 1992), except for the attractant effects of white lights (Minoli and Lazzari 2006), which are contingent upon the surrounding vegetation and relief. Hence, a large fraction of undirected radial flights may reach unsuitable habitats and delay or even compromise the establishment of new colonies.

Model predictions were sensitive to the assumed dispersal capacity (α^{-1}) and insensitive to the threshold for certain extinction (A0), compatible with *T. sordida* having a limited colonizing ability.

This is supported by contrasting the outputs of simulations including all suitable habitats (which predicted increasing occupancies) versus those considering only prime habitats (in which occupancies remained almost constant) indicating the relevance of intersite distances for occupancy regardless of habitat quality.

Secondly, regarding habitats playing different roles, long intersite distances prevented the invasion of artificial structures by *T. sordida* when no other intermediate, invasible habitats were available (Forattini et al. 1979). Other less frequent habitats (e.g., dead trees) may serve as stepping stones during dispersal bouts (Moilanen et al. 1998). In our study, simulations including only prime habitats led to half of the occupancy predicted by simulations including all suitable habitats. Both systems differed in intersite distances and in the total number of patches. Nonetheless, the initial pattern of occupancy only had 17 (of 317) occupied secondary habitats, whose carrying capacities were lower than for prime habitats; therefore, the contribution of secondary habitats to colonization during the initial time steps of the simulation is expected to be small. As the simulation for all suitable habitats progressed, the empty secondary patches became occupied and emitted propagules that colonized nearby prime and secondary patches at a mean distance of ~40 m. In contrast, as the simulation restricted to prime habitats progressed, only prime-to-prime colonization events could occur through longer interpatch distances (approximately 100 m). Although increasing interpatch distance was expected to reduce the *S* parameter, the 45% increase in *S* highlights that vector carrying capacity in prime habitats substantially exceeded that in secondary habitats, compensating patch isolation with population persistence over time. The major difference between both simulations was mainly caused by interpatch distances. Therefore, secondary habitats may play an important role as stepping stones allowing triatomine dispersal through the patch network. Their relevance for establishment may exceed that for achieving a complete reproductive cycle (Abad-Franch et al. 2010b).

Thirdly, in reference to the population dynamics of *T. sordida*, the implemented IFM included several time-invariant variables (e.g., foundation and colonization, development, and sex-specific arrival times). Including stage-structured vital rates, which may account for extended developmental times (approximately 1 yr for *T. sordida*) and sex structure (relevant for flight dispersal and colony foundation), may provide a more realistic scenario leading to reduced occupancy.

Fourthly, stochasticity is expected to create a recurrent disturbance dynamics that reduces the occupancy of *T. sordida*. Peridomestic habitats are subject to aperiodic modifications
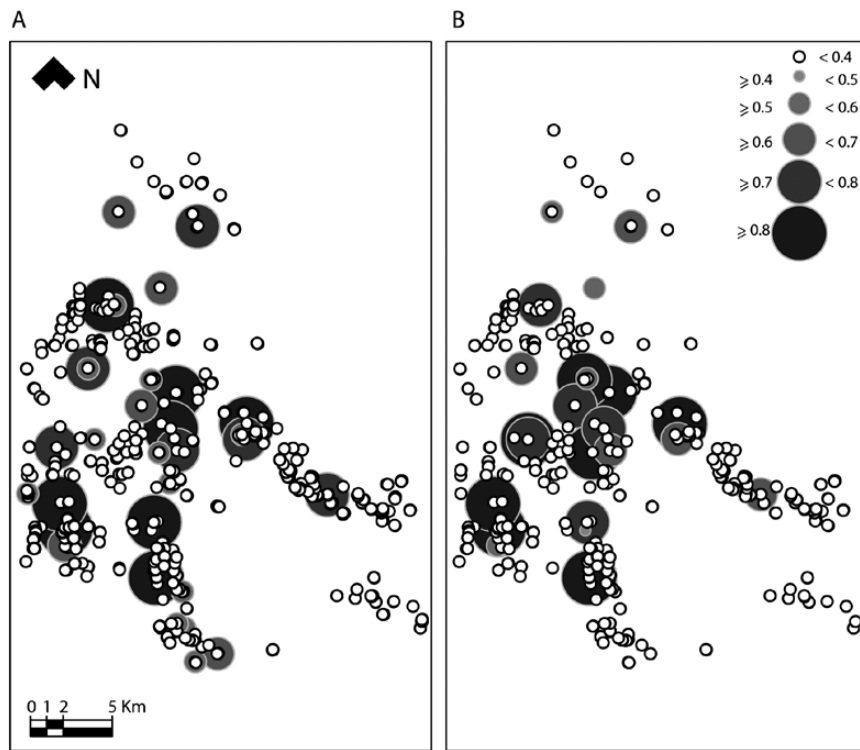
Fig. 4. Incidence of occupancy map for *T. sordida* based on the observed patch occupancy in Pampa del Indio, Chaco, 2007, for all (A) and prime (B) suitable sites. Size and grey gradients show fitted incidences with probabilities lower than 0.4 in empty circles, and bigger than 0.8 in black.

(including reconstruction, destruction, relocation within the same compounds, and main function), strong climatic, and microclimatic variations (i.e., environmental stochasticity) depending on habitat type. For example, in the dry Chaco, the type of building materials and housing structure exerted large effects on variations in microsite temperature and humidity, which affect triatomine vital rates (Vazquez-Prokopec et al. 2002). In addition, demographic stochasticity is particularly relevant for the small populations of *T. sordida* and likely contributes to local extinctions and colonization failure.

Finally, imperfect detection is a typical source of error in presence/absence data, leading to underestimation of abundance, preference, co-existence, and occupancy (MacKenzie et al. 2006, Abad-Franch et al. 2010a). This problem is enhanced when the probability of detecting (and catching) an individual is positively associated with the true abundance of the local population, especially in recently established (small) populations. Our cross-sectional data represent a retrospective analysis in which the original detection probability remains unknown. However, established triatomine populations most likely had reached detectable numbers given the time elapsed since the last vector control campaign and the substantial search efforts invested. In addition, recently founded or very small (nonviable) triatomine populations may not reflect long-term (asymptotic) patch occupancy, and thus would be less relevant for identifying the key (peri)domestic habitats of *T. sordida*.

The interpretation of current findings is limited by additional aspects. First, despite of the sizable search efforts, under-registration of sites potentially occupied with *T. sordida* is possible. This is relevant for IFMs, which require the complete enumeration of potential habitats. For example, including all trees in small forest patches in between houses (few of which were occupied with *T. sordida*) would reduce the incidence fitted by the model for each patch. Second,

although half of local households reportedly applied low-concentration insecticides, such applications were mainly restricted to domestic premises, sporadic, and nonsystematic (Gurevitz et al. 2011), and thus were unlikely to affect the establishment and persistence of *T. sordida* populations. Third, a requisite for the correct use of the IFM is that the metapopulation is in a dynamic equilibrium between extinction and colonization (Hanski 1994). However, when the simulated fraction of occupied patches displays a time trend, the dynamics under assumed quasistability conditions is close to that in the original time series (Moilanen 2000). The quasistability assumption is a conservative choice when there is no evidence of recent disturbance, as in our case.

Our study has implications for research and vector control. The study triatomines are more compatible with *T. sordida Argentina* than with *T. sordida sensu stricto*, as suggested by its strong association with peridomestic structures used by chickens and a random spatial distribution at site level, unlike *T. sordida* from Brazil, where adults stay shortly in recently founded colonies, out-migrate, and generate spatially aggregated foci (Forattini et al. 1975). However, the precise taxonomic identity and relevance of *T. sordida* as a secondary vector of *T. cruzi* in the ongoing context of land-use change and deforestation in the Gran Chaco requires further investigation, as does its flight range. Adequate management of peridomestic premises is essential to prevent colonization (Guhl et al. 2009, Gorla et al. 2013) and allows the early detection of new triatomine colonies. *T. sordida* is ubiquitous within its distribution range, and both peridomestic and sylvatic populations are likely connected and may contribute to the (peri)domestic (re)invasion process (Waleckx et al. 2015). In our study, the central habitat patches showing a high fitted incidence coincided with a local hot-spot of *T. cruzi* infection in peridomestic *T. sordida* (Macchiaverna et al. 2015) and small sylvatic
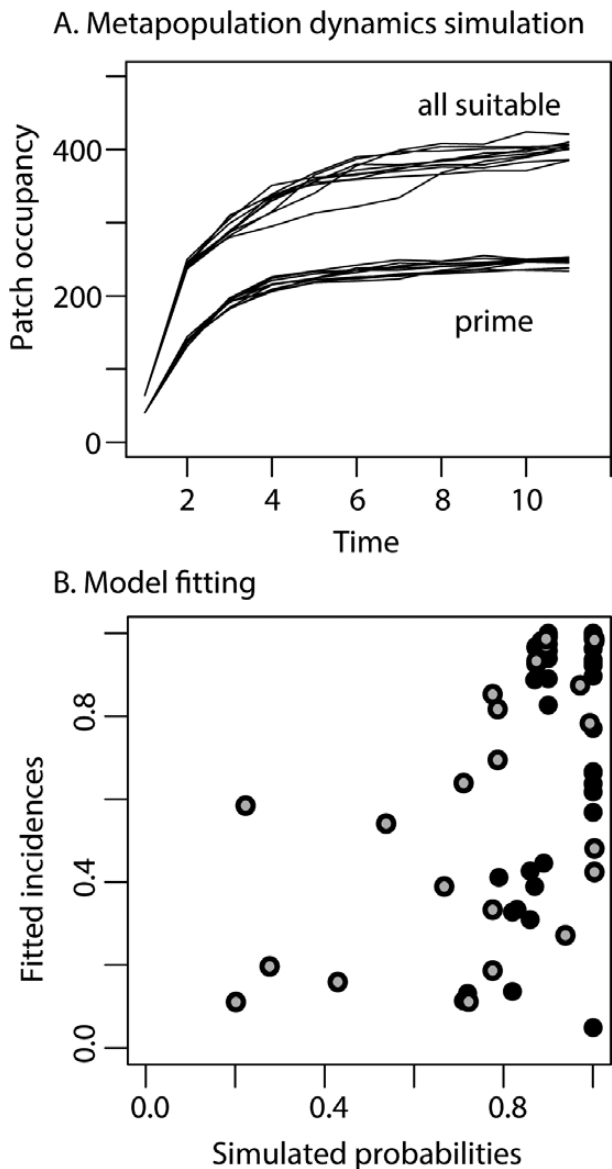
A. Metapopulation dynamics simulation

B. Model fitting

Fig. 5. (A) Patch occupancy in 10 replicate simulations of the *Triatoma sordida* metapopulation using the parameter values given in Table 3 and A0 set to 2 triatomines for all suitable and prime habitats. Only the first 10 time steps are shown; the number of occupied patches remained the same until the end of the simulation. (B) Simulated versus fitted incidences of the *T. sordida* metapopulation for all suitable (black dots) and prime (gray dots) habitats.

mammals (Orozco et al. 2013, 2014). This co-occurrence highlights the underlying process of contact between *T. sordida, T. cruzi,* and vertebrate hosts in (peri)domestic and sylvatic habitats, and the potential for spillover events remain to be established.

Supplementary Data

Supplementary data are available at *Journal of Medical Entomology* online.

Acknowledgments

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