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PROGRAMA DE MAESTRÍA Y DOCTORADO EN CIENCIAS DE LA PRODUCCIÓN Y DE LA SALUD ANIMAL
FACULTAD DE MEDICINA VETERINARIA Y ZOOTECNIA

DISTRIBUCIÓN Y ABUNDANCIA DE ROEDORES RESERVORIOS DE PATÓGENOS ZOONÓTICOS EN AMBIENTES ANTROPIZADOS

TESIS

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PRESENTA

MVZ VÍCTOR HUGO MENDOZA GUTIÉRREZ

TUTOR PRINCIPAL

DR. GERARDO SUZÁN AZPIRI

PROGRAMA DE MAESTRÍA Y DOCTORADO EN CIENCIAS DE LA PRODUCCIÓN Y DE LA SALUD ANIMAL

COMITÉ TUTOR

DRA. ROSA ELENA SARMIENTO SILVA

DR. GABRIEL ERNESTO GARCÍA PEÑA

PROGRAMA DE MAESTRÍA Y DOCTORADO EN CIENCIAS DE LA PRODUCCIÓN Y DE LA SALUD ANIMAL

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Fernando Pessoa

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Resumen

La mayoría de las enfermedades zoonóticas se originan en animales de vida silvestre. Cambios en el medio ambiente y la genética de los animales que sirven como reservorios, no reservorios, vectores y patógenos pueden promover la aparición de enfermedades zoonóticas. La antropización (i.e. efecto de las actividades humanas sobre el medio ambiente) es uno de los mayores mecanismos que promueven la aparición de zoonosis, ya que la modificación de la biodiversidad y la pérdida del hábitat resultantes incrementan el contacto entre reservorios infectados y el ser humano. Varias especies de roedores generalistas e invasores pueden verse beneficiadas por la antropización de sus hábitats, aumentando sus abundancias relativas y densidades; además, algunas de esas especies han sido identificadas como reservorios importantes de una gran variedad de patógenos zoonóticos (e.g. *Rattus rattus* y *Mus musculus*). Con el fin de entender la relación entre roedores reservorios de patógenos zoonóticos y la antropización de sus hábitats, realizamos dos estudios a diferentes escalas. A escala local, evaluamos si la antropización interviene en la estructura de las comunidades de roedores (reservorios y no reservorios) en el noroeste de México. Para probar esto, desarrollamos un índice de antropización y ordenamos los sitios de captura de menor a mayor grado de antropización. El análisis de las comunidades se realizó desde la perspectiva de la teoría de metacomunidades, la cual nos permite identificar patrones de ensambles de especies. En nuestros resultados, encontramos que las comunidades de roedores en Bahía de Kino, Noroeste de México, presentan una estructura metacommunitaria Clementsiana (es decir, que las comunidades se reemplazan entre sí como un grupo, donde las especies funcionan en conjunto como un "superorganismo") cuando ordenamos la matriz de presencias-ausencias de especies con base en el grado de antropización. En el segundo capítulo, llevamos a cabo un metanálisis a escala global para evaluar el efecto del cambio de uso del suelo sobre la abundancia de roedores en relación con su estado de reservorio

para las enfermedades zoonóticas transmitidas por roedores. En general, los roedores reservorios fueron significativamente más abundantes en hábitats modificados, mientras que las especies no reservorios fueron más abundantes en hábitats no modificados. Nuestros hallazgos proporcionan evidencia adicional, tanto a escala local como a escala global, de que la antropización generalmente tiene un impacto en la biodiversidad de tal manera que puede implicar un mayor riesgo de transmisión de patógenos zoonóticos al favorecer un incremento en las abundancias y distribuciones de sus reservorios roedores.

Palabras clave: antropización, zoonosis, teoría de metacomunidades, estructura Clementsiana, cambio de uso del suelo

Abstract

Most zoonotic diseases are originated in wildlife. Changes in the environment and organisms serving as genetic reservoirs and non-reservoirs, vectors and pathogens can promote the emergence of zoonotic diseases. "Anthropization" (i.e., the effect of human activities on the environment) is one of the major drivers that promotes the emergence of zoonoses, as biodiversity modification and habitat loss increase contact between infected reservoirs and humans. Species of generalist and invasive rodents can be benefitted from anthropization of their habitats, increasing their relative abundances and densities. In addition, some of these species have been identified as important reservoirs of a considerable number of zoonotic pathogens (e.g. *Rattus rattus* and *Mus musculus*). In order to understand the relationship between rodent reservoirs of zoonotic pathogens and the anthropization of their habitats, we conducted two studies at different scales. At the local level, we examined whether anthropization leads to changes in the structure of rodent communities (reservoirs and non-reservoirs) in Bahía de Kino, Sonora State (northwestern Mexico). To test this, we developed an anthropization index and ranked the capture sites from lowest to highest anthropization. Analysis of the animal communities was made from the metacommunity theory framework, which allows identifying patterns of assemblages of species. In our results, we found that rodent communities in Bahía de Kino, have a Clementsian metacommunity structure (i.e. communities are considered to be discrete entities that replace each other as a group, and where species function in concert as a 'superorganism') when we order the presence-absence species matrix based on the degree of anthropization. In the second chapter, we conducted a meta-analysis on a global scale to evaluate the effect of land-use change on the abundance of rodents in relation to their reservoir status for rodent-borne zoonotic diseases. In general, reservoir rodents were significantly more abundant in modified habitats, while non-reservoir species were more abundant in non-modified habitats. Our findings provide additional evidence, both locally and globally, that anthropization generally has an impact on biodiversity such that may imply an increased risk of

zoonotic pathogen transmission via the increase in their rodent reservoirs abundance and distribution.

Key words: anthropization, zoonoses, metacommunity theory, Clementsian structure, land-use change

Distribución y abundancia de roedores reservorios de patógenos zoonóticos en ambientes antropizados

Introducción general

Las actividades humanas que impactan a los ecosistemas (i.e. antropización), tales como la deforestación, la agricultura, la ganadería y la urbanización, tienen un efecto directo sobre los procesos ecológicos naturales (Scheffer et al. 2001; Kehoe et al. 2017). Algunos factores resultantes de la antropización (e.g. la fragmentación del hábitat, la modificación de las redes tróficas y el cambio de uso del suelo) pueden provocar la pérdida de la biodiversidad (Pimm et al. 2014; Newbold et al. 2015), el filtrado ambiental de especies invasoras (Kraft et al. 2015; Suzán et al. 2015) y la modificación de la estructura comunitaria, a veces favoreciendo especies invasoras que pueden ser reservorios de patógenos zoonoóticos (Suzán et al. 2015; Chalkowski et al. 2018). La continua coexistencia entre especies reservorio y no reservorio, así como con sus patógenos relacionados, dentro de un paisaje antropizado, es uno de los mecanismos que más favorecen la aparición de enfermedades zoonóticas (Ostfeld y Keesing 2001; Guo et al. 2018).

Las enfermedades zoonóticas representan a más del 60% de las enfermedades infecciosas humanas (Taylor et al. 2001) y la mayoría son originadas en animales de vida silvestre (Jones et al. 2008). Las enfermedades transmitidas por roedores son un excelente modelo para entender la relación entre la antropización y la aparición de enfermedades zoonóticas (Mills 2006; McCauley et al. 2015; Morand et al. 2015; Plourde et al. 2017). Los roedores comprenden el orden más diverso de mamíferos con 2272 especies registradas (aproximadamente el 43% del total), además son el grupo animal con mayor distribución mundial después de los humanos (Wolff y

Sherman 2008). Las adaptaciones de los roedores a diferentes condiciones ambientales facilitan la coexistencia de este grupo de mamíferos con diferentes tipos de patógenos (Luis et al. 2013; Plourde et al. 2017) y se estima que los roedores están asociados con más de 80 patógenos zoonóticos (Han et al. 2016).

El aumento en la abundancia de roedores es un mecanismo subyacente para el aumento del riesgo de enfermedad como consecuencia de la conversión del hábitat (Mills 2006; Gottdenker et al. 2014; McCauley et al. 2015). Un aumento en la densidad de roedores reservorios puede aumentar la frecuencia de los contactos entre reservorios (infectados y susceptibles) de patógenos con transmisión denso-dependiente y horizontal, como el hantavirus (Khalil et al. 2014). Para las enfermedades transmitidas por roedores dependientes de vectores (e. g. Bartonellosis, enfermedad de Lyme y peste), la prevalencia de la infección en vectores puede aumentar como resultado de una mayor tasa de contacto entre vectores y reservorios debido a las mayores densidades de roedores reservorios (Ostfeld y Keesing 2001; Gage y Kosoy 2005; Young et al. 2014). Además, si los reservorios son más resistentes al cambio de uso del suelo que los no reservorios, puede producirse una pérdida del efecto de dilución (cuando una mayor diversidad de especies reservorios puede reducir el riesgo de enfermedad) cuando hay una disminución en la riqueza de especies o diversidad ecológica de los reservorios (Keesing et al. 2006).

Algunas especies de roedores con capacidad invasora, como *Rattus rattus* y *Mus musculus*, han sido identificadas como reservorios de patógenos zoonóticos que provocan enfermedades muy importantes para la salud pública, tales como la fiebre de Lassa y la Leptospirosis (Meerburg et al. 2009; McMahon et al. 2018). Por otro lado, especies nativas e invasoras están asociadas con hantavirus causante del síndrome pulmonar por hantavirus en América, como *Peromyscus maniculatus* en el norte, *Oligoryzomys fulvescens* en el centro y *O. longicaudatus* en el sur del continente (Jonsson et al. 2010).

Los roedores reservorios y no reservorios, así como sus vectores y patógenos relacionados, pueden formar comunidades que están interconectadas mediante la

dispersión de individuos de diferentes especies, es decir, pueden formar una metacomunidad (Leibold y Mikkelsen 2002). En ese sentido, el estudio de las enfermedades zoonóticas desde el enfoque de la teoría de metacomunidades (Mihaljevic 2012) nos permite vislumbrar la dinámica patógeno-reservorio en una escala mayor a la de una comunidad clásica. Suzán et al. (2015) propusieron tres procesos que pueden definir la prevalencia de un patógeno en un paisaje desde el enfoque de la teoría de metacomunidades: 1) la dispersión, colonización y extinción de patógenos, reservorios y no reservorios; 2) los procesos antropogénicos que pueden conducir al filtrado ambiental de reservorios, no reservorios y patógenos; y 3) la diversidad filogenética relativa al reservorio o vector.

Para probar la hipótesis de que la antropización es un factor determinante para la modificación de la biodiversidad, la alteración en los procesos metacommunitarios y la emergencia y proliferación de enfermedades zoonóticas transmitidas por roedores. en esta tesis abordaremos el efecto de la antropización sobre los roedores reservorios de patógenos zoonóticos en una escala metacommunitaria local y en una escala global. En el primer capítulo, aplicaremos el enfoque metacommunitario de la ecología de enfermedades propuesto por Suzán et al. (2015). Para ello, evaluaremos las comunidades de roedores en una localidad del noroeste mexicano (Bahía de Kino, Sonora) a lo largo de un gradiente de antropización. Nuestros objetivos son 1) conocer si la antropización modifica la estructura comunitaria de roedores, reservorios y no reservorios, en cinco sitios con diferentes usos del suelo y diferentes grados de antropización, y 2) determinar si la antropización puede favorecer la distribución, la riqueza y la abundancia de especies de roedores reservorios de patógenos zoonóticos. Nuestra hipótesis fue que la antropización modifica la estructura comunitaria de roedores, promoviendo el intercambio de individuos de distintas especies entre comunidades interconectadas (i.e. que forman una metacomunidad). Así mismo, predijimos que la antropización está positivamente correlacionada con la riqueza y la abundancia de roedores reservorios.

En el segundo capítulo, en una escala global, abordamos el efecto del cambio de uso del suelo sobre la abundancia de roedores reservorios de patógenos zoonóticos. A partir de un meta análisis con información mundial, nuestro objetivo fue evaluar si el tipo de hábitat, modificado o no modificado por actividades humanas, favorece la abundancia de roedores reservorios y no reservorios de patógenos zoonóticos. Nuestra hipótesis fue que los roedores reservorios son más abundantes en los hábitats modificados, mientras que los roedores no reservorios son más abundantes en los sitios con hábitats no perturbados.

Capítulo I

Landscape anthropization determines metacommunity structure of rodents and facilitate the presence of reservoir species of zoonotic pathogens

Landscape anthropization determines metacommunity structure of rodents and facilitate the presence of reservoir species of zoonotic pathogens

Mendoza, Hugo¹, García-Peña, Gabriel E.^{1,2}, Sotomayor-Bonilla, José de Jesús¹, Álvarez-Mendizábal, Paulina¹, Tolsá-García, María J.¹, Sarmiento-Silva, Rosa E.³, and Suzán, Gerardo^{1*}

1. Departamento de Etología, Fauna Silvestre y Animales de Laboratorio, Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, 04510 Ciudad de México, México.

2. Centro de Ciencias de la Complejidad C3, Universidad Nacional Autónoma de México, 04510 Ciudad de México, México.

3. Departamento de Microbiología e Inmunología, Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, 04510 Ciudad de México, México.

Key Words: Clementsian structure, rodent reservoir, metacommunity theory, zoonotic disease

*** Corresponding Author**

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Abstract

Anthropization is a major driver for biodiversity and habitat loss that can modify community structure of many species, resulting in an increase of zoonotic disease risk. The assemblages of species in anthropized landscapes can be evaluated from a metacommunity perspective that allows understanding of the patterns and dynamics of spatially interconnected communities. Metacommunity theory can be used as a tool that helps us to understand the distribution of pathogens and reservoirs in an anthropized landscape. In this study, we examined metacommunity structure in a rodent-reservoir system depending on the degree of anthropization of habitats in Bahía de Kino, Sonoran Desert. To that end, we developed an anthropization index composed of four variables: introduced vegetation, distance to human settlements, presence of roads and highways, and presence of buildings. Then, we generated presence/absence species matrices and arranged them along an anthropization gradient. Finally, we examined if captured species had been reported as reservoirs of zoonotic pathogens and we performed a Spearman's correlation test to evaluate the relationship between anthropization and richness/abundance of rodent reservoirs. Our results showed that rodent communities in Bahía de Kino have a positive turnover (i.e. number of times in which one species replaces another species between communities) with distinct clumps arranged along the anthropization gradient. Besides, we found a positive correlation between anthropization and richness/abundance of rodent reservoirs for the third season. Thus, rodent metacommunities are structured in a Clementsian-type pattern resulting from the anthropization gradient, whereby the most anthropized sites (cropland sites) had highest abundance of rodent reservoirs of zoonotic

pathogens. Likewise, we found that as anthropization increases, the richness and abundance of reservoir rodents also increases. These results support our hypothesis that anthropization modifies the composition of rodent species within interconnected communities in Bahía de Kino, Mexico. To our knowledge, this is the first study where an anthropization index is applied to metacommunity theory in a zoonotic multi-reservoir system.-This research has multiple implications for animal community ecology and health sciences, and highlights the importance of biodiversity conservation regarding zoonosis prevention via the identification of zoonotic reservoir hotspots.

Introduction

Human activities, such as deforestation, pollution or habitat fragmentation (i.e., anthropization), are a major driver of biodiversity and habitat loss that can modify animal community structure (Patz et al. 2004; Loh et al. 2015; Newbold et al. 2015). Anthropized landscapes are usually dominated by invasive species (McMahon et al. 2018), characterized by being able to rapidly increase their abundance and frequently expand their original geographical distribution, displacing native species through ecological niche usurpation (Chalkowski et al. 2018). In addition, these invasive species have ecological traits that facilitate pathogenic disease augmentation, such a fast-paced life history strategy, high abundance and high population density, promoting encounters between pathogens and reservoirs (Rubio et al. 2014; Han et al. 2015).

Several rodent species act as invasive species, many of them associated with more than 80 zoonotic pathogens (Han et al. 2015), including Lassa virus, Smallpox virus, *Leptospira* spp., *Bartonella* spp., and *Giardia* spp., among others (Meerburg et al. 2009). Thus, rodent reservoirs of zoonotic pathogens can be easily affected by the anthropization of their habitats, increasing their abundance and contact rates between reservoirs and non-reservoirs (including humans), thus increasing the risk of rodent-borne zoonotic diseases (Ostfeld and Keesing 2001; Khalil et al. 2014; Young et al. 2014). Each rodent community, including both reservoirs and non-reservoirs, can form a set of communities in different sites linked by dispersion (i.e., metacommunity) (Leibold and Mikkelsen 2002). In fact, species distribution along metacommunity gradient can modify contact rates between pathogens, reservoirs and potential reservoirs favoring or decreasing the risk of pathogens

transmission (Suzán et al. 2015; García-Peña et al. 2016). In this situation, prevalence of an infection at local and regional level might be influenced by three mechanisms that occur at the landscape level: 1) dispersion, colonization and extinction of pathogens, reservoir hosts, and non-reservoirs species; 2) anthropogenic processes leading to environmental filtering of hosts, non-hosts and pathogens; and 3) phylogenetic diversity relative to host or reservoir vector, which can influence the presence and circulation of pathogens (Suzán et al. 2015).

Metacommunity structure depends of 1) coherence, the response of species to an environmental gradient quantified with the number of embedded absences (i.e., absences that have at least one presence toward each extreme in a row or a column) of a species distribution, 2) species turnover, the number of times in which one species replaces another species between communities, and 3) boundary clumping, the distribution of species edges along the environmental gradient given by Morisita's index, that measures the clumping of species distributional boundaries by counting the number of terminal boundaries at each site (Leibold and Mikkelsen 2002). Theoretically, rodent metacommunities can be arranged into seven main idealized patterns: Nested subsets, Checkerboards, Clementsian gradients, Gleasonian gradients, Evenly-spaced gradients and Random (Leibold and Mikkelsen 2002; Leibold et al. 2004). Rodent species can be structured in a metacommunity based on different types of gradients, such as geographical and environmental gradients (e. g. Presley et al. 2012; Stevens and Tello 2012) and conservation gradients (e. g. de la Sancha et al. 2014; López-González and Lozano 2015). Nevertheless, the effect of anthropization on rodent reservoirir and non-reservoir metacommunities is still unknown.

To assess the effect of anthropization on rodent communities, we applied a metacommunity approach of Disease Ecology (Suzan et al., 2015) to a rodent-reservoir

system in Bahía de Kino, Mexico (Figure 1). Our hypothesis is that anthropization modifies the community structure of rodents, promoting the exchange of individuals of different species between interconnected communities (i.e. comprising a metacommunity). Likewise, we predict that species of rodent reservoirs of zoonotic pathogens are more abundant in the most anthropized sites. To test our hypothesis and predictions, we first developed an anthropization index by measuring features of the landscape produced by human activities in five areas with different vegetation type. Subsequently, we assessed the metacommunity structure based on anthropization index. Finally, we determined what reservoir species are distributed among sites.

Methods

Study site

Bahía de Kino (Figure 1) is a RAMSAR site (No. 2154) and one of the twenty critical areas for biodiversity conservation of the Gulf of California, Mexico (Enríquez-Andrade et al. 2005). Bahía de Kino is immersed in a heterogeneous landscape due to different land use types determined by different anthropogenic activities promoting the presence of exotic species (Hafner, 2012). The native vegetation of Bahía de Kino includes xerophilous, microphilous chaparral, crassicaule- and halophile-dominated scrubs, with restricted areas of vegetation with mesquital and arborescent bushes, and areas of croplands and urban matrices (CONABIO, 2016). We designated five sampling localities, based on their main land use: cropland, halophyte vegetation, mangrove, mesquital and periurban (Figure 1).

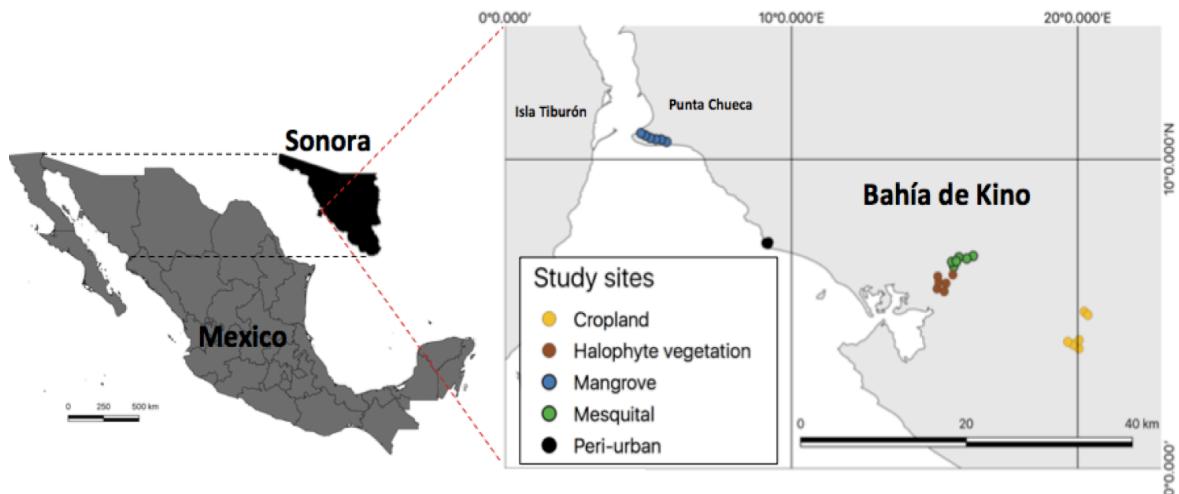


Figure 1. Map of Bahía de Kino, Sonora, showing the five different study sites.

Anthropization index

Anthropization is defined as the set of changes in the environment produced directly or indirectly by human activities (Magalhaes et al. 2014). To quantify anthropization we conducted a spatial analysis in 27 sites using a Geographic Information System. We defined impacted area by using 1000 m buffers in LandSat 8 satellite images (Google Earth, 2017). We measured four different variables of anthropization:

- a. *Introduced vegetation.* We use land use and vegetation vector data set, scale 1: 250,000 (series VI, INEGI, 2016). We discard all types of native vegetation and we only use data for non-native vegetation (e.g. cropland), human settlements and urban areas. We obtained the result as a percentage. To do this, we used the following equation:

$$\text{Induced vegetation \%} = \frac{A_{iv} \times 100}{A_{buffer}}$$

Where A_{iv} is the area of introduced vegetation and A_{buffer} is the 1000m buffer total area.

- b. *Distance to human settlements.* We determined linear distance (m) from each quadrant to nearest human settlement.
- c. *Presence of roads and highways.* We made polygons to measure the total area representing roads and highways. We use the following equation to obtain results in percentage value:

$$\text{Presence of roads and highways \%} = \frac{A_{rh} \times 100}{A_{buffer}}$$

Where A_{rh} is the total area representing roads and highways.

d. *Presence of buildings.* We implemented polygons that represent areas defined by constructions. To obtain the percentage of the total area, we use the following equation:

$$\text{Presence of Buildings \%} = \frac{A_b \times 100}{A_{buffer}}$$

Where A_b is the total area representing buildings.

Because the variables we measured are represented in different units, we performed a standardization of variables with following equation:

$$\text{Standardized variable} = \log_{10}(\text{variable} + 1) - \log_{10}(\text{mean(variable} + 1)$$

We performed a Principal Component Analysis (PCA) to combine data of all variables. Since PCA explained 97% of the variance, we used component analysis 1 for the anthropization analysis. We obtained an anthropization index from the PCA-eigenvector, thus we designated a level of anthropization for each study site.

Sampling method

Each locality was composed of six sites except periurban, where only three sites were available. To collect small rodents we set a 7 X 7 grid of 49 Sherman Traps (HB Sherman Traps, Inc., Tallahassee, FL) in each site, with traps located at 10-m intervals. We covered a total area of 0.49 ha per site. For each site, we activated the traps for three different nights. We sampled rodents in three samplings seasons: 1) October-November 2015 (autumn), 2) January-February 2016 (winter) and 3) August-September 2016 (summer). Captured individuals were identified by species, sex, reproductive status (scrotal, inactive, pregnant, lactating), and age (adult, juvenile); also, morphometric measurements were taken (body length, tail length, total length, right ear length). Individuals were released immediately after processing. The sampling was carried under collection permit SGPA/01610/16 issued by the Secretaría de Medio Ambiente y Recursos Naturales (Secretary of Environment and Natural Resources) of Mexican Government, approval of the Subcomité Institucional para el Cuidado y Uso de Animales Experimentales (Institutional Subcommittee for the Care and Use of Experimental Animals) of the Universidad Nacional Autónoma de México (sheet number MC-2017/1-12), following the approved protocols of The American Society of Mammalogists (Sikes et al. 2011).

To identify rodent reservoirs species in communities from Bahía de Kino, we used the database published by Han et al. (2015), where 2272 recognized rodent species were classified based on their status of pathogen hosts. We grouped species in two main categories: 1) reservoir species, which have been linked to at least one pathogen, and 2) non-reservoir species, which have not been linked to any pathogen or have not been

analyzed. We performed a Sperman's correlation test to prove if rodent reservoirs species was higher in sites with higher anthropization degree.

Metacommunity structure

To determine if rodent communities are structured in a metacommunity by anthropization gradient, we estimated coherence, turnover and boundary clumping parameters of rodent species distribution in the study area (Leibold and Mikkelsen, 2002; Presley et al. 2010) by ordinating site-by-species interaction matrices. Each matrix was ordered via reciprocal averaging (Gauch et al. 1977), which optimizes the simultaneous proximity of sites with similar species compositions and the proximity of species with similar environmental distributions (Presley et al. 2011). Besides, we ordered species incidence matrix from anthropization index, i.e., from the highest anthropized site to the lowest anthropized site. Random matrices were generated with 1000 simulations using a null model in which is assumed that habitats are saturated, i.e., the habitat maintains species richness of sites and habitat heterogeneity (Presley at al. 2010). We compared results of analyses with sites ordered by anthropization degree against analysis without ordered sites based on their anthropization. Analyses to determine metacommunity structure were assessed separately for three seasons.

Results

Anthropization scores were obtained for each of 27 sites analyzed with PCA. The first principal component (PC1) contained 97% of data. ‘Introduced vegetation’ was the variable with the highest statistical weight in PC1, followed by the variable ‘Presence of buildings’. Following our results, as PC1 increases anthropization increases. Thus, periurban and cropland areas represent sites with highest anthropization index, while mangrove and mesquital included sites with lowest anthropization (Table 1).

Table 1. Species of reservoir and non-reservoir rodents per site.

Site	Anthropization index*	Species richness	Reservoir	Non-reservoirs	Rodent species
Cropland	12.51562164	8	6	2	<i>Chaetodipus intermedius</i> <i>C. penicillatus</i> <i>Mus musculus</i> <i>Neotoma albigenula</i> <i>Peromyscus eremicus</i> <i>P. spp</i> <i>Rattus rattus</i> <i>Sigmodon hispidus</i>
Halophyte-vegetation	1.401470944	11	4	7	<i>Ammospermophilus harrisii</i> <i>C. intermedius</i> <i>C. penicillatus</i> <i>Dipodomys deserti</i> <i>D. merriami</i> <i>M. musculus</i> <i>N. albigenula</i> <i>Onychomys torridus</i> <i>P. eremicus</i> <i>P. spp</i> <i>Spermophilus tereticaudus</i>
Mangrove	0.65119015	8	3	5	<i>A. harrisii</i> <i>C. baileyi</i> <i>C. intermedius</i> <i>D. merriami</i> <i>N. albigenula</i> <i>O. torridus</i>

					<i>P. eremicus</i> <i>P. spp</i>
Mesquital	0.743478584	11	5	6	<i>A. harrisii</i> <i>C. intermedius</i> <i>C. penicillatus</i> <i>D. merriami</i> <i>M. musculus</i> <i>N. albigula</i> <i>O. torridus</i> <i>P. eremicus</i> <i>P. spp</i> <i>S. hispidus</i> <i>S. tereticaudus</i>
Peri-urban	1.451912567	9	3	6	<i>A. harrisii</i> <i>C. baileyi</i> <i>C. intermedius</i> <i>C. penicillatus</i> <i>D. merriami</i> <i>N. albigula</i> <i>O. torridus</i> <i>P. eremicus</i> <i>P. spp</i>

* Anthropization index is shown as the average of all locations per site

We captured 1721 individuals in three sampling seasons corresponding to 10 genera and 13 species. Invasive species such as *Rattus rattus*, *Peromyscus* spp., *Mus musculus*, *Sigmodon hispidus* and *Neotoma albicula* (Table 1) are species identified as reservoir for Hantavirus, West Nile Virus, Arenavirus, *Leptospira* spp., *Bartonella* spp, and *Giardia* spp., among others (Meerburg et al. 2009; Han et al. 2015). The number of rodent reservoir species (richness) varied between sites, being higher in cropland and lower in halophyte-vegetation site. There was a positive correlation between anthropization and reservoir richness for the third season (summer) ($\rho=0.5709667$, $p\text{-value}=0.002874$), but not for the first two seasons (autumn and winter) ($p\text{-value}>0.05$). The abundance of rodent reservoirs did not vary significantly between sites, however there was a positive correlation between anthropization and abundance of rodent reservoirs for the third season ($\rho= 0.5257807$, $p\text{-value}=0.006947$), but not for the first two seasons ($p\text{-value}>0.05$) (Figure 2).

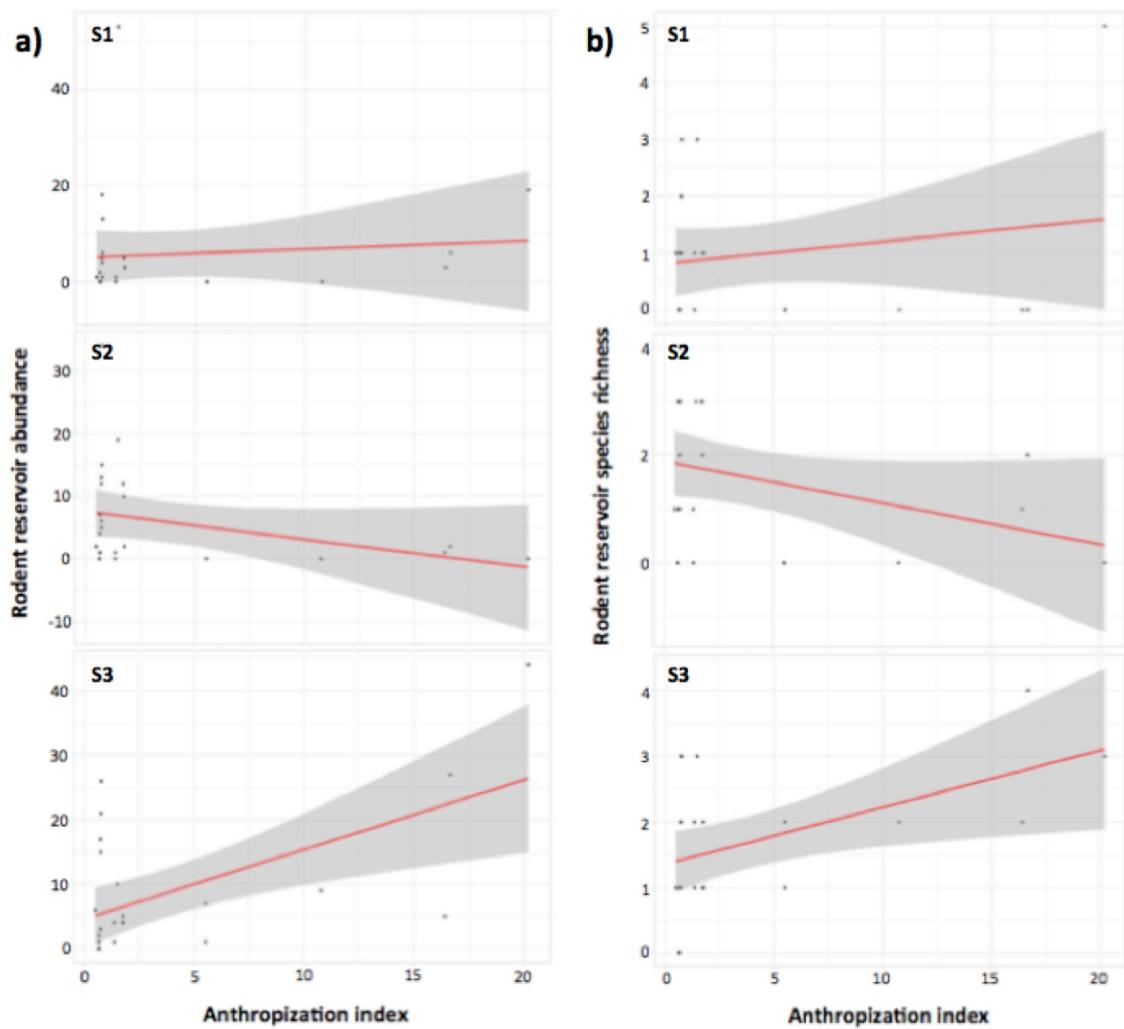


Figure 2. Correlation between anthropization and reservoirs. We performed a Spearman's correlation test to evaluate the correlation between a) anthropization and richness of rodent reservoirs, and b) anthropization and abundance of rodent reservoirs. X-axis is represented by anthropization index of each locality and Y-axis is represented by number of species (a) and number of individuals (b). Standard errors are represented in grey. S1 first season, S2 second season, S3 third season.

Results for the three seasons show that each metacommunity exhibits positive Coherence, indicating that the distributions of species within each community were molded by the same latent environmental gradient, that is, biotic and abiotic environmental characteristics to which species respond (Leibold and Mikkelsen 2002; Presley et al. 2012). Metacommunities exhibit positive Turnover across communities, measured as the number of times one species replaces another between two sites (i.e. number of replacements) for each possible pair of species and for each possible pair of sites (Leibold and Mikkelsen 2002; Presley et al. 2010). Finally, Morisita's (1971) index (I) result was clumped boundaries ($I > 1.0$). According with Leibold and Mikkelsen (2002) and Presley et al. (2010). Following the framework proposed by Suzán et al (2015), our results indicate a Clementsian structure of metacommunities for the three different seasons when we take into account anthropization as an environmental gradient (Table 2, Figure 3).

Table 2. Metacommunity analysis. We evaluated coherence, turnover (TO) and boundary clumping (BC) (Presley et al., 2010) for rodent communities. Presences-absences matrix was ordered based on anthropization index and compared with a matrix ordered by reciprocal averaging (results not shown, S1). EA embedded absences, SM simulated mean, I Morisita's index.

Season	Coherence				Turnover				BC		Structure
	EA	SM	p	z	TO	SM	p	z	I	p	
1	112	163.32	>0.05	3.69	370	1387.5	>0.05	6.93	4.307	0	Clementsian
2	95	119.06	>0.05	2.41	275	1113.1	>0.05	7.05	5.533	0	Clementsian
3	142	184.24	>0.05	4.34	503	2124.3	>0.05	7.62	1.571	0.054	Clementsian

Discussion

Our analysis showed that rodent metacommunities are structured in a Clementsian-type pattern (Leibold and Mikkelsen 2002) resulting from environmental gradient given by the anthropization (Figure 3). Rodent distributions in Bahía de Kino have a positive turnover and exhibit clumped range boundaries that are coincident with anthropization. In nature, Clementsian metacommunities are communities regarded to be discrete entities that replace each other as a group where species function in concert as a ‘superorganism’ (Clements 1916). Animal species distributions can be directly affected by the biotic dynamics such as vegetation associations and animal interactions along an environmental gradient, or due to abiotic characteristics, such as climate and temperature (Presley et al. 2012). Because distributions of species are molded primarily by habitat specializations, the variation in resource availability and/or habitat type due to anthropization tolerance could be the main drivers of metacommunity structure (Drake and Hunt 2009; Presley et al. 2012; de la Sancha et al. 2014). Our results are consistent with the hypothesis of Presley et al (2012), where habitat type is an important determinant of local community composition and metacommunity structure of rodents in an elevation gradient.

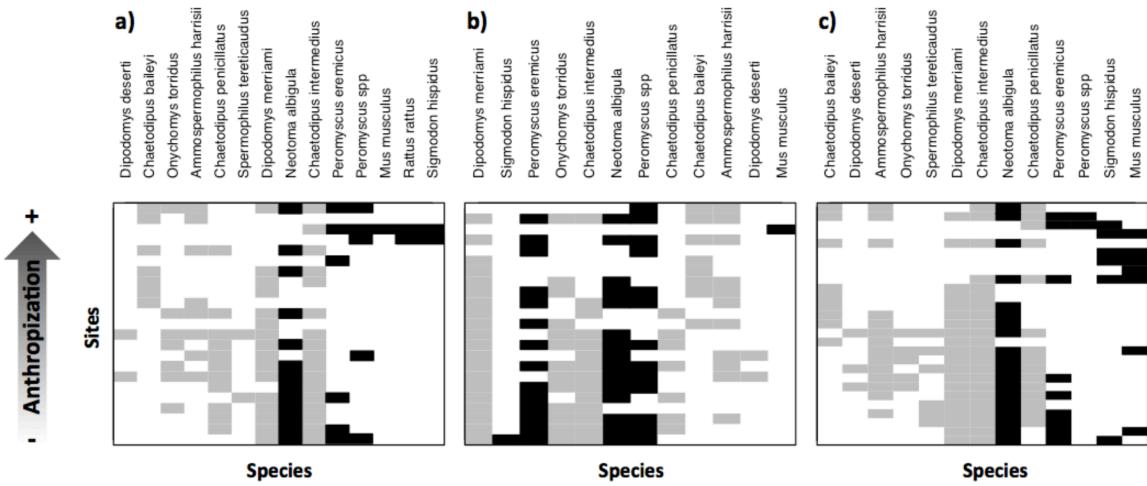


Figure 3. Metacommunity structure of rodents in Bahía de Kino shows a Clementsian type pattern for summer (a), autumn (b) and winter (c) seasons. Black cells represent presence of reservoir rodent species in study sites and gray cells represent presence of non-reservoir species, while white cells correspond to embedded absences (Presley et al., 2010). We ordered sites from lowest to highest anthropization index. Rodent species are listed on upper axis.

Despite some rodent reservoirs are more abundant in the most anthropized sites (cropland) for the three sampling seasons, there was only positive correlation between anthropization and richness/abundance of rodent reservoirs for third season, but not for the first two seasons (Figure 2). Thus, it is very likely that the relationship of reservoirs and anthropization is also a seasonal-dependent event. Season three corresponds to summer, a time of the year in which Bahía de Kino exhibits a higher human population density due to tourist activities, which may explain the increase of richness and abundance of reservoirs due to the facilitating of resources.

Reservoir species are also distributed along the entire anthropization gradient (see Figure 3). Therefore, rodent species composition along the metacommunities in Bahía de Kino is related to anthropization but they are not entirely co-dependent. This is especially important because a continuous distribution of reservoirs through different communities interconnected by dispersal of individuals can serve as a trigger for zoonotic pathogens circulation (Suzán et al. 2015), regardless of whether transmission is horizontal or vector-borne (Khalil et al. 2014; Young et al. 2014). Likewise, most anthropized sites with high reservoir abundance can act as a reservoir source-sink for other communities, maintaining cycles of pathogens due to the generalized occurrence of reservoirs (Leibold et al. 2004; Suzán et al. 2015). In the same way, species that are most tolerant to anthropogenic landscape changes are often the most competent, and therefore could also contribute to maintenance of a pathogen at meta-community landscape level (Mills 2006; Roche et al. 2012; Suzán et al. 2015). For example, food provision by human settlements is a facilitating factor for generalist reservoir species presence (e.g. *Rattus spp* and *Mus musculus*) (Drake and Hunt 2009; Meerbburg et al., 2009) whose high synanthropism degree raises the risk for zoonotic diseases such as Lymphocytic choriomeningitis, virus-hemorrhagic fever or Leptospirosis (Hugot et al. 2001; Himsworth et al. 2013).

We confirmed our hypothesis that anthropization modifies the composition of rodent species within interconnected communities in Bahía de Kino, Mexico. Likewise, we identified that rodent reservoirs of zoonotic pathogens are distributed along the metacommunity-anthropization gradient where the most anthropized sites (cropland sites) had the highest abundance of rodent reservoirs of zoonotic pathogens. Besides, we found a positive correlation between anthropization and richness/abundance of rodent reservoirs,

that is, as anthropization increases, the richness and abundance of reservoir rodents also increases. To our knowledge, this is the first study where an anthropization index is applied to metacommunity theory in a multi-reservoir system. This research has multiple implications for ecological and health sciences, including planning and management biodiversity conservation and zoonosis prevention due to identification of reservoirs hotspots (Dirzo et al. 2014; Rubio et al. 2014; Magalhaes et al. 2015; Suzán et al. 2015).

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Capítulo II

**Does anthropogenic land-use change increase the abundance of
zoonotic pathogens reservoirs? Rodents say yes**

Does land-use change increase the abundance of zoonotic pathogens reservoirs?

Rodents say yes

Hugo Mendoza¹, André V. Rubio^{2*}, Gabriel E. García-Peña^{1,3}, Gerardo Suzán¹, Javier A. Simonetti⁴

1. Departamento de Etología, Fauna Silvestre y Animales de Laboratorio, Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, 04510 Ciudad de México, México.

2. Departamento de Ciencias Biológicas Animales, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile., Av. Santa Rosa 11735, La Pintana, Santiago, Chile

3. Centro de Ciencias de la Complejidad C3, Universidad Nacional Autónoma de México, 04510 Ciudad de México, México.

4. Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile.

***Corresponding Author**

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Abstract

Land-use change can raise the risk of human exposure to zoonotic diseases by increasing reservoir host abundances. In this study, we conducted a meta-analysis to assess the effect of land-use change on abundance of rodent species in relation to their reservoir status for rodent-borne diseases. Using the PREDICT database, we retrieved 58 case studies comprising 54 species from eight countries for our analysis. In general, rodent reservoirs were significantly more abundant in modified habitats (anthropogenically altered sites), whereas non-reservoir species were more abundant in non-modified habitats. To our knowledge, this is the first meta-analysis that evaluates the response of rodents to land-use change with a focus on the potential implications for epidemiological risks. Our findings give further evidence that land-use change may impact biodiversity in ways that imply higher risk of zoonotic pathogen transmission.

Key Words: Biodiversity, disease risk, land-use change, reservoirs, Rodentia, zoonosis

Introduction

Zoonotic diseases represent more than 60% of human infectious diseases (Taylor et al. 2001), largely originating in wildlife (Jones et al. 2008). Rodents are one of the most important groups of zoonotic disease reservoirs, being associated with more than 80 zoonotic diseases (Han et al. 2016). Major rodent-borne diseases include Hantavirus Pulmonary Syndrome, Hemorrhagic Fever with Renal Syndrome, Plague, and Leptospirosis, among others (Meerburg et al. 2009).

Human impact on native ecosystems such as deforestation, agricultural development and urbanization, have been associated with the emergence and transmission of infectious diseases, making land-use change a major driver of emerging zoonotic diseases (Gottdenker et al. 2014). Land-use changes might modify biodiversity, favoring wild host species of zoonotic pathogens and consequently elevating the risk of disease (Mills 2006; Gottdenker et al. 2014; Guo et al. 2018). In fact, a number of studies have reported land-use change as a key driver for increasing infection prevalence of zoonotic pathogens in wild rodents (e.g. Mills 2006; McCauley et al. 2015; Young et al. 2017). The increase in rodent abundance is an underlying mechanism for the rise of disease risk as a consequence of habitat conversion (Mills 2006; Gottdenker et al. 2014; McCauley et al. 2015), which may also increase the prevalence of zoonotic pathogens regardless of the type of pathogen or its mode of transmission (e.g. direct contact, mediated by vectors; Ostfeld and Holt 2004).

Reservoir rodents differ from non-reservoir rodents in features such as greater geographic range size and a fast-paced life history strategy (e.g. earlier sexual maturity and higher reproduction rate) (Han et al. 2015). Therefore, rodent reservoirs would capitalize on reproduction and increase population size rapidly, reducing their vulnerability to

demographic stochasticity (Pimm 1991). Thus, reservoir species would be more resilient to anthropogenic disturbances, such as land-use change (Rubio et al. 2014; Guo et al. 2018).

The response of reservoirs and non-reservoir rodents to land-use change has not been assessed at a global scale. Within this framework, we hypothesized that land-use change increases abundance of reservoir rodents in anthropogenic-modified habitats (e.g. agricultural lands, pasturelands) relative to non-modified habitats, and decreases the abundance of non-reservoir species in anthropogenic-modified habitats. To test this hypothesis, we conducted a meta-analysis to assess the effects of land-use changes on rodent abundances according to their reservoir status for zoonotic pathogens.

Material and methods

To analyze the response of rodents to land-use changes (assessed here as changes in abundance), we used the data from the PREDICTS database (Hudson et al. 2017), a large compilation of data from published comparisons of species assemblages at sites facing different degrees of anthropogenic pressures. In our analysis, we considered publications that report rodent abundance in modified habitats (i.e. sites under some anthropogenic change) and non-modified habitats (i.e. sites of native vegetation). We recorded the abundance of each rodent species separately and each comparison was considered as an independent case study (Rubio et al. 2014). As many studies had differences in sampling effort between modified and non-modified habitats, we used the “effort-corrected abundance values” from the PREDICTS database, which standardize abundance by the sampling effort across sites (Hudson et al. 2017). We then grouped rodent species into two categories using the data from Han et al. (2015): (1) non-reservoir species, that is rodent species that have not been described as carriers of zoonotic agents, and (2) reservoir species, that is those rodent species known to carry one or more zoonotic agents. We also include in this group rodent species that have not been described as carriers of zoonotic agents, but based on their life histories and ecological traits, they might serve as reservoirs of future zoonotic diseases (Han et al. 2015).

To determine whether there is a pattern of change in the abundance of rodent reservoirs and non-reservoirs in response to land-use change, we used the relative abundance index (RAI), according to Vanderwel et al. (2007):

$$RAI = \frac{N_{modified\ habitats} - N_{non-modified\ habitats}}{N_{modified\ habitats} + N_{non-modified\ habitats}}$$

where $N_{modified\ habitats}$ and $N_{non-modified\ habitats}$ are the abundance of rodents reported for modified habitats and non-modified habitats, respectively. The relative abundance index ranges from +1 (species found only in modified habitats) to -1 (species found only in non-modified habitats), and equals zero when species are equally abundant in both modified and non-modified habitats (Vanderwel et al. 2007). We calculated RAI for each independent case study and then we calculated mean and standard errors for both reservoir and non-reservoir rodents separately. We used this approach instead of other commonly used effect sizes based on variance, such as Hedges' g because in some cases the number of replicates for each treatment (modified or non-modified habitats) was too small to calculate a variance (Rosenberg et al. 2000).

Studies with significant results are more likely to be published than those with non-significant results (Murtaugh 2002), therefore, we assessed publication bias by testing a Spearman correlation between RAI and sample size (abundance of rodents), as suggested by Egger et al. (1997). A significant correlation between RAI and sample size may indicate a publication bias where larger RAI in one direction (e.g. positive effects) are more likely to be published than smaller RAI. We found no relationship between RAI and sample size ($\rho = 0.23$, $p = 0.09$), and thus, there was no significant evidence of publication bias in our data.

Table 1. Information used for the meta-analysis. Data were retrieved from the PREDICTS database (Hudson et al. 2017). Rodents were separated by their reservoir status according to Han et al. (2015).

Reference	Reservoir species	Non-reservoir species	Ecoregion of non-modified habitats	Modified habitat-type	Country
Garcia et al. 2013	<i>Abrothrix longipilis, Abrothrix olivaceus, Loxodontomys micropus, Oligoryzomys longicaudatus, Reithrodon auritus</i>	<i>Chelemys macronyx, Geoxus valdivianus, Irenomys tarsalis,</i>	Valdivian Temperate Forests	Pasture, plantation forest	Chile
Garmendia et al. 2013	<i>Cuniculus paca, Dasyprocta punctata</i>	--	Peten-Veracruz Moist Forests	Pasture	Mexico and Guatemala
Gheler-Costa et al. 2012	<i>Akodon montensis, Calomys tener, Necromys lasiurus, Oligoryzomys nigripes</i>	<i>Rhipidomys mastacalis</i>	Cerrado	Pasture, plantation forest	Brazil
Granjon and Duplantier 2011	<i>Cricetomys gambianus, Lemniscomys striatus, Lemniscomys zebra, Mastomys erythroleucus, Mastomys natalensis, Mus minutoides, Praomys daltoni, Xerus erythropus</i>	<i>Acomys johannis, Arvicanthis ansorgei, Dasymys rufulus, Funisciurus pyrropus, Gerbilliscus guineae, Gerbilliscus kempi, Heliosciurus gambianus, Lemniscomys linulus, Praomys rostratus, Steatomys caurinus,</i>	West Sudanian Savanna	Cropland, urban	Mali

			<i>Taterillus gracilis,</i> <i>Uranomys ruddi</i>			
Kittle et al. 2012	<i>Hystrix indica</i>	--	Sri Lanka Lowland Rain Forests	Plantation forest	Sri Lanka	
Kutt and Woinarski 2007	--	<i>Pseudomys delicatulus,</i> <i>Pseudomys desertor</i>	Mitchell Grass downs	Pasture	Australia	
Martin et al. 2012	<i>Calomys tener,</i> <i>Cavia aperea,</i> <i>Necromys lasiurus,</i> <i>Oligoryzomys flavescens,</i> <i>Oligoryzomys nigripes,</i> <i>Oryzomys subflavus,</i> <i>Rattus rattus</i>	<i>Juliomys pictipes,</i> <i>Rhagomys rufescens</i>	Cerrado	Pasture, plantation forest	Brazil	
McShea et al. 2009	<i>Hystrix brachyura</i>	<i>Hystrix crassispinis,</i> <i>Trichys fasciculata</i>	Borneo Lowland Rain Forests	Plantation forest	Malaysia	
Woinarski et al. 2009	<i>Hydromys chrysogaster,</i> <i>Mesembriomys gouldii,</i> <i>Rattus tunneyi</i>	<i>Leggadina lakedownensis,</i> <i>Melomys burtoni,</i> <i>Pseudomys delicatulus,</i> <i>Pseudomys nanus,</i> <i>Zyzomys argurus</i>	Arnhem Land Tropical Savanna and Kimberly Tropical Savanna	Cropland, pasture	Australia	

Results and Discussion

In total, nine articles from the PREDICTS database met our search criteria, providing 58 case studies dealing with 54 rodent species. Data included 41 genera of eight families of rodents (Caviidae, Cricetidae, Cuniculidae, Dasyprotidae, Hystricidae, Nesomyidae, Muridae and Sciuridae (Table 1)). These studies comprised a variety of anthropogenic land-use types (forestry plantations, croplands, pasturelands and urban areas) from eight countries: Australia, Brazil, Chile, Guatemala, Malaysia, Mali, México and Sri Lanka. Twenty-seven case studies were grouped into the non-reservoir species category, and 31 case studies were grouped into the reservoir species category (Table 1).

Land-use change had a significant positive effect in the abundance of rodent reservoir species. In contrast, non-reservoir species were more abundant in non-modified habitats (Figure 1). These findings support the contention that land-use change drives the emergence of wildlife-borne infectious diseases. An increase in reservoir rodent density can increase frequency of contacts between infected and susceptible hosts of pathogens with density-dependent and horizontal transmission, such as hantavirus (Khalil et al. 2014). For rodent-borne diseases transmitted by vectors (e.g. bartonellosis, Lyme disease and plague), infection prevalence in vectors can increase as a result of a higher rate of contact between vectors and reservoirs due to higher densities of rodent reservoirs (Ostfeld et al. 2001; Gage and Kosoy 2005; Young et al. 2014). Furthermore, if reservoir hosts are more resilient to land-use change than non-reservoir hosts, a loss of the dilution effect (when higher host species diversity can reduce disease risk) can occur when there is a decrease in richness/diversity of hosts (Keesing et al. 2006).

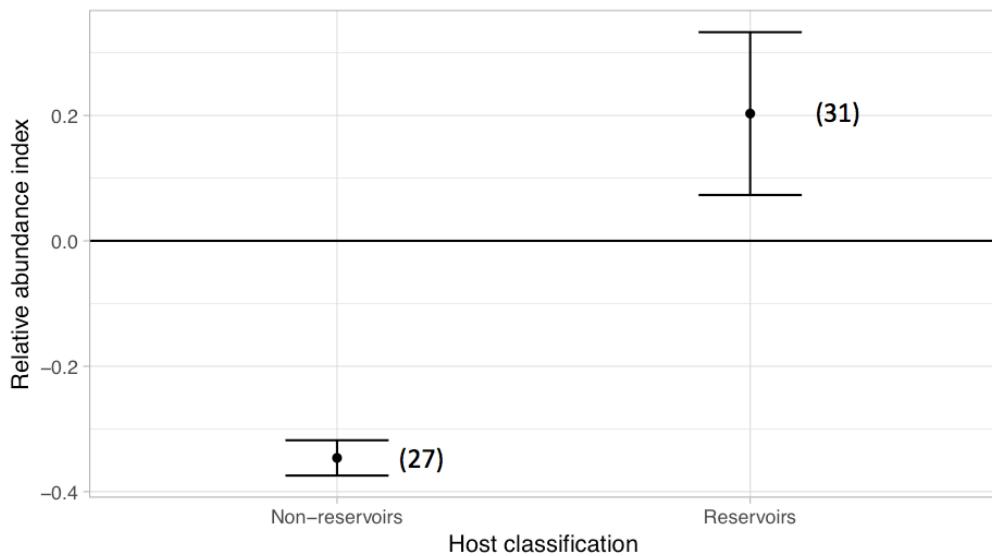


Figure 1. Relative abundance indexes (RAI) of rodent reservoir species and non-reservoir species. Positive values of RAI indicate higher abundance in modified habitats than non-modified habitats, whereas negative values mean lower abundance in modified habitats than non-modified habitats. Bars represent standard errors and numbers inside parentheses denote sample sizes.

To our knowledge, this is the first meta-analysis that evaluates the response of rodents to land-use change with direct implications for epidemiological risks. Although our study comprised a small number of species of the order Rodentia, the species analyzed come from a variety of geographic areas, ecosystems and types of land-use. Our findings give further evidence that land-use change generally impacts biodiversity in ways that might involve higher risk of zoonotic pathogen transmission.

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Discusión general

Nuestros resultados apoyan la afirmación de que la antropización favorece el incremento en la riqueza y abundancia de reservorios, pudiendo favorecer la aparición de enfermedades infecciosas transmitidas por la fauna silvestre. Por un lado, obtuvimos que la estructura metacommunitaria de roedores está siendo influenciada por las actividades humanas en una escala local. Además, encontramos que existe una correlación positiva entre la antropización y la riqueza y la abundancia de roedores reservorios. Por otro lado, en una escala global, el cambio de uso del suelo tuvo un efecto positivo significativo en la abundancia de especies de roedores reservorios de patógenos zoonóticos.

Nuestro análisis mostró que las metacommunidades de roedores están estructuradas en un patrón de tipo Clementsiano (Leibold y Mikkelsen 2002) como resultado del gradiente ambiental dado por la antropización. En la naturaleza, las metacommunidades Clementsianas son comunidades consideradas como entidades discretas que se reemplazan entre sí como un grupo donde las especies funcionan como un "superorganismo" (Clements 1916). Las distribuciones de especies animales pueden verse directamente afectadas por la dinámica biótica, como las asociaciones de vegetación y las interacciones entre animales a lo largo de un gradiente ambiental, o debido a las características abióticas, como el clima y la temperatura (Presley et al. 2012). Debido a que las distribuciones de especies se moldean principalmente por especializaciones de hábitat, la variación en la disponibilidad de recursos y/o el tipo de hábitat debido a la tolerancia a la antropización podrían ser los principales impulsores de la estructura metacommunitaria (Drake y Hunt 2009; Presley et al. 2012; de la Sancha et al. 2014). Nuestros resultados son consistentes con la hipótesis de Presley et al. (2012), donde el tipo de hábitat es un determinante importante de la composición de la comunidad local y la estructura de la metacommunidad de roedores en un gradiente de ambiental (de elevación en el caso de Presley et al., y de disturbio antropogénico en el presente estudio).

Los roedores reservorios se distribuyeron a lo largo de toda la metacomunidad, siendo más abundantes en los sitios correspondientes a cultivo. Así mismo, existió una correlación positiva entre la antropización y la abundancia y la riqueza de roedores reservorios. Esto es especialmente importante porque una distribución continua de reservorios a través de diferentes comunidades interconectadas por la dispersión de individuos puede servir como un desencadenante para la circulación de patógenos zoonóticos (Suzán et al. 2015). Asimismo, la mayoría de los sitios antropizados con alta abundancia de reservorios puede actuar como una fuente-sumidero de reservorios para otras comunidades, manteniendo los ciclos de patógenos debido a la aparición generalizada de reservorios (Leibold et al. 2004; Suzán et al. 2015). De la misma manera, las especies que son más tolerantes a los cambios antropogénicos son a menudo las más competentes y, por lo tanto, también podrían contribuir al mantenimiento de un patógeno a nivel del paisaje metacommunitario (Mills 2006; Roche et al. 2012; Suzán et al. 2015).

Confirmamos nuestra hipótesis de que la antropización modifica la composición de las especies de roedores dentro de comunidades interconectadas en Bahía de Kino, México. Identificamos que los roedores reservorios se distribuyen a lo largo del gradiente de antropización-metacomunidad donde los sitios más antropizados tuvieron la mayor abundancia de reservorios. Así mismo, hubo una correlación positiva entre la antropización y la riqueza/abundancia de reservorios. Hasta donde sabemos, este es el primer estudio en el que se aplica un índice de antropización a la teoría de la metacomunidad en un sistema multi-reservorio. Esta investigación tiene múltiples implicaciones para las ciencias ecológicas y de la salud, incluida la planificación y gestión de la conservación de la biodiversidad y la prevención de zoonosis debido a la identificación de sitios clave donde circulan roedores reservorios en sistemas interconectados (Dirzo et al. 2014; Rubio et al. 2014; Magalhaes et al. 2015; Suzán et al. 2015).

En el segundo capítulo, la abundancia de roedores reservorios de patógenos zoonóticos fue significativamente mayor en sitios con hábitats antropogénicamente

modificados comparada con hábitats no modificados. En contraste, las especies no reservorio fueron más abundantes en los hábitats no modificados. Estos hallazgos apoyan la afirmación de que el cambio de uso del suelo impulsa la aparición de enfermedades infecciosas transmitidas por roedores. Por lo tanto, el aumento en la densidad de roedores reservorios puede aumentar la frecuencia de contactos entre reservorios infectados y susceptibles de patógenos con transmisión horizontal y denso-dependiente (Khalil et al. 2014). Para las enfermedades transmitidas por roedores dependientes de vectores (e.g. Bartonellosis, enfermedad de Lyme y peste), la prevalencia de la infección en vectores puede aumentar como resultado de una mayor tasa de contacto entre vectores y reservorios debido a densidades elevadas de reservorios (Ostfeld et al. 2001 ; Gage y Kosoy 2005; Young et al. 2014). Además, si los reservorios son más resistentes al cambio de uso del suelo que los no reservorios, esto puede disminuir el efecto de dilución (Keesing et al. 2006). Este es el primer estudio que evalúa la respuesta global de los roedores al cambio de uso del suelo con implicaciones directas para los riesgos epidemiológicos. Si bien nuestro estudio comprendió un pequeño número de especies, las especies analizadas provienen de una variedad de áreas geográficas, ecosistemas y tipos de uso del suelo. Nuestros hallazgos proporcionan evidencia adicional de que el cambio de uso del suelo generalmente afecta a la biodiversidad, de manera que podría implicar un mayor riesgo de transmisión de patógenos zoonóticos.

Conclusión general

En este trabajo pudimos evaluar a escala local y global que la antropización del paisaje promueve la distribución e incremento de la abundancia de roedores reservorios de patógenos zoonóticos, elevando el riesgo de enfermedad hacia los humanos. En primer lugar, la evaluación de la estructura metacomunitaria de roedores en Bahía de Kino, nos permitió desarrollar un índice de antropización con diversos usos potenciales para la evaluación del impacto de las actividades humanas en los ecosistemas. La coexistencia entre roedores reservorios y humanos en los sitios más antropizados, resultado del filtrado ambiental, representa un riesgo inminente para la presentación de enfermedades zoonóticas. En segunda instancia, se pudo comprobar que de manera global existe un efecto directo positivo del cambio de uso del suelo sobre la abundancia de roedores reservorios, incrementando el riesgo de enfermedades zoonóticas. La continua evaluación del efecto de las actividades humanas sobre la biodiversidad, incluyendo aquellas especies que pueden ser reservorios de patógenos zoonóticos, es de suma importancia para entender los mecanismos subyacentes a la presentación de una enfermedad zoonótica en una población humana, sobre todo cuando la coexistencia entre humanos y reservorios, en este caso roedores, es constante y va en aumento dentro un sistema globalizado con elevadas tasas de perturbación ambiental.

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