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Diversidad funcional, taxonómica y dispersión de semillas por murciélagos filostómidos en un paisaje antropizado: un análisis multi-escala

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Resumen

La urbanización constituye una de las más drásticas y profundas modificaciones del paisaje, la cual puede tener implicaciones ecológicas en términos de la simplificación de las comunidades biológicas y la reducción de la biodiversidad. La respuesta de la biota nativa a la transformación del paisaje, está mediada no sólo por la escala espacial en que las especies perciben y son afectadas por la heterogeneidad espacial, sino también por sus atributos funcionales en particular. En este sentido, los murciélagos filostómidos son un grupo que por su diversidad de rasgos contribuyen en múltiples funciones en el ecosistema, y presentan un amplio espectro de respuestas a la degradación ambiental. En este trabajo investigué, desde una aproximación taxonómica y funcional, la respuesta escala-dependiente de los murciélagos filostómidos a la composición y estructura de un paisaje antropizado en Villavicencio-Meta. Para esto, en círculos concéntricos de 0.5, 1.25 y 2 km de radio, cuantifiqué la cobertura de bosque, potrero, área construida, y variables relacionadas con el arreglo espacial de la cobertura vegetal remanente. En el centroide de cada uno de estos círculos, capturé murciélagos usando redes de niebla para estimar su riqueza, composición y abundancia. A cada individuo le fue medida la masa corporal, relación de aspecto del ala, carga alar y envergadura alar, para realizar agrupamientos funcionales y estimar índices de diversidad funcional. Así mismo, registré la riqueza de especies de semillas consumidas por los murciélagos filostómidos, para relacionar sus cambios en función de los índices. La riqueza de especies y la complejidad del ensamble fue menor en áreas con mayor área urbanizada. En efecto, la composición y estructura del ensamble respondieron a la composición del paisaje a las escalas de 1.25 y 2 km, mientras que a nivel de especie la respuesta a la escala espacial fue idiosincrática. Así mismo, el número de grupos funcionales decreció con el aumento del área urbanizada. La equidad (EF) y la riqueza funcional (RF) tendieron a ser mayores en áreas con mayor cobertura nativa, mientras que la divergencia funcional (DF) mostró una tendencia inversa. Los modelos lineales generalizados revelaron, que la EF y la DF respondieron a las variables de paisaje a 0.5 y 1.25 km respectivamente, mientras que la fragmentación del bosque a 0.5 km benefició a los murciélagos grandes con alas largas y en forma de punta. También, la riqueza de especies de semillas aumentó con la RF de murciélagos y decreció con su EF. En general, mis resultados soportan la idea de que la urbanización puede reducir la diversidad funcional y taxonómica de los murciélagos, lo cual parece tener efectos en la riqueza de especies de semillas que pueden ser dispersadas en el paisaje. La aproximación basada en rasgos desde una perspectiva multiescala, puede mejorar nuestra capacidad de detectar las escalas espaciales en las que el filtrado ambiental opera para determinar la estructura de los ensambles de murciélagos en ambientes dominados por humanos.

Abstract

Urbanization is one of the most drastic and pervasive process of landscape transformation, which may have ecological implications in terms of the simplification of biotic communities and biodiversity loss. The responses of indigenous biota to the landscape conversion, is mediated not only by the spatial scale in which the species perceive and are affected by the spatial heterogeneity, but also by their particular functional traits. On this regard, phyllostomid bats present a variety of traits that influence their contribution in many functional processes, and allow them a wide range of responses to the environmental degradation. I evaluated, using a functional and taxonomic approach, the scale-dependent response of phyllostomid bats to the composition and structure of the urban-rural landscape in Villavicencio. I measured in concentric circles of 0.5, 1.25 and 2 km of radius, the forest cover, grassland, built area and landscape variables related with the spatial arrangement of natural cover. At the centroid of these circles, I used mist nets to sampling bats and estimate species richness, composition and abundance. From each individual captured I recorded body mass, aspect ratio, wing loading and wing span, to classify functional groups and estimate functional diversity indices. Also, I recorded the species richness of seeds consumed by bats, to relate its changes as a function of functional indices. Species richness and complexity of assemblage structure decrease in highly urbanized areas. Indeed, composition and structure of bat assemblage were best predicted by the landscape composition at 1.25 and 2 km scales, whereas at species level the response to the spatial scale was idiosyncratic. Species grouping by regression/classification trees, showed that number of phyllostomid functional groups decrease in most degraded areas. Moreover, functional evenness (FE) and richness (FR) tended to increase with forest cover, while functional divergence (FD) exhibited the opposite trend. Generalized linear models revealed that FE and FD responded to the landscape factors at 0.5 and 1.25 km, respectively, and forest fragmentation at 0.5 km benefited those large-bodied bats with long-pointed wings. Additionally, species richness of seeds increased with bat FR and decreased with the FE. Overall we found greater support for the idea that urbanization process may be an important driver for bat functional and taxonomic diversity loss, which is in line with global trends for other groups of bats. This loss of bats functional diversity seems to reduce the species richness of seed consumed, which in turn probable have implication in the seed dispersal process in urban environments. The trait-based approach seen from a multiscale perspective, may improve our capacity to detect particular spatial scales, in which environmental filtering influence the bats assemblage structure in human dominated landscapes.

Introducción

El desplazamiento de las comunidades rurales a las grandes ciudades es una tendencia global que, exacerbada por un crecimiento exponencial de la población humana, ha generado la acelerada expansión de los centros urbanos y profundiza la transformación y degradación del paisaje natural (Foley et al. 2005; Grimm et al. 2008). Esta tendencia en la intensificación en el uso del suelo conlleva a la extirpación de las especies nativas, la simplificación de las comunidades biológicas y la degradación de procesos ecosistémicos (Cumming et al. 2014; Gómez-Baggethun & Barton 2013; Marzluff et al. 2008; McKinney 2008). Dicha pérdida de la integridad de la biodiversidad, ha recibido una creciente atención pública dado el entendimiento de que la estabilidad ecosistémica y buena parte del bienestar humano dependen de la conservación y el manejo de la naturaleza (Dearborn & Kark 2010; Hooper et al. 2005). En este sentido, la planificación de la conservación de la biodiversidad en ambientes urbanos reposa, al menos en parte, en nuestra comprensión acerca de los aspectos que limitan la adaptación de las especies a estos ambientes creados por los humanos, y los efectos derivados de la pérdida de especies en las funciones y servicios ecosistémicos (Dearborn & Kark 2010; Gómez-Baggethun & Barton,2013; Montis et al. 2015).

Los murciélagos son un grupo que por su diversidad de hábitos tróficos, rasgos morfo-fisiológicos y comportamentales, cumplen con funciones ecosistémicas como la polinización, dispersión de semillas y el control de la población de insectos (Kunz et al. 2011). En ambientes dominados por humanos, estos rasgos pueden traducirse no sólo en la contribución de los murciélagos al control de insectos plaga y/o a la revegetalización de zonas deforestadas (Boyles et al. 2011), sino también a su grado de tolerancia a la intensificación en el uso del suelo (Jung & Threlfall 2016; Meyer et al. 2016). Los procesos de urbanización operan a diferentes escalas espaciales limitando la distribución y abundancia de los quirópteros (Cisneros et al. 2016; Grimm et al. 2008). Por ejemplo, el uso del hábitat por algunas especies a escala local puede estar limitado por el arreglo espacial de los parches de forrajeo inmersos en la matriz (e.g., Avila-Flores & Fenton 2005; Threlfall et al. 2011), mientras que su abundancia local puede ser el resultado de dinámicas metapoblaciones que ocurren a escala regional (e.g., Cisneros et al. 2015; López-González et al. 2012). Por lo tanto, la manera en que se configuran los ensambles de murciélagos en ambientes antropizados, es el reflejo de procesos que ocurren a diferentes escalas espacio en el paisaje (Cisneros et al., 2016).

En el Neotrópico, el uso de una aproximación multiescala para evaluar el efecto de la transformación del paisaje en murciélagos filostómidos, se ha enfocado principalmente en su diversidad taxonómica en términos de la composición del ensamble (e.g., Gorresen & Willig 2004; Gorresen et al. 2005), la riqueza de especies (e.g., Klingbeil & Willig, 2009), y su abundancia (e.g., Mendes et al. 2016; Pinto & Keitt 2008), mientras que la evaluación de su respuesta desde una perspectiva funcional ha sido poco explorada (Cisneros et al. 2014; García-Morales et al 2016). El estudio multiescala de la diversidad funcional de murciélagos filostómidos en paisajes antropizados, podría rendir importantes frutos en términos de: (1) el entendimiento de los mecanismos que limitan la adaptación de estos organismos en ambientes urbanos (Jung & Threlfall 2016), (2) el desarrollo de un marco conceptual que nos permita predecir cuáles ensambles pueden ser más susceptibles a la intensificación en el uso del suelo (Voigt & Kingston 2016), (3) la

detección de aquellas escalas espaciales en las que el filtrado ambiental opera sobre los murciélagos con base en sus rasgos (Cisneros et al. 2016), y (4) el entendimiento de la manera en que ciertas funciones ecosistémicas de los filostómidos persisten en ambientes dominados por humanos (Luck et al. 2013). En el Neotrópico estas ideas permanecen pobremente estudiadas y llenar estos vacíos en el conocimiento, podría brindar herramientas que faciliten la planificación de la conservación de murciélagos en paisajes altamente transformados (Cisneros et al. 2014; Jung & Kalko 2011).

Con base en lo anterior, pretendo contestar la pregunta *¿De qué manera afectan diferentes elementos de un paisaje antropizado, a diferentes escalas espaciales, en un gradiente urbano-rural en Villavicencio-Meta, la diversidad funciona y taxonómica de los murciélagos filostómidos y las semillas que consumen?* Planteo dar respuesta a esta pregunta basado en los siguientes objetivos:

Objetivo general

Evaluar el efecto de la composición y estructura, a diferentes escalas espaciales, de un paisaje antropizado en Villavicencio – Meta, sobre la diversidad funcional y taxonómica de los murciélagos filostómidos y las semillas que consumen. Esto, con el fin de determinar los mecanismos que podrían explican los patrones de diversidad taxonómica de los murciélagos en ambientes urbanos, así como aquellos factores que condicionan su respuesta a la transformación del paisaje y pueden incidir en el proceso de dispersión de semillas.

Objetivos específicos

1. Determinar cambios en la riqueza de especies, composición y estructura del ensamble de murciélagos filostómidos, en función de la composición y estructura del paisaje de Villavicencio a tres diferentes escalas espaciales.
2. Detectar posibles respuestas especie-específicas de los murciélagos filostómidos al efecto de la escala, la composición y estructura del paisaje de Villavicencio.
3. Determinar cambios en la riqueza, equidad y divergencia funcional de los murciélagos filostómidos, en función de la composición y estructura del paisaje de Villavicencio a tres diferentes escalas espaciales.
4. Evaluar el efecto de la composición y estructura del paisaje antropizado de Villavicencio, a diferentes escalas, sobre la masa corporal y los rasgos asociados a la morfología alar de los murciélagos filostómidos.
5. Determinar cambios en la riqueza de especies de semillas consumidas por murciélagos, en función de cambios en la riqueza, equidad y divergencia funcional del ensamble de filostómidos.

Este trabajo está dividido en dos capítulos presentados en formato de artículo científico cada uno. El primer artículo (capítulo 1), se encuentra en el formato de sometimiento para la revista *Journal of Tropical Ecology* y desde una perspectiva taxonómica abarca los objetivos específicos uno y dos. Por su parte, el segundo artículo (capitulo 2) está presentado en el formato de sometimiento a *Biodiversity and Conservation* y usando una aproximación funcional, comprende los objetivos específicos tres, cuatro y cinco. En el Anexo 1, encontrará los criterios que justifican la selección de las revistas para una eventual publicación de ambos documentos.

Capítulo 1

MANUSCRIPT TITLE: Scale-dependent response of phyllostomid bats to landscape composition and structure in an urban-rural interface in the Colombian Orinoquia

RUNNING TITLE: Bat's assemblage response to landscape transformation

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ABSTRACT

Understand the scale-dependent response of fauna to land use intensification is a fundamental issue for species conservation in human-dominated landscapes. We evaluated the effects of landscape transformation on the composition taxonomic diversity of a phyllostomid assemblage in an urban-rural interface of the Colombian Orinoquia. To do so, we quantified at concentric circles of 0.5, 1.25 and 2 km of radius landscape composition and structure, and we sampled bats at the centroid of these circles. Bat assemblage responded at 1.25 and 2 km scales and presented low species richness, composition and structure in more degraded areas. Small-frugivorous bats, were affected at 0.5 km, whereas large-bodied frugivorous bats responded at 1.25 and 2 km scales. Our findings support the idea that urbanization had negative effects on phyllostomid assemblages. Composition bats probably respond to landscape variables at the largest scales, since it should encompass the aggregated response of all species at smaller, such as small-size frugivorous, and larger scales, such as big-sized frugivorous. Our study shows a species-specific response to the landscape degradation, which is probably due by differences in tolerance to ecosystem degradation of generalist and specialist bats. Thus, a multi-scale approach provides a more complete picture of the interaction between phyllostomid bats and the landscape features in urbanized environments.

INTRODUCTION

Land use and cover change are amongst the main drivers of landscape transformation at global scale (Foley et al. 2005), and it generates biodiversity loss through human-dominated environments (Dirzo et al. 2014). Indeed, about 40% of the Earth surface has been designated for agricultural and livestock production (Foley et al. 2005), and in regions such as the Colombian Orinoquia about 80% of the natural savanna ecosystems have been replaced with grasslands for cattle, and African oil palm or sugar cane crops (Etter et al. 2006; Romero-Ruiz et al. 2012). Indeed, the loss of landscape heterogeneity, i.e. composition and structure of land cover types, may generate environmental filters responsible for the decline of specialized species and whereas favor generalist ones (Gámez-Virués et al. 2015).

A human-dominated matrix generally includes gradients of land use intensification, from degraded patches of natural cover embedded in rural productive systems to urbanized areas, which include the most drastic landscape transformations (Marzluff et al. 2008; Mcdonnell & Pickett 1990). These differences in environmental degradation influence species population dynamics among the remaining patches of natural cover (Jules & Shahani, 2003), due to differences in habitat availability perceived by each species and the potential use of the artificial cover as foraging sites (Franklin & Lindenmayer 2009; Prugh et al. 2008). The effects of anthropogenic environments on biotic communities is affected by matrix composition (Watling et al. 2011), and also by spatial scale in which each species perceives and is affected by the environmental heterogeneity (Gámez-Virués et al. 2015). Indeed, spatial heterogeneity is a scale-dependent attribute (Wu 2004) and therefore, patterns of variation in the landscape elements have particular spatial scales in which influence species abundance and presence (McGill 2010; Wu et al. 2002). Hence,

the evaluation of the effects associated to landscape composition and structure on faunal assemblages, should be addressed from a multi-scale approach (McGill 2010; Rahbek 2005; Sandel & Smith 2009). Evidences from tropical forest of Brazil, show the influence of both local (canopy cover, tree density or understory eight) and landscape variables (forest cover or number of patches) on site occupancy of Neotropical bats, suggesting that bat assemblage response is a consequence of particular habitat preferences (Mendes et al. 2016). Indeed, response to the spatial scale appear to be related with species-specific capabilities to perceive environmental heterogeneity (Mendes et al. 2016; Rahbek 2005). Also, in temperate forest of North America at small scale, less than 100 linear meters (following Mcgill 2010), the availability of roosting sites is the main constrain for bat species richness, whereas availability of foraging patches becomes more relevant at the landscape level (Brooks & Ford, 2006). Furthermore, scale-specific effects seem to be responsible for the simplification of phyllostomid assemblages in fragmented tropical forests in Paraguay and Mexico (García-Morales et al. 2016; Gorresen et al. 2005; Pinto & Keitt 2008). Similarly, forest fragmentation in the Ecuadorian Amazon at multiple spatial scales, from 1 to 5 km, may increase the abundance of frugivorous bats, whereas gleaning animalivores show the opposite trend (Klingbeil & Willig 2009). In summary, Neotropical bats appear to respond to the loss of natural cover at multiple spatial scales, and the effect seems to be highly idiosyncratic regarding the species identity and habitat preferences of each species.

Urbanization processes cause deforestation, changes in landscape structure (e.g. number, size or density of forest patches (Wu 2004)), artificial light and pollution, among other factors that may reduce species' habitat quality (Marzluff et al. 2008; Russo & Ancillotto 2015; Threlfall et al. 2012). This environmental degradation has different effects on biological communities depending on the urbanization intensity and/or taxonomic

identity of species (McKinney 2008). For instance, the rise of housing density may reduce species richness of fauna by the extremely loss of habitable area (McKinney 2006, 2008), whereas moderate urbanizations may present the opposite effect, by increasing the range of exploitable resources, and allowing the coexistence of many species (McKinney 2008). This general rule seems to remain true for bats in human environments, where species richness decreases as a function of urbanization level, benefiting those bats with flexibility in the choice of roosting sites and food resources, whereas reducing the presence of the specialist species (Russo & Ancillotto 2015). Indeed, several authors have recorded that urbanized areas containing fragments of natural cover, may support high levels of species richness and foraging activity of insectivorous bats, due to the range of resources available to both clutter and open-adapted species (Avila-Flores & Fenton 2005; Luck et al. 2013; Threlfall et al. 2012). Also, Saldaña-Vázquez & Schondube (2016) in a global meta-analysis, found that big-sized frugivorous bats of the Phyllostomidae family, tend to be the most successful species in urban environments, which is probably because they are able to exploit food resources that may be common in this novel ecological context.

In the light of the above, we hypothesized that the differences in abundance, species richness and composition of phyllostomid bats are related to changes in various landscape properties: number of forest patches, mean forest patch size, forest patch size standard, forest patch density, and percentage of land cover types such as built area, grassland and forest cover (Klingbeil & Willig 2009; Meyer et al. 2016; Sparks et al. 2005). Additionally, since the way in which species perceive and are affected by spatial heterogeneity is a function of behavioral, morphological and life history traits (Marinello & Bernard 2014; Norberg & Rayner 1987), we also expect that the response to spatial

scale to be species-specific and should be identified by changes in species' abundance and presence (García-Morales et al. 2016; Gorresen et al. 2005).

METHODS

Study area

We tested our hypothesis in an urban-rural gradient in the Colombian Orinoco region. This region has experienced gradual human colonization since the 1950s (Etter et al. 2008). Substantial changes in land use and cover have been produced since 1970s due to extensive livestock ranching, African oil palm crops, timber exploitation, and oil production (Romero-Ruiz, et al. 2012; Sánchez-Cuervo et al. 2012). Currently, in the region remain natural ecosystems such as gallery forests, piedmont savannas, high plains and tropical rain forest remnants (Sánchez-Cuervo et al. 2012).

We did the study in Villavicencio, which is the largest urban center in the Colombian Orinoquia, at 319 to 483 m a.s.l (Figure 1). Villavicencio presents a marked rainfall seasonality with high precipitation between April and October, and low values between November and March (Bernal et al. 2013). Annual mean precipitation is ~2600 mm, but decreases from west to east, and daily air temperature, below 500 m a.s.l is about 26ºC (Bernal et al. 2013). The weather and vegetation are strongly influenced by both the piedmont, i.e. lower slopes of the Eastern Cordillera (Bates 1948), and the lowland ecosystems such as savanna, gallery forest and high plains (Bates 1948; Rangel et al. 1997). Historically, piedmont forest has been described as a rain forest with a heavy canopy with little understory (Bates 1948; Blydenstein 1967), but since the expansion of Villavicencio, which increased around 1950's decade, this ecosystem has been highly cleared and replaced by grassland dominated by species of the family Poacea such as,

Homolepis aturensis, *Panicum pilosum*, *P. trichoides*, *P. versicolor* and *Melinis minutiflora* originally from Africa (Blydenstein 1967; Rangel et al. 1997).

Bat sampling

In the urban-rural interface of Villavicencio, we selected five sampling sites with different landscape composition, called landscape units (LU). LU refers to the specific area from which we measured landscape composition and structure variables (Figure 1), while sites refers to the centroid of each LU in which mist nets were set. Sites were selected considering: (a) enough tree cover to place mist-nets and (b) a separation among LU's centroid of at least 4.3 km to prevent spatial autocorrelation bias (Pinto & Keitt, 2008). On each site we set two to three mist-nets of 12×3m, separated more than 50 m from each other, and we kept them open from 17:30 h until 01:00 h in every sampling session. We visited each site five times between January and July of 2016, selecting nights with moon illumination levels below of 60% (Rowse et al. 2016). Sampling effort in each site ranged from 288 to 300 m^2×nights, and the total sampling effort was 1484 m^2×nights.

To avoid bias in quantification of species abundance and to assess the independence of bat captures among mist-nets in each site, we marked all captured individuals with an unique numerical code using a rabbit tattoo (Powell & Proulx 2003). We identified all individuals to species level using specialized taxonomic references based on external characters (e.g., Díaz et al. 2016; Gardner 2007), and those we could not identify in the field were collected for accurate taxonomic identification using dental and cranial characters (Díaz et al. 2016), and by comparison with specimens in the Museum of Natural History – Universidad de los Llanos, MHN-U-M. We deposited the specimens collected at the MHN-U-M.

Land use classification

We processed DigitalGlobe satellite images from Google Earth taken between 2014 and 2015, with a resolution of 2 m^2 per pixel, to characterize landscape composition and structure. We used supervised classification method of ArcGIS 10.1 to generate maps with three land uses: built area, grassland and forest (Mendes et al. 2016; Pinto & Keitt 2008). We did not include in the analysis other land uses and landscape elements as crops, water bodies or bared ground, since they covered less than 5% of each area and were not present in all LU's (Figure 1).

We defined concentric buffers around sampling sites, to delimit LU's at three spatial scales of 0.5, 1.25 and 2 km of radius (Gorresen et al. 2005; Klingbeil & Willig 2009; Pinto & Keitt 2008; Figure 1). The smallest scale was delimited considering the average distance traveled by *Glossophaga soricina*, 0.5 km (Alvarez et al. 1991; Lemke 1984), one of the smallest species recorded in the study area, while the largest, 2 km, was selected to prevent spatial overlapping among buffers of all analyzed LU's (Gorresen et al. 2005). At each spatial scale, we measured the percentage of built area, grass land and forest cover, number of forest patch, mean forest patch size, forest patch size standard deviation and forest patches density (Garmendia et al. 2013; Pinto & Keitt 2008; Wu et al. 2002). For all the analyses, we employed as response variables composition, abundance and species richness of phyllostomid bats.

[Figure 1]

Data analyses

To compare species richness among LU's, we used Estimates 9.0 to build individual-based rarefactions curves, because this method allows comparison among sites with

different sampling efforts (Colwell et al. 2012). We randomized samples 100 times to obtain 95% confidence intervals and, we also used the estimator of total richness Jackknife 1 to evaluate the inventory completeness at each LU and for the whole landscape (Colwell et al. 2012). Jackknife 1 richness estimator is adequate for heterogeneous samples such as LUs (Magurran 2004). We used rank-abundance curves to compare the bat assemblage structure pattern, in terms of the species abundance and evenness in each of the LU's (Feisinger, 2001). We evaluated similarity bat composition and identified the species responsible of the variation among LU's using a SIMPER subroutine (Clarke & Gorley 2015).

To determine changes in bat composition and structure among LU's we used a permutational multivariate analysis of variance (PERMANOVA). Our experimental design had three factors: mist-net location (fixed factor) nested in LU (fixed factor) and sampling visite (fixed factor). We did PERMANOVA analyses based on a Bray-Curtis similarity matrix, type III sums of squares and 9999 random permutations under the reduced model (Anderson & Ter Braak 2003). When statistical significance was detected for a factor or pair of factors, we used an *a posteriori* pair-wise comparison using t-test. We visualized differences in bat assemblage composition among sites, using a SIMPROF subroutine with 9999 random permutations (Clarke et al. 2008), then we overlaid classification results into a principal coordinates analysis (PCoA) (Anderson & Willing 2003), and finally we show those bat species that have more than 20% of correlation with the two first principal coordinates.

We did non-parametric correlation analysis between landscape composition and structural variables to identify linear relationships, and exclude collinear variables from further analyses (Quinn & Keough 2002). We generated distance-based linear models

(DistLM), to relate changes of bat composition and structure as a function of landscape composition and structure (Legendre et al. 2005). We selected different models at each spatial scale (0.5, 1.25 and 2 km) and used Akaike's information criterion for small samples (AIC$_c$), to select those models that better predicted changes in bat assemblages given a less number of predictor variables (Johnson & Omland 2004; Snipes & Taylor 2014). Using the best fitted model, we did an ordination and visualization with a distance-based redundancy analysis (dbRDA; Legendre & Anderson 1999). We did these statistical analysis using PRIMER V 7 & PERMANOVA add on program (Anderson et al. 2008; Clarke & Gorley 2015).

To analyze changes in the abundance of most common species as a function of landscape composition and structure, we used generalized linear models at each spatial scale. Then, we ranked the models using AICc and selected the best one using *glmulti* package in R 3.3.2 (Calcagno 2013; R Core Team 2016). Subsequently, we used *MuMIn* package to average the first five best ranked models (Barton 2016), and then evaluated variable importance in relation to the bat's abundance response. Partial residuals of selected models and their confidence intervals were plotted using *visreg* package (Breheny & Burchett, 2016).

RESULTS

Bat capture and species richness

We captured 615 individuals of 13 genera in 20 species of the Phyllostomidae family (Table 1). During the sampling period we recorded seven recaptures in all the landscape. The most frequently captured species were *Artibeus planirostris* and *Carollia perspicillata* with 233 and 209 individuals, respectively. In all LU's, capture success was

estimated over 1 individual/net×-hour and the inventory completeness was greater than 77.8% in four of the five sites, whereas for the whole landscape it was over 80%. We did not find overlapping among confidence intervals of species richness estimation of LU1 and LU3, and LU2 with LU3, LU4 and LU5, suggesting significant differences of species richness among them. Species richness and total abundance tended to increase with the distance to the centroid of the urban center (Table 1).

[Table 1]

Species composition and structure

Bat structure and composition were different among LU's (Pseudo-F= 6.4; p-perm < 0.01), conforming two groups: LU3 and LU5, and LU1, LU2 and LU4 (Pi= 2.3; p= 0.01) (Figure 2a). The interaction of LU and sampling visit affected bat composition and structure (Pseudo – F= 1.7; p-perm < 0.01), with differences among LU's during the trips two and five. The first two axes of the PCoA explained 65.4% of the total variation: axis 1 explained 43.2% of total variation and discriminated LU's between those having higher amount of forest cover with low built area, i.e., LU3 and LU5, from other LU's. Axis 2, explained 22.2% of variation and better reflected the internal variability of survey units inside each LU (Figure 2a). Species most related with LU3 and LU5 were *Phyllostomus elongatus*, *C. perspicillata*, *C. castanea* and *Desmodus rotundus*, whereas *P. discolor*, *A. lituratus* and *A. planirostris* were more associated with LU1, LU2 and LU4 (Figure 2b).

Across the urban-rural interface, rank-abundance patterns of bat assemblage structure indicate the existence of few abundant species, followed by an increasing number of rare species, particularly in LU3 and LU5 (Table 1; Figure 3). LU3 and LU5 showed an average similarity between them of 50.4% with *C. perspicillata* (80.5%), *A. planirostris*

(86.2%) and *Desmodus rotundus* (86.9%) as the most important species contributing to this similarity. In general, similarities among all LU's were between 32.8 and 52.7%, and in most cases *C. perspicillata* and *A. planirostris* were the most contributing species (SIMPER subroutine).

[Figure 2]

[Figure 3]

Effect of composition and structure of the landscape on the phillostomid assemblage

Variation of landscape composition and structure through LU's was mainly explained by changes in built and grassland areas, at all spatial scales, and by patch number at 1.25 and 2 km scales (Figure 4). Indeed, forest patch number were highly associated with axis 1 (56.9% of total variation explained; Table 2, Figure 4), and grassland and built area variables with axis 2 (32.3% of total variation explained). Along landscape gradient LU1 and LU2, the nearest to the urban center (Figure 1), were mainly associated with high percentage of built area and forest patch number, respectively (Table 2, Figure 4). LU4 were associated with forest patch number, whereas LU3 and LU5 were mainly related with grassland area and forest cover (Figure 4; Table 2).

[Table 2]

[Figure 4]

Linear relations among landscape metrics varied depending on each spatial scale, i.e. collinearity of two or more variables was not consistent at all spatial scales. Therefore, we excluded from the 0.5 km scale analysis percentage of grassland, because it was highly negatively correlated with percentage of forest (p= 0.03; *rho*= -0.9). Forest patch size

standard deviation was excluded of the analysis at 1.25 and 2 km, because it was correlated with percentage of forest, mean forest patch size, forest patch number and forest patch density at both spatial scales (all p= 0.03; all *rho*= -0.9).

At the 0.5 km scale, forest patch number was the predictor that best explained changes in bat composition and structure (adjusted R^2= 11.8%). However, interactions between forest cover – mean forest patch size (adjusted R^2= 17.02%) and forest cover – mean forest patch size – patch number (adjusted R^2= 24.3%), showed the highest explanatory values (Table 3; Figure 5). At the 1.25 km scale, built area percentage was the factor with the best explanatory value (adjusted R^2= 8.9%), followed by the interactions of built area – mean forest patch size (adjusted R^2= 15.7%), forest cover – grassland – forest patch number (adjusted R^2= 23.02) and forest cover – grassland – built area – patch density (adjusted R^2= 26.2%). Finally, the best explanatory variables at 2 km scale were: built area (adjusted R^2= 9.5%), interactions among built area – mean forest patch size (adjusted R^2= 18.6%), forest cover – built area– mean forest patch size (adjusted R^2= 20.1%) and grassland – forest percentage – built area percentage – mean patch size (adjusted R^2= 26.2%) (Table 3; Figure 5).

[Table 3]

[Figure 5]

Effect of landscape metrics on bats species abundance

Changes in *A. planirostris* abundance were best explained by the interaction of three factors at the 1.25 km scale: forest patch number – built area – forest cover (Figure 6). These three variables exhibited a positive relationship with *A. planirostris* abundance and, after averaging the best five ranked models, were the most important followed by

percentage of grassland (Vi= 0.50) and patch density (Vi= 0.26) (Figure 6). Similarly, abundance of *A. lituratus* was best explained by the interaction of forest cover – forest patch number at the 1.25 km scale. These two variables were followed in importance by grassland (Vi= 0.14), built area (Vi= 0.11) and patch density (Vi= 0.11) (Figure 6). In contrast, changes in *C. perspicillata* abundance were mainly explained, at the 0.5 km scale, by the interaction of structural landscape factors, forest patch size standard deviation – forest patch number (Figure 6). Indeed, these two variables presented a negative relationship with *C. perspicillata*'s abundance, and were the most important landscape metrics followed by patch density (Vi= 0.45), forest cover (Vi= 0.37) and mean patch size (Vi= 0.11) (Figure 6).

[Figure 6]

DISCUSSION

We recorded about 80 percent of the expected species for the whole urban-rural landscape. Indeed, the composition of bats assemblage recorded in this study is the expected for the Llanero piedmont, being the frugivorous species the most abundant followed by insectivorous, omnivorous and hematophagous species (Sánchez *in press*). Inventory completeness was not consistent at all LU's, LU1, LU2, LU3 and LU4 reached an inventory completeness above of 77 percent, but we only recorded 57 percent of the species expected in LU5. These differences on species records are probably due to two possible factors: (a) rainfall and atypical low temperature occurred during a sample visits to the LU5. This weather conditions could reduce bat activity during that night, consequently reducing detectability (Erickson & West 2002; Parsons et al. 2003). (b) LU5 was the most distant sampling site to the Llanero piedmont, therefore a higher influence of the savanna ecosystems may reduce the abundance of some species, e.g., *Sturnira*

lillium, and present unique ones, e.g., *Rhinophylla* sp. and *Lophostoma brasiliense* (Table 1). Changes in forest structure complexity at local scales, e.g., canopy density, tree density, number of lianas or height of understory, may generate heterogeneous conditions that influence bat movements and resources use at local scales, affecting in turn its site occupancy and species detectability (Hanspach et al. 2012; Mendes et al. 2016).

Our results support the hypothesis that the effects of urbanization go beyond of species richness, affecting species abundance, and composition, in a scale dependent context. The composition and structure of a community is the result of the interaction of many factors (e.g., climate, geographic locality or vegetation structure) that operate at a range of different spatial scales (Cisneros et al. 2015; López-González et al. 2012). For instance, metapopulation dynamics may determine local bat abundance in human environments, due to the landscape connectivity perceived by each species and the immigration flow among populations at regional scales (Cisneros et al. 2015). In contrast, habitat disruption may generate local conditions that modulate the resource use dynamics and would account for bat structure and composition at local spatial scales (Mendes et al. 2016). These patterns have been broadly documented across different Neotropical localities (Cisneros et al. 2014; Gorresen et al. 2005; Klingbeil & Willig 2009; Pinto & Keitt 2008), and they seem to remain true for the phyllostomid assemblage in Villavicencio. We found that landscape composition and the spatial arrangement of patch forest at the 1.25 and 2 km scales, were the main factors responsible for the assemblage structure. For phyllostomid bats, empirical studies have indicated the importance of the interaction of matrix permeability and spatial distribution of forest remnants, predicting the structure of bat assemblages in anthropogenic landscapes (Cisneros et al. 2016; Farneda et al. 2015; Gorresen & Willig 2004; Jung & Threlfall 2016). For instance, the increase of housing density has proven to be an important driver for homogenization of bat communities in

urban contexts (Jung & Threlfall 2016; Threlfall et al 2012). These effects may be dependent on the particular context of landscape transformation and the remaining natural cover embedded in the anthropogenic matrix (Avila-Flores & Fenton 2005; Jung & Threlfall 2016; Meyer et al. 2016). Also, the spatial compactness of forest fragments may increase the evenness of species abundance (Cisneros et al., 2016; Gorresen & Willig, 2004), whereas the conversion of natural cover in small forest patches seems to benefit generalist frugivorous bats, that are able to take advantage of food resource spatially dispersed through the landscape, in forest with different successional stages (Gorresen & Willig 2004; Klingbeil & Willig 2009). This guild-specific response of phyllostomid bats, is given by behavioral and morphological constrains that negatively affect those species that need vertically complex forest, which in human dominated environments are scarce or non-existent (Cisneros et al. 2016; Klingbeil & Willig 2009; Meyer & Kalko 2008). This has repercussions probably on taxonomic diversity of phyllostomid bats in highly transformed areas (Threlfall et al. 2012), and would explain that in the most degraded LU's we recorded the lowest assemblage complexity of phyllostomids, in terms of the species richness, composition and abundance.

We also found support for the prediction that bat species are not equally affected by landscape transformations at a particular spatial scale. Even the most abundant species, with presence throughout LU's, showed contrary responses to landscape structure and composition gradients. Indeed, the abundance of *A. planirostris*, *A. lituratus* and *C. perspicillata* were mainly predicted by landscape composition and structure at 2, 1.25 and 0.5 km scales, respectively. The frugivorous *A. planirostris* and *A. lituratus*, are middle to big-sized bats with high dispersal capability (Trevelin et al. 2013), that usually forage resources spatially scattered (Soriano 2000). In contrast, small-sized frugivorous of the genus *Carollia* tend to feed on plants distributed homogeneously in the landscape, which

in turn lead to smaller foraging areas (Soriano 2000; Trevelin et al. 2013). Given these differences in use of space by frugivorous phyllostomids, the assumption that they perceive and are affected by the spatial heterogeneity at different spatial scales results intuitive. Empirical studies in tropical forests of Mexico proved that abundance of *Carollia* spp. and *Sturnira* spp. are mainly influenced by habitat loss at spatial scales below of 0.5 km, whereas the abundance of big-sized bats such as *Artibeus* spp.,was predicted by forest cover at scales above of 1.5 km (Pinto & Keitt 2008). Although similar patterns have been found in other Neotropical localities (Gorresen et al. 2005; Klingbeil & Willig 2009; Trevelin et al. 2013), the scale-dependent response of bats to the landscape heterogeneity is sensitive to the particular contexts of land cover transformation and to the temporal scale of the analysis (Cisneros et al. 2016). For instance, mating season or exploratory flights of migrant individuals may increase the movements of bats through the landscape (Trevelin et al. 2013), and it would lead to a likely variation of the spatial scale in which bats respond to the land cover during different periods of time. Long-term studies of the interaction between temporal and spatial scales modulating the way on which bat assemblages respond to the landscape transformation, should bring up valuable insights about the factors that influence population dynamic of Neotropical bats in urban landscapes (Marzluff et al. 2008).

We found that the abundance of *A. planirostris* and *A. lituratus* increased with forest fragmentation and forest cover. Large-bodied bats of the Stenodermatinae group are well known to thrive in human-altered areas, due to their tolerance to habitat fragmentation and because they feed on plants that can persist following clear-cutting of the forest (Meyer et al. 2016; Rocha et al. 2016; Saldaña-Vázquez & Schondube 2016). Indeed, in our study area one of the main food items for *A. planirostris* were fruits of *Ficus* spp. (Ramírez-Mejía et al., see chapter 2), which are common in the urbanized area of

Villavicencio. Also, the remaining forest patches embedded in the urbanized matrix, may serve for *Artibeus* spp. as roosting sites after feeding on resources distributed in the urbanized matrix (Avila-Flores & Fenton 2005; Jung & Kalko 2011), which would account for the high number of individuals captured in the most degraded LU's. Also, forest fragmentation has been documented to favor the abundance *C. perspicillata*, due the increase of plants of early successional stages that may provide a continuous pulse of food resources (Gorresen & Willig 2004; Rocha et al. 2016). However, this is contrary to our findings, since the abundance of *C. perspicillata* decreased as a function number of forest patches. The context of land use/cover change in Villavicencio, presents different degrees of matrix intensification that may reduce the abundance and quality of food resources from which some frugivorous phyllostomid depends (Jara-Servín et al. 2016). Bats of the genus *Carollia* tend to feed on fruits from understory plants (Fleming 1981; Soriano 2000), which in urbanized areas may be less common or replaced by novel resources that would not fulfill the energetic requirements of those bats (Jara-Servín et al. 2016).

Final considerations: research and conservation of phyllostomid bats in urbanized environments

Our study demonstrate that using a multi-scale perspective provides a more comprehensive framework, and a broad picture to understand the interaction between phyllostomid bats and landscape features in urbanized environments. This approach has not only practical implications on the research of bat response to land uses intensification, but also for the planning of conservation strategies in human dominated environments. For instance, based in our results, management plants to conserve the whole assemblage of phyllostimids in Villavicencio, should be addressed in a range of spatial scales above

1.25 km, since it likely encompass the aggregate response of each specie in terms of their abundance, and must consider the vegetal enrichment of the landscape matrix to improve its permeability to bats species. In contrast, if the conservations goals are focused in small-bodied species such as *Carollia* spp., focusing efforts in a radius of 0.5 km may be enough to facilitate their local persistence in human-transformed environments. However, it is important to point out that processes occurring at regional scales, e.g., metapopulation dynamics (Cisneros et al. 2015; López-González et al. 2012), go beyond of the spatial scales of our analysis and must be taken account regarding the relationship between structural and functional connectivity of the landscape and species home range, in the local abundance of bats species.

Future studies should focus on the morphological, physiological and behavioral mechanisms, underlying the different range of response displayed by phyllostomid bats to the landscape transformation (Jung & Threlfall 2016; Meyer et al. 2016). Indeed, research on bat functional diversity in urban environments, should contribute to a theoretical framework to predict which species and phyllostomid assemblages may be more susceptible to the land uses intensification (Cisneros et al. 2016), and would help understanding of the consequence of environmental degradation on the ecosystem functions involving Neotropical bats (Kunz et al. 2011).

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Tables

Table 1. Capture success, species richness and inventory completeness of bats in an urban-rural interface of Villavicencio municipality, Colombian Orinoquia. Distance to the centroid of Villavicencio urban center increase with landscape units (LU) numeration. CI: confidence interval. Bold letters on parenthesis correspond to the species abbreviation.

	LU1	LU2	LU3	LU4	LU5	Total
Carollia perspicillata (cp)	12	48	36	27	86	209
Carollia castanea (cc)	0	0	7	0	5	12
Artibeus lituratus (al)	10	4	4	8	1	27
Artibeus planirostris (ap)	62	49	20	80	22	233
Sturnira lilium (sl)	0	2	4	34	0	40
Platyrrhinus sp. 1 (p1)	0	0	1	0	0	1
Platyrrhinus sp. 2 (p2)	1	0	0	0	0	1
Uroderma bilobatum (ub)	0	0	3	4	1	8
Mesophylla macconnelli (mm)	0	0	1	0	1	2
Desmodus rotundus (dr)	0	0	15	0	2	17
Glossophaga soricina (gs)	2	0	1	1	0	4
Anoura sp. (a)	1	0	0	0	0	1
Phyllostomus discolor (pd)	3	10	0	6	1	20
Phyllostomus elongatus (pe)	0	0	8	1	5	14
Phyllostomus hastatus (ph)	0	0	0	2	1	3
Gardnerycteris crenulatum (gc)	0	0	2	14	0	16
Tonatia saurophila (ts)	0	0	1	1	1	3
Micronycteris sp. (m)	0	0	2	0	0	3
Lophostoma brasiliense (lb)	0	0	0	0	1	1
Rhinophylla sp. (r)	0	0	0	0	1	1
Total number of individuals	91	113	105	178	128	615
Capture percentage	14.8	18.4	17.1	29.1	20.6	100
Capture success (individuals/net×-hour)	1.01	1.3	1.2	2	1.4	1.4
Species richness based on rarefaction estimation (CI 95%)	7 (4.5 - 9.4)	5 (5 – 5)	14 (11.08 - 16.9)	11 (7.5 - 14.5)	13 (7.05 - 18.9)	20 (15.7 - 24.3)
Jack 1 mean ± SD	8.9 ± 1.3	5 ± 0	17.9 ± 1.9	13.9 ± 1.7	20.9 ± 2.7	24.9 ± 2.2
Inventory completeness (%)	77.8	100	77.8	78.6	57.1	80.3
Sampling effort (m^2 net×nights)	296	300	288	300	300	1484

Recaptures		3	0	2	0	2	7

Table 2. Landscape composition at three spatial scales in an urban-rural interface at Villavicencio, Colombian Orinoquia. Distance to the centroid of urban area increases with landscape units (LU) numeration.

Scale	Land cover	LU1	LU2	LU3	LU4	LU5
	Forest (%)	39.56	16.86	40.75	42.32	36.97
0.5 km	Grassland (%)	5.30	60.60	25.42	45.22	62.23
	Built area (%)	55.14	22.54	33.83	12.45	0.80
	Forest (%)	39.99	14.08	37.06	18.43	42.08
1.25 km	Grassland (%)	5.61	44.25	43.06	69.84	56.41
	Built area (%)	54.40	41.66	19.89	11.73	1.51
	Forest (%)	28.56	16.36	30.03	19.33	36.03
2 km	Grassland (%)	12.78	36.36	57.88	71.51	62.79
	Built area (%)	58.66	47.29	12.10	9.16	1.17

Table 3. Best fitted distance-based linear models (DistLM) at three spatial scales, explaining composition and structure of phyllostomid bats in an urban-rural interface at Villavicencio. At 0.5 km scale, 1: forest; 3: Built area; 10: patch number; 11: mean patch size; 12: patch size standard deviation; 13: Patch density. At 1.25 km scale, 4: forest; 5: grassland; 6: built area; 14: patch number; 15: mean patch size; 17: patch density. At 2 km scale, 7: forest; 8: grassland; 9: built area; 18: patch number; 19: mean patch size; 21: patch density. (*) Models selected considering its explanatory value and variables number.

	Adjusted R^2	Residuals sum of squared deviation	Number of variables	Models. Selected variables
0.5 km	0.119	62445	1	10
	0.170	57836	2	1;11
	0.243	51879	3	1;10;11*
	0.237	52296	4	3;10;12;13
	0.262	49741	5	1;10-13
	0.262	49741	6	1;3;10-13
1.25 km	0.089	64472	1	6
	0.158	58711	2	6;15
	0.230	52775	3	4;5;14
	0.262	49741	4	4-6;17*
	0.262	49741	5	4-6;14;15
	0.262	49741	6	4-6;14;15;17
2 km	0.095	64098	1	9
	0.186	56721	2	9;19
	0.201	54779	3	7;9;19
	0.262	49741	4	7-9;19*
	0.262	49741	5	7-9;19;21
	0.262	49741	6	7-9;18;19;21

Figure legends

Figure 1. Landscape units (LU) in an urban-rural interface in Villavicencio. Top right, location of Villavicencio in Colombia. We sampled bats in sites at the centroid of each concentric circle. Concentric circles at each LU, set the limits of each spatial scale (0.5, 1.25 and 2 km of radius) in which landscape variables were measured. The land use category "other", includes bare ground, small crops and body waters. DU: distance to the centroid of the urban area. F: forest cover. G: grassland area. B: built area. P#: number of forest patches. mps: mean size of forest patches (ha). pssd: patch forest size standard deviation. pd: forest patch density (P#/ha). Landscape variables provided correspond to the 2 km scale.

Figure 2. Principal coordinates analysis (PCoA) of bats composition and structure in an urban-rural interface at the Villavicencio municipality. The first two axes explain 65.4% of the total variation. a. Differences in bat composition and structure among landscape units (LU) were statistically significant (circles). b. Species with over 20% of correlation with both or one of the axes are presented. Species codes are provided in Table 1. Length and direction of blue arrows show the species association with axes and LU's.

Figure 3. Rank-abundance curves of phyllostomid bats in an urban-rural interface in the Colombian Orinoquia. Distance to the urban centroid increases with the landscape unites (LU) numeration. Species codes are provided in Table 1. Bat assemblages nearest to the urban centroid tend to have low number of rare species, of species richness and of species evenness.

Figure 4. Principal coordinates analysis (PCoA) of landscape composition and structure in an urban-rural interface at Villavicencio. PCoA axes explained 89.2% of total variation

and landscape metrics with over 30% of correlation with both or one of the axes are presented. Length and direction of each metric show the association with axes and LU's. LU: landscape unit. G: grassland. B: built area. P#: number of forest patches.

Figure 5. Distance-based redundancy analysis (dbRDA) of bat structure and composition according landscape variables at three spatial scales in Villavicencio's urban-rural interface. All dbRDA analysis explained 28.2% of total variation with the first two axes. Length and direction of each factor denotes its explanatory value and axes relationship. LU: landscape unite. F: forest. P#: number of forest patches. G: grassland. PD: patch density. B: built area. MPS: mean patch size. At the 1.25 and 2 km scale, bat composition in the nearest LU's to the urban center, LU1 and LU2, are mainly explained by the built area. At LU`s with the highest amount of forest cover, LU3 and LU5, bat composition are mainly predicted by the percentage of forest cover and mean forest patch size.

Figure 6. Partial residual plots of the best fitted models explaining changes in the abundance of *A. planirostris*, *A. lituratus* and *C. perspicillata*, as a function of different landscape metrics at three spatial scales: 0.5, 1.25 and 2 km. Shaded bands denote 95% confidence intervals. Variable importance (Vi) AICc weight (W_i) and delta (Δ_i) goes from 0 to 1, and were calculated by averaging the first five ranked models. Reliability of the model increase as Δ_i decrease to cero and W_i increase to 1. pssd: patch forest size standard deviation. P#: number of forest patches. F: forest cover
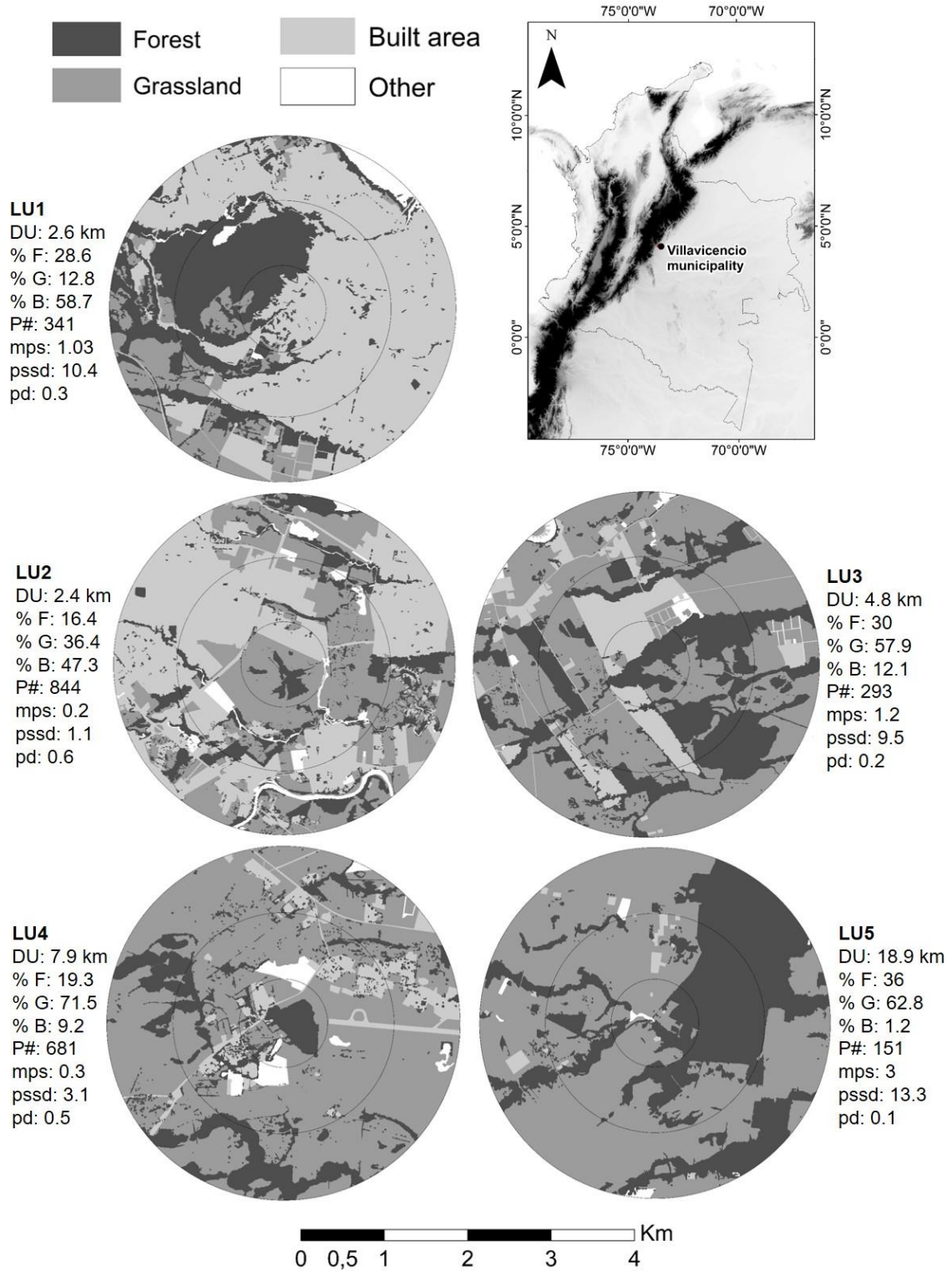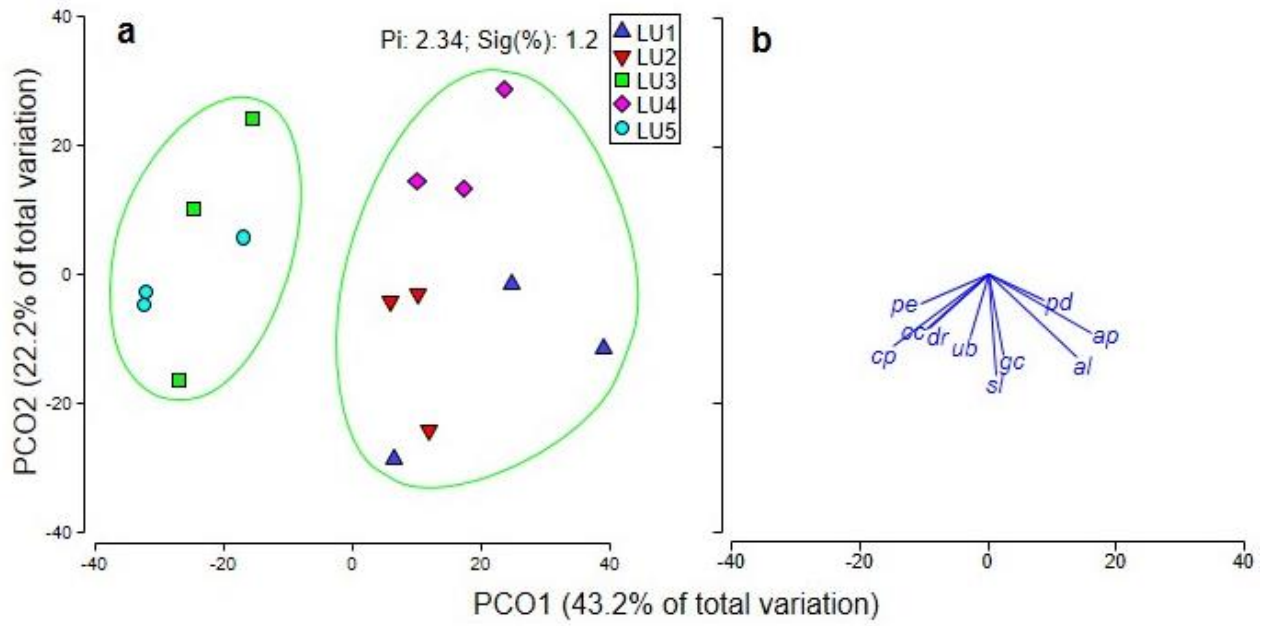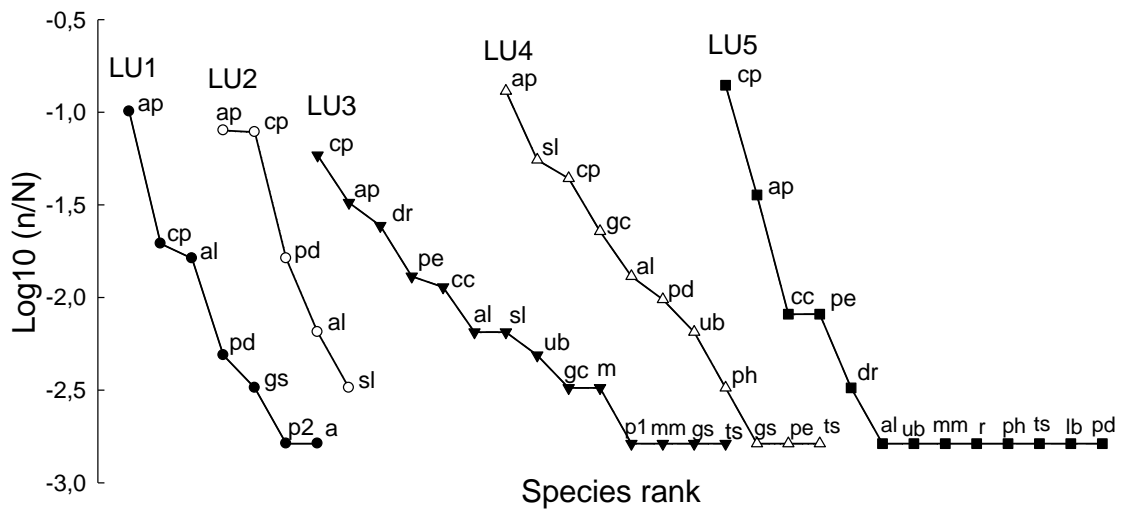
FIGURES

Figure 1

LU1
DU: 2.6 km
% F: 28.6
% G: 12.8
% B: 58.7
P#: 341
mps: 1.03
pssd: 10.4
pd: 0.3

LU2
DU: 2.4 km
% F: 16.4
% G: 36.4
% B: 47.3
P#: 844
mps: 0.2
pssd: 1.1
pd: 0.6

LU3
DU: 4.8 km
% F: 30
% G: 57.9
% B: 12.1
P#: 293
mps: 1.2
pssd: 9.5
pd: 0.2

LU4
DU: 7.9 km
% F: 19.3
% G: 71.5
% B: 9.2
P#: 681
mps: 0.3
pssd: 3.1
pd: 0.5

LU5
DU: 18.9 km
% F: 36
% G: 62.8
% B: 1.2
P#: 151
mps: 3
pssd: 13.3
pd: 0.1

Forest   Built area
Grassland   Other

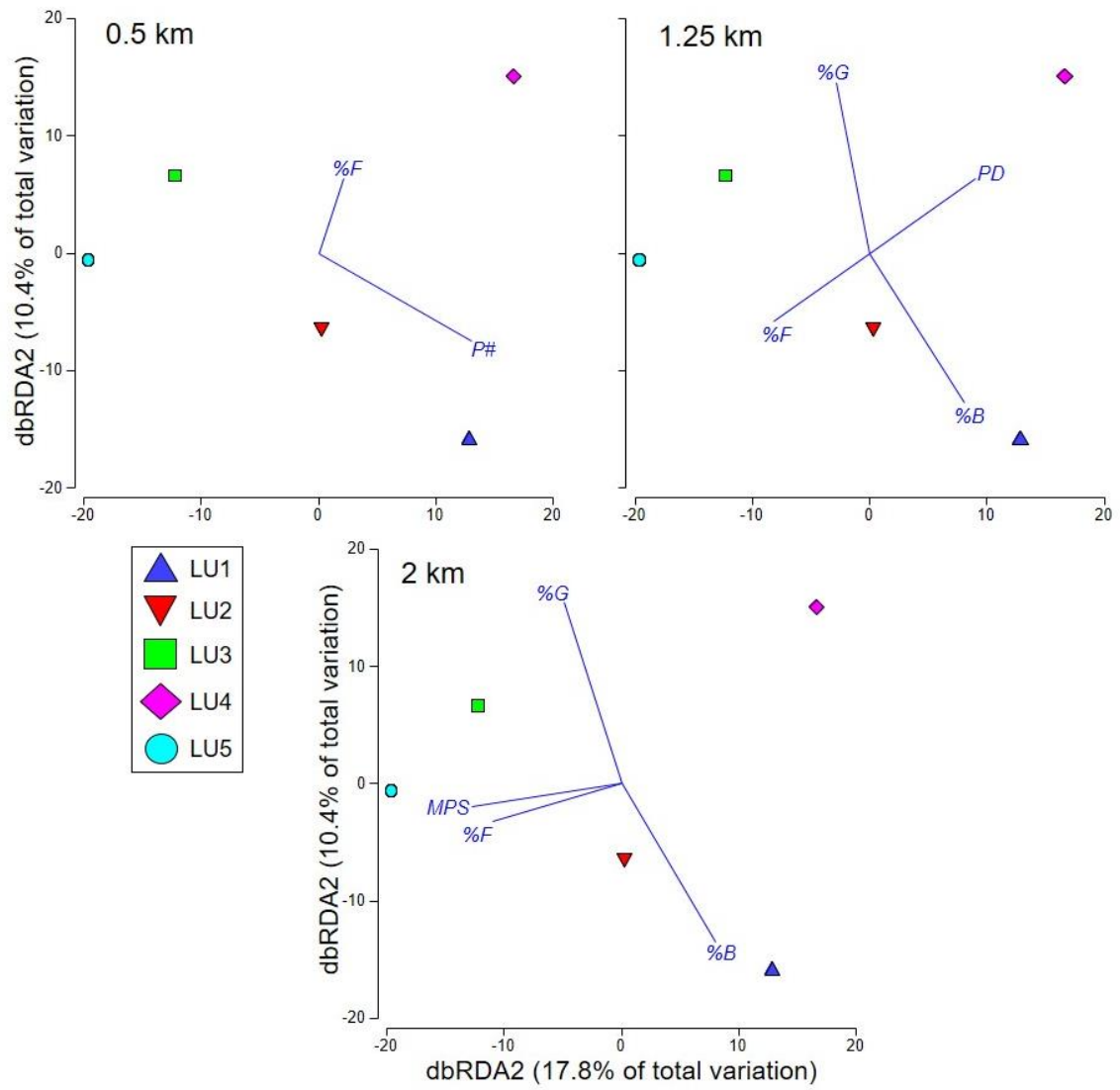Villavicencio municipality

Km
0 0,5 1   2   3   4

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

A. planirostris **1.25 km**

Model	df	LogLik	AICc	Δ_i	w_i
P#+BA+F	5	-108.9	229.2	0.0	0.27

β= 0.4, Vi= 1 (Abundance vs Number of forest patches)

β= 0.15, Vi= 0.87 (Abundance vs Built area)

β= 3.56, Vi= 0.63 (Abundance vs Forest cover)

A. lituratus **1.25 km**

Model	df	LogLik	AICc	Δ_i	w_i
F+P#	4	-26.93	65.5	0.0	0.38

β= 0.94, Vi= 0.51 (Abundance vs Forest cover)

β= 0.1, Vi= 0.62 (Abundance vs Number of forest patches)

C. perspicillata **0.5 km**

Model	df	LogLik	AICc	Δ_i	w_i
pssd+P#	4	-58.37	126.7	0.0	0.26

β= -2.84, Vi= 1 (Abundance vs pssd)

β= -0.6, Vi= 0.55 (Abundance vs Number of forest patches)

Capítulo 2

Seed dispersal and functional diversity of phyllostomid bats in a human dominated landscape: a scale-dependence analysis in the Colombian Orinoquia

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Abstract

Urbanization is one of the most pervasive landscape agents, affecting wildlife in a variety of ways. Bats may persist on those human-dominated environments, but the mechanisms responsible of their adaptability and the effects on their ecological functions remain understudied. We investigate the scale-dependent functional response of phyllostomid to the landscape transformation, in an urban-rural gradient on the Colombian Orinoquia. We used wing morphology traits and body mass to calculate indices of functional diversity (FD), and to classify species in functional groups. We measured in concentric circles of 0.5, 1.25 and 2 km of radius, compositional and structural landscape variables, to evaluate bat's responses to landscape transformation. Also, we relate changes on seed richness consumed by bats, as function of phyllostomid FD. Number of functional groups, functional richness (FRic) and functional evenness (FEve) tended to be higher in areas less degraded, whereas functional divergence (FDiv) exhibited the opposite trend. Changes on FEve and FRic were best explained by landscape structural variables at 0.5 and 1.25 km scales, respectively. Species richness of seeds increased with bat FRic and decreased with the FEve. Our results suggest a negative effects of urbanizations in bat's FD, affecting species richness of seed consumed. Our findings suggest an environmental filtering by landscape structure variables at 0.5 km, benefiting bats with long pointed wings. Recognizing the scale-dependent nature of phyllostomid functional response to

environmental transformation, appear as a fundamental issue to address bats conservation planning in urban-rural landscapes such as the Llanero Piedmont.

Key words: Chiroptera, ecological grouping, functional trait, Llanero piedmont, Neotropiacal bats, urban-rural landscape.

Introduction

The ecological consequences of biotic homogenization are receiving public attention given its potential consequences on human wellbeing and the realization that human persistence depends on nature (Grimm et al. 2008; Naeem et al. 1999). Functional diversity has been a concept developed not only to link the role of biodiversity to ecosystem processes and services, but also as a tool to understand the mechanisms underlying the species response to environmental filtering (Cadotte et al. 2011; Diaz and Cabido 2001; Hooper et al. 2005). This framework is particularly useful to study biodiversity patterns across human-dominated landscapes, because it is robust to predict which traits influence the ecological structure of communities in urban and/or rural contexts (Jung and Threlfall 2016; Luck et al. 2013).

In functional terms, the response of wildlife to landscape transformation depends on particular life history traits, ecological attributes of the species pool and the intensification of land use or the spatial scale (Carmona et al. 2016; González-Maya et al. 2016; Luck et al. 2013; Vandewalle et al. 2010). Examples in birds and mammals show that particular patterns of traits combination may predict the community ecological structure in human-dominated environments (e.g., Flynn et al. 2009; Vandewalle et al. 2010). Indeed, research on bats' functional response to urbanization, suggest that the main environmental filters predicting community composition are roosting sites and food availability, artificial illumination and forest cover (Jung and Threlfall, 2016; Luck et al. 2013; Threlfall Law, and Banks 2012). Particularly, since flight is a fundamental aspect of bats' life history (Marinello and Bernard 2014; Norberg and Rayner 1987), the study of wing morphology in human-dominated landscapes, may be used to understand the mechanisms responsible of their adaptation to environmental changes (Jung and Threlfall 2016; Meyer et al. 2016). For instance, the loss of natural forest cover in urban and suburban areas seems to be related with an increase in aspect ratio and wing loading of insectivorous bats (Jung and Threlfall 2016), since these traits favor high-speed flight at low energy cost, which is ideal for the exploitation of open environments (Marinello and Bernard 2014; Norberg and Rayner 1987). Several authors have reported the positive relationship of bat's body mass, wing loading and aspect ratio, with the intensification of land uses in human environments (e.g., Cisneros et al. 2014; Saldaña-Vázquez and Schondube 2016; Threlfall et al. 2011; Wordley et al. 2017), which may have implications in different functional diversity facets of bats at assemblage level (Wordley et al. 2017). Indeed, the evidences suggest that the response of functional diversity facets of birds and bats assemblages in gradients of environmental degradation, may be independent from each other and not necessarily are negatively affected by the landscape transformation (Barbaro et al. 2013; Luck et al.

2013; Wordley et al. 2017), it likely has repercussions on the ecosystem functions involving those organisms in human dominated landscapes.

Frugivorous bats are among the most abundant mammals in the Neotropics (Fleming and John Kress 2011; Medellín and Gaona 1999). In consequence, their role on seed dispersal and plant recruitment impacts forest composition and natural succession (Kunz et al. 2011). In Neotropical savanna ecosystems the reduction of frugivorous bats may lead to high losses on plant functional and taxonomic diversity (Cianciaruso et al. 2013), which in turn, could affect ecosystem process such as primary productivity. Several authors have pointed out the importance of the seed rain provided by bats, on the recovering of natural forest in fragmented landscapes (Abelleira-Martínez et al. 2015; Galindo-González et al. 2000; Medellín and Gaona 1999). Also, patterns of seed consumption and its relationship with phyllostomid functional traits has been studied using trophic categories of frugivorous species (e.g., Suárez-Casttro and Montenegro 2015) and bat physiological attributes (e.g., González and Murillo-García 2016; Saldaña-Vázquez et al. 2015), although the relationship between different facets of bat functional diversity and the seeds consumed diversity remains unknown.

The study of the effects of landscapes anthropization in Neotropical bat assemblages in megadiverse countries such as Colombia has been limited (e.g., Cortés-Delgado and Pérez-Torres 2011; Roncancio-D and Estéves-V, 2007; Sánchez, 2011), and as far as we know, few of this efforts have taken place in the Colombian Orinoquia (Suárez-Casttro and Montenegro 2015). Thus, our main goal was to evaluate the functional response of phyllostomid bats to the landscape transformation at multiple scales in an urban-rural landscape, and its potential relationship with the seed dispersal process. Particularly, as functional traits we used wing morphology, body mass and trophic guild. We expect that functional richness, functional evenness and functional divergence will be a function of the forest cover due to loss of habitat availability (García-Morales et al. 2016). Particularly, we expected a scale-dependent response of bat functional diversity dimensions, due to differences in which each bat species may be affected by the spatial heterogeneity (Gorresen et al. 2005; Pinto and Keitt 2008). Also, we predicted that the abundance of open-adapted species should increase with landscape transformation and, therefore, high aspect ratio and wing loading becomes more common at the assemblage as forest cover decreases (Jung and Threlfall 2016; Marinello and Bernard 2014; Norberg and Rayner 1987). Finally, we expected changes in species richness of seeds consumed by phyllostomid bats across the urban-rural gradient, as a function of bats functional

richness, evenness and divergence (Jung and Threlfall 2016), due that changes on these functional attributes may influence the use of food resources by the assemblage (Luck et al. 2013).

Methods

Study area

We conducted the study in an urban-rural gradient of the Llanero Piedmont, at the Villavicencio municipality in the Colombian Orinoquia. It is a transition zone between the savanna and Andean ecosystems (Rangel et al. 1997), and has experience deep land cover change processes since the early 1950s (Etter et al. 2008). Further details about vegetation and the ecological context of Villavicencio's landscape, are provided in Ramírez-Mejía et al. (see unpublished chapter 1).

Bat sampling

We sampled bat in five sites with different landscape composition, landscape units (LU), along Villavicencio's urban-rural interface. LU refers to the specific area from which we measured landscape composition and structure variables (Figure 1), while sites refers to the centroid of each LU in which mist nets were set. In each site we set two to three mist-nets of 12×3m, which were visited five times between January and July of 2016, selecting nights with moon illumination levels below of 60% (Rowse et al. 2016). We used a rabbit tattoo to mark each individual captured with an unique numerical code (Powell and Proulx 2003), to avoid bias in quantifying species abundance and to assess the independence of bat capture among mist-nets in each site. We identified individuals using taxonomic keys based on external characters (e.g., Díaz et al. 2016; Gardner, 2007), and those which we could not identify in the field, were collected for accurate taxonomic identification using dental and cranial characters (Díaz et al. 2016). Sampling design, sampling effort and sites selection criteria are deeply described in Ramírez-Mejía et al. (see unpublished chapter 1).

[Figure 1]

Bat functional traits

We selected five morphological and life-history traits under the hypothesis that bat species respond to landscape transformation factors depending on trait attributes or states. Wing span (Ws), aspect ratio

(Ar) and wing loading (Wl), influence flight performance and food acquisition, affecting in turn seed dispersal process and the capability of bats to respond to habitat disruption due to landscape transformation (Luck et al. 2012; Marinello and Bernard 2014; Norberg and Rayner 1987). Also, body mass (Bm) affects flight maneuverability (Stockwell 2001), and is related with home-range and the species contribution to seed dispersal due the amount and type of fruits consumed (Luck et al. 2012; Soriano 2000). Trophic guild (Tg) is strongly related with ecosystem function and may be linked to the species sensitivity to environmental change in relation to diet specialization (Luck et al. 2012). We use information in the literature to assign trophic categories to each bat species (Schnitzler and Kalko 2001; Soriano 2000). Additionally, we recorded seed species consumed by bats confining each individual captured in separates cotton bags for a period of one to two hours to collect feces (García-Morales et al. 2016). All the seeds collected were dried and identified to the highest possible taxonomic resolution, using the reference collection of the Natural Science Institute of National University of Colombia.

We measured the bats' Bm using a digital balance, of 0.1g of resolution, and wing morphology traits were measured as follows: (a) we took a photo of the left wing fully extended in a ventral position against a paper with millimeter scale (Korine and Pinshow, 2004). Then, (b) those images were processed using ImageJ 1.6 (Abramoff et al. 2004) to measure Ws and wing area. Finally, (c) Ar was calculated as the square of Ws divided by wing area, and Wl was estimated by dividing Bm into the product of gravitational acceleration, 9.81 m/s^2, by wing area (Norberg and Rayner 1987).

Land use classification (predictors variables)

We delimited concentric buffers of 0.5, 1.25 and 2 km of radius around sample sites, to characterize landscape composition and structure (Pinto and Keitt 2008). To do so, we used supervised classification tool of ArcGIS 10.1, and DigitalGlobe satellite images from Google Earth taken between 2014 and 2015 with a resolution of 2m^2 per pixel, to generate maps with three land uses: built area, grassland and forest (Figure 1). At each spatial scale, we measured the percentage of built area, grass land and forest cover, number of forest patch, mean forest patch size, forest patch size standard deviation and forest patches density (Garmendia et al. 2013; Pinto and Keitt 2008; Wu et al. 2002). For all the analysis we considered as response variables functional diversity indices of bat assemblage. Further details about landscape digitalization and scale delimitation criteria are given in Ramírez-Mejía et al. (see unpublished chapter 1).

Data Analysis

We used Estimates 9.0, to evaluate inventory completeness of bats and seeds recorded, using the estimator of total richness Jackknife 1 after randomized the samples 100 times (Gotelli and Colwell 2009). This estimator is adequate for heterogeneous samples such as LU's (Magurran 2004). To estimate functional diversity indices we considered the median of quantitative traits for each specie, and additionally for cluster analysis we transformed categorical traits in dummy variables of presence-absence (Pla et al. 2012). We used a regression and classification tree (LINKTREE) (Clarke et al. 2008), to identify functional groups using a similarity matrix of Gower modified Log10. We detected threshold values for each of the traits, in which the binary divisions were defined in groupings of bats, by a non-parametric measure of multivariated differences R and B%. We did LINKTREE analysis using PRIMER V 7 and PERMANOVA add on program (Anderson et al. 2008; Clarke and Gorley 2015).

We described the functional diversity facets of bat community across the urban-rural landscape, calculating indices of functional richness (FRic), evenness (FEve) and divergence (FDiv) (Villéger et al. 2008), as follows: (a) we standardized all trait values to avoid the effects of unit of measure (Pla et al. 2012), by subtracting the trait value of each species with the mean of the trait value for all species and dividing by the standard deviation of the trait value of all species (García-Morales et al. 2016). (b) We used Euclidean distance as measure of ecological distance and we weighted each trait by the abundance of each species (Luck et al. 2013; Mason et al. 2005). Additionally, we used the original trait data to calculate the community weighted mean index (CWM) (Díaz et al. 2007), to evaluate the expected mean value of each trait for the bats assemblage across each LU. We used the software FDiversity to calculate all functional diversity indices (Casanoves et al. 2011). For LINKTREE and functional indices, we included trait values of rare species ($n < 2$) since they may generate aggregate effects that could contribute to ecosystem functioning (Lyons et al. 2005).

We did non-parametric correlation analyses between landscape composition and structural variables to identify linear relationships, and to exclude collinear variables from further analyses (Quinn and Keough 2002). We evaluated changes on FRic, FEve, FDiv and all CWM indices as a function of landscape variables, using generalized linear models (GLM) and considering as response variables the indices values during each file visit. We generated every possible model at each spatial scale and we ranked them using Akaike's information criterion for small samples (AIC_C) and selected the best adjusted models using *glmulti* package in R 3.3.2 (Calcagno 2013; R Core Team 2016). Subsequently, we used *MuMIn*

package to average the first five best ranked models (Barton 2016), and then evaluated the importance of each variable with regard to functional diversity indices changes. Partial residuals of selected models and their confidence intervals were plotted using *visreg* package (Breheny and Burchett, 2016).

By GLM's we evaluate changes of species richness of seeds consumed by bats as function of bats FRic, FEve and FDiv. For this analysis, we used as a response variable the number of seed species recorded per each field visit at each LU and as predictor variables the cumulative value of all indices at each LU. The process to obtain, ranking, averaging and plotting the models is described above.

Results

We captured 615 individuals of 20 species belonging to 13 genera of the Phyllostomidae family, and during the sampling period we recorded seven recaptures in all the landscape. The highest number of bat captures was recorded in LU4, whereas the lowest was at LU1. Inventory completeness was over 80% for the whole landscape, and over 77% for four of the five LU's. Further details about bat captures, species recorded, species richness and abundance, are provided in Ramírez-Mejía et al. (see unpublished chapter 1).

Bat functional groups along urban-rural landscape

We detected 11 functional groups of bats for the whole landscape (Figure 2). Most of the groups included two or three species, but five groups included only one species (Figure 2, Table 1). Main traits contributing to species classification were body mass, wing span, wing loading and trophic guild (Figure 2). Number of functional groups recorded increased with distance to the centroid of urban center (Figure 2). Cumulative values of FRic and FEve also showed a similar trend whereas FDiv decrease with distance to the urban centroid (Figure 2). Foliage gleaners (SSFG and BSFG), hematophagous bats (H) and micro-sized frugivorous bats (MiF), were only recorded on LU's with the highest proportion of forest cover. Middle and big-sized nomadic frugivorous (MSNF and BSNF), sedentary frugivorous (SSSF and MSSF) and meddle-sized omnivorous (MSO) bats were recorded, at any proportion, throughout the urban-rural interface (Figure 2, Table 1). Also, the nectarivorous group was more redundant on LU1, which presented the highest proportion of urbanized area, in comparison to the others ones.

[Table 1]

[Figure 2]

Functional diversity and landscape metrics

Functional diversity dimensions of phyllostomid bats exhibited a scale-dependent response to landscape factors, at 1.25 and 0.5 km scales, but not at the 2 km scale. Changes in bat FDiv were best explained with the increase of forest cover at 1.25 km scale, showing a negative trend (Figure 3). Although this explanatory model was the best ranked and presented the highest weight (Figure 3), the second ranked model containing number of forest patches presented a similar AICc (-42.20), but a lower weight ($W_i=$ 0.22). The interaction between built area and forest patch size standard deviation at 0.5 km scale was the best explanatory model of changes in bat FEve in the landscape (Figure 3). Built area presented a negative effect with FEve, whereas forest patch size standard deviation exhibited the opposite trend and its effects on FEve at intermediates levels was highly variable (Figure 3). After averaging the first five best ranked models, the most important variable to explain changes on FEve was forest patch size standard deviation (Figure 3), followed by number of forest patches (Vi= 0.36), built area and density of forest patches (Vi= 0.18). Best ranked model explaining changes in FRic included only the constant, i.e. null model. This suggests that variation in this functional dimension was not accounted by any of the landscape predictor variables.

[Figure 3]

CWM Ws was highly correlated with CWM Bm (*Rho*= 0.9; p< 0.01), and in consequence we excluded CWM Ws from the GLM analysis, considering that the other wing morphology traits were good measures of the bats movement capabilities. Changes in CWM Bm were best accounted by the interaction of forest patch size standard deviation – mean forest patch size – number of forest patches at the 0.5 km scale (Figure 4). Indeed, these were the most important variables for the first five ranked models, followed by patch density (Vi= 0.5) and forest cover (Vi= 0.35) (Figure 3). Changes in CWM Wl were mainly explained by the interaction among forest cover – built area – number of forest patches at 0.5 km scale (Figure 4), being these the most important variables followed by density of forest patches (Vi= 0.8). Finally, the interaction of forest patch size standard deviation – number of forest patches at 0.5 km scale, was the

best ranked model to explain changes in CWM Ar (Figure 4). These were the most important variables after averaging the first five ranked models, followed by forest patch density (0.44) and forest cover (0.31).

[Figure 4]

Seed richness and bat functional diversity

We recorded 21 seed species from 229 bat feces, belonging to six genera and six families (Table 2). According to the estimator of total richness Jackknife 1 (mean= 23.99; SD= 1.72), we recorded 87.5% of seed species consumed by bats for the landscape. Most frequent seed on feces samples belonged to the families Hypericaceae (two species; n= 74), Urticaceae (seven species, n= 66), Moraceae (five species, n= 44) and Solanaceae (four species, n= 29) (Table 2). We also registered mango, *Mangifera indica*, as the unique non-native item consumed by bats at the study area (Table 2).

Seeds of families Urticaceae and Moraceae were mainly consumed by MidNF followed by MSSF (Table 2). Indeed, number of samples recorded from MidNF and MSSF for six of the seven species of Urticaceae were almost the same, except for *Cecropia* sp. 2 which was much more consumed by MidNF (Table 2). Samples of the Moraceae family showed a similar trend, being *Ficus* sp. 1 the species more recorded and mainly consumed by MidNF (Table 2). In contrast, seeds of de families Piperaceae, Solanaceae and Hypericaceae were mostly consumed by MSSF (Table 2). A lower proportion of seed species of these three families were recorded from feces of MidNF, BSNF, SSNF and MSO and species such as *Piper* sp. 2, *Solanum* sp. 1, *Vismia* sp. 1 and *Vismia* sp. 2 were almost exclusively consumed by MSSF (Table 2).

[Table 2]

Changes in richness of seed species consumed by bats were best explained, across the landscape, by the interaction FRic – Feve of phyllostomid bats (Figure 5). Seed richness and FRic exhibited a positive relationship, whereas seed richness and FEve showed the opposite trend (Figure 5). After averaging the first five best ranked models, FRic was the most important variable explaining changes in seed richness (Vi= 0.97), followed by FEve (Vi= 0.92) and with less explanatory importance FDiv (Vi= 0.15).

[Figure 5]

Discussion

Previous studies have used functional diversity of phyllostomid bats to categorize functional groups in tropical rainforest and Andean cloud forest, through trophic categories and foraging strategies (Soriano 2000). Also, this approach has been used to explain patterns of phyllostomid distribution along altitudinal and geographical gradients (Aguirre et al. 2016; Cisneros et al. 2014), and as a theoretical framework to explore the functional response of Neotropical bats assemblages to habitat loss and transformation (Cisneros et al. 2014; García-Morales et al. 2016; Klingbeil and Willig 2009). As far as we know, to date our study is the first integrating the response of different facets of phyllostomid functional diversity to landscape anthropization, and seed dispersal processes.

In this study, functional groups of fruit-eating and middle-sized omnivorous species were found across the whole urban-rural interface, whereas foliage gleaners and hematophagous groups were almost exclusively recorded in LU's with the large proportion of forest cover (Figure 2). This pattern is consistent with previous studies in Central and South America (Gorresen et al. 2005; Klingbeil and Willig 2009; Pinto and Keitt 2008), and is likely explained by behavioral traits, such as the foraging strategy, and use of resource (e.g., food, roosting sites) (Klingbeil and Willig 2009; Meyer and Kalko 2008; Soriano 2000). Foliage gleaners, i.e., SSFG and BSFG, are clutter-adapted bats with a sit-and-wait foraging strategy and a slow and maneuverable flight, which suggest a low dispersal capability and small foraging areas (Marinello and Bernard 2014; Norberg and Rayner 1987; Soriano 2000). These traits may make these functional groups particularly sensitive to the habitat loss and fragmentation, decreasing their abundance in human-transformed landscapes (Klingbeil and Willig 2009; Meyer and Kalko 2008; Meyer et al. 2016). The hematophagous group was composed by one species, *Desmodus rotundus*, and was only recorded in the LU's with highest amount of forest cover and livestock. Vampire bats are known to be highly associated to rural contexts, where cattle ranching is a common economical practice (Delpietro et al. 1992; Estrada and Coates-Estrada 2002), and vampires can take advantage of preying on cattle in the grassland systems near the forest cover (Delpietro et al. 1992; Estrada and Coates-Estrada 2002). In contrast, the higher redundancy of nectarivorous functional group in the most urbanized LU, is likely explained by two main factors: (a) nectarivorous bats tend to present wings with intermediate to high values of wing loading and aspect ratio (Marinello and Bernard 2014; Norberg and Rayner, 1987), allowing them move across the matrix to exploit remnants of natural forest cover embedded in the Villavicencio's urban core. Additionally, (b) nectar-eating bats can, eventually, feed upon insects, fruits, pollen and other flower parts (Alvarez et al. 1991; Ortega and Alarcón-D 2008), probably increasing their adaptability to changes food availability. Indeed, these

results are in agreement with Flynn et al. (2009), who found in a global meta-analysis that functional diversity of nectarivorous birds may be maintained in human-dominated landscapes, allowing these species to contribute to pollination process in such degraded environments. Also, the increase of some functional groups of fruit-eating bats with land uses intensification has been already recorded in tropical forest of Central and South America (Gorresen et al. 2005; Klingbeil and Willig 2009; Meyer and Kalko 2008; Pinto and Keitt 2008). Natural forest fragmentation may present different successional stages that would increase the fruit availability for different functional groups of fruit-eating bats (Pinto and Keitt 2008). Indeed, these functional groups present intermediate values of aspect ratio and wing loading (Marinello and Bernard 2014), which may allow them take advantage of resources in both, forest patch interior and cleared environments in human dominated landscapes.

Phyllostomid FEve tended to be higher in LU's with lower landscape transformation, and was positively related to forest patch size standard deviation and negatively affected by built area. In contrast, FDiv increased in most urbanized LU`s and was affected negatively by forest cover. These results are in agreement with empirical studies on birds in Oceania (Barbaro et al. 2013; Luck et al. 2013), where FEve and FDiv exhibited opposite responses according to a gradient of environmental degradation. LU's with large and small forest patches may provide suitable habitat for both clutter and open-adapted bats (Farneda et al. 2015), which likely explain the highest values of FEve in the LU's with high forest patch standard deviation. This suggests that Neotropical bat assemblages in less degraded LU's may be more resilient than those in urbanized areas, by presenting a wider set of responses on the face of landscape transformation processes (Luck et al. 2013; Mason et al. 2005). In addition, increase of FDiv with the loss of forest cover suggests a high niche differentiation and low resource competition among phyllostomid species in most transformed LU's (Mason et al. 2005). This indicates that urbanization may leave limited set of resources for only some functional types of bats that become extremely dominant, whereas others become more rare (Jung and Threlfall 2016; Luck et al. 2013; Saldaña-Vázquez and Schondube 2016).

In partial support to our hypothesis, the effects of landscape variables on FEve and FDiv were scale-dependent and operated at two scales: 0.5 and 1.25 km. These results are in contrast to previous studies in Central America, where the effect of landscape transformation in functional aspects of phyllostomid assemblages was consistent at multiple spatial scales (Cisneros et al. 2014; García-Morales et al. 2016). However, comparing scale-dependence of bats functional diversity across different studies should be seen with caution, mainly because many factors may influence its variation including the

ecological context of each Neotropical localities, matrix quality, historical processes of land uses/cover change, environmental variability, sampling effort and/or methodology (Cisneros, Fagan, and Willig, 2016). Those differences on landscape context and transformation, may have repercussion on the spatial scale in which particulars environmental filters influence selectively the functional diversity of a community (Carmona et al. 2016). Below, we will further discuss this idea on the light of the spatial scales in which phyllostomid functional traits may be filtered.

We found that CWM values for Bm, Wl and Ar were best explained, at the 0.5 km scale, by factors related to forest fragmentation and matrix quality. This may suggests that the environmental filtering due to landscape transformation, may operates at local spatial scales influencing phyllostomid functional diversity facets. This result is in agreement with previous studies reporting that functional diversity facets in bats in the palaeotropic, are the result of environmental degradation that selectively filter bats based on their wing morphology attributes (Wordley et al. 2017). Indeed, several studies have reported that forest fragmentation (e.g., Farneda et al. 2015; Wordley et al. 2017) and urban intensification (e.g., Jung and Kalko 2011; Luck et al. 2013; Saldaña-Vázquez and Schondube 2016), may causes the increase of Bm, Wl and Ar values in the bat community. Habitat disruption presents negative conditions at local scales that may affect the use of space by phyllostomid bats (Mendes et al. 2016), and as a result would filter species based on their capability to pass through disrupted areas (Croci et al. 2008). Global evidences suggests that habitat disruption derived from urbanization and fragmentation processes, may filter bat species based on their diet, wing morphology and body mass (Jung and Threlfall 2016; Meyer et al. 2016; Saldaña-Vázquez and Schondube 2016; Wordley et al. 2017). Bats with high Bm, Ar and Wl tend to be open-adapted bats with long-pointed wings, that allow them a fast flight with low energetic cost ideal to exploit uncluttered environments (Norberg and Rayner 1987; Stockwell 2001). Therefore, middle to big-sized bats with long pointed wings, may be able to travel across the human dominated landscape to exploit resources spatially scattered, whereas the aerodynamic constrains would limit the dispersion of small-sized bats with short rounded wings (Jung and Threlfall 2016; Saldaña-Vázquez and Schondube 2016). That is, clutter-adapted bats would be relegated to forest remnants embedded in the anthropogenic matrix, being likely exposed to the effects of population isolation, edge effects and stochastic processes associated to small populations (Franklin and Lindenmayer 2009; Jung and Threlfall 2016; Prugh et al. 2008).

For most traits, CWM values were highly variable at intermediate levels of predictor variables, in comparison to extremes. Studies in Europe, Oceania and South America, have found that at forest edges,

intermediate level of degradation considering interior – edge – matrix, reptiles functional groups and birds functional diversity increase due the invasion of species from the landscape matrix and forest interior (Barbaro et al. 2013; Carvajal-Cogollo and Urbina-Cardona, 2015). Therefore, it is possible that the inclusion of functional groups of open and clutter-adapted bats, accounted for the highest variability of the traits at intermediates levels of forest fragmentation (e.g., forest patch size standard) and/or land uses intensification (e.g., low level of urbanization).

Seed dispersion and phyllostomid functional diversity

The composition of seeds consumed by bats recorded in our study is in agreement with previous findings in other Neotropical localities (e.g., González and Murillo-García 2016; Medellín and Gaona 1999), and in the Colombian Orinoquia (Suárez-Casttro and Montenegro 2015). In addition, our results reveal that seeds of the genera *Cecropia*, *Ficus*, *Piper*, *Solanum* and *Vismia* are mainly dispersed by two functional groups, middle-sized sedentary frugivorous bats and middle-sized nomadic frugivorous bats. The interactions among these species of bats and plants have been well documented in the Neotropics (e.g., Fleming 1981; Fleming and Williams 1990; Lobova et al. 2003; Mikich et al. 2003; Suárez-Casttro and Montenegro, 2015), and show the importance of bats on seed dispersal in degraded areas (Abelleira-Martínez et al. 2015; Medellín and Gaona 1999). This flexibility displayed by some fruit bats in terms of the food use, is likely attributed to their digestive capacity that allow them take advantage of a variety of items with different nutritional composition (Saldaña-Vázquez et al., 2015), and would be an additional functional traits that explain their adaptation to the land uses intensification (Luck et al. 2012). These ideas may suggest that functional groups of generalist frugivorous bats, would partially insurance the seed dispersal process in human dominated environments. However, it should receive deeper analysis considering the ecological role of rare species, regarding their particular biotic interactions and the aggregated ecological effects of their loss in the ecosystem (Lyons et al. 2005).

We found a negative relation of seed species richness with bats FEve, and a positive one with FRic. These results may be explained by two main factors: (1) increasing functional richness of phyllostomid bats, would also lead an increment of the functional space occupied by the assemblage (Mason et al. 2005) and as a result would be expectable that the number of food resources used by bats increase too. On the other hand, (2) LU's with highest values of FEve presented lower abundance of generalist bats, in consequence it may lead to a reduction of species richness of seeds consumed, since those dominant

species tend to be those who most contribute to the seeds consumption in the ecosystem (Kunz et al. 2011; Mikich et al. 2003; Suárez-Casttro and Montenegro 2015). In Bolivian Andes suggest that high values of FRic in frugivorous bird assemblages, imply with a large number of interactions with plants, which in turn would lead to an increment of seed consumption and dispersal function (Saavedra et al. 2014). Moreover, the inverse relationship between seed richness consumed and FEve of bats, suggests a reduction in resources use flexibility as bats abundance evenness increases (Saavedra et al. 2014), since dietary spread of the assemblage may be reduced as rare specialist species become more abundant. This idea is supported by our results, considering that uncommon functional groups of frugivorous bats with low abundance, tended to consume a low number of seed species.

Conclusions, future directions and implications for bats conservation in anthropogenic landscapes

Research on bat functional diversity patterns in urban-rural gradients may help to understand, at least in part, how certain ecosystem functions linked to bats are affected by the land use intensification (Mcdonnell and Pickett 1990; McKinney 2006; Sparks et al. 2005), and may serve as foundation to develop strategies for their conservation via landscape planning (Montis et al. 2015).

Studies such as ours reveal that phyllostomid functional diversity present a scale-dependent response and is best explained by landscape factors at medium and small spatial scales. Indeed, our data suggest that environmental filtering operates at local spatial scales to filter species traits of the bat assemblage. Recognizing the scale-dependent nature of phyllostomid functional response to environmental transformation, is a fundamental issue for bats conservation planning in human dominated environments, because as the competition for space between human development and natural ecosystems is increasing (Foley et al. 2005; Grimm et al. 2008), the understanding of those particular spatial scales in which conservation efforts may be best invested will become more valuable. For instance, according to our results, planning for conservation of bats functional diversity in Villavicencio's landscape should be addressed at local spatial scales. That is, the conservation of large patches of natural cover, use of dispersed trees in the anthropogenic matrix and reducing forest fragmentation at focal areas of ~78 ha (area covered by a circle of 0.5 km of radius), would contribute to mitigate the environmental filtering that reduce the diversity of bats, and may guaranty the seed dispersal function of phyllostomids in this human-dominated landscape.

Our results suggest an important effect of environmental filtering by forest fragmentation variables and matrix quality, which selectively benefit frugivorous species with long pointed wings and prove that a

trait-based framework is a good predictor of bats vulnerability to habitat transformation. In addition, our data show that changes in functional diversity facets of phyllostomid bats depends on both matrix quality and the spatial arrangement of the remainder natural cover in the landscape. The loss of functional diversity and the biotic homogenization driven by urbanization, may present pervasive consequences nor only for ecosystem functioning but also on phylogenetic attributes of the assemblage (Díaz et al. 2013; Morelli et al. 2016). Phylogenetic distance may be considered as a surrogate of ecological differences among species, and as a consequence it is related to ecosystem stability (Cadotte et al. 2012). Thus, future studies of Neotropical bats in urban-rural landscapes should involve both functional and phylogenetic diversity, since it would bring up valuable insights on the mechanisms underlying bats adaptability and evolutionary potential in anthropogenic environments (Morelli et al. 2016). On this regard, we highly that upcoming analysis of phyllostomids in urban environment, should consider explore the influence of a likely phylogenetic signal at the subfamily level (See Table 1), on the species response to the landscape transformation.

On this work we found that functional groups with more flexible food and space use were who most contribute to the seed dispersal function in the urban-rural landscape of Villavicencio. Also, this study shows that the number of seed species potentially dispersed depends on the functional diversity facet of phyllostomid bats. We recommend that future studies of seed dispersion by bats in human environments, should also include a more complex picture with additional ecological aspects such plant phenology, complementary dispersal services by common and rare bats, plant recruitment and the effects of species abundance fluctuations on seed dispersal function (Corlett 2011; Escribano-Avila et al. 2014).

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FIGURE CAPTIONS

Figure 1. Landscape units (LU) in an urban-rural interface in Villavicencio. Top right, location of Villavicencio in Colombia. We sampled bats in sites at the centroid of each concentric circle. Concentric circles at each LU, set the limits of each spatial scale (0.5, 1.25 and 2 km of radius) in which landscape variables were measured. The land use category "other", includes bare ground, small crops and body waters. DU: distance to the centroid of the urban area. F: forest cover. G: grassland area. B: built area. P#: number of forest patches. mps: mean size of forest patches (ha). pssd: patch forest size standard deviation. pd: forest patch density (P#/ha). Landscape variables provided correspond to the 2 km scale.

Figure 2. Regression and classification trees, clustering functional groups of phyllostomid bats based on five traits (body mass (Bm), wing span (Ws), wing loading, aspect ratio and guild (G)), in an urban-rural at Villavicencio. Distance to the centroid of urban center increase with the landscape unite (LU) numeration. R= non parametric measure of degree of separation between binary division; B% = absolute measure of group difference. Acronyms of functional groups are given in Table 1. G= guild, Wl= wing loading, Ws= wing span, Bm= body mass. Cumulative values of functional richness (FRic), evenness (FEve) and divergence (FDiv) indices, are provided for entire landscape and each LU.

Figure 3. Best fitted models explaining changes of functional attributes of phyllostomid bat assemblage (FEve and FDiv), as a function of different landscape metrics at three spatial scales (0.5, 1.25 and 2 km) in Villavicencio. Shaded bands and black dotes denotes 95% confidence intervals and partial residuals, respectively. Variable importance (Vi) AICc weight (W_i) and delta (Δ_i) goes from 0 to 1, and were calculated by averaging the first five ranked models. Reliability of the model increase as Δ_i decrease to cero and W_i increase to 1. pssd: forest patch size standard deviation. ba: built area. F: forest cover.

Figure 4. Best fitted models explaining changes on community weighted mean (CWM) values for three functional traits of bats, as a function of different landscape metrics at three spatial scales (0.5, 1.25 and 2 km) in Villavicencio. Shaded bands and black dotes denotes 95% confidence intervals and partial residuals, respectively. Variable importance (Vi), AICc weight (w_i) and (Δ_i) goes from 0 to 1, and were calculated by averaging the first five ranked models. Reliability of the model increase as Δ_i decrease to cero and W_i increase to 1. pssd= forest patch size standard deviation, mps= mean patch size, p#= number of forest patches, f= forest cover, ba= built area.

Figure 5. Best fitted models explaining changes richness of seed species consumed by bats, as a function of FRic and FEve of phyllostommid bats in Villavicencio. Shaded bands and black dotes represents 95% confidence intervals and partial residuals, respectively. Variable importance (Vi), AICc weight (w_i) and delta (Δ_i) goes from 0 to 1, and were calculated by averaging the first five ranked models. Reliability of the model increase as Δ_i decrease to cero and W_i increase to 1. FRic= functional richness index, FEve= functional evenness index.

FIGURES

Figure 1

LU1
DU: 2.6 km
% F: 28.6
% G: 12.8
% B: 58.7
P#: 341
mps: 1.03
pssd: 10.4
pd: 0.3

LU2
DU: 2.4 km
% F: 16.4
% G: 36.4
% B: 47.3
P#: 844
mps: 0.2
pssd: 1.1
pd: 0.6

LU3
DU: 4.8 km
% F: 30
% G: 57.9
% B: 12.1
P#: 293
mps: 1.2
pssd: 9.5
pd: 0.2

LU4
DU: 7.9 km
% F: 19.3
% G: 71.5
% B: 9.2
P#: 681
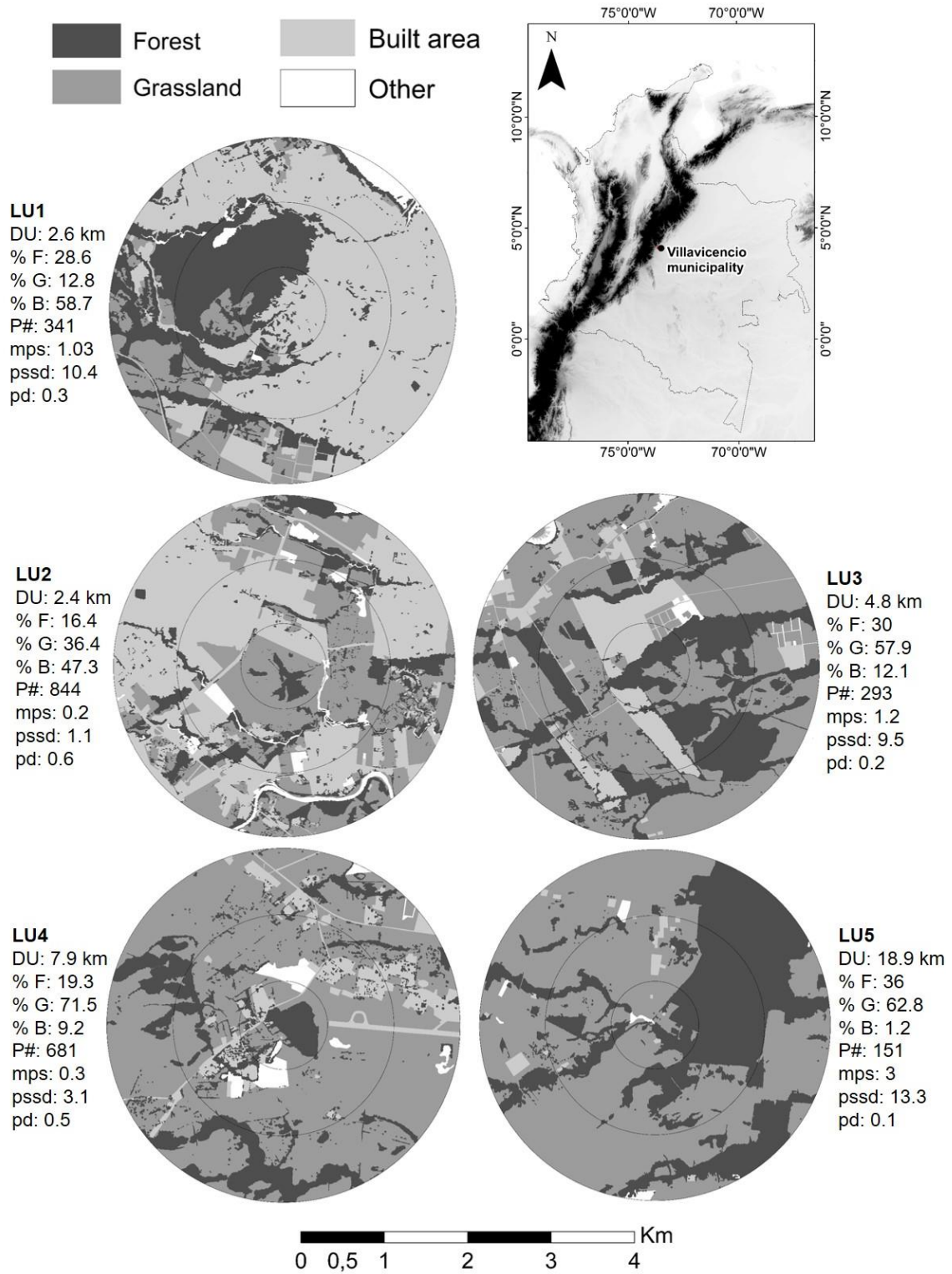mps: 0.3
pssd: 3.1
pd: 0.5

LU5
DU: 18.9 km
% F: 36
% G: 62.8
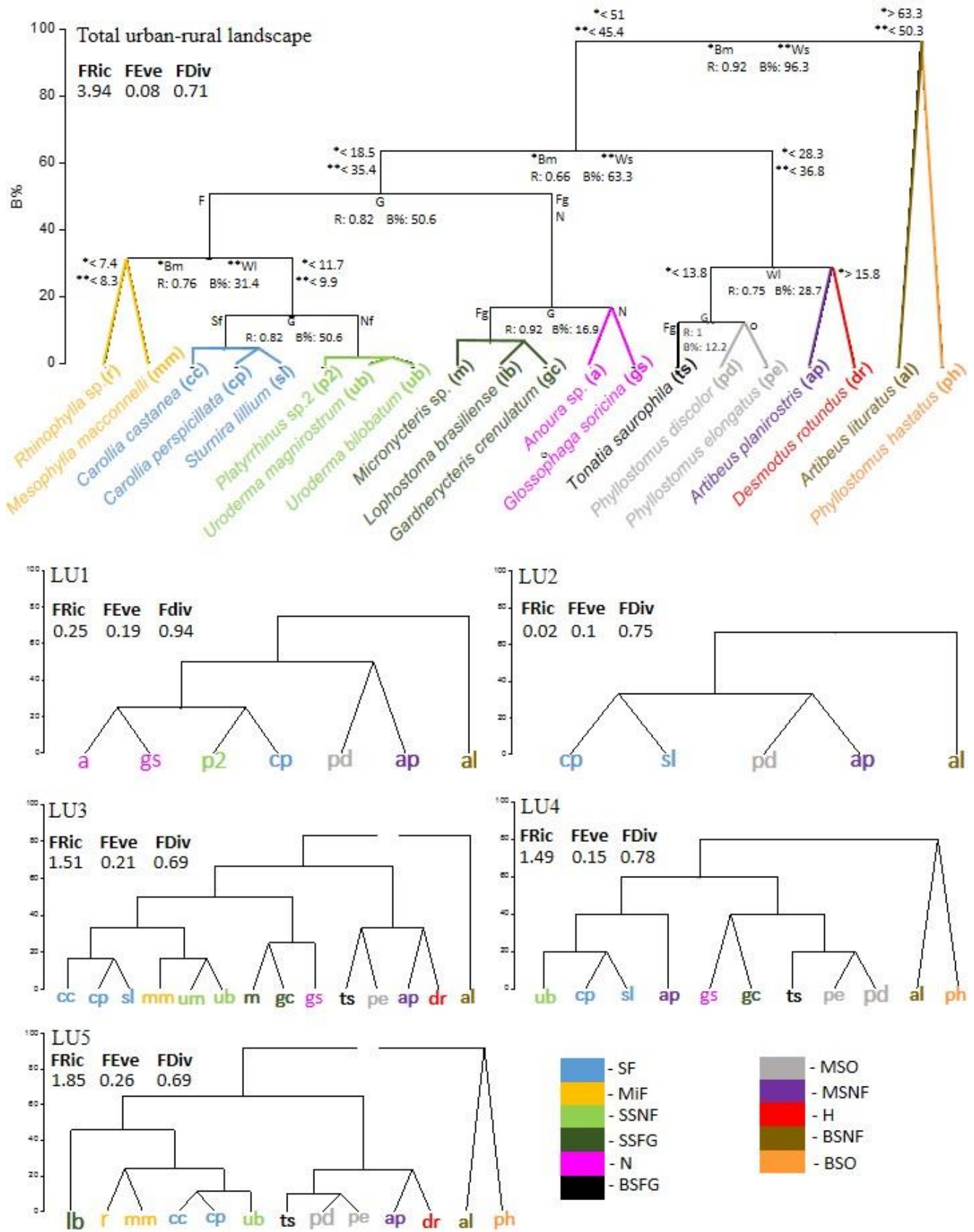% B: 1.2
P#: 151
mps: 3
pssd: 13.3
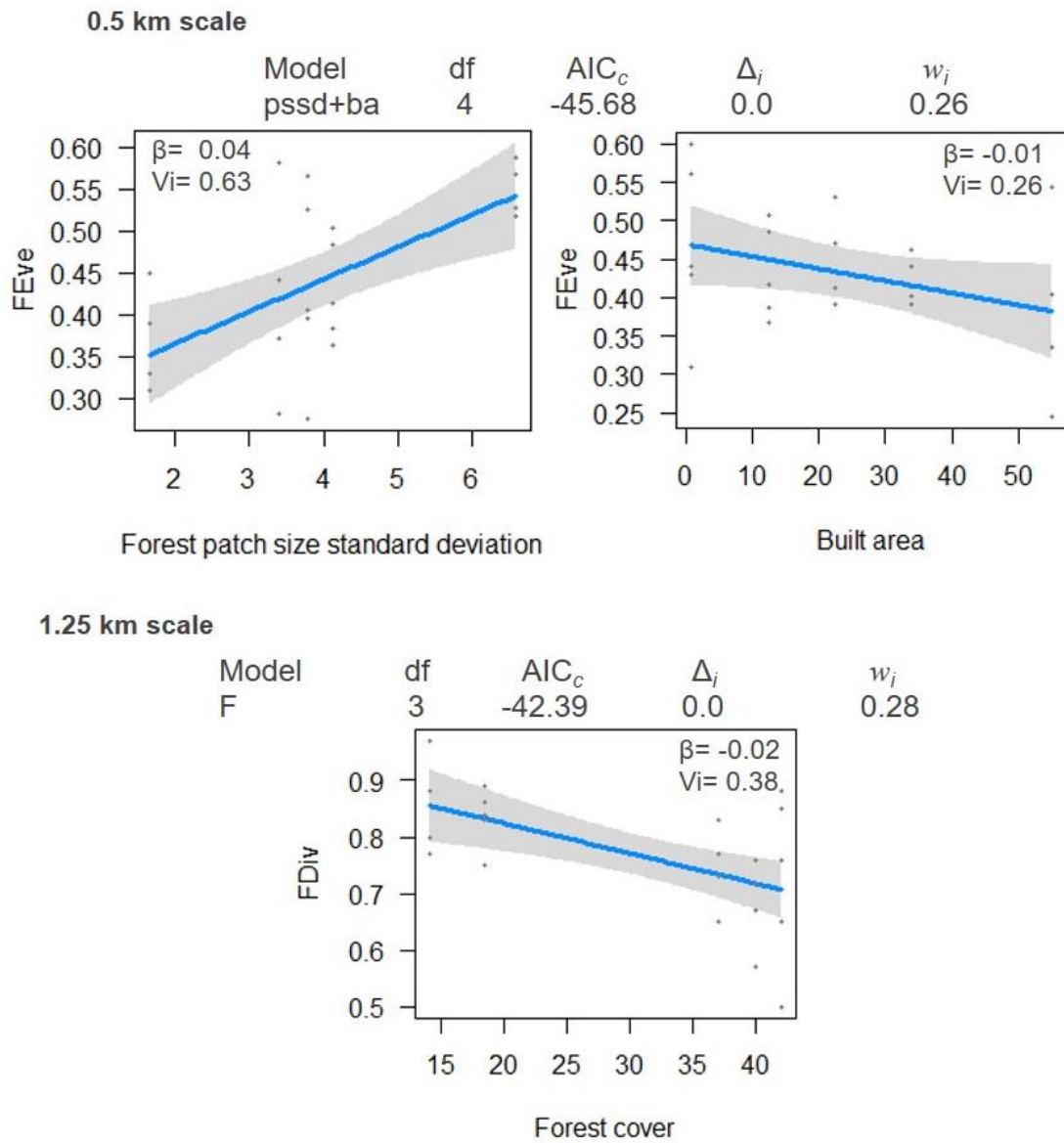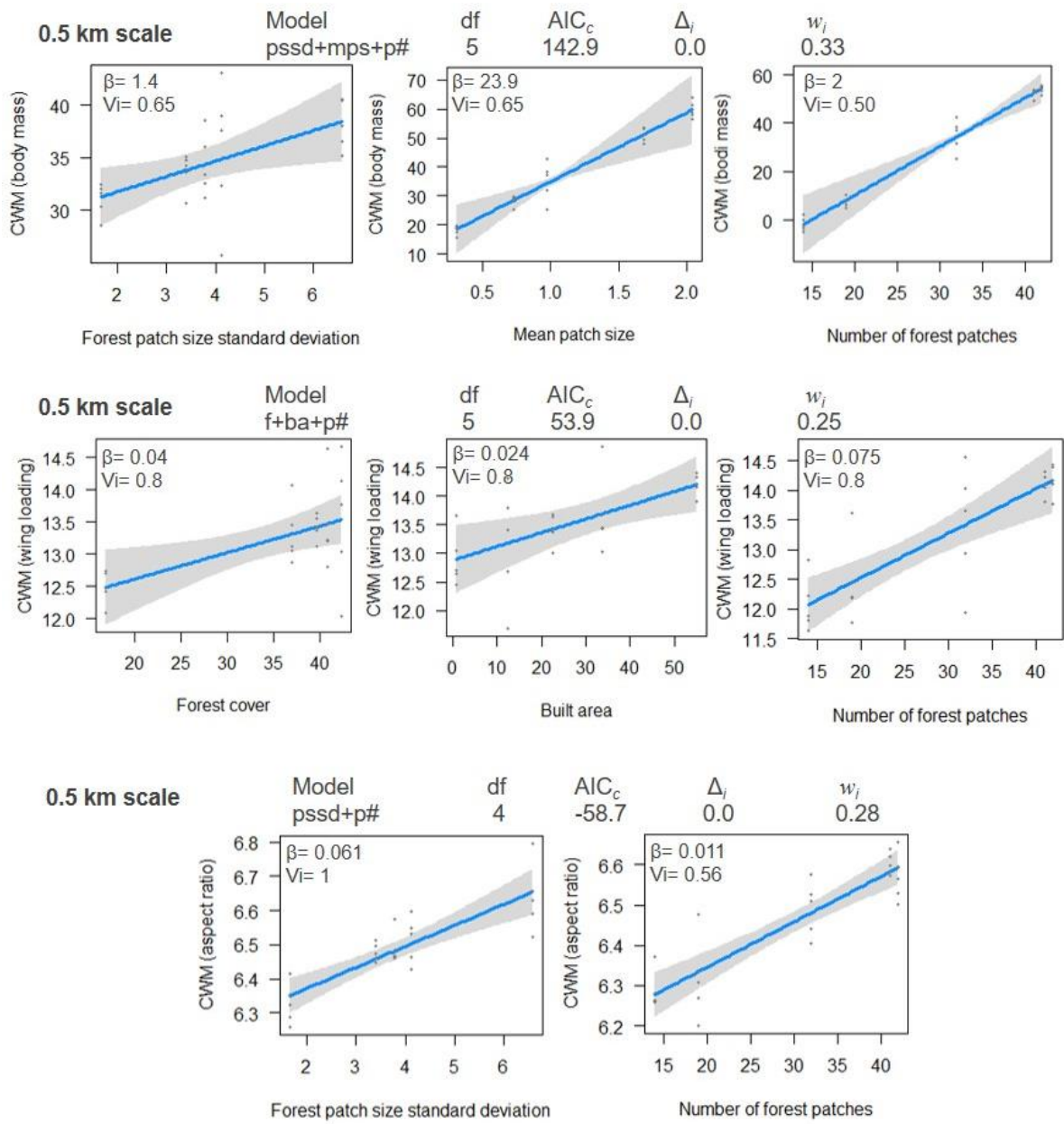pd: 0.1

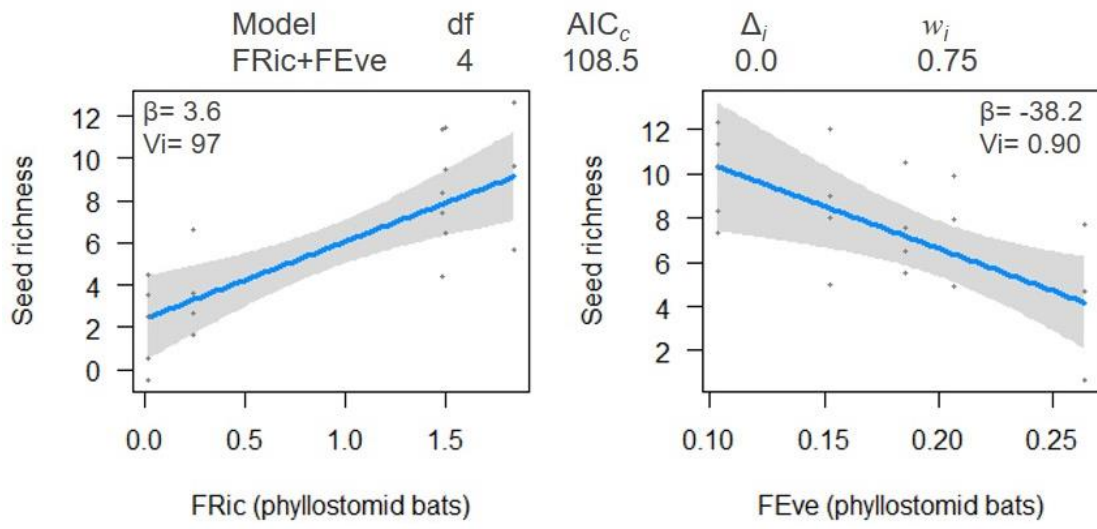Figure 2

Figure 3

Figure 4

Figure 5

TABLES

Table 1. Description of functional groups of phyllostomid bats in the urban-rural landscape of Villavicencio. Species integrating each group and the subfamily each belong, are provided.

Functional group	General description	Species	Subfamily
SF	Sedentary frugivorous bats	*Carollia castanea*	Carollinae
		Carollia perspicillata	Carollinae
		Sturnira lillium	Stenodermatinae
SSNF	Small-sized nomadic fugivorous bats	*Platyrrhinus* sp.	Stenodermatinae
		Uroderma magnirostrum	Stenodermatinae
		Uroderma bilobatum	Stenodermatinae
SSFG	Small-sized foliage gleaners bats	*Mycronicteris* sp.	Micronycterinae
		Lophostoma brasiliense	Phyllostominae
		Gardnerycteris crenulatum	Phyllostominae
MSO	Middle-sized omnivorous bats	*Phyllostomus discolor*	Phyllostominae
		Phyllostomus elongatus	Phyllostominae
N	Nectarivorous bats	*Anoura* sp.	Glossophaginae
		Glossophaga soricina	Glossophaginae
MiF	Micro-sized frugivorous bats	*Rhinophylla* sp.	Carollinae
		Mesophylla macconnelli	Stenodermatinae
BSFG	Big-sized foliage gleaners bats	*Tonatia saurophila*	Phyllostominae
MidNF	Middle-nomadic frugivorous bats	*Artibeus planirostris*	Stenodermatinae
H	Hematophagous bats	*Desmodus rotundus*	Desmodontinae
BSNF	Big-sized nomadic frugivorous bats	*Artibeus lituratus*	Stenodermatinae
BSO	Big-sized omnivorous bats	*Phyllostomus elongatus*	Phyllostominae

Table 2. Seeds recorded from feces of phyllostomid functional groups (FG) in an urban-rural landscape at the Villavicencio municipality. Codes of FG's are provided on Figure 2.

Family	Species	Sample recorded	Number of samples recorded by bats FG	Percentage seed families consumed by bats FG
Urticaceae	*Cecropia* cf. m*etensis*	6	MSSF (1), MidNF(2), BSNF (1), SSNF(1), MSO (1)	MidNF (56.01) MSSF (27.3) BSNF (10.6) BSO (3) SSNF (1.5) MSO (1.5)
	Cecropia engleriana	19	MSSF (8), MidNF(8), BSNF (3)	
	Cecropia membranacea	5	MSSF (2), MidNF(3)	
	Cecropia peltata	6	MSSF (2), MidNF(3), BSO (1)	
	Cecropia sp. 1	21	MSSF (2), MidNF(16), BSNF (2), BSO (1)	
	Cecropia sp. 2	8	MSSF (2), MidNF(5), BSNF (1)	
	Cecropia sp. 3	1	MSSF (1)	
Moraceae	*Ficus* sp. 1	26	MSSF (3), MidNF(23)	MidNF (81.8) MSSF (18.2)
	Ficus sp. 2	1	MidNF(1)	
	Ficus sp. 3	2	MidNF(2)	
	Ficus sp. 4	6	MSSF (2), MidNF(4)	
	Ficus sp. 5	9	MSSF (3), MidNF(6)	
Anacardiaceae	*Mangifera indica*	1	MidNF(1)	MidNF (100)
Piperaceae	*Piper* sp. 2	10	MSSF (8), BSNF (1)	MSSF (73.3) MidNF (20) BSNF (6.7)
	Piper sp. 1	5	MSSF (3), MidNF(3)	
Solanaceae	*Solanum* sp. 1	14	MSSF (10), MidNF(1), SSNF(1), MSO (2)	MSSF(69) MidNF(17.2) MSO(10.3) SSNF(3.4)
	Solanum sp. 2	2	MSSF (2)	
	Solanum sp. 3	8	MSSF (4), MidNF(3), MSO (1)	
	Solanum sp. 4	5	MSSF (4), MidNF(1)	
Hypericaceae	*Vismia* sp. 1	37	MSSF (29), MidNF(1), BSNF (5), SSNF(1), MSO (1)	MSSF (83.8) BSNF(8.1) MidNF(5.4) SSNF(1.3) MSO(1.3)
	Vismia sp. 2	37	MSSF (33), MidNF(3), BSNF (1)	
	Total	229		

Conclusiones y recomendaciones

Mi trabajo demuestra que la intensificación en el uso del suelo en el paisaje urbano-rural de Villavicencio, tiene implicaciones en la simplificación del ensamblaje de filostómidos en términos de su diversidad taxonómica y la riqueza y equidad funcional. Estos resultados son congruentes con evidencias globales con comunidades de aves y murciélagos en paisajes antropizados de Oceanía (Luck et al. 2013; Luck et al. 2013a; Threlfall et al. 2012), América (Cisneros et al., 2014; Farneda et al., 2015; Meyer & Kalko, 2008) e India (Wordley et al. 2017). En efecto, mis datos sugieren que la divergencia funcional es inversa a la riqueza de especies de murciélagos, lo cual podría sugerir que la diversidad taxonómica puede no ser un buen sustituto para esta facetas de la diversidad funcional (Luck et al. 2013).

Los resultados muestran que la transformación del paisaje en Villavicencio, opera en diferentes escalas espaciales para afectar tanto la diversidad taxonómica, como la diversidad funcional de murciélagos. En efecto, este trabajo muestra por primera vez en el Neotrópico que el filtrado ambiental en un gradiente de intensificación en el uso del suelo, puede operar a escala local (0.5 km) para beneficiar sólo aquellas especies de murciélagos con alta masa corporal, alas largas, delgadas y en forma de punta. Estos rasgos, posiblemente hacen parte del conjunto de mecanismos que explican la simplificación taxonómica y la diversidad funcional del ensamblaje de murciélagos filostómidos en el paisaje de Villavicencio. Futuros estudios que incluyan rasgos asociados a la tolerancia fisiológica de los murciélagos a la contaminación y sus implicaciones en la eficacia biológica de estos organismos, podrían brindarnos un panorama más amplio de los factores que determinan la adaptación de murciélagos en áreas urbanas (Salmón et al. 2016; Voigt & Kingston 2016).

Entender la naturaleza multiescala de la respuesta de los murciélagos a diferentes elementos del paisaje en áreas urbanizadas, podría servir para direccionar las acciones de conservación a las particulares escalas espaciales en las que los beneficios para los murciélagos podrían ser mayores. Por ejemplo, con base en mis resultados, la conservación de grandes remanentes de cobertura nativa y la prevención de su fragmentación a una escala local de ~ 78 ha (área ocupada por un círculo de 0.5 km de radio), podría contribuir a reducir los efectos del filtrado ambiental que probablemente influencia la diversidad del ensamblaje, dado que favorecería la presencia y abundancia de murciélagos pequeños con alas, cortas, anchas y redondeadas dependientes del interior de bosque. En efecto, este tipo de plan debería ir acompañado del uso de árboles dispersos alrededor de estas áreas, para aumentar la permeabilidad de la matriz urbanizada y potencialmente favorecer la dispersión de las especies a través del paisaje (Threlfall et al. 2011).

Este trabajo es el primero en reportar una relación positiva de la riqueza y una negativa de la equidad funcional de murciélagos, con la riqueza de especies de semillas consumidas por ellos. Es decir, mis datos sugieren que en la medida que el ensamble de filostómidos ocupa un espacio funcional mayor con especies muy dominantes y otras raras, el número de especies de semillas dispersadas en el paisaje tendería a crecer. En efecto, los grupos funcionales más dominantes y que parecen ser favorecidos, o por lo menos no afectados, por la transformación del paisaje fueron aquellos que consumieron

una mayor diversidad semillas. Esto, podría sugerir que en paisajes urbanizados el proceso de dispersión de semillas podría estar parcialmente asegurado por dichos murciélagos tolerantes a la degradación ambiental. Sin embargo, es necesario continuar investigando el rol ecológico de aquellas especies raras de las cuales desconocemos la importancia de sus interacciones en ciertas propiedades del ecosistema (Morelli & Tryjanowski 2016), y los potenciales efectos sinérgicos derivados de su pérdida en el ensamblaje (Lyons et al. 2005). Finalmente, resalto que además del estudio de la dieta de los dispersores, el entendimiento del proceso de dispersión de semillas en paisajes altamente degradados debería involucrar aspectos relacionados con la variación fenológica de las plantas, el reclutamiento efectivo de las semillas dispersadas en nuevas poblaciones e incluso rasgos asociados a la capacidad de germinación de las semillas (Corlett 2011).

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Anexos

Anexo 1. Criterio de selección para elección de las revistas científicas

	País	Ubicación según tema	Criterio de selección
Biodiversity and conservation	**Holanda**	**Cuartil 1:** "ecology", "ecology, evolution, behavior and systematics", "nature and landscape conservation"	Es una revista internacional de alto impacto en la que estos nuevos hallazgos de diversidad funcional de murciélagos prodrían ser más visibles. La potencial aplicación de los resultados en el manejo del paisaje para la conservación de murciélagos en áreas urbanizadas, podría ser de interés para los editores dado el enfoque de la revista y su particular interés en la publicación de contribuciones provenientes de paices en desarrollo.
Journal of tropical ecology	**Reino Unido**	**Cuartil 2:** "ecology, evolution, behavior and systematics"	Es una revista de alto impacto especializada en la publicación de contribuciones relacionadas con ecología tropical. La publicación de nuestro trabajo podría contribuir a visibilizarlo, dada la tradición de la revista. En efecto, consideramos que nuestro diseño experimental y tamaño de muestra podrían ser aceptables para los editores de la revista.