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Multiscale environmental determinants of rats' infestation on households in a subtropical urban to rural gradient in Latin America

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ABSTRACT. Strategies for the prevention and control of commensal rodents would improve with better knowledge of their response to environmental factors from different spatial scales. In this research we evaluated which different scales environmental characteristics determine rodent infestation levels in a subtropical urban to rural landscape gradient in Misiones, Argentina. A total of 87 households from an urban, a periurban and a rural landscape were surveyed at least once, with nine households surveyed repeatedly along five consecutive seasons. Rodent infestation levels were estimated using nontoxic bait stations set up in the backyard and garden of each household. Different environmental characteristics at several spatial scales were obtained from field surveys and land cover classification based on a satellite image. *Rattus* spp. was detected in 42.5% of the households. The lowest rodent infestations occurred in winter.Infestation levels showed spatial dependence up to 2500 m. Rodent infestation was associated with landscape types and environmental characteristics at the macro and microhabitat scales. Macrohabitat characteristics explained 53.7% of the variation of rodent infestation levels, whereas microscale explained 28.0% and landscape type only 2%. This multiscale study provides evidence that households' characteristics may not be the most important factor to explain variations in the abundance of commensal rodents' around human dwellings. As a consequence, prevention and control measures would be more effective if applied at the neighborhood level and during winter, since it is a critical time for preventing compensatory population responses in rodent infestations.

[Keywords: hair traps, household characteristics, landscape, predictive map, *Rattus rattus*, spatial scale]

RESUMEN. Determinantes ambientales a múltiples escalas de la infestación de ratas en hogares en un gradiente urbano rural en una zona subtropical de América Latina. Las estrategias para la prevención y control de roedores comensales podría mejorar con el conocimiento de sus respuestas a factores ambientales que actúan a diferentes escalas espaciales. En este trabajo evaluamos qué características ambientales a diferentes escalas determinan los cambios en los niveles de infestación de roedores en un gradiente de paisaje subtropical urbano-rural en Misiones, Argentina. Se seleccionaron y muestrearon al menos una vez 87 hogares de un paisaje urbano, uno periurbano y uno rural, y nueve de ellos fueron, además, muestreados durante cinco estaciones consecutivas. La infestación de roedores se estimó usando estaciones de cebo no tóxico colocadas en los patios y jardines de los hogares. Las características ambientales a diferentes escalas se obtuvieron por medio de encuestas y relevamientos de campo y de una clasificación de la cobertura del suelo a partir de una imagen de satelital. Se detectaron *Rattus* spp. en el 42.5% de los hogares. Los menores valores de infestación de roedores se registraron en invierno. Los niveles de infestación mostraron una dependencia espacial hasta 2500 m. La infestación de roedores se asoció con el tipo de paisaje y las características ambientales a escala del macro- y del microhábitat. Las características del macrohábitat explicaron 53.7% de la variación de la infestación de roedores, mientras que las de la microescala explicaron 28% y el paisaje solo 2%. Este estudio provee evidencia de que las características de los hogares no serían los factores más importantes para explicar las variaciones de la abundancia de roedores comensales en las viviendas. En consecuencia, las medidas de prevención y control serían más efectivas si se aplicaran a la escala del macrohábitat (i.e., el vecindario) y en el invierno, dado que es el momento crítico, evitando las respuestas compensatorias de sus poblaciones.

[Palabras claves: características de las viviendas, escalas espaciales, mapa predictivo, paisaje, *Rattus rattus*, trampas de pelo]

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Introduction

Anthropic pressure causes biodiversity loss through processes of habitat degradation and fragmentation (McKinney 2008; Avigliano et al. 2019; Iezzi et al. 2019). As these processes occur, understanding the relationship between urban and rural human environments, on the one hand, and wildlife, synanthropic and domestic fauna on the other, becomes an important issue for conservation and health policies (Daszak et al. 2001; Cavia et al. 2009).

Many animal species that manage to adapt to anthropized environments are reservoirs for zoonotic pathogens, being relevant to public health (Daszak et al. 2001; Meerburg et al. 2009; Himsworth et al. 2013; Lydecker et al. 2019). Rodent species that have accompanied human migrations and expansion processes are the commensal rodents *Rattus rattus* (Linnaeus, 1758), *R. norvegicus* (Berkenhout, 1769) and *Mus musculus* (Linnaeus, 1758) (Coto 2014). The growth of urban areas and the expansion of agricultural frontiers at the expense of the surrounding environments provide refuge and food resources for these species, which are involved in the transmission of numerous diseases to humans, household animals and cattle (Meerburg et al. 2009; Battersby 2015; Lovera et al. 2017). They also inflict economic losses by damaging crops, stored food and buildings (Drummond 2001; Brown et al. 2020).

The Upper Paraná Atlantic Forest is one of the most important ecosystems in the world because of its biodiversity conservation value (Myers et al. 2002). It is also one of the most threatened due to anthropogenic pressures (Ribeiro et al. 2011). Currently, after suffering intense processes of fragmentation, degradation and habitat loss, only about 7.8% of its surface is conserved (Di Bitetti et al. 2003; Izquierdo et al. 2008), mostly in the province of Misiones, Argentina, where it is fragmented by human advancement: urbanization, agriculture and forestry activities (Izquierdo et al. 2008). Approximately eleven species of rodents have been cited in northern Misiones (Lanzone et al. 2018; Teta et al. 2018), including the commensal *R. rattus* and *M. musculus* (Fernández et al. 2018; Galliari and Pardiñas 2021). In Argentina, both commensal species have been directly implicated in leptospirosis outbreaks (Vanasco et al. 2003; Boey et al. 2019; Ricardo et al. 2020). In addition, they were found to be infected with several zoonotic pathogens (*Leptospira* spp., *Trichinella* spp., *Brucella* spp., *T. gondii* and lymphocytic choriomeningitis virus) on rural or urban areas (Castillo et al. 2003; Hancke and Suárez 2017; Lovera et al. 2017; Manabella Salcedo et al. 2021).

Rodent studies involving the entire area of a city are scarce since their sampling is difficult using traditional methods such as rodent traps (Channon et al. 2006; Cavia et al. 2012). Studies that embraced whole cities were done in New York (Childs et al. 1998), São Paulo (Masi et al. 2010), Budapest (Bajomi 1983), Madrid (Tamayo-Uria et al. 2014), several cities all over England (Langton and Cowan 2001) and Buenos Aires (Cavia et al. 2009; Cavia et al. 2015). None of these studies used traps to estimate rodent abundance (except for Cavia et al. 2009), and most could not be easily replicated in other cities because of the extraordinary amount of information (i.e., Childs et al. 1998) or resources (i.e., Langton and Cowan 2001) needed. These studies showed that abundance of commensal rodents may respond to urban characteristics at the microhabitat, macrohabitat or landscape scales (Traweger et al. 2006; Cavia et al. 2009; Masi et al. 2010; Tamayo-Uria et al. 2014; Cavia et al. 2015). However, studies that simultaneously quantify environmental conditions at multiple spatial scales are also scarce. A multiscale approach helps finding the critical scales at which different environmental factors act (Turner and Gardner 2015; Fletcher and Fortin 2018) and how these spatially structured factors could explain the observed variations in the abundance of organisms (Wiens et al. 1989).

Knowledge on the factors that affect rodent abundances and their spatial and temporal variations in urban, periurban and rural areas allows for the development and better application of preventive and control measures. These public policies are needed to reduce contact between rodents and humans (Gómez Villafañe et al. 2001; Cavia et al. 2009; Hulme-Beaman et al. 2016). The development of easy-to-apply and low-cost alternative tools to assess rodent infestation would help both to systematically monitor their population fluctuations and to identify areas for the implementation of control programs (Fernández et al. 2007; Cavia et al. 2009; Cavia et al. 2012).

The aim of this research was to evaluate the characteristics that determine rodent infestation levels at different scales in a subtropical urban to rural environmental gradient within the Upper Paraná Atlantic Forest in Misiones, Argentina. Besides, we used an economic field technique that may allow for bigger, city-wide rodent exploratory studies and monitoring programs.

Materials and Methods

Study area

The study area lies within the Department of Iguazú (25°35′ S - 54°35′ W), Misiones, Argentina. It is located in the Upper Paraná Atlantic Forest, a subtropical humid forest from the Amazonian domain (Cabrera 1994; Oyarzabal et al. 2018). The weather is subtropical, fully humid with warm summers (Peel et al. 2007). Average minimum and maximum temperatures are 11 °C and 32 °C, respectively (Plací and Di Bitetti 2005). Rainfalls are abundant throughout the year, with average annual values of 2000 mm, with minimums in winter (July, August) and maximum precipitation in spring (October, Nobember) (Plací and Di Bitetti 2005).

We studied four areas within the department: the city of Puerto Iguazú (25°35′ S - 54°35′ W, 42849 inhabitants), the village of Puerto Libertad (25°39′ S - 54°26′ W, 6694 inhabitants) (INDEC 2012) and two rural areas (Cooperativa, and San Cayetano) (Figure 1). The city of Puerto Iguazú is limited by the Paraná and the Iguazú rivers, the international boundaries with Paraguay and Brazil, the Iguazú National Park and the Peninsula Provincial Park. The village of Puerto Libertad is located along the Paraná river, 35 km south to the city of Puerto Iguazú. These four areas include a broad range of environmental conditions classified in this study as urban (the city of Puerto Iguazú), periurban (the village of Puerto Libertad) and rural zones (Cooperativa and San Cayetano).

Rodent survey

We divided the city of Puerto Iguazú and the village of Puerto Libertad into grids of 54 and 15 square areas of 400x400 m^2, respectively. Within each one of these areas one household was selected, and a total of 19 households in the two rural zones (Figure 1). To study the spatial variation in rodent infestation, we sampled each selected household only once between November 2014 and January 2015 (late spring and early summer). Additionally, a subgroup of nine households from the city of Puerto Iguazú were selected and sampled throughout the four following seasons, from March 2015 (early fall) to February 2016 (summer), to study the temporal variation in rodent infestation levels.

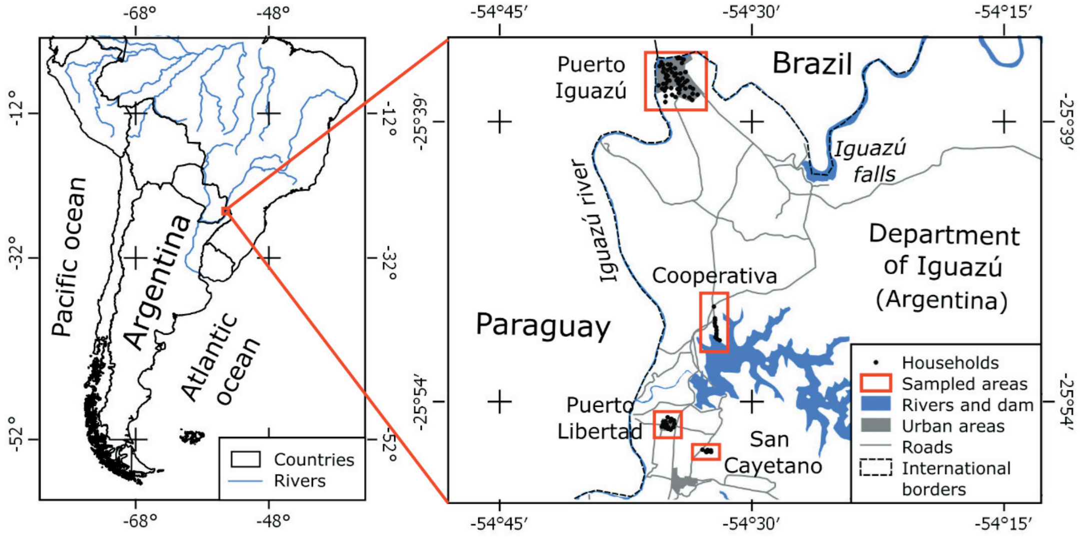

Figure 1. Distribution of the sampled households (black dots) in four areas (red squares) of Iguazú department, Misiones, Argentina: the city of Puerto Iguazú (urban, 54 households sampled), the town of Puerto Libertad (peri urban, 15) and the rural areas of Cooperativa (rural, 10) and San Cayetano (rural, 9).

Figura 1. Distribución de los hogares muestreados (puntos negros) en cuatro áreas (cuadrados rojos) del departamento Iguazú, Misiones, Argentina: la ciudad de Puerto Iguazú (urbano, 54 hogares muestreados), la localidad de Puerto Libertad (periurbano, 15) y las zonas rurales de Cooperativa y San Cayetano (rural, 10 y 9, respectivamente).

Ten bait stations were set in each household backyard or garden every 5-10 m. Bait stations consist of polystyrene vessels with a non-toxic bait composed by a mix of peanut butter and bovine fat and an adhesive tape to capture hairs of the animals that visit them (Figure 2A-C) (Gurnell et al. 2001; Cavia et al. 2012). The presence of rodent activity signs (incisor marks on the bait and/or rodent hair left on the adhesive tape) was recorded at each bait station after three days of exposure (Figure 2B-C) (Cavia et al. 2012). An infestation index for each household was calculated as the number of bait stations with rodent signs over the total number of valid bait stations inspected (broken or lost stations were not counted). These indexes have already shown to be useful to estimate and monitor small mammals' relative abundances in other urban and rural environments (Aplin et al. 2003; Cavia et al. 2012; Barja et al. 2016). The identification of rodent species visiting the baits was based on gnawing patterns and sizes and the external morphology of hairs trapped in the adhesive tapes, following criteria in Cavia et al. (2008).

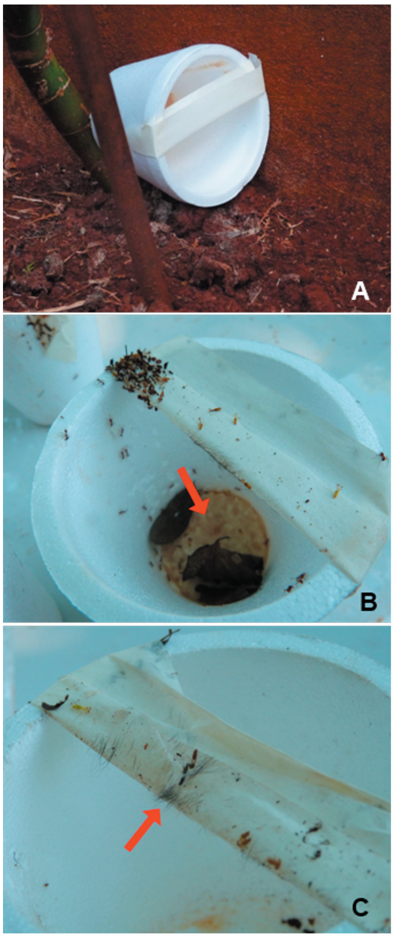

Figure 2. Non-toxic bait stations used to detect rodents' activity. A) A bait station located in a household garden. B) The red arrow shows signs of gnawing by rats on the surface of the bait (a mix of peanut butter and bovine fat). C) The red arrow shows rat hairs stuck on the adhesive tape.

Figura 2. Estaciones de cebo no tóxico utilizadas para detectar la actividad de los roedores. A) Una estación de cebo ubicada en el jardín de una casa. B) La flecha roja muestra signos de roído de rata en la superficie del cebo (una mezcla de mantequilla de maní y grasa bovina). C) La flecha roja muestra pelos de rata pegados en la cinta adhesiva.

Environmental characteristics

Environmental characteristics at different spatial scales were recorded simultaneously along the spring/summer rodent surveys. We defined three scales: microhabitat, macrohabitat and landscape, considering the known extent of the home range of *R. rattus* individuals (15-61.8 m of radius) (Whisson et al. 2007; Coto 2014; Byers et al. 2019). The microhabitat scale represents where individuals find different resources within their home range to satisfy each of their different requirements such as foraging, nesting or shelter (Morris et al. 1987). Correspondingly, features associated to areas smaller than individual home ranges were considered characteristics of the microhabitat. The macrohabitat represents the scale in which home ranges of individuals or social groups is included (Morris 1987), so environmental characteristics corresponding to areas of this extent were considered characteristics of the macrohabitat. Lastly, the landscape scale included several macrohabitats and was determined by the variability of habitat patches (Turner and Gardner 2015; Fletcher and Fortin 2018).

At the microhabitat scale, we recorded 14 field variables representing the characteristics of the focal houses and their backyards or gardens (Table 1) since *R. rattus* home range would include more than one garden or backyard. These variables were selected based on urban rodent ecology, rodent habitat requirements and landscape characteristics that have been described to influence the distribution of rodents within cities (Langton and Cowan 2001; Cavia et al. 2009; Feng and Himsworth 2014).

At the macrohabitat scale, we recorded the availability of public services (i.e., garbage collection) and land cover characteristics in the neighborhood around focal households (Traweger et al. 2006; Cavia et al. 2009; Tamayo-

Uria et al. 2014), which would include the whole home range of one or several *R. rattus* individuals. We delimited two concentric areas of 100 and 250 m of radius centered on each focal household and measured 13 environmental and land cover characteristics (Table 1). A Spot5-HRG2 Multispectral image of the study area with a pixel size of 2.5x2.5 m^2 and a vector support machine (SVM) classifier was used for land cover classification. Land cover classes included: 1) trees or shrubs vegetation, 2) herbaceous vegetation, 3) crops, 4) bare soil, 5) impervious or constructed surfaces, and 6) water bodies

Table 1. Macro and microhabitat scale environmental characteristics recorded on urban, periurban and rural households in the department of Iguazú, Misiones. (*) These characteristics were also estimated for a buffer area of 50 and 25 m radius, but considered from the microhabitat scale (see text).

Tabla 1. Características ambientales a escala de macro y microhábitat registradas en viviendas urbanas, periurbanas y rurales dentro del departamento de Iguazú, Misiones. (*) Estas características también fueron estimadas para un área de 50 y 25 m de radio, pero consideradas desde la escala del microhábitat (ver texto).

Environmental characteristics
Macrohabitat scale (neighborhood)
Neighborhood garbage collection service (presence/absence)
Drinking water service (presence/absence)
Public sewage connection (presence/absence)
Electrical energy network (presence/absence)
Paved road (presence/absence)
Services Index: an index of public services from the presence of six services: paved road, drinking water, electricity, garbage collection, sewer, street lighting. The index ranges from 0 (no services) to 1 (all services)
Distance to water bodies (km)
Tree, herbaceous, bare soil, crops and impervious or constructed surfaces cover (%) within 100 and 250 m radius (*)
Land cover richness and Shannon index for land cover within 100 and 250 m radius
NDVI and NDWI within 100 and 250 m radius
Microhabitat scale (backyards or gardens)
Ground burned waste (presence/absence)
Water tanks (presence/absence)
Cement (presence/absence)
Artesian wells (presence/absence)
Cesspit (presence/absence)
Lighting (presence/absence)
Dogs (presence/absence)
Grass (presence/absence)
Scrubs (presence/absence)
Bare soil (presence/absence)
Tree (presence/absence)
Flooded soil (without flooded soil (0), least than 1 m^2 of flooded soil (1) and more than 2 m^2 of flooded soil)
Domestic garbage (without domestic garbage (0), least than 1 m^2 of domestic garbage (1) and more than 2 m^2 of domestic garbage)
Fallen leaves and fruit (without fallen leaves and fruit (0), least than 1m^2 of fallen leaves and fruit (1); and more than 2 m^2 of fallen leaves and fruit)

(Supplementary Material 1). The configuration used for the SVM classifier was: a) kernel function=RBF; b) constant C=1000; c) gamma parameter=1, and d) probability threshold=0. We used the homogeneity variable to increase the precision of the classification of the maps (Tucker 1979). Environmental heterogeneity at this scale was estimated by the richness of land cover classes and the Shannon diversity index (Fletcher and Fortin 2018). We also estimated overall vegetation cover using the average of the NDVI and NDWI indices for each pixel of the image (Landis and Koch 1977; Coulibaly 2006). Satellital and spatial data were analyzed using ENVI+IDL v.4.8 (ITT Visual Information Solutions) and QuantumGis 2.14.15-Essen (QGIS Development Team 2014), respectively. All the same characteristics were estimated also at the microhabitat scale in concentric areas of 25 and 50 m radius. Finally, we defined the characteristics at the landscape scale as a categorical variable with three levels, based broadly on the number of inhabitants in each area and all the correlated factors: urban (Puerto Iguazú), periurban (Puerto Libertad) or rural areas (Cooperativa and San Cayetano).

Data analysis

The magnitude and range of spatial dependence of the rodent infestation index was estimated with a correlogram of the permutation test for Moran's I statistic according to Fletcher and Fortin (2018) with the spdep package (Bivand and Wong 2018) in the R environment (R Core Team 2020). The association between the rodent infestation index and measured microhabitat and macrohabitat environmental characteristics and landscape type was evaluated using a multiscale approach (Fletcher and Fortin 2018). Relevant environmental variables were included in generalized linear models (GLM) with binomial distributions and logit-links following a forward stepwise procedure (McCullaugh and Nelder 1989; Crawley 2007; Zuur et al. 2009). Variables with significant and greater change in deviance were included in each step. We evaluated collinearity among variables with variance inflation factors (VIF) (Zuur et al. 2007) and tested several possible additive combinations of variables and quadratic variables to determine the final candidate models. Non nested candidate models obtained by forward selection were compared with Akaike's information criterion, selecting only those most parsimonious (ΔAIC<2 compared to the lowest AIC) (Burnham and Anderson 2002) (Supplementary Material 2). GLM were fitted with the package MASS (Venables and Ripley 2002) within the R software (R Core Team 2020). Variance partitioning analyses for the final model(s) to estimate the effect of each predictor variable on the rodent infestation index were performed with the package variancePartition (Hoffman and Schadt 2016) in R (R Core Team 2020). Spatial dependence of the residuals was checked with permutation tests based on Moran's I correlograms (Fletcher and Fortin 2018).

Spatially explicit predictive maps of rodent infestation levels were built using the selected environmental models when required values for the predictive variables were available for the whole area. Otherwise, constant and contrasting values for the whole area were assumed (see Results). For this, maps of the selected explanatory variables were built using the moving windows procedure using the packages raster (Hijmans 2021) and landscapemetric (Hesselbarth et al. 2019) in R (R Core Team 2020).

The seasonal variation of the rodent infestation index from November 2014 to February 2016 was analyzed using a generalized linear mixed models (GLMM) with binomial distribution of the errors and logit-link function. In these models, season was included as an explanatory variable and focal households were considered a random factor since each of them was sampled repetitively (Zuur et al. 2007). *A posteriori* multiple comparisons with Bonferroni correction were performed if necessary to compare levels of fixed factors, with differences considered significant when P<0.2. Models and tests were performed with the packages lme4 (Bates et al. 2014) and multcomp (Hothorn et al. 2008) in R (R Core Team 2020).

Results

Rodent activity was detected in 42.5% of the households sampled (n=87), including 39.6% of the urban (n=53), 60% of the periurban (n=15) and 36.8% of the rural households (n=19). According to the signs in bait stations (hairs and marks), all rodents detected were *Rattus* spp. The rodent infestation index showed positive spatial autocorrelation between sampled sites up to ~2500 m (Figure 3A). According to the multiscale environmental analysis, the most parsimonious model

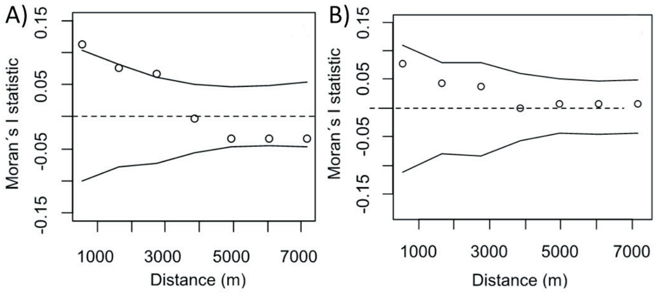

Figure 3. Moran's I statistic correlogram. A) On the rodent infestation index. B) On the residuals of the selected environmental model (see Table 2). The solid lines show the 95% null envelope from the permutation test; observed values higher than the limits of the envelope indicate positive spatial autocorrelation.

Figura 3. Correlograma del estadístico I de Moran. A) Sobre el índice de infestación de roedores. B) Sobre los residuos del modelo ambiental (ver Tabla 2). Las líneas continuas muestran la envolvente nula al 95% de la prueba de permutación; valores observados más altos que los límites de la envolvente implican autocorrelación espacial positiva.

Table 2. Estimates for the explanatory environmental variables (see Table 1) according to the model selected to explain the variation of the rodent infestation index in urban, periurban and rural households in department of Iguazú, Misiones. The model was fitted assuming binomial error structure and a logit-link function following a forward stepwise procedure. SE: standard error.

Tabla 2. Estimaciones de las variables ambientales (ver Tabla 1) incluidas en el modelo seleccionado para explicar las variaciones del índice de infestación de roedores en viviendas urbanas, periurbanas y rurales del departamento Iguazú, Misiones. El modelo fue ajustado suponiendo una estructura de error Binomial con función de enlace logit y siguiendo un procedimiento por pasos hacia adelante (*forward stepwise*). SE: error estándar.

	Estimate	SE	z-value	Variance partition
Intercept (rural)	7.740***	1.7017	4.548	
Landscape scale				0.020
Periurban area	2.060***	0.6245	3.299	
Urban area	1.020*	0.4806	2.122	
Macrohabitat scale				
Shannon Index within 100 m radius	-8.645***	1.4854	-5.820	0.140
Impervious surfaces (%) within 100 m radius	0.080	0.0522	1.533	0.098
[Impervious surfaces (%) within 100 m radius]^2	-0.002**	0.0008	-2.781	0.252
Trees cover (%) within 250 m radius	-0.047***	0.0139	-3.366	0.047
Microhabitat scale				
Bare soil cover (%) within 25 m radius	0.077**	0.0276	2.791	0.135
[Bare soil cover (%) within 25 m radius]^2	-0.001**	0.0003	-2.843	0.139
Trees presence	-0.726*	0.3607	-2.012	0.006

to explain rodent infestation levels in the households included variables from the three spatial scales considered ($\text{AIC}_{\text{model}}$=183.10; AIC_{null}=253.81) (Table 2). At the landscape scale, rodent infestation was higher in households in the periurban area (mean±SD=0.23±0.24 bait stations with rat signs) than in the urban (0.12±0.20) and rural areas (0.07±0.09) (Table 2, Figure 4A). Among macrohabitat characteristics, rodent infestation was higher in households with lower Shannon index of land cover types within 100 m radius (Table 2, Figure 4B) and with lower tree cover within 250 m radius (Table 2, Figure 4C). The amount of impervious surface within the first 100 m of a household (macrohabitat) and the bare soil cover within 25 m radius (microhabitat) were also included with quadratic relationships with higher infestation levels associated with intermediate values of both environmental characteristics (Table 2, Figure 4D and 4E). The presence of trees in the household's gardens or backyards —a microhabitat scale characteristic— was associated with lower values of rodent infestation (Table 2, Figure 4F). According to the variance partition analysis, the macrohabitat characteristics were the most relevant in this model, summarizing 53.7% of the variance of the infestation index while those at the microhabitat scale explained 28.0% and landscape type only 2% (Table 2). The residuals of this model showed non-significant spatial autocorrelation (Figure 3B).

According to the selected multiscale model, maps of predicted rodent infestation were built assuming two possible scenarios at the microhabitat scale: with trees (Figure 5A-D) or without trees (Figure 5E-H) in the household

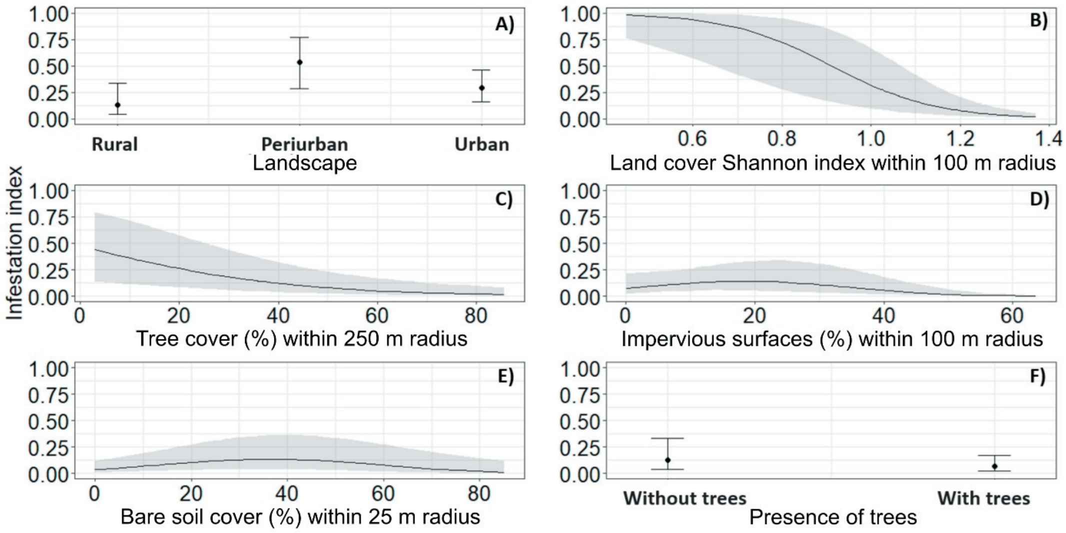

Figure 4. Relation between the rodent infestation index and the environmental characteristics according to the environmental model selected (see Table 2). Predicted values for each of the explanatory variables. A) Landscape (urban, periurban and rural areas). B) Land cover Shannon index within 100 m radius. C) Trees cover within 250 m radius. D) Impervious surfaces within 100 m radius. E) Bare soil cover within 25 m radius buffer area. F) Presence or absence of trees.

Figura 4. Relación entre el índice de infestación de roedores y las características ambientales según el modelo ambiental (Tabla 2). Valores predictivos en relación con las variables explicativas. A) Paisaje (zonas urbanas, periurbanas y rurales). B) Índice de Shannon de cobertura del suelo a 100 m. C) Cobertura de árboles a 250 m. D) Superficies impermeables a 100 m. E) Cobertura de suelo desnudo en un área de amortiguación de 25 m de radio. F) Presencia o ausencia de árboles.

backyard or garden, because this information is not available for all the non-sampled households in the study area. Despite the appearance of a spatially dispersed pattern, under both scenarios the highest rodent infestation occurs in areas of lower household density and on the outskirts of the populated agglomerations either in the city, the village or the rural areas. This pattern is clearer in the city of Puerto Iguazú, with observed and predicted areas with rodent infestation index greater than 0.2 located mainly in the north, south-center and south of the city (Figure 5A and E). In the scenario without-trees on the gardens of backyards, the spatial prediction is the same but with higher rodent infestation values.

The temporal analysis showed a seasonal variation in the rodent infestation index (LRT=9.150, df=3, P=0.027, residual deviance=212.8, $\mathrm{df}_{\mathrm{resid}=}$81, $\mathrm{AIC}_{\mathrm{model}=}$222.77, $\mathrm{AIC}_{\mathrm{null}=}$225.92). In winter, the rodent infestation index was an order of magnitude smaller than in summer (mean=0.0138 and 0.160 bait stations with rat signs, respectively; estimate=-2.345, se=1.076, z-value=-2.179, P=0.176) and autumn (mean=0.147 bait stations with rat signs; estimate=-2.344; se=1.099, z-value=-2.134, P=0.197). Differences were not as significative between winter and spring or between the other seasons compared (P>0.20).

Discussion

This study shows that not only the characteristics of the households explain the abundance of commensal rats´ in human settlements of different size. We observed that land cover around the focal households (macrohabitat, up to 100-250 m around) was more important than characteristics measured at the household scale (microhabitat). While the simultaneous effects of factors acting at different scales has been already robustly demonstrated (Kotliar and Wiens 1990; Wiens 1989; Klijn and de Haes 1994), with population abundance the result of multiscalar processes (Johnson 1980; Morris 1987, 1996; Orians and Wittenberger 1991), multiscalar studies such as ours are not abundant, possibly due to methodological and resource limitations. In any case, the identification of the relative importance of scale-dependent interactions may prove not only interesting but practical in cases with health and economic implications, such as the presence of commensal rats in northern Misiones. We

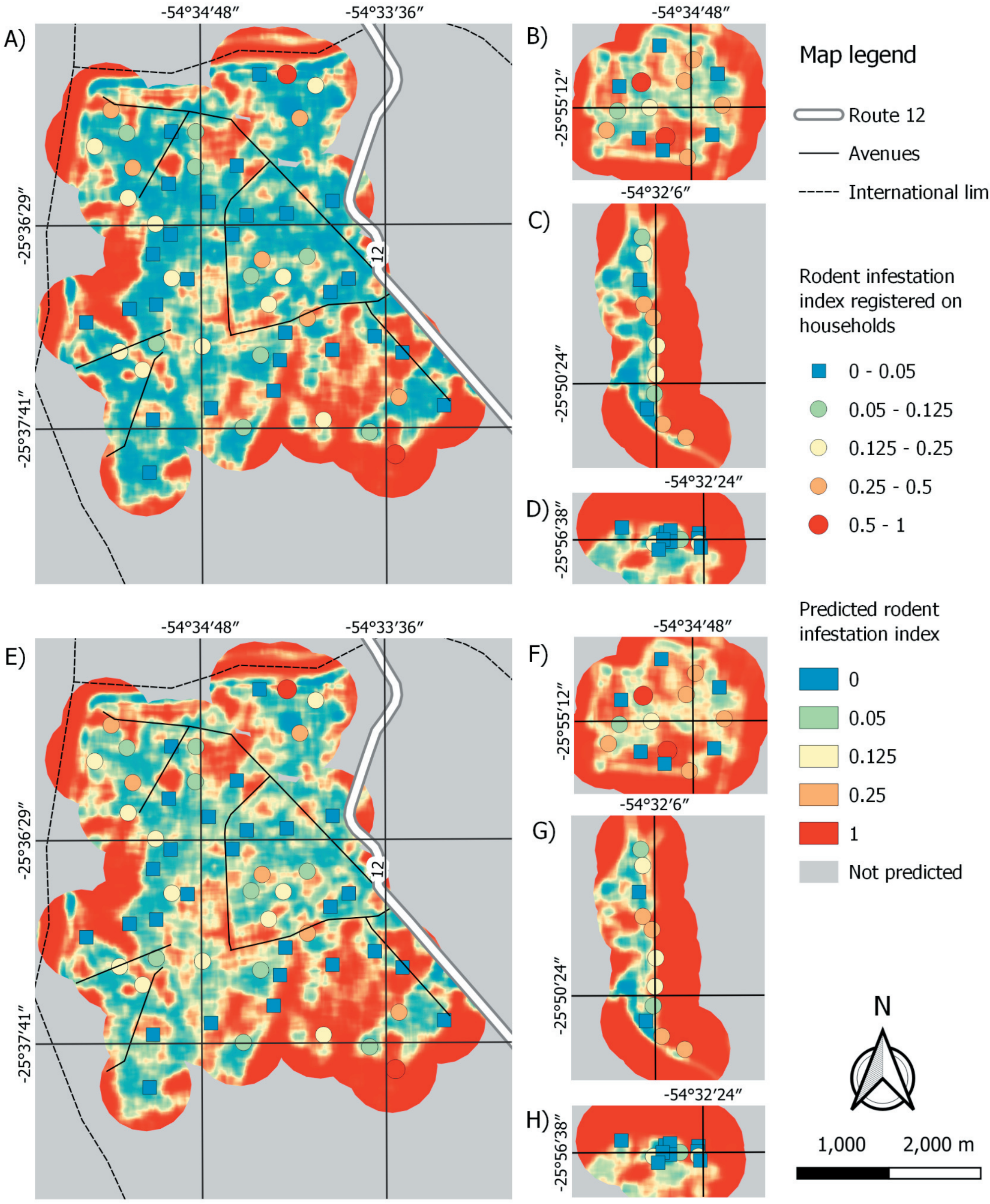

Figure 5. Spatial predictions for the rodent infestation index (proportion of bait stations with rodent activity) in households with trees in the backyards or gardens in A) the city of Puerto Iguazú, B) the town of Puerto Libertad, C) the rural areas of Cooperativa and D) San Cayetano; or without trees in their gardens (same locations: E-H) in the Department of Iguazú, Misiones, Argentina.

Figura 5. Predicciones espaciales para el índice de infestación de roedores (proporción de estaciones de cebo con actividad de roedores) en viviendas con árboles en los patios en A) la ciudad de Puerto Iguazú, B) la localidad de Puerto Libertad, C) las zonas rurales de Cooperativa y D) San Cayetano; o sin árboles (mismos lugares: E-H) en el departamento de Iguazú, Misiones, Argentina.

show that rat abundance in cities, villages and rural areas have spatial dependences at larger than households or block-sized areas that can be related to several environmental characteristics. This knowledge contrasts with the usual approach by residents and local authorities, who concentrate rodent-control efforts on individual houses or their immediate neighborhood providing short-term solutions that prove hard to sustain in the long term (Lambropoulos et al. 1999; Fernández et al. 2007). Our results support proposals by Lambropoulos et al. (1999) and Fernández et al. (2007) regarding the need for coordinated citizen work in order to achieve a more effective rodent control strategy, thus, ecologically-based rodent management strategies would be adopted in urban areas.

Although it is not yet understood how different types of land cover at the neighborhood level (macrohabitat scale) are either favoring or limiting the population size of rats, our results show that these variables have a strong influence on the spatial structure of rat infestation levels. This allowed us to make spatial predictions of rat infestation throughout the study area showing that, as has been observed in other experiences, there are relatively large areas with similar levels of rat abundance (Childs et al. 1998; Traweger and Slotta-Bachmayr 2005; Tamayo-Uria et al. 2014; Cavia et al. 2015). If this spatial distribution pattern proves consistent over the years, it could help guide rodent control efforts and monitoring efforts in the region. At household scale, only the absence of trees in the gardens or backyards (among the fourteen microhabitat characteristics evaluated) was associated with higher rat abundance, probably related to less availability of perches for flying predators of rodents (Yonas and Leirs 2019; Zagorski and Swihart 2020). Despite the important diversity of raptors in the Department of Iguazú (Ferguson-Lees and Christie 2004; López Lanús 2017), information about which of them prey on rodents in the urban areas is scarce. Some research carried out on other urban and periurban areas in Argentina mention *Tyto alba* as a main predator on *Rattus* spp. and *Mus musculus* (Teta et al. 2012; Rimoldi and Curti 2021). On the other side, and contrary to our expectations (cf. Childs 1986; Montes de Oca et al. 2020), possession of cats or dogs in the household, potential terrestrial predators of rodents, did not associate with rat abundances.

Seasonal variations in abundance have frequently been reported for commensal rodents throughout the world, with the patterns in rats infestation observed in this study similar to the seasonal variation observed for *R. norvegicus* elsewhere in urban (Gómez Villafañe et al. 2012; Vadell et al. 2014) and rural areas of temperate Argentina (Gómez Villafañe and Busch 2007; Gómez Villafañe et al. 2012; Lovera et al. 2015) and other countries (Glass et al. 1988; McGuire et al. 2006; Panti-May et al. 2016). In all cases, winter is the season with the lowest abundance (Traweger et al. 2006; Vadell et al. 2010, 2014; Cavia et al. 2015), even in the subtropical weather (without cold winters) of northern Misiones, as our results shown.

Bait stations coupled with hair traps provide an easy economical method to identify the presence of rodents in urban areas and estimate rodent infestation levels (Fernández et al. 2007; Cavia et al. 2012). Our experience using this non-invasive technique shows that it can be applied along extended areas both inside households and in public places (Fernández et al. 2007). Hair structure and morphology allow the distinction between different groups of mammal species. Hair from *R. rattus* and *R. norvegicus* can be easily differentiated from those of *Mus musculus* and *Didelphis albiventris* —the most frequent marsupial in the study area— because of their different hair size and color patterns (Cavia et al. 2008, Cavia et al. unpublished data). In this way, this method has shown to be useful to identify the presence of rodents in urban areas as well as to estimate the infestation levels (Fernández et al. 2007; Cavia et al. 2012). Although requiring proper calibration for focal species and environments before absolute rodent population sizes can be estimated, it still allows the comparison of relative abundances between sites and/or time periods, as well as any other sampling method (Aplin et al. 2003). Although with incisor marks and hairs we cannot differentiate between *Rattus* species, *R. rattus* is the only *Rattus* species cited for the north of Misiones (Cavia et al. 2019a,b) and it is frequently captured in the Department of Iguazú (Burgos unpublished data; Cavia unpublished data) while *R. norvegicus* has not been cited in the area yet (Cavia et al. 2019a). In consequence, we can safely assume that all rodent signs recorded in this study correspond to *R. rattus*.

In conclusion, the number of signs of rats recorded in household gardens and backyards represent a health risk for local people and domestic animals, since they are important disease agents in urban areas (Himsworth et al. 2013; Hancke and Suárez 2017; Boey et al. 2019). Systematic identification and mitigation of the causes of disease are key factors for effective prevention actions (Childs 2007; Ellwanger et al. 2019). This study showed how priority areas for management actions can be identified with a low-cost and easy-to-use sampling tool. Also, we showed that urban rat infestation can be predicted with information on environmental factors acting at different scales, particularly those that integrate information at the neighborhood scale. The management of commensal rodents should consider the specific ecology and spatial scales of each target species. Prevention and control actions would be more effective if greater efforts are made to apply management actions at specific moments of the year (i.e., during the winter) and on the critical areas within the urban-rural gradient.

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```
####Models####

library(lme4)
library(MuMIn)
library(MASS)
library(pscl)
library(car)
library(boot)
library(multcomp)
library(AICcmodavg)
library(vegan)
y=cbind(SIGN2, REV2-SIGN2)
summary(y)

M0=glm(y~1, data=datos, family = binomial, na.action=na.omit)
summary(M0)
AIC(M0)

add1.test <- add1(M0,scope=y~1+zona+quemaentierrabasura2+basuradomestica2+hojasfrutascaidas2+servic_index+calle_pav+cemento2+aguadered2+pozosartesianos2+cloaca2+pozociego2+alumbrado2+tierraanegada2+recolecciondebasura2+energiaelectrica2+cisternas2+perros_pres+gallinas_pres+tierra_d+cesped_d+arbustos_d+arboles_d+distancia_agua_km+I(distancia_agua_km^2)+arboles_25+I(arboles_25^2)+arboles_50+I(arboles_50^2)+arboles_100+I(arboles_100^2)+arboles_250+I(arboles_250^2)+herbaceas_25+I(herbaceas_25^2)+herbaceas_50+I(herbaceas_50^2)+herbaceas_100+I(herbaceas_100^2)+herbaceas_250+I(herbaceas_250^2)+suelo_25+I(suelo_25^2)+suelo_50+suelo_100+suelo_250+I(suelo_50^2)+I(suelo_100^2)+I(suelo_250^2)+urbano_25+I(urbano_25^2)+urbano_50+I(urbano_50^2)+urbano_100+I(urbano_100^2)+urbano_250+I(urbano_250^2)+cultivos_100+I(cultivos_100^2)+cultivos_250+I(cultivos_250^2)+shannon25+I(shannon25^2)+shannon50+I(shannon50^2)+shannon100+I(shannon100^2)+shannon250+I(shannon250^2)+diver_cob_25+I(diver_cob_25^2)+diver_cob_50+I(diver_cob_50^2)+diver_cob_100+I(diver_cob_100^2)+diver_cob_250+I(diver_cob_250^2)+ndvi_25+I(ndvi_25^2)+ndvi_50+I(ndvi_50^2)+ndvi_100+I(ndvi_100^2)+ndvi_250+I(ndvi_250^2)+ndwi_25+I(ndwi_25^2)+ndwi_50+I(ndwi_50^2)+ndwi_100+I(ndwi_100^2)+ndwi_250+I(ndwi_250^2), test="Chisq", x=NULL, k=2, trace=T)
```

```
M1=glm(y ~1+ shannon100, family = binomial,data = datos, na.action = na.omit)
summary(M1)

add1.test <- add1(M1,scope=y~1+zona+quemaentierrabasura2+basuradomestica2+hojasfrutascaidas2+servic_index+calle_pav+cemento2+aguadered2+pozosartesianos2+cloaca2+pozociego2+alumbrado2+tierraanegada2+recolecciondebasura2+energiaelectrica2+cisternas2+perros_pres+gallinas_pres+tierra_d+cesped_d+arbustos_d+arboles_d+distancia_agua_km+I(distancia_agua_km^2)+arboles_25+I(arboles_25^2)+arboles_50+I(arboles_50^2)+arboles_100+I(arboles_100^2)+arboles_250+I(arboles_250^2)+herbaceas_25+I(herbaceas_25^2)+herbaceas_50+I(herbaceas_50^2)+herbaceas_100+I(herbaceas_100^2)+herbaceas_250+I(herbaceas_250^2)+suelo_25+I(suelo_25^2)+suelo_50+suelo_100+suelo_250+I(suelo_50^2)+I(suelo_100^2)+I(suelo_250^2)+urbano_25+I(urbano_25^2)+urbano_50+I(urbano_50^2)+urbano_100+I(urbano_100^2)+urbano_250+I(urbano_250^2)+cultivos_100+I(cultivos_100^2)+cultivos_250+I(cultivos_250^2)+shannon25+I(shannon25^2)+shannon50+I(shannon50^2)+shannon100+I(shannon100^2)+shannon250+I(shannon250^2)+diver_cob_25+I(diver_cob_25^2)+diver_cob_50+I(diver_cob_50^2)+diver_cob_100+I(diver_cob_100^2)+diver_cob_250+I(diver_cob_250^2)+ndvi_25+I(ndvi_25^2)+ndvi_50+I(ndvi_50^2)+ndvi_100+I(ndvi_100^2)+ndvi_250+I(ndvi_250^2)+ndwi_25+I(ndwi_25^2)+ndwi_50+I(ndwi_50^2)+ndwi_100+I(ndwi_100^2)+ndwi_250+I(ndwi_250^2), test="Chisq", x=NULL, k=2, trace=T)

add1.test[order(add1.test$"Pr(>Chi)"),]

M1 <- update(M1, .~.+zona)
vif(M1)
anova(M1, test="Chisq")
summary(M1)

M1 <- update(M1, .~.+urbano_100+ I(urbano_100^2))
vif(M1)
anova(M1, test="Chisq")
summary(M1)
M1 <- update(M1, .~.+arboles_250)
vif(M1)
anova(M1, test="Chisq")
summary(M1)
M1 <- update(M1, .~.+ suelo_25 + I(suelo_25^2))
```

```
vif(M1)
anova(M1, test="Chisq")
summary(M1)
M1.1 <- update(M1, .~.+ arboles_d)
vif(M1)
anova(M1, test)

M1.1=glm( y ~1+ shannon100 + zona + urbano_100 + I(urbano_100^2) + arboles_250 + suelo_25 + I(suelo_25^2)+arboles_d, family = binomial,data = datos, na.action = na.omit)
summary(M1.1)

#pruebo rama distancia al agua en km

M0=glm(y~1, data=datos, family = binomial, na.action=na.omit)
summary(M0)
AIC(M0)

add1.test <- add1(M2,scope=y~1+zona+quemaentierrabasura2+basuradomestica2+hojasfrutascaidas2+servic_index+calle_pav+cemento2+aguadered2+pozosartesianos2+cloaca2+pozociego2+alumbrado2+tierraanegada2+recolecciondebasura2+energiaelectrica2+cisternas2+perros_pres+gallinas_pres+tierra_d+cesped_d+arbustos_d+arboles_d+distancia_agua_km+I(distancia_agua_km^2)+arboles_25+I(arboles_25^2)+arboles_50+I(arboles_50^2)+arboles_100+I(arboles_100^2)+arboles_250+I(arboles_250^2)+herbaceas_25+I(herbaceas_25^2)+herbaceas_50+I(herbaceas_50^2)+herbaceas_100+I(herbaceas_100^2)+herbaceas_250+I(herbaceas_250^2)+suelo_25+I(suelo_25^2)+suelo_50+suelo_100+suelo_250+I(suelo_50^2)+I(suelo_100^2)+I(suelo_250^2)+urbano_25+I(urbano_25^2)+urbano_50+I(urbano_50^2)+urbano_100+I(urbano_100^2)+urbano_250+I(urbano_250^2)+cultivos_100+I(cultivos_100^2)+cultivos_250+I(cultivos_250^2)+shannon25+I(shannon25^2)+shannon50+I(shannon50^2)+shannon100+I(shannon100^2)+shannon250+I(shannon250^2)+diver_cob_25+I(diver_cob_25^2)+diver_cob_50+I(diver_cob_50^2)+diver_cob_100+I(diver_cob_100^2)+diver_cob_250+I(diver_cob_250^2)+ndvi_25+I(ndvi_25^2)+ndvi_50+I(ndvi_50^2)+ndvi_100+I(ndvi_100^2)+ndvi_250+I(ndvi_250^2)+ndwi_25+I(ndwi_25^2)+ndwi_50+I(ndwi_50^2)+ndwi_100+I(ndwi_100^2)+ndwi_250+I(ndwi_250^2), test="Chisq", x=NULL, k=2, trace=T)

add1.test[order(add1.test$"Pr(>Chi)"),] #AIC Pr(>Chi)
M2=glm (y ~1+ distancia_agua_km, family = binomial, data = datos,
```

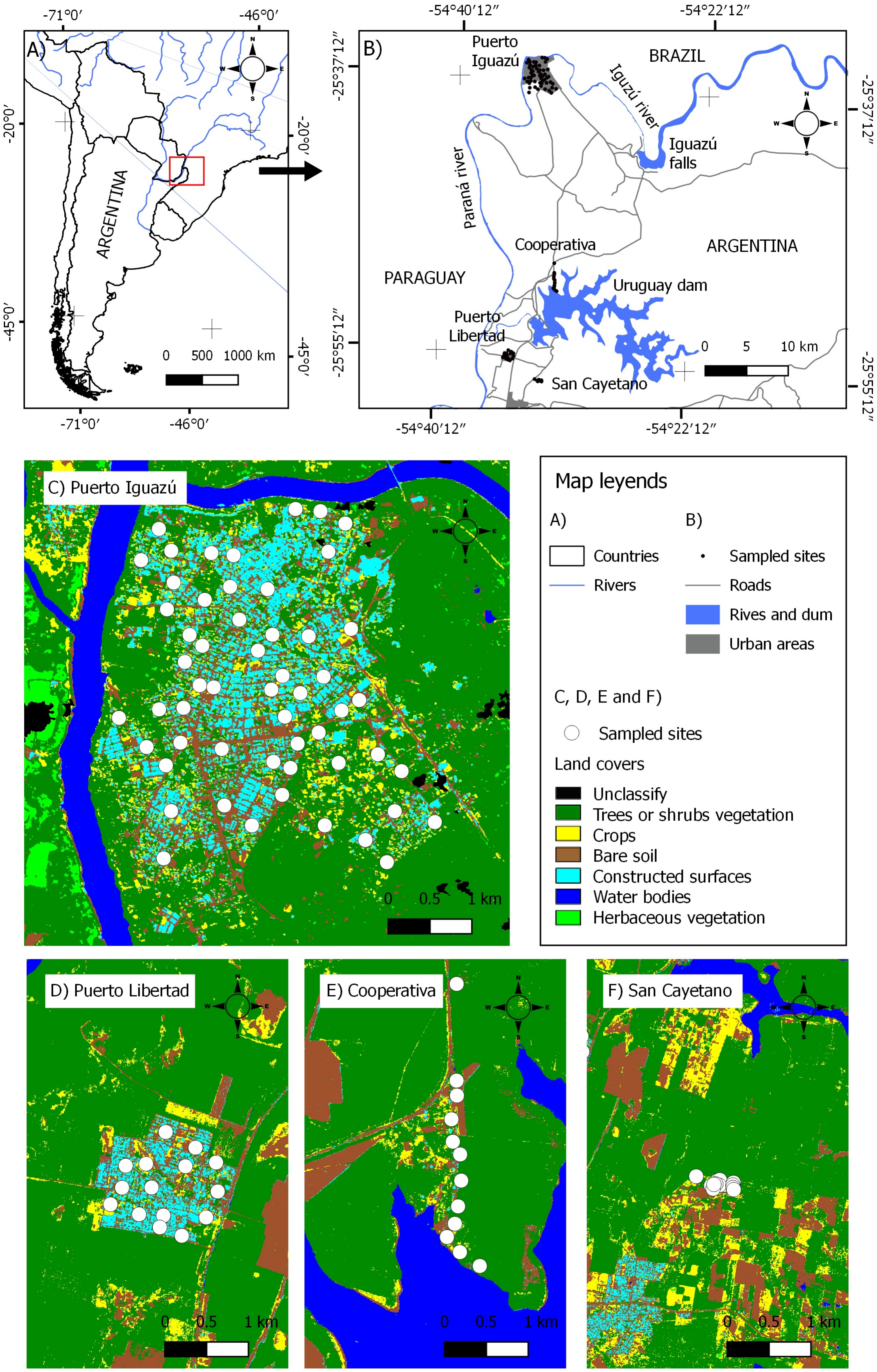
```
          na.action = na.omit)
summary(M2)
M2 <- update(M2, .~.+shannon100)
vif(M2)
anova(M2, test="Chisq")
M2 <- update(M2, .~.+arboles_250)
vif(M2)
anova(M2, test="Chisq")
M2 <- update(M2, .~.+ urbano_100 + I(urbano_100^2))
summary(M2)
vif(M2)
anova(M2, test="Chisq")

M2.1=glm (y ~1+ distancia_agua_km + shannon100 + arboles_250 +
            urbano_100 + I(urbano_100^2), family = binomial, data = datos,
          na.action = na.omit)
summary(M2.1)

modlist=list(M0,M1.1,M2)

modnames=c("M0","M1.1","M2")

aictab(modlist, modnames =modnames)

M1.1=glm( y ~1+ shannon100 + zona + urbano_100 + I(urbano_100^2) + arboles_250 +
suelo_25 + I(suelo_25^2)+arboles_d, family = binomial,data = datos, na.action = na.omit)
summary(M1.1)
(((M1.1$null.deviance-M1.1$deviance)/M1.1$null.deviance)*100)

contr_zona<-glht(M1.1, linfct = mcp(zona="Tukey"))
summary(contr_zona)
```

```
library(ggplot2)
windows()
plot(contr_zona)

####Predichos####
datos$zona1 <- factor(datos$zona, labels=c("Rural","Peri urban", "Urban"))
datos$arboles_d1 <- factor(datos$arboles_d, labels=c("Without trees","With trees"))

library(ggplot2)
library(ggeffects)
pred.shannon<-ggpredict(M1.1, terms = "shannon100 [all]")
pred.urbano<-ggpredict(M1.1, terms = "urbano_100 [all]")
pred.arboles<-ggpredict(M1.1, terms = "arboles_250 [all]")
pred.suelo<-ggpredict(M1.1, terms = "suelo_25 [all]")
pred.zona<-ggpredict(M1.1, terms = "zona1")
pred.presarbol<-ggpredict(M1.1, terms = "arboles_d1")

#numericas#
shannon <- plot(pred.shannon)+ theme_bw()+labs(x="Shannon index at 100 m", y="Infestation
index")+
  theme(plot.title=element_blank(), legend.position = c(0.1,0.9),
        axis.title=element_text(size=rel(2)),axis.text= element_text(size = rel(2)))
+scale_y_continuous(limits = c(0,1))+ ggtitle("A") +
  theme(
    axis.title.x = element_text(colour="black", size=20),
    axis.text.x = element_text(colour="black", size=20),
    axis.title.y = element_text(colour="black", size=20, angle = 90),
    axis.text.y = element_text(colour="black", size=20))

arb_cob <- plot(pred.arboles)+ theme_bw()+labs(x="Trees cover at 250 m", y="")+
  theme(plot.title=element_blank(), legend.position = c(0.1,0.9),
```

```
      axis.title=element_text(size=rel(2)),axis.text= element_text(size = rel(2)))
+scale_y_continuous(limits = c(0,1)) + ggtitle("B") +

  theme(

    axis.title.x = element_text(colour="black", size=20),

    axis.text.x = element_text(colour="black", size=20),

    axis.title.y = element_text(colour="black", size=20, angle = 90),

    axis.text.y = element_text(colour="black", size=20))



imper_sourface <- plot(pred.urbano)+ theme_bw()+labs(x="Impervious surfaces at 100 m",
y="")+

  theme(plot.title=element_blank(), legend.position = c(0.1,0.9),

      axis.title=element_text(size=rel(2)),axis.text= element_text(size = rel(2)))
+scale_y_continuous(limits = c(0,1))+ ggtitle("C") +

  theme(

    axis.title.x = element_text(colour="black", size=20),

    axis.text.x = element_text(colour="black", size=20),

    axis.title.y = element_text(colour="black", size=20, angle = 90),

    axis.text.y = element_text(colour="black", size=20))



suel <- plot(pred.suelo)+ theme_bw()+labs(x="Bare soil cover at 25 m", y="")+

  theme(plot.title=element_blank(), legend.position = c(0.1,0.9),

      axis.title=element_text(size=rel(2)),axis.text= element_text(size = rel(2)))
+scale_y_continuous(limits = c(0,1))+ ggtitle("D") +

  theme(

    axis.title.x = element_text(colour="black", size=20),

    axis.text.x = element_text(colour="black", size=20),

    axis.title.y = element_text(colour="black", size=20, angle = 90),

    axis.text.y = element_text(colour="black", size=20))


zone <- plot(pred.zona)+ theme_bw()+labs(x="Landscape", y="")+
```

```
  theme(plot.title=element_blank(), legend.position = c(0.1,0.9),
        axis.title=element_text(size=rel(2)),axis.text= element_text(size = rel(2))) +scale_y_continuous(limits = c(0,1))+ ggtitle("D") +
  theme(
    axis.title.x = element_text(colour="black", size=20),
    axis.text.x = element_text(colour="black", size=20),
    axis.title.y = element_text(colour="black", size=20, angle = 90),
    axis.text.y = element_text(colour="black", size=20))

arb_pres_aus <- plot(pred.presarbol)+ theme_bw()+labs(x="Tree presence", y="")+
  theme(plot.title=element_blank(), legend.position = c(0.1,0.9),
        axis.title=element_text(size=rel(2)),axis.text= element_text(size = rel(2))) +scale_y_continuous(limits = c(0,1))+ ggtitle("D") +
  theme(
    axis.title.x = element_text(colour="black", size=20),
    axis.text.x = element_text(colour="black", size=20),
    axis.title.y = element_text(colour="black", size=20, angle = 90),
    axis.text.y = element_text(colour="black", size=20))



require(cowplot)
windows()
par(mfrow = c(3,2), mar = c(2,2,2,2))
plot_grid(suel,imper_sourface, shannon, arb_cob , zone, arb_pres_aus, nrow=3)


###Variance Partition####
M1.1=glm( y ~1+ shannon100 + zona + urbano_100 + I(urbano_100^2) + arboles_250 + suelo_25 + I(suelo_25^2)+arboles_d, family = binomial,data = datos, na.action = na.omit)#Mejor modelo selecto!
library(variancePartition)
calcVarPart(M1.1)
```

```
M1=glmer(y~estacion+ (1|Codigo_sitio), data=datos, family = binomial, na.action=na.omit)
summary(M1)
AIC(M1)#222.7759

library(emmeans)
Tukey <- emmeans(M1, pairwise~estacion, adjust = "tukey")
summary(Tukey)

residuos<-resid(M1)
predichos<-predict(M1)

qqnorm(residuos)
qqline(residuos)
shapiro.test(residuos)
```



Supplementary Material 1. Study area (a, b) and distribution of the sampling sites (c–f) in Iguazú Department, Misiones, Argentina.
Material Suplementario 1. Área de estudio (a, b) y distribución de los sitios de muestreo (c-f) en el departamento de Iguazú, Misiones, Argentina.