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Redes de interacción entre murciélagos frugívoros y plantas quiropterócoras en un paisaje rural cafetero

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Doctorado en Ciencias Biológicas

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A ti que fuiste mi motor en este proceso,

sin ti nada de esto hubiera sido posible

y a los frutos que están por venir

Tabla de contenido

RESUMEN

La transformación del paisaje inducida por el hombre ha resultado en la pérdida y fragmentación de hábitats naturales; afectando negativamente las especies a través de pérdida o disminución en la calidad de su hábitat. Sin embargo, la transformación de hábitats naturales puede resultar en un mosaico de parches de diferentes calidades y características, donde las especies pueden ser capaces de usar, además de aquellos recursos encontrados en el hábitat original, recursos alternativos provenientes de hábitats modificados. Las especies no funcionan como entidades aisladas, más bien están involucradas en redes complejas de interacciones que sostienen los procesos ecológicos que proporcionan servicios ecosistémicos de valor para las sociedades humanas. Conocer la estructura de estas redes permite entender la robustez de las comunidades ante la pérdida de especies. También permite identificar especies clave, es decir, aquellas relativamente más importantes para mantener la estructura de la comunidad y el funcionamiento de los ecosistemas. Para muchos lugares se desconoce cómo varía la estructura de las redes, o el papel de las especies, en diferentes escenarios rurales modificados por el hombre. Aunque se ha reconocido el aporte del paisaje rural cafetero colombiano a la conservación de la biodiversidad, aún no hay consenso sobre cuál debe ser la composición y configuración del paisaje rural que asegure la persistencia de la biodiversidad y la provisión de servicios ecosistémicos a largo plazo. El objetivo de este trabajo fue evaluar el efecto de la configuración y composición espacial del paisaje sobre la estructura de las redes de interacción murciélagos frugívoros (MF) y plantas quiropterócoras (PQ) en tres escenarios (bosques, fragmentos de bosque y agroeosistemas) que representan la transformación del paisaje rural cafetero de Risaralda, Colombia. Se establecieron nueve parcelas de 1km de radio (tres por cada tipo de paisaje); se clasificaron las diferentes coberturas presentes en cada una de las parcelas, se describió la composición (porcentaje de cobertura) y la configuración del paisaje (número de parches de bosque, tamaño promedio de los parches de bosque, densidad de bordes de bosque y los índices de Simpson y Shannon). En la región central de cada parcela se capturaron murciélagos frugívoros utilizando redes de niebla y se colectaron sus muestras fecales para conocer las plantas consumidas. Se evaluó el cambio en seis métricas de la estructura de las redes de interacción entre murciélagos frugívoros - plantas quiropterócoras, y el papel de las especies dentro de las redes (centralidad) en tres los escenarios de transformación del paisaje rural cafetero. Se describió la estructura de 34 redes de interacción MF-PQ que representaron cada una de las cuatro visitas en cada uno de los nueve sitios de estudio. Se realizaron modelos lineales generalizados, para determinar qué variables de composición y configuración del paisaje influyeron sobre el tamaño de la red, la riqueza de plantas, la riqueza de murciélagos y la riqueza de interacciones en la red. Capturamos 1146 murciélagos pertenecientes a 32 especies, (Familias Molossidae, Phyllostomidae, Thyropteridae y Vespertilionidae). Para los análisis de estructura se considerarron solamente 13 especies (subfamilias Carolliinae y Stenodermatinae) que consumieron frutos de 37 especies vegetales pertenecientes a las familias Araceae, Campanulaceae, Cyclanthaceae, Ericaceae, Gesneriaceae, Hypericaceae, Moraceae, Myrtaceae, Piperaceae, Solanaceae y Urticaceae. Se encontró que la riqueza de interacciones y de especies en las redes fue menor en los bosques que en los otros escenarios transformados, no obstante, el anidamiento y la modularidad se mantuvieron. Se evidenciaron cambios en el papel de las especies, donde los agroecosistemas presentaron interacciones menos especializadas y las especies mantuvieron su papel entre escenarios de bosques y fragmentos; pero cambiaron su papel en agroecosistemas. En las coberturas con presencia de árboles se incrementó el número de interacciones. En particular el porcentaje de cobertura de bosque, de plantación forestal, de matorrales y de cuerpos de agua, y el número de parches de bosque favorecieron el número de interacciones en las redes MF-PQ, donde la cobertura de pastizales incrementó el número de interacciones. Por otra parte, la densidad de bordes tuvo un efecto negativo sobre el número de interacciones. Este es el primer estudio que evalúa el efecto de la estructura y composición del paisaje sobre las redes de interacción MF-PQ. Los resultados dan luces en la manera que la biodiversidad responde a trasformaciones antrópicas, mostrando una estabilidad superior a lo predicho teóricamente y apoya la idea que en el paisaje cafetero la matriz rural ofrece recursos para los murciélagos y mantiene los servicios ecosistémicos. Los paisajes con mayor cobertura de matorrales, cuerpos de agua, y número de parches de bosque afectaron positivamente el número de interacciones y la riqueza de especies, tanto de plantas como de murciélagos. Identificar esta relación tiene implicaciones en el papel que pueden cumplir los paisajes agrícolas en el mantenimiento de la biodiversidad y de servicios ecosistémicos.

OBJETIVOS

Objetivo general:

Evaluar el efecto de la configuración y composición espacial del paisaje sobre la estructura de las redes de interacción murciélagos frugívoros (MF) y plantas quiropterócoras (PQ) en tres escenarios de transformación del paisaje rural cafetero de Risaralda.

Objetivos específicos

Primer objetivo específico

Comparar la estructura de las redes de interacción entre MF-PQ en tres escenarios (bosque continuo, fragmentos de bosque inmersos en una matriz de agroecosistemas y agroecosistemas sin bosque) de transformación del paisaje rural cafetero de Risaralda.

Segundo objetivo específico

Analizar los cambios del papel de las especies dentro de las redes de interacción MF-PQ en los tres escenarios de transformación.

Tercer objetivo específico

Analizar cómo afecta los atributos de composición y configuración del paisaje las propiedades estructurales de las redes de interacción MF-PQ en los tres escenarios de transformación del paisaje rural cafetero de Risaralda.

INTRODUCCIÓN

Los ecosistemas del planeta, especialmente las regiones tropicales, están perdiendo biodiversidad a una tasa acelerada (Hagen et al. 2012) debido principalmente a cambios en el uso del suelo inducidos por el hombre, dada la fuerte demanda de tierras para la producción de alimentos (Fahrig et al. 2011). Es así que, la mayoría de regiones tropicales carecen de grandes masas de bosque primario viables para ser declaradas áreas de conservación (Tilman et al. 2011). Sin embargo, los paisajes rurales modificados por el hombre pueden ser una oportunidad para conservar la biodiversidad; al crear escenarios donde las tierras productivas coexistan con áreas de bosque natural y donde se promuevan prácticas culturales más "amigables" con la biodiversidad (Melo et al. 2013).

Se reconoce el aporte de los paisajes rurales de la zona cafetera colombiana, también conocido como Paisaje Cultural Cafetero (PCC) a la conservación de la biodiversidad (Castaño *et al*. 2004, Sánchez Clavijo *et al*. 2009, Henao *et al*. 2014, Castaño y Carranza-Quiceno 2015). El PCC ha sido considerado patrimonio cultural de la humanidad de la UNESCO; comprende 47 municipios de los departamentos de Caldas, Quindío, Risaralda y Valle del Cauca (Martínez Moreno 2011). En esta región se ha producido café a escala familiar desde mediados del siglo XIX y actualmente se encuentran cerca de 24 mil fincas cafeteras en las que viven alrededor de 80 mil personas (Martínez Moreno 2011). El resultado de esto es un paisaje rural altamente heterogéneo, dominado por agroecosistemas que incluyen cultivos de café, pastizales para ganadería, frutales, plantaciones forestales de eucalipto y pino; además de fragmentos de bosque húmedo pre-montano que hacen parte del sistema municipal de áreas protegidas (Villamil-Echeverri et al. 2015). Aún no hay consenso sobre cuál debe ser la cantidad de bosque o sobre cómo deber ser la composición y configuración del paisaje rural que permitan asegurar la permanencia de la biodiversidad y la provisión de servicios ecosistémicos a largo plazo (Smith *et al*. 2011, Melo *et al*. 2013, Arroyo-Rodríguez *et al*. 2016).

A escalas locales, la biodiversidad está organizada en redes complejas de interacciones entre especies; éstas son las que desarrollan los procesos ecológicos que finalmente proporcionan los servicios ecosistémicos de valor para las sociedades humanas (Bascompte and Jordano 2014, Zapata-Mesa et al. 2017). Por lo tanto, un reto importante para predecir las consecuencias de los cambios del paisaje sobre la biodiversidad es entender la complejidad de los sistemas naturales y los pasos para conservarlos en un escenario dinámico (Hagen et al. 2012). Entender las causas y consecuencias de la pérdida de interacciones de especies permitiría entender cómo cambia el funcionamiento de las comunidades ante las perturbaciones (Tylianakis *et al*. 2010, Valiente-Banuet *et al*. 2014). Una aproximación simplificada para estudiar interacciones entre muchas especies es a través de redes de interacción conocidas también como redes ecológicas (Bascompte y

Jordano 2014). Pocos trabajos han estudiado cómo se afecta la estructura de las redes de interacción ante transformaciones del paisaje (Sabatino *et al*. 2010, Hagen *et al*. 2012, Aizen *et al*. 2012, Spiesman y Inouye 2013, Nielsen y Totland 2014, Moreira *et al*. 2015). La mayoría de éstos han estudiado redes de planta-polinizador y hasta el momento no se conoce ningún estudio que evalúe el efecto de la transformación del paisaje sobre redes planta-dispersor y sus consecuentes efectos sobre el servicio de dispersión de semillas**.**

Este trabajo evalúa el efecto de la composición y de la configuración espacial del paisaje sobre la estructura de las redes de interacción murciélagos frugívoros-plantas quiropterócoras en tres escenarios de transformación del paisaje rural cafetero de Risaralda. Ese documento está organizado en dos capítulos que contribuyen a alcanzar el objetivo general y tres anexos con información relevante para llenar vacíos teóricos respecto a riqueza de mamíferos en el área de estudio, estructura de interacciones entre murciélagos frugívoros y plantas en ambientes montanos, y el papel de los murciélagos en la germinación de las plantas que consumen.

En el capítulo 1 titulado "**Bat-fruit networks structure resist habitat modification but species roles change in the most transformed habitats"** se evaluó cómo varía la estructura de las redes de interacción entre murciélagos frugívoros - plantas quiropterócoras (MF-PQ) en tres escenarios que representan la transformación del paisaje en la ecorregión del eje cafetero, y evaluamos si cambia el papel de las especies entre los escenarios. En el capítulo 2 titulado "**Importancia de los elementos del paisaje rural cafetero para las redes de interacciones entre murciélagos frugívoros y plantas quiropterocóricas"** se evaluó el efecto de las diferentes coberturas de uso de suelo y su configuración sobre el número de interacciones y la riqueza de especies que conforman las redes de interacción entre MF-PQ en el paisaje rural cafetero de Risaralda (Colombia).

En el anexo 1 titulado "**Responses of bats to landscape transformation in an Andean agricultural landscape**" se presentan los resultados generales del muestreo de murciélagos y se compara la abundancia y diversidad de murciélagos en tres escenarios de transformación del paisaje rural cafetero. En el anexo 2 titulado **"Diet and trophic structure in assemblages of montane frugivorous phyllostomid bats"** se presenta una revisión de la dieta de murciélagos frugívoros montanos y se evalúa su estructura trófica en elevaciones intermedias y altas combinando datos obtenidos de literatura con los datos obtenidos en el desarrollo de esta tesis. Aquí se usó el concepto de modularidad para probar si los murciélagos montanos tienen preferencias dietarias observadas en tierras bajas. Este artículo fue publicado en la revista Acta Oecologica. En el anexo 3 titulado **"Does seed ingestion by bats increase germination?: a new meta-analysis 15 years later"** se presenta un meta-análisis donde se evalúa el efecto de los murciélagos frugívoros sobre la germinación de las plantas consumidas. Usando datos de revisión de literatura y experimentos de germinación desarrollados durante el trabajo de campo. Este manuscrito fue sometido a la revista Mammal Review. Finalmente, el anexo 4 titulado **“Mamíferos del departamento de Risaralda, Colombia”** se presenta la lista actualizada de los mamíferos del departamento de Risaralda, la cual fue complementada con los resultados de muestreos de campo desarrollados durante esta tesis; este artículo fue publicado en la revista Biota Colombiana.

Capítulo 1

Bat-fruit networks structure resist habitat modification but species roles change in the most transformed scenario

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Abstract

Species do not function as isolated entities, rather they are organized in complex networks of interactions; these networks develop the ecological processes that provide ecosystem services for human societies. Understand the causes and consequences of changes in ecological networks due to landscape modification would allow us to understand consequences for ecological processes. However, there is still theoretical controversy and few empirical data regarding the effects of the loss of natural environments on network characteristics. We investigate how the bat–fruit network responds to three landscapes representing the modification from pre-montane forest to a heterogeneous agricultural landscape in the Colombian Andes (continuous forests, forest fragments and crops). We observed that Forest contained smaller bat–fruit networks than forest fragments and crops. Modified landscapes had similar ecological network structures to forest (nestedness and modularity), but crops contained less specialized network compared to forests and fragments and the species role in this scenario changes. The networks in the rural coffee landscape maintain their structure in the different transformation scenarios, indicating that the seed dispersal service is maintained even in the most transformed scenario, this could be related to the high heterogeneity present in this rural landscape. Although the number of species does not decrease due to transformation, species change their role in the most transformed scenario. This result sheds light on the way that biodiversity responds to anthropogenic transformations, showing higher stability than theoretically predicted.

Key words: Colombia´s Coffee Cultural Landscape, Complex networks, Chiropterocorous plants, Ecological networks, Phyllostomids.

Introduction

Anthropogenic landscape transformations have produced the loss and fragmentation of many natural habitats, with progressive and detrimental effects on species abundances and the continuous decrease of habitat quality and quantity (Fahrig et al. 2011). This is why forest loss due to anthropogenic landscape transformations is considered the single most pervasive threat to biodiversity worldwide (Fahrig 2013). However, more often than not, land use changes produce a mosaic of habitat patches with different quality and characteristics, where species may be able to use resources from patches of alternative and modified habitats in addition to resources usually found in patches of their original natural habitats (Brotons et al. 2005).

Species do not function as isolated entities, instead they are organized in complex networks of interactions between species (REF), and these networks substantiate the ecological processes that ultimately provide valuable ecosystem services for human societies (Bascompte and Jordano 2014). Therefore, if species' ocurrences and abundances change as a consequence of landscape modification, the interactions between species and the structure of the interaction networks is also expected to change (Woodward et al. 2010). By understanding what causes changes in ecological networks and the consequences these changes would have on species interactions, it would be possible to predict how ecological processes and ecosystem services can respond to further landscape transformations (Valiente-Banuet et al. 2014).

The organization of ecological networks structure can be explained by the variation in the community structure, such as species richness and relative abundance (Vásquez et al. 2009) The importance of those relationships is that network structure may be related with the ecological systems' emerging properties such as nestedness, modularity and complementary specialization; which are key factors to the stability of ecological communities, maintenance of ecological processes and biodiversity conservation (Tylianakis et al. 2010).

Nestedness measures how much of the interactions among specialists species are a subset of the interactions among generalists species (Jordano et al. 2003). A nested structure minimizes competition and increases the number of coexisting species (Bastolla et al. 2009), and also makes the community more robust to both random extinctions (Burgos et al. 2007) and habitat loss (Fortuna and Bascompte 2006). Modular patterns are characterized by the existence of densely connected, non-overlapping subsets of species (i.e. modules), which are composed of species having many interactions among themselves but very few interactions with species from other modules (Castaño et al. 2018). Modularity increase network stability, retaining the impacts of a perturbation within a single module and minimizing impacts on other modules (Fortuna et al. 2010). Complementary specialization (H2′) measure the extent by which specialist species interact with other specialist species (Blüthgen et al. 2006). H2′ informs if there is high or low niche differentiation in the network and can be used to compare networks to describe which has more interactions between generalist or specialist species (Soares et al. 2017).

Not all species are equally important for the dynamics and stability of an ecological network (Martín González et al. 2010). Some species are central to the stability of the network; the structure of the network breaks down faster when central species are selectively removed compared to random removals of other species (e.g. Memmott et al. 2004). Centrality metrics are a useful tool for assessing the relative importance of species

(Palacio et al. 2016). Different centrality indices measure different aspects related to the position of a species within its network; for example closeness centrality (CC) measures the proximity of a node to all other nodes in the network, i.e. nodes with high CC values can rapidly affect other nodes and vice versa. Alternatively, betweenness centrality (BC) describes the importance of a node as a connector between different parts of the network. Nodes with BC > 0 connect areas of the network that would otherwise be sparsely or not connected at all (Martín González et al. 2010). Furthermore, species may be ranked according to each of these metrics as a way to choose target species for conservation efforts (Palacio et al. 2016). Such target species may also serve as proxies to evaluate changes due to habitat loss, fragmentation, and climate change (Nielsen and Totland 2014).

Even though it is expected that land use changes should modify network characteristics, there is still theoretical controversy and few empirical studies that show how the loss of natural environments affect network nestedness, modularity, complementary specialization and centrality (Moreira et al. 2018). In this study, we investigated how bat–fruit networks responds to land use change in the Colombian Andes. We studied bat-fruit networks in three different scenarios; continuous forests, forest fragments and crops, representing the transformation from pre-montane forest to a heterogeneous agricultural matrix known as the “Colombia´s Coffee Cultural Landscape”. The “Colombia´s Coffee Cultural Landscape” is a particular combination of coffee-growing cultural customs and sustainable practices, which show how farmers have adapted to the difficult geographic conditions of the area (Martínez Moreno 2011).

By analyzing bat–fruit networks from three scenarios we empirically validate whether the composition and structures of mutualistic networks are conserved after land use change in an active agricultural landscape. We ask the following questions: 1) are network structural properties of bat–fruit networks conserved along three scenarios of modification? 2) Does the species’ role within the bat–fruit network change along the transformation scenarios? We hypothesize that the bat–fruit networks in all the studied scenarios, despite contrasting modification history, will display structural properties such as nestedness, modularity and specialization, previously found in other mutualistic networks (Tylianakis et al. 2010).

Methods

Study area

The study area is located on the western slope of the Colombian Cordillera Central of the Andes, in the municipalities of Santa Rosa de Cabal, Marsella and Dosquebradas (Departament of Risaralda ca 4°54′N, 17°39′W). The study area ranges in elevation from 1600 m to 2000 m. UNESCO recognizes this region (including the departments of Risaralda, Quindío, Caldas and Valle del Cauca) as a World Heritage site known as the “Colombia´s Coffee Cultural Landscape”. In this region, coffee has been produced for more than 100 years and is one of the most important crops in the area. Other important crops are pastures, bananas, vegetables, forest plantations and other fruits (Villamil-Echeverri et al. 2015). The annual mean temperature oscillates between 16 - 24 °C, the mean relative humidity is 79% and the mean precipitation is 3358.4 mm (Cenicafé 2011, Jaramillo et al. 2011).

We selected three scenarios representing land transformation: (1) continuous forests, (2) forest fragments, which are immersed in a matrix of crops, and (3) crops. Three sampling points were located in the center of a 1 km buffer of each scenario totaling nine sampling localities. Each sampling point was separated by at least 4 km from other sampling points.

Data sampling

We captured bats using mist nets (12 meters long) located at 1–5 m above the ground between August 2016 and August 2017. Each locality was surveyed four consecutive nights every three months. We used 5–7 mist nets (12×2.5m; 30mm mesh) per survey, opened mist nets at 18:00 p.m. and closed them at 06:00 a.m. In the event of ongoing heavy

rain, nets were closed. We avoided surveys during full moon nights in order to prevent the influence of lunar phobia (Saldaña-Vázquez y Munguía-Rosas 2013). In total, we accumulated 47012 net hours of sampling effort (forests: 12297; fragments: 19116; crops: 18599). Species were identified using the most updated taxonomic key for the region (Diaz et al. 2016). Captured bats were held in cloth bags for no longer than 2h to allow them to defecate so we could maximize sample yield. We cleaned the bags thoroughly between captures to prevent cross-contamination of fecal samples. Bats were released after the collection of data and fecal samples. Voucher specimens were collected to represent the species diversity of bats at each sampling locality and were deposited in “Colección de Vertebrados UNISARC (CUS-M 283-321)”. Each sample from each individual was collected separately and then dried and stored in plastic bags. Seeds were identified up to species level based on a reference collection of the study area (Rodríguez-Duque 2018). Seed samples were finally deposited in “Herbario UNISARC (CUS-P)”.

Bat-fruit network structure

To analyze bat-fruit network structure we created binary and weighted matrices, with bat species in rows and plant species in columns. Inside binary matrices, cell values of 1 (presence) represented an interaction between a specific bat species and a specific plant species. Ceros (absence) indicate no interaction. Weighted matrices were filled with the number of “consumption events”, defined as the sum of the presences of plant seeds in the fecal samples of each bat species (Castaño 2009). We created matrices for each of the nine study plots separately and for the three scenario types by pooling the data obtained from the three study plots within each scenario.

Species and interaction richness

For each of the nine study plots matrices, we calculated plant network species richness (P), bat network species richness (B), network size (S=B+P) and interaction richness (I= cell values of 1 inside binary matrices.

Complex network metrics

For each of the three scenario types matrices (by pooling the three study plots within each scenario) we calculated: (1) *Complementary Specialization* (H2′), which determines high or low niche differentiation in the network, and can be used to compare which networks have more interactions between generalist or specialist species (Blüthgen et al., 2006). H2' varies from 0 (all bat species interacting with the plant species) to 1 (each species interacts with a particular subset of partners). (2) *Weighted Nestedness* (WNODF) measures how strongly species interactions of little connected species are nested within those of highly connected species (Almeida-Neto and Ulrich 2011). WNODF ranges from 0 (non-nested) to 100 (fully nested). To test whether estimates of WNODF differed significantly from networks with randomly interacting species, we compared the observed nestedness with the nestedness of 1000 random networks based upon a Patefield null model (Dormann et al. 2009). (3) *Quantitative Modularity* (QuanBiMo) using the algorithm QuanBiMo (Dormann and Strauss 2014). This algorithm uses the hierarchical random graph approach, which organizes interacting species into a graph so that close species are more likely to interact. Then it swaps branches randomly at different levels and reassesses the modularity of the network selecting the more modular organization. QuanBiMo ranges from 0 (non-modular) to 100 (fully modular). To test the significance of modularity, we generated 1000 random networks fixing the probability that two species would interact based on the observed real networks. We used the Patefield null model to estimate the significance of the observed network metrics. We then calculated the modularity of the networks and evaluated whether observed modularity fell within the 95% confidence interval calculated from the randomized matrices. We finally standardized the modularity by calculating the Z-score Q (ZQ).

Species roles within the networks

In each of the scenario types matrices we assessed the functional role of bat and plant species using three centrality metrics: (1) *Degree centrality* (DC), which measures the number of interactions of a given species, reflecting its degree of generalization versus specialization; (2) *Betweenness centrality* (BC), which measures the extent by which a species acts as a connector on the lowest number of direct or indirect interactions among other pairs of species; and (3) *Closeness centrality* (CC), which is the mean of the lowest number of direct or indirect interactions from one species to every other species in the network, with higher numbers yielding lower CC scores (Palacio et al. 2016).

Comparison between landscapes

To compare if there were any effect of habitat modification on the species and interaction richness in the network, we made post hoc comparisons using a Duncan test. Variables were log transformed to meet assumptions of the tests. In order to compare if there were any effect of habitat modification on the complex network metrics (H2′, WNODF and Q) we compared pairs of networks using Monte Carlo procedures (Muylaert and Dodonov 2016).

To test whether a particular species’ functional role within the networks varied among the three scenarios, we used the Pearson correlation coefficient for each centrality metric (DC, BC, CC) between pairs of scenarios. Our goal was to assess whether the functional role of a species in one scenario could explain the same species functional role in another.

In these analyses, we pooled the three networks over three study plots rather than the nine separate networks as the number of species found in all nine networks was smaller.

Results

We captured 1146 bats from 32 species (Families Molossidae, Phyllostomidae, Thyropteridae and Vespertilionidae (ANEXO 1) Thirteen species (Phyllostomidae, subfamilies Stenodermatinae and Carolliinae) consumed 37 plant species belonging to 11 botanical families (Araceae, Campanulaceae, Cyclanthaceae, Ericaceae, Gesneriaceae, Hypericaceae, Moraceae, Myrtaceae, Piperaceae, Solanaceae y Urticaceae) (Supplementary material figure A1). The plants most consumed by bats were *Cecropia telealba* (Urticaceae, 22% of all fecal samples), *Solanum aphiodendrum* (Solanaceae, 17%), *Ficus americana* (Moraceae, 9%), *Piper aduncum* (Piperaceae, 6%), *Piper crassinervium* (Piperaceae, 6%), and *Ficus tonduzi* (Moraceae, 5%).

The continuous forest contained the lowest network size, interaction richness, and richness of plant, on average; the bat network species richness was not different between scenarios (Figures 1 and 2). The three networks (each scenario) were all nested, modular and specialized compared with respective null models (Supplementary material Table A1). Moreover, there were no differences between scenarios in nestedness or modularity, however the crop scenario contained less specialized network compared to continuous forests and fragments (Figure 3).

Species' roles within the network across scenarios

The most central bat in continuous forest and fragments was *Carollia brevicauda*, whereas in crops it was *Artibeus lituratus*. In the same way, the most central plant species in forest and fragments was *C. telealba*, whereas in crops it was *S. aphiodendrum* (Supplementary material Table A2). There was no pairwise correlation in DC, BC and CC for particular plants species between crop and the other two scenarios (forest fragment and continuous forest). For bats, however, the DC (number of interacting partners) showed low correlation ($R^{2=}$ 0.39, $P < 0.05$) between crop and forest fragment; there was no pairwise correlation in BC and CC between crop and the other two scenarios. A negative correlation would have indicated a systematic change, but the lack of correlation suggests a more random pattern. The pair-wise correlations between forest fragments and continuous forest were significant (R^2 = 48%-94%, $P < 0.05$) in all centrality metrics for both plant and bat species (Table1).

Discussion

By analyzing the bat–fruit networks along 3 scenarios of increasing habitat modification in the "Colombia´s Coffee Cultural Landscape" we observed that 1) The non-modified scenario (continuous forest) contained smaller bat–fruit networks than the modified forest fragments and crops. 2) Modified scenarios had similar ecological network structures comparted to continuous forest, with no significant differences observed for nestedness and modularity metrics. 3) Despite similar network properties among the three levels of habitat modification, the more modified scenario induce a homogenization of the bat–fruit networks; crops contained less specialized network and the species' roles in crops changed in relation to the roles in continuous forests and fragments.

Species and interaction richness

The non-modified scenario (continuous forest) contained, on average, smaller network size, lower interaction richness, and lower plant richness than forest fragment and crop. Although no significant differences in bat richness were detected among scenarios, continuous forest had a slightly lower bat richness than the modified scenarios. Although the effect of landscape transformation on seed dispersal networks had not been evaluated hitherto (Hagen et al. 2012), this result is consistent with previous studies on plant-pollinator network where forest contained smaller plant–pollinator network than the more disturbed scenarios (Hagen and Kraemer 2010, Nielsen and Totland 2014). These results may indicate that agricultural landscape are not completely hostile for bat and plant species; in fact, it can harbor complementary resources (*sensu* Brotons et al., 2005) favoring interactions that are typical of both modified and unmodified habitats.

Complex network metrics

Modified scenarios (e.g. forest fragments and crops) had similar bat-fruit network structures to continuous forest, with no significant differences observed for nestedness and modularity metrics. Few empirical studies have shown that structural properties of ecological networks withstand habitat degradation (Tylianakis et al. 2007, Nielsen and Totland 2014). However, theoretical models have suggested that networks can remain robust as long as habitat loss does not exceed 80%. Below this threshold, networks showed massive and rapid species extinction (Fortuna and Bascompte 2006). The fact that the bat-plant networks maintain their structure in our agricultural landscape, and the fact that species and interaction richness were high even in scenarios with a high degree of modification, suggests that forest loss in our agricultural system does not necessarily lead to a cascade of secondary extinctions that would lead to an ecosystem collapse. Rather, new interactions are reconfigured where bats feed on plants that grow in the crops (e.g. *Psidium guajava* or *Solanum aphyodendrum*). This result sheds light on the way that biodiversity responds to anthropogenic transformations, showing higher stability than theoretically predicted. This is consistent with previous studies that have shown that the heterogeneity of the "Colombia´s Coffee Cultural Landscape" is able to maintain high levels of biodiversity that provide valuable ecosystem services (Carranza-Quiceno et al. 2018). Thus, appropriately managed agroecosytems can retain ecological networks that are structurally and functionally similar to unmodified habitats (Tylianakis et al. 2007).

Nonetheless, we must take these results with caution because despite similar network properties among the three levels of habitat modification, the more modified a scenario is, its bat–fruit networks become more homogeneous; for example, the crops habitat contained less specialized network and the species role in this habitat changed compared to those in continuous forests and fragments.

Species role within the network in three scenarios

The role of bat and plant species in continuous forest was correlated with their role in forest fragments; on the contrary, the species role in crop did not correlate with the other scenarios. This means that both plants and bats fulfill similar roles in less transformed scenarios, which present forest cover, but change their role in crop that represent the highest transformation of the study area landscape, here open areas with isolated trees and shrub vegetation predominate.

With regards to bats, *C. brevicauda* has been considered the most important frugivore montane bat both in Central and South América in terms of richness of plants consumed (Castaño et al. 2018). In this study, *C. bravicauda* was the most central bat in forests and fragments, however in crops it was replaced by *Artibeus lituratus* as the most central bat. This switch in centrality suggest that functional traits could be influencing the species role; for example *A. lituratus* is a larger and heavier bat and probably faces lower predation risk compared to other frugivores (Cohen et al. 1993), traits that seem more suitable for occupying modified landscapes (Saldaña-Vázquez and Schondube 2015). The smaller but more maneuverable *C. bravicauda* would favor its performance to fly in spatially complex environments such as the interior of forests and fragments of forest (Marinaello and Bernard 2014).

With regards to plants, *C. telealba* is a tall tree, and was considered the plant most consumed by bats in a subandean landscape (Aguilar-Garavito et al. 2014). In our study, we also found that *C. telealba* was the most central plant in forest and fragment, however in crops it was replaced by a bush *Solanum aphyodendrum*,, the latter, having a smaller size and faster maduration would be more likely to inhabit in high changing enviroments as crops (Falster et al. 2018).

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Although we attribute that the species' role within interaction networks is related to their functional traits, another study that evaluated the change in the species role within interaction networks in transformation scenarios (Nielsen and Totland 2014) attributed the lack of correlation in the species role between transformed scenarios to the spatial and temporal variation of the interactions. Future studies should evaluate which variables affect changes in the role played by species in interaction networks.

Conclusion

As far as we are aware, this is the first study that evaluates the response of bat-fruit networks to habitat transformation. Our results suggest that the networks in the "Colombia´s Coffee Cultural Landscape" maintain their structure across scenarios in a landscape with different land uses, which indicates that the seed dispersal service is maintained even in the most transformed habitat. High network richness could be related to the high heterogeneity present in this agroecosystem. Future studies should evaluate how landscape heterogeneity affects interaction networks. Our results have important implications for the conservation of biodiversity and the maintenance of ecosystem services, particularly seed dispersal, because we have documented the most central and important plant and animal species in the network. Even though the number of species does not decrease due to habitat transformation, species change their role in the most transformed habitat.

Declarations

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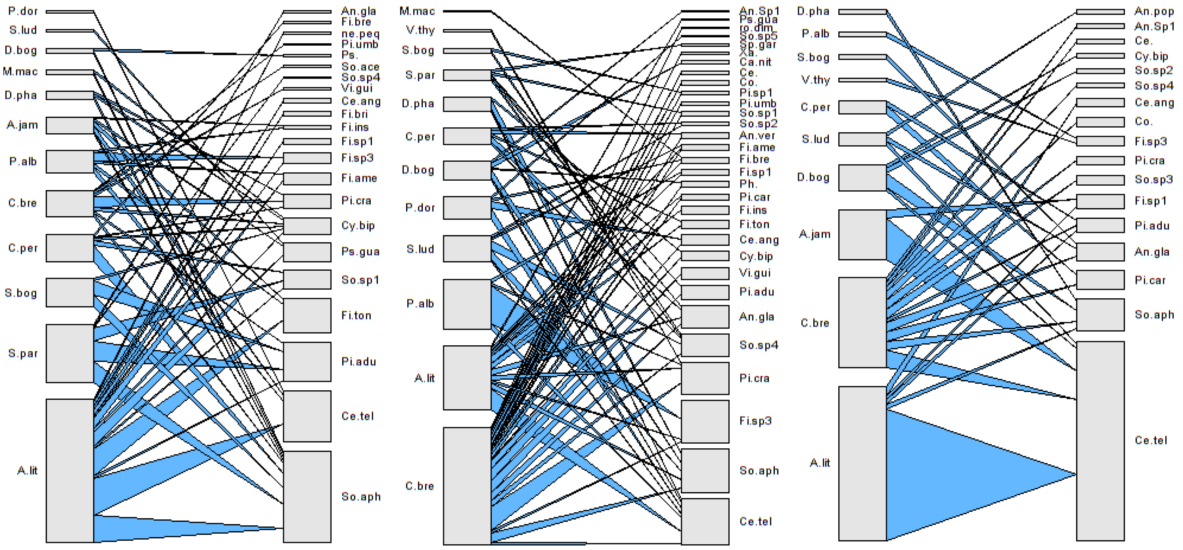

Figure 1. Quantitative bat–fruit networks along three scenarios of increasing habitat modification (right to left). For each web, left bars represent bat abundance and right bars represent fruit plant abundance, drawn at different scales. Linkage width indicates frequency of each trophic interaction.

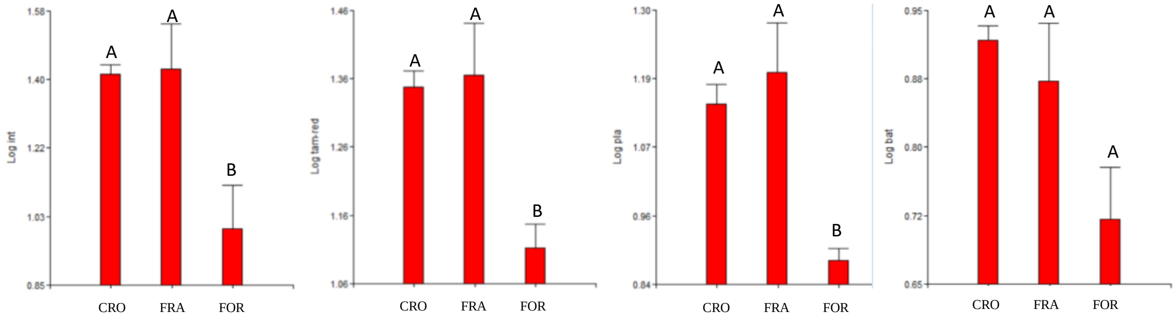

Figure 2. The effects of habitat modification on four qualitative network metrics (plant richness, bat richness, network size and interaction richness). Whiskers represents standard error, letters above individual means indicate significant differences (P≥0.05) among habitat types (FOR:continuous forests, FRA: forest fragments and CRO: crops) for that particular metric, letters in common indicates no significant difference.

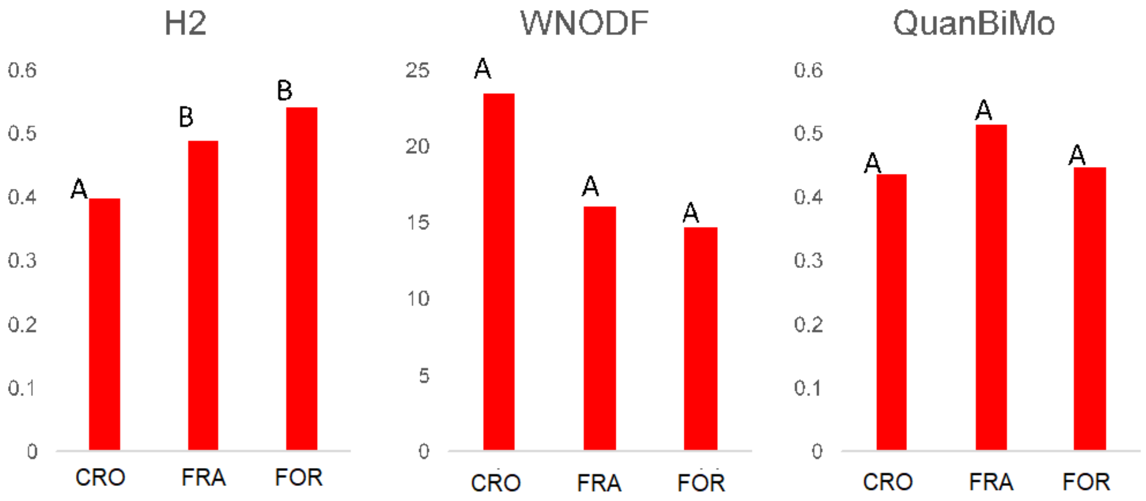

Figure 3. The effects of habitat modification on three quantitative complex network metrics (H2′, WNODF and QuanBiMo). **H2′** Complementary Specialization varies from 0 (all species interacting with the same partners) to 1 (each species interacts with a particular subset of partners). **WNODF** Weighted Nestedness ranges from 0 (non-nested) to 100 (fully nested). **QuanBiMo** Quantitative Modularity ranges from 0 (non-modular) to 100 (fully modular). Letters indicate significant differences (P≥0.05) among habitat types (FOR:continuous forests, FRA: forest fragments and CRO: crops) for that particular metric, letters in common indicates no significant difference. we compare pairs of networks using Monte Carlo procedures (Muylaert and Dodonov 2016).

Table 1. Pair-wise correlation tests (Pearson's correlation) between the three landscape types (continuous forests, forest fragments and crops) based on three centrality metrics (DC,BC,CC). **DC** Degree Centrality indicate the number of interacting species of the species occurring in all three landscapes sampled in Colombian cofee landscape. **BC** Betweenness Centrality measures the extent to which a species acts as a connector on the lowest number of direct or indirect interactions among other pairs of species. **CC** Closeness Centrality is the mean of the lowest number of direct or indirect interactions from one species to every other species in the network. (*) = *P* < 0.05, (**) = *P* <0.01.

	Dc		**Bc**		**Cc**	
Landscapes	**R^2 Bat**	**R^2 Pla**	**R^2 Bat**	**R^2 Pla**	**R^2 Bat**	**R^2 Pla**
For-Fra	0.94**	0.48**	0.94**	0.69**	0.57*	0.16
Fra-Cro	0.39*	0.1	0.36	0.09	0.12	0.07
Cro-Fra	0.17	0.18	0.16	0.23	0.22	0.05

Supplementary material figure A1. General interaction matrix describing plant species consumed by Phyllostomid bats in the study area.

Fam pla	Plantas	Carollia brevicauda	Carollia perspicillata	Artibeus jamaicensis	Artibeus lituratus	Dermanura bogotensis	Dermanura phaeotis	Mesophylla macconnelli	Platyrrhinus albericoi	Platyrrhinus dorsalis	Sturnira bogotensis	Sturnira ludovici	Sturnira parvidens	Vampyressa thyone
Araceae	*Anthurium* sp1	1	0	0	0	1	0	0	0	0	0	0	0	0
	Anthurium glaucospadix	6	3	0	3	0	0	0	0	0	1	1	2	0
	Anthurium stipitatum	0	0	0	0	0	0	0	0	0	0	1	0	0
	Anthurium versicolor	1	2	0	0	0	0	0	0	0	0	0	0	0
	Phylodendron sp.	2	0	0	0	1	0	0	0	0	0	0	0	0
	Xanthosoma sp.	1	0	0	0	0	0	0	0	0	0	0	0	0
Campanulaceae	*Centropogon* sp.	3	0	0	0	0	0	0	0	0	0	0	0	0
Cyclanthaceae	*Cyclanthus bipartitus*	6	1	0	2	1	2	1	0	0	1	0	0	0
	Spharadenia garciae	0	0	0	0	0	0	0	0	0	0	0	1	0
Ericaceae	*Cavendishia nitida*	0	0	0	0	2	0	0	0	0	0	0	0	0
	Psamisia penduliflora	0	0	0	0	1	0	0	0	0	0	0	0	0
Gesneriaceae	*Columnea*	4	0	0	0	0	0	0	0	0	0	0	0	0
Hypericaceae	*Vismia guianensis*	7	0	0	0	0	0	0	0	0	0	0	0	0
Moraceae	*Ficus americana*	1	0	0	6	0	0	0	1	0	0	1	0	0
	Ficus brevibracteata	0	1	0	1	0	0	1	0	1	0	0	0	0
	Ficus sp2	0	0	0	2	0	0	0	0	0	0	0	0	0
	Ficus insipida	0	0	1	4	0	0	0	1	0	0	0	0	0
	Ficus sp1	0	0	2	5	0	0	0	2	0	0	0	0	0
	Ficus sp3	1	0	0	2	0	0	0	24	0	0	0	0	1
	Ficus tonduzi	0	1	2	16	0	0	0	2	0	0	0	0	0
Myrtaceae	*Psidium guajava*	0	0	1	8	0	0	0	0	0	0	1	0	0
Piperaceae	*Piper aduncum*	8	1	0	2	0	0	0	0	0	7	0	11	0
	Piper carpunya	4	2	0	1	0	0	0	0	0	0	0	0	0
	Piper crassinervium	19	1	0	2	0	1	0	1	0	0	0	0	1
	Piper sp1	1	0	0	0	0	0	0	0	0	1	0	0	0
	Piper umbellatum	3	0	0	0	0	0	0	0	0	0	0	0	0
Solanaceae	*Solamun sp5*	0	0	0	0	0	0	0	0	1	0	0	0	0
	Solanum acerifolium	1	0	0	0	0	0	0	0	0	0	0	0	0
	Solanum aphyodendron	9	8	1	17	8	8	1	0	0	6	5	10	0
	Solanum sp1	1	2	0	1	0	0	0	0	0	0	0	7	0
	Solanum sp2	0	1	0	0	1	0	0	0	0	0	1	0	0
	Solanum sp3	2	0	0	0	0	0	0	0	0	0	0	0	0
	Solanum sp4	4	1	0	0	0	0	0	0	0	1	5	2	0
Urticaceae	*Cecropia angustifolia*	1	0	0	4	0	0	0	0	4	0	0	0	0
	Cecropia telealba	5	0	12	58	2	1	0	6	6	0	2	0	0
Indeterminada	negra pequeña	0	0	0	1	0	0	0	0	0	0	0	0	0
	rojiza diminuta	1	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary material Table A1. Qualitative measures of the three bat–fruit networks studied in Colombiaian Coffee Cultural Landscape . ‘Cro, Fra and For represents the pooled bat–fruit networks from three sample plots. H2 is the Complementary Specialization index. WNODFis the nestedness index, we compared the observed nestedness with the nestedness of 1000 random networks based upon a Patefield null model. QuanbiMo is the modularity index calculated, we compared the observed modularity with the modularity of 1000 random networks based upon a Patefield null model Three asterix (***) behind the value indicates that the value is significantly higher than would be expected by chance.

Habitat	H2	WNODF	Z-sc WNODF	QuanbiMo	Z-score Q
Agr	0.397***	23.43***	1059.955	0.434***	13.24965
Bos	0.54***	14.66***	285.3356	0.446***	9.51909
Fra	0.488***	16.00***	797.0995	0.517***	14.44294

Supplementary material table A2 Centrality metrics (Dc, Bc, Cc) per bat and plant species in the three landscape types sampled in Colombiaian Coffee Cultural Landscape . Degree centrality (DC) Betweenness centrality (BC) and Closeness centrality (CC).

Cro				Fra				For			
Bats											
	Dc	Cc	**Bc**		**Dc**	Cc	**Bc**		**Dc**	Cc	**Bc**
A.lit	13	0.5	0.5	C.bre	21	0.6	0.6	C.bre	11	0.5	0.5
C.bre	7	0.4	0.2	A.lit	12	0.5	0.3	A.lit	5	0.4	0.1
A.jam	5	0.4	0.1	C.per	5	0.3	0	D.bog	4	0.4	0.1
C.per	5	0.4	0.1	D.bog	5	0.4	0.1	S.lud	3	0.3	0.1
P.alb	5	0.3	0	S.lud	5	0.4	0	C.per	2	0.3	0
S.par	5	0.4	0.1	S.par	5	0.3	0.1	A.jam	2	0.3	0
D.pha	3	0.4	0	P.alb	4	0.4	0	D.pha	1	0.3	0
S.bog	3	0.4	0	P.dor	4	0.4	0.1	P.alb	1	0.1	0
M.mac	2	0.4	0	D.pha	3	0.3	0	S.bog	1	0.3	0
P.dor	1	0.3	0	S.bog	2	0.3	0	V.thy	1	0.1	0
S.lud	1	0.3	0	M.mac	1	0.3	0				
				V.thy	1	0.3	0				
Plants											
					Dc	Cc	**Bc**		**Dc**	Cc	**Bc**
So.aph	9	0.6	0.4	Ce.tel	7	0.5	0.2	Ce.tel	5	0.5	0.2
Cy.bip	6	0.4	0.1	So.aph	5	0.5	0.1	So.aph	4	0.4	0.2
Ce.tel	4	0.4	0.1	So.sp4	5	0.4	0.1	An.gla	3	0.4	0.1
Pi.adu	4	0.4	0.1	An.gla	4	0.4	0.1	Pi.adu	3	0.4	0.1
Fi.ton	3	0.4	0	Pi.cra	4	0.4	0.1	Fi.sp1	2	0.3	0
Pi.cra	3	0.3	0	Fi.ame	3	0.4	0	Fi.sp3	2	0.1	0
Ps.gua	3	0.4	0.1	Fi.bre	3	0.3	0.1	Pi.car	2	0.3	0
So.sp1	3	0.4	0	Fi.sp3	3	0.4	0	An.pop	1	0.2	0
Fi.ame	2	0.4	0	An.ver	2	0.4	0	An.Sp1	1	0.3	0
Fi.ins	2	0.3	0	Ce.ang	2	0.4	0	Ce.	1	0.3	0
Fi.sp3	2	0.4	0	Cy.bip	2	0.4	0	Ce.ang	1	0.3	0
Ce.ang	1	0.4	0	Fi.sp1	2	0.3	0	Co.	1	0.3	0
Fi.bre	1	0.3	0	Fi.ton	2	0.3	0	Cy.bip	1	0.3	0
Fi.bri	1	0.4	0	Ph.	2	0.4	0	Pi.cra	1	0.3	0
Fi.sp1	1	0.4	0	Pi.adu	2	0.4	0	So.sp2	1	0.3	0
ne.peq	1	0.4	0	Pi.car	2	0.4	0	So.sp3	1	0.3	0
Pi.umb	1	0.3	0	Pi.sp1	2	0.4	0	So.sp4	1	0.3	0
Ps.	1	0.3	0	So.sp1	2	0.4	0				
So.ace	1	0.3	0	So.sp2	2	0.3	0				
So.sp4	1	0.3	0	An.Sp1	1	0.3	0				
Vi.gui	1	0.3	0	Ca.nit	1	0.3	0				
An.gla	1	0.3	0	Ce.	1	0.4	0				
				Co.	1	0.4	0				
				Fi.ins	1	0.3	0				
				Pi.umb	1	0.4	0				
				Ps.gua	1	0.3	0				
				ro.dim	1	0.4	0				
				So.sp5	1	0.3	0				
				Sp.gar	1	0.3	0				
				Vi.gui	1	0.4	0				
				Xa.	1	0.4	0				

Capítulo 2

Importancia de los elementos del paisaje rural cafetero para las redes de interacciones entre murciélagos frugívoros y plantas quiropterocóricas

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Resumen

Se ha reconocido el aporte de los paisajes rurales de la zona cafetera colombiana a la conservación de la biodiversidad, sin embargo, aún no hay consenso sobre cuál debe ser la composición y configuración del paisaje rural que asegure la persistencia de la biodiversidad y la provisión de servicios ecosistémicos a largo plazo. El objetivo de este trabajo fue evaluar el efecto de las diferentes coberturas de uso de suelo y su configuración sobre el número de interacciones y la riqueza de especies que conforman las redes de interacción entre murciélagos frugívoros y plantas quiropterocoras (MF-PQ) en el paisaje rural cafetero de Risaralda (Colombia). Se establecieron nueve parcelas de 1km de radio en tres tipos de paisajes (bosques continuos, fragmentos de bosque en una matriz de agroecosistemas y agroecosistemas sin bosque). Se clasificaron las diferentes coberturas presentes en cada una de las parcelas, se describió la composición (Porcentaje de cobertura) y la configuración del paisaje (Número de parches de bosque, Tamaño promedio de los parches de bosque (Densidad de bordes de bosque los índices de Simpson y Shannon-Wiener). Entre agosto de 2016 y agosto de 2017 se capturaron murciélagos frugívoros utilizando redes de niebla ubicadas en la región central de cada parcela, obtuvimos sus muestras fecales para conocer las plantas consumidas por los murciélagos. Describimos la estructura de 34 redes de interacción MF-PQ que representaron cada una de cuatro visitas en cada uno de los nueve sitios de estudio. Se realizaron modelos lineales generalizados, para determinar qué variables de composición y configuración del paisaje influyeron sobre el tamaño de la red, la riqueza de plantas, la riqueza de murciélagos y la riqueza de interacciones en la red. El porcentaje de cobertura de bosque, de plantación forestal, de matorrales, de pastizales y de cuerpos de agua; y el número de parches de bosque

incrementaron el número de interacciones en las redes MF-PQ; por otra parte, la densidad de bordes tuvo un efecto negativo sobre el número de interacciones. Identificar estas relaciones tiene implicaciones en manejo y conservación de la biodiversidad La intensificación del uso del suelo ha sido considerado como el factor más amenazante para la biodiversidad, no obstante, los paisajes agrícolas pueden cumplir un papel fundamental en el mantenimiento de la biodiversidad y de servicios ecosistémicos, si se mantiene diferentes tipos de vegetación nativa como bosques y matorrales, así como la vegetación ribereña.

Introducción

La transformación del paisaje y el cambio en el uso de suelo conllevan a la pérdida de bosques, lo cual es considerado como una de las principales amenazas a la biodiversidad a escala global (Sala et al. 2000, Fahrig 2013). Una estrategia de conservación de la biodiversidad y de aprovechamiento de los recursos naturales es el mantenimiento de la heterogeneidad del uso de suelo en el paisaje (Fahrig et al. 2011, Hass et al. 2018). Especialmente en paisajes rurales, donde, al mantener la heterogeneidad se albergan comunidades ecológicas muy diversas y ofrecen oportunidades para la conservación (Harvey et al. 2008, Melo et al. 2013). En el contexto actual de deterioro acelerado de los ecosistemas a escala global, regional y local; se plantea la necesidad de integrar los paisajes rurales en las estrategias de conservación (Melo et al. 2013). Estas iniciativas son aún más importantes si se considera que las áreas protegidas son insuficientes para la conservación (Chazdon et al. 2009).

Se ha planteado que la heterogeneidad de los paisajes rurales se relaciona positivamente con la riqueza de especies (Benton et al. 2003, Heim et al. 2015) en la medida que permanezcan parches de vegetación natural y que el manejo de los agroecosistemas favorezca la conectividad entre los parches (Harvey et al. 2008). Se ha reconocido que en paisajes agrícolas los árboles aislados (Manning et al. 2006), matorrlaes (Marshall and Moonen 2002) y ríos (Williams et al. 2004), proporcionan refugio y alimento para animales (Forman and Baudry 1984, Saab 1999). Por lo tanto, son elementos clave para mantener la funcionalidad de la biodiversidad local y la provisión de servicios ecosistémicos. Estos elementos también sirven como corredores conectando hábitats adecuados para especies silvestres (Getzin et al. 2012) e incrementan la heterogeneidad de hábitat (Kalda et al. 2015).

La estructura espacial de los paisajes afecta la riqueza de especies (Benton et al. 2003, Fahrig et al. 2011, Arroyo-Rodríguez et al. 2016). Las variables de configuración del paisaje, como el número de parches de bosque y la densidad de bordes de bosque pueden tener efectos negativos, positivos o neutros sobre la biodiversidad (Ewers and Didham 2006). Por ejemplo la fragmentación y la densidad de bordes beneficia a aquellas especies que persisten en parches pequeños, desarrollan movimientos largos de dispersión y hacen uso de recursos presentes en la matriz y en los bordes (Ethier and Fahrig 2011). La proliferación de plantas pioneras altamente productivas en los bordes aumenta la disponibilidad de recursos para murciélagos frugívoros en paisajes con mayor grado de fragmentación y mayor densidad de bordes (Arroyo-Rodríguez et al. 2016).

Paisaje rural cafetero

Los paisajes andinos en la Cordillera Central de Colombia se han transformado en respuesta a la compleja dinámica social y económica desde hace más de 200 años (Guhl 2004). La ocupación de nuevos territorios, el avance del cultivo del café y el crecimiento de las ciudades, han generado un mosaico de paisaje muy heterogéneo en el que se entremezclan parches de vegetación natural con agroecosistemas y zonas urbanizadas (Burel and Baudry 2005). Además de remanentes de vegetación natural, se integran árboles aislados en los agroecosistemas y se mantienen corredores de vegetación ribereña que favorecen la conectividad en el paisaje (Marín et al. 2008).

Se ha reconocido el aporte de los paisajes rurales de la zona cafetera colombiana a la conservación de la biodiversidad (Castaño et al. 2004a, Sánchez Clavijo et al. 2009, Henao et al. 2014, Cardona et al. 2016). Sin embargo, aún no hay consenso sobre cuál debe ser la composición y configuración del paisaje rural que asegure la persistencia de la biodiversidad y la provisión de servicios ecosistémicos a largo plazo (Smith et al. 2011, Arroyo-Rodríguez et al. 2016).

Inrteracciones entre los murciélagos frugívoros y las plantas quiropterocoras (MF-PQ)

Ninguna especie está aislada, más bien están ligadas a otras formando redes complejas de interacciones (Bascompte and Jordano 2014). Éstas interacciones desarrollan los procesos ecológicos que finalmente proporcionan beneficios naturales, no materiales, como la dispersión de semillas (Hagen et al. 2012, Díaz et al. 2018). Proceso importante para la regeneración de los bosques (Wang and Smith 2002, Muscarella and Fleming 2007). Por esta razón, conocer las interacciones entre los murciélagos frugívoros y las plantas quiropterocoras (MF-PQ) es fundamental para entender el funcionamiento de los ecosistemas y particularmente el servicio de dispersión de semillas.

Algunos estudios han demostrado que los murciélagos se ven favorecidos por la heterogeneidad del uso de suelo en paisajes agrícolas (Heim et al. 2015, Arroyo-Rodríguez et al. 2016). Sin embargo, aún se desconoce la importancia de los elementos del paisaje rural en la estructura de las redes de interacciones entre murciélagos frugívoros y las plantas; en interacciones mutualistas, tales como las relación entre frugívoros y plantas, la pérdida de interacciones puede amenazar la dispersión de las plantas o reducir el fitness de los frugívoros, al disminuir la disponibilidad de recursos (Aizen et al. 2012).

El objetivo de este trabajo fue evaluar el efecto de las diferentes coberturas de uso de suelo y su configuración sobre el número de interacciones y la riqueza de especies que conforman las redes de interacción entre MF-PQ en el paisaje rural cafetero de Risaralda (Colombia). Las predicciones fueron: 1) los paisajes con mayor heterogeneidad en su composición de paisaje, es decir, con mayor porcentaje de matorral, jardín-urbano, policultivos, plantaciones forestales, bosque maduro y cuerpo de agua presentarán valores altos de tamaño de red y número de interacciones, 2) los paisajes que tengan mayor porcentaje de pastizales y monocultivos tendrán valores bajos de tamaño de red y número de interacciones, y 3) los paisajes más heterogéneos en su configuración presentarán redes más grandes y con mayor número interacciones.

Materiales y métodos

Este trabajo se realizó en los municipios de Santa Rosa de Cabal, Dosquebradas y Marsella del departamento de Risaralda ubicados entre los 1642 y 2000 m de elevación, en la vertiente occidental de la Cordillera Central de Colombia. El clima de esta región está caracterizado por un régimen de lluvias bimodal (marzo-junio y septiembre-diciembre), condicionado por los fenómenos del Niño (aumento de temperaturas) y la Niña (enfriamiento) (Jaramillo et al. 2011). La precipitación promedio anual es de 2300 a 3000 mm y la temperatura promedio es cercana a los 20°C (Cenicafé 2011, Jaramillo et al. 2011).

Se establecieron nueve parcelas de 1km de radio en tres tipos de paisajes: tres parcelas en paisaje boscoso (cobertura de bosque superior al 70%), tres parcelas en paisaje fragmentado (cobertura de bosque entre 7% y 30% inmersos en una matriz de agrícola) y tres parcelas en paisajes agrícola sin cobertura de bosque (dominados por policultivos y pastizales) El centro geográfico de cada parcela estaba separado por lo menos cuatro kilometros entre si para asegurar la independencia de las réplicas.

En cada una de las nueve parcelas se describió la composición y la configuración del paisaje. La composición se evaluó a través del *Porcentaje de coberturas* que se consideró como el porcentaje de espacio que ocupa cada una de las diferentes coberturas dentro de la parcela. Para definir las coberturas de cada parcela, se analizaron imágenes satelitales recientes extraídas del software Google Earth Pro® versión 7.1.7.2602. Se les asignó el Sistema de Referencia Espacial (SRC) WGS84 (Baiocchi et al. 2010), a partir del programa QGIS® versión Las Palmas de G. C. 2.18 por medio de la extensión "*Georreferenciador GDAL*". Se digitalizó cada uno de los usos del suelo que componen el paisaje, éstos fueron revisados y confrontados en campo de acuerdo a las ocho categorías definidas a continuación: 1. *Monocultivo*: Cultivos perennes, transitorios y/o anuales, (maíz, tomate, pasifloras caña panelera). 2. *Policultivo*: Definidos por mosaicos de cultivos de diferente tipo (principalmente café en asociación con otros cultivos). 3. *Jardín-Urbano*: zonas ocupadas por edificaciones que incluyen casas, vías pavimentadas y jardines. 4. *Pastizal*: Zonas de ganadería usadas para el pastoreo tanto intensivo como extensivo (incluyó pastos arbolados, pastos limpios, pastos enmalezados). 5. *Plantación forestal*: Áreas para la producción de madera (eucaliptos o pinos). 6. *Bosque*: Vegetación nativa con predominancia de cobertura arbórea, en estados de sucesión intermedia a madura excluyendo matorrales. 7. *Matorral*: Vegetación nativa definidos por su estado de sucesión temprana, generalmente en cercanía a afluentes hídricos en movimiento, predominaron gramíneas de gran porte como la guadua (*Guadua angustifolia*). 8. *Cuerpos de agua*: Incluyen principalmente ríos y ocasionalmente lagunas.

La configuración del paisaje fue descrita a partir de métricas del paisaje propuestas por Farina (2008) dónde se determinó: 1) el *Número de parches de bosque,* 2) el *Tamaño promedio de los parches de bosque (ha),* 3) la *Densidad de bordes de bosque* (m/km2), y 4) los índices de estructura de *Simpson* ($\lambda=\sum p_i^2$) y *Shannon-Wiener* ($H' = -$□ p_i □ $ln\ p_i$), donde se consideró p_i como la proporción de cada tipo de vegetación dentro de la parcela (para descripción detallada de cada parcela ver Material suplementario 1).

Muestreo de murciélagos frugívoros

En la región central de cada paisaje se ubicaron entre 5 y 7 redes de niebla (12 m x 2.5 m; 30 mm ojo de malla) que permanecieron abiertas toda la noche (18:00-06:00 horas), durante cuatro noches consecutivas en cada sitio. Cada sitio fue visitado cuatro veces en un período comprendido entre agosto de 2017 y agosto de 2017, para un total de 108 noches de muestreo, el orden de visita dentro del mismo bloque se eligió aleatoriamente, y se evitaron muestreos durante luna llena para disminuir sesgos debido a la fobia lunar de los murciélagos (Saldaña-Vázquez and Munguía-Rosas 2013). Se revisaron las redes a intervalos de 20 minutos y los animales capturados fueron depositados individualmente en bolsas de tela limpias por espacio de dos horas, para obtener sus muestras fecales. Ocasionalmente se obtuvieron también frutos transportados por los animales al momento de su captura. Antes de ser liberado, cada ejemplar fue identificado usando claves taxonómicas para murciélagos (Diaz et al. 2016). Cuando fue imposible identificar algún ejemplar en el campo, o representó un nuevo registro para la zona, fue colectado de acuerdo a las normas de la Sociedad Americana de Mastozoología (Sikes et al. 2011). Los individuos colectados fueron depositados en la colección de Corporación Universitaria de Santa Rosa de Cabal (CUS-M 283-321). Los permisos marco de colección institucional que respaldarán estas capturas y colectas fueron UNISARC (resolución CARDER 2004 de 5 de septiembre de 2016) y PUJ (resolución ANLA 0546 de 29 de mayo de 2014).

Muestreo de plantas quiropterocóricas

Para conocer las plantas consumidas por los murciélagos, fueron colectadas y etiquetadas las muestras fecales y los frutos obtenidos de los murciélagos frugívoros capturados en el campo. Estas fueron secadas y posteriormente identificadas por comparación con una colección de referencia de frutos y semillas, realizada para este estudio (Rodríguez-Duque 2018). Para realizar la colección de referencia se hicieron recorridos diurnos en busca de plantas que se encuentren en producción de frutos carnosos maduros. Las muestras botánicas debidamente herborizadas fueron identificadas a nivel de especie y sus frutos y semillas fueron comparados con los obtenidos a partir de los animales capturados en redes. Las muestras fueron depositadas en los herbarios de las Universidades de Santa Rosa de cabal.

Análisis de la estructura de interacciones

Describimos la estructura de 34 redes de interacción MF-PQ que representaron cada una de las cuatro visitas en cada uno de los nueve sitios de estudio (excepto dos visitas en las que no se obtuvieron registros de interacciones). Construímos matrices de interacción donde las filas representan las especies de plantas consumidas por murciélagos (*P*) y las columnas representan las especies de murciélagos frugívoros (*F*). Donde, $r_{ij}=1$ si el fruto de la planta *i* es consumida por el frugívoro *j*, y $r_{ij}=0$, si no hay interacción en la matriz cualitativa (Bascompte et al. 2003).

Se realizaron modelos lineales generalizados (MLG) en el programa R 3.2.4 (R Core Team 2016), para determinar qué variables de composición y configuración del paisaje influyeron sobre el tamaño de la red, la riqueza de plantas, la riqueza de murciélagos y la riqueza de interacciones en la red. Se realizó un análisis post hoc $\chi 2$ para los coeficientes estandarizados y se usó la distribución Poisson de error, debido a que las variables de respuesta eran conteos. La estrategia de análisis fue la de optimización de modelos, donde se inicia con un modelo con todas las variables explicativas y posteriormente se van eliminando aquellas que no sean significativas, finalmente se seleccionan aquellos modelos con la menor devianza residual y los menores valores del Criterio de Información Akaike (AIC; Crawley 2007).

Resultados

En total registramos 374 individuos de 13 especies de murciélagos (familia Phyllostomidae) pertenecientes a las subfamilias Carolliinae y Stenodermatinae que consumieron frutos de 37 especies vegetales (420 muestras) pertenecientes a las familias Araceae, Campanulaceae, Cyclanthaceae, Ericaceae, Gesneriaceae, Hypericaceae, Moraceae, Myrtaceae, Piperaceae, Solanaceae y Urticaceae. (Material suplementario 2).

Se generaron 26 modelos para las variables espaciales que influyen el tamaño de la red, la riqueza de plantas, la riqueza de murciélagos y la riqueza de interacciones en las redes; de los cuales se consideraron 12 que presentaron un $\Delta AIC \leq 2$ (Material suplementario 3).

Importancia de las variables del paisaje sobre el número de interacciones

Como se esperaba, las coberturas con presencia de árboles fueron importantes para incrementar el número de interacciones. En particular el porcentaje de cobertura de bosque ($p < 0.01$), de plantación forestal ($p < 0.01$), de matorrales ($p < 0.001$) y de cuerpos de agua ($p < 0.001$); y el número de parches de bosque ($p < 0.05$), favorecieron el número de interacciones en las redes MF-PQ. Contrario a nuestra segunda predicción, la cobertura de pastizales incrementó el número de interacciones ($p < 0.01$); por otra parte, la densidad de bordes tuvo un efecto negativo sobre el número de interacciones (Tabla1).

Importancia de las variables del paisaje sobre riqueza de especies en la red

El tamaño de la red y la riqueza de especies de plantas se vieron afectadas por las mismas coberturas, incrementando proporcionalmente con el aumento de matorrales ($p < 0.001$ y $p < 0.01$ respectivamente), de cuerpos de agua ($p < 0.001$ y $p < 0.001$) y de pastizales ($p < 0.001$ y $p < 0.05$); y con el número de parches de bosque ($p<0.05$ y $p < 0.05$). Por el contrario, la densidad de bordes de bosque ($p < 0.001$ y $p < 0.05$) y el tamaño promedio de los parches ($p < 0.001$ y $p < 0.001$) afectaron negativamente a estas variables. En el caso del componente animal de las redes, la riqueza de murciélagos solamente se relacionó positivamente con el porcentaje de cuerpos de agua y pastizales ($p < 0.001$ y $p<0.05$), y negativamente con la densidad de bordes de bosque ($p < 0.05$)(Tabla 1).

Tabla 1. Resultados estadísticos de los Modelos lineares generalizados (MLG) con distribución Poisson. Se presentan las variables explicativas del paisaje y su respectivo efecto sobre los parámetros de la red de interacciones entre murciélagos frugívoros y plantas quiropterocoras en el Paisaje rural cafetero de Risaralda. (E.S.)= , (n.s.) = no significativo, (*) = $P < 0.05$, (**)= $P <0.01$, (***)= $P<0.001$, (□)= . En negrilla las variables que resultaron significativas $P(□^{2})$.

Parámetro de la red	Variable explicativa	Pendiente	E.S.	z value	Pr(>|z|)	χ2	P(χ2)
Número de interacciones	**Matorral**	**0.25**	**0.07**	**3.39**	***	**143.73**	***
	Jardín-urbano	-0.07	0.02	-3.30	***	143.72	n.s.
	Bosque	**0.03**	**0.01**	**2.13**	*	**135.72**	**
	Policultivo	-0.02	0.01	-2.77	**	135.71	n.s.
	Plantación forestal	**0.04**	**0.01**	**2.66**	**	**128.55**	**
	Cuerpo de agua	**1.19**	**0.26**	**4.61**	***	**107.42**	***
	Monocultivo	-0.05	0.02	-2.52	*	164.88	n.s.
	Pastizal	**0.02**	**0.01**	**4.31**	***	**145.87**	***
	N° Parches de Bosque	**0.14**	**0.04**	**3.78**	***	**4.36**	*
	Tamaño parches bosque	-0.01	0.00	-1.92	.	33.45	***
	Densidad de bordes	**-0.01**	**0.00**	**-2.80**	**	**15.95**	***
	Simpson	0.21	0.63	0.34	n.s.	0.15	n.s.
	Shannon-Wiener	0.40	0.60	0.66	n.s.	0.43	n.s.
	Estación	0.21	0.13	1.61	n.s.	2.60	n.s.
Tamaño de red	**Matorral**	**0.17**	**0.07**	**2.57**	*	**124.37**	***
	Jardín-urbano	-0.08	0.02	-3.61	***	124.00	n.s.
	Bosque	0.02	0.01	1.43	n.s.	115.64	**
	Policultivo	-0.01	0.01	-2.45	*	115.64	n.s.
	Plantación forestal	0.02	0.01	1.91	.	105.98	**
	Cuerpo de agua	**0.93**	**0.24**	**3.94**	***	**88.78**	***
	Monocultivo	-0.04	0.02	-2.42	*	138.26	n.s.

	Pastizal	**0.02**	**0.00**	**3.96**	*******	**122.29**	*******
	N° Parches de Bosque	**0.14**	**0.03**	**4.29**	*******	**5.10**	*****
	Tamaño parches bosque	**-0.01**	**0.00**	**-2.61**	******	**25.76**	*******
	Densidad de bordes	**-0.01**	**0.00**	**-3.19**	******	**12.49**	*******
	Simpson	0.81	0.59	1.36	n.s.	1.91	n.s.
	Shannon-Wiener	-0.02	0.57	-0.04	n.s.	0.00	n.s.
	Estación	0.16	0.12	1.35	n.s.	1.83	n.s.
Riqueza de murciélagos	**Cuerpo de agua**	**0.41**	**0.12**	**3.43**	*******	**43.46**	*******
	Monocultivo	-0.04	0.02	-1.68	.	55.15	n.s.
	Pastizal	**0.02**	**0.01**	**3.14**	******	**49.25**	*****
	N° Parches de Bosque	0.13	0.05	2.52	*	0.54	n.s.
	Tamaño parches bosque	-0.01	0.01	-1.50	n.s.	8.09	**
	Densidad de bordes	**-0.01**	**0.01**	**-2.26**	*****	**5.97**	*****
	Simpson	0.82	0.90	0.91	n.s.	0.85	n.s.
	Shannon-Wiener	-0.15	0.87	-0.18	n.s.	0.03	n.s.
	Estación	0.02	0.18	0.09	n.s.	0.01	n.s.
Riqueza de plantas	**Matorral**	**0.22**	**0.09**	**2.41**	*****	**83.26**	******
	Jardín-urbano	-0.09	0.03	-3.19	**	83.05	n.s.
	Bosque	0.02	0.01	1.33	n.s.	77.00	*
	Policultivo	-0.02	0.01	-2.65	**	76.59	n.s.
	Plantación forestal	0.03	0.02	1.86	.	70.76	*
	Cuerpo de agua	**1.08**	**0.31**	**3.48**	*******	**55.76**	*******

	Monocultivo	-0.04	0.02	-1.68	.	90.40	n.s.
	Pastizal	**0.02**	**0.01**	**3.14**	******	**80.32**	******
	N° Parches de Bosque	**0.15**	**0.04**	**3.46**	*******	**5.48**	*****
	Tamaño parches bosque	**-0.01**	**0.01**	**-2.15**	*****	**17.93**	*******
	Densidad de bordes	**-0.01**	**0.00**	**-2.24**	*****	**6.41**	*****
	Simpson	0.79	0.79	1.00	n.s.	1.04	n.s.
	Shannon-Wiener	0.07	0.76	0.10	n.s.	0.01	n.s.
	Estación	0.27	0.16	1.70	.	2.92	n.s.

Discusión

Este es el primer estudio que evalúa el efecto de la estructura y composición del paisaje sobre las redes de interacción MF-PQ. Nuestro análisis revela que la estructura y composición del paisaje tiene incidencia sobre la estructura de interacciones entre murciélagos frugívoros y plantas quiropterocoras. Los paisajes con mayor cobertura de matorrales, cuerpos de agua, mayor número de parches de bosque afectaron positivamente el número de interacciones y la riqueza de especies tanto de plantas como de murciélagos. Identificar esta relación tiene importantes implicaciones en manejo y conservación de la biodiversidad ya que permite explicar los mecanismos potenciales que afectan las redes de interaccione entre murciélagos y plantas y los servicios ecosistémicos que prestan.

Influencia de la composición del paisaje sobre las redes de interacción MF-PQ

Los matorrales, fueron un elemento del paisaje rural muy importante para incrementar el número de interacciones, tamaño de red y la riqueza de plantas. Los matorrales al presentarse en los estados iniciales de la sucesión de los bosques luego del abandono de las prácticas productivas, coexisten con los cultivos (Forman and Baudry 1984) y se convierten en refugio de biodiversidad de plantas y animales (Marshall and Moonen 2002). Particularmente en los matorrales estudiados abundaron plantas importantes como fuente de alimento para los murciélagos frugívoros (e.g Familias Solanaceae y Piperaceae), lo que favoreció las interacciones. Varios estudios han mostrado el alto consumo de las especies de estas familias de plantas por parte de los murciélagos frugívoros (Castaño 2009, Andrade et al. 2013, Castaño et al. 2018). Esto además resalta la importancia de mantener parches de vegetación natural en diferentes estados sucesionales en el paisaje rural (Estrada-Carmona et al. 2014).

Los cuerpos de agua fueron un elemento del paisaje rural que explicó el incremento del número de interacciones, el tamaño de red y la riqueza de plantas, así como la cantidad de especies de murciélagos. En la región los cuerpos de agua están representados principalmente por una alta densidad de ríos (entre 1.92 y 4.59 km/km^2) protegidos por vegetación ribereña (Ríos 1999) estas características estructurales (canales con vegetación ribereña) proporcionan rutas de vuelo lineales sin obstrucciones que facilitan el desplazamiento y el forrajeo de los murciélagos (Hagen and Sabo 2011, Zarazúa-Carbajal et al. 2017) lo cual puede favorecer la conectividad de las diferentes coberturas (Marín et al. 2008) pues al usar los ríos y quebradas como corredores, los murciélagos acceden fácilmente a otras áreas de forrajeo para consumir recursos (de la Peña-Cuéllar et al. 2015), incrementando así la riqueza de plantas con las que interactúan.

Contrario a lo esperado, cuando incrementaba la presencia de pastizales aumentó el número interacciones, la riqueza de plantas y animales, y el tamaño de red. Aunque se han planteado los efectos negativos de los pastizales sobre la biodiversidad, árboles en medio de pastizales pueden servir como alimento o refugio para los frugívoros, y al arribo de semillas y subsecuente regeneración (Galindo-González and Sosa 2003, Ragusa-Netto et al. 2015). En la región de estudio los pastizales presentaron áreas pequeñas, la ganadería no era intensiva y allí se presentan árboles (e.g. *Cecropia* spp, *Solanum* spp.*Psidium guajava*) y cercas vivas (*Piper* spp. *Solanum* spp.) que pueden favorecer la heterogeneidad ambiental y las redes de interacción MF-PQ.

Importancia de la configuración del paisaje sobre las redes de interacción MF-PQ

El número de parches de bosque mostró un efecto positivo sobre el número de interacciones y la riqueza de especies de plantas y el tamaño de red, sin embargo, no presentó un efecto sobre los murciélagos. El incremento en el número de parches de bosque en el paisaje puede incrementar la disponibilidad de recursos (Dunning et al. 1992, Arroyo-Rodríguez et al. 2016), en particular los frutos de los cuales se alimentan los murciélagos. Tales recursos estarían más disponibles en paisajes con mayor número de parches, donde habría menores distancias de aislamiento entre parches (Fahrig 2003). Esta situación permitiría a los murciélagos acceder fácilmente a una mayor variedad de ítems alimenticios, favoreciendo el número de interacciones y la riqueza de especies de plantas en la red. Aunque se a demostrado efectos positivos de la fragmentación sobre las especies de murciélagos (Ethier and Fahrig 2011, Arroyo-Rodríguez et al. 2016), en este trabajo encontramos que los efectos fueron principalmente sobre las plantas que ellos consumen y sobre las interacciones, y no sobre las especies de murciélagos, de hecho en la región no hubo diferencias en la riqueza ni abundancia de murciélagos en los tres escenarios del paisaje rural (Vélez-Orozco 2017).

Este hallazgo soporta la idea que incluso pequeños remanentes de vegetación nativa pueden tener un efecto significativo para mantener la biodiversidad en paisajes agrícolas (Pacheco et al. 2013, Cardona et al. 2016). Es así que en el paisaje rural cafetero, la presencia de varios fragmentos de bosque esta positivamente relacionada con el número de interacciones MF-PQ y el servicio de dispersión de semillas en escenarios rurales.

Por el contrario, la densidad de bordes presentó una relación negativa con el número de especies de murciélagos, de plantas tamaño y de interacciones, tal patrón puede ser reflejo de los efectos negativos de borde, los cuales pueden alterar la naturaleza de las interacciones entre especies modificando procesos y dinámicas, por ejemplo aumentando la herbivoría, y depredación de semillas, y el riesgo de depredación para los animales (Ewers and Didham 2006).

Conclusiones e implicaciones para la conservación

La intensificación del uso del suelo ha sido considerado como el factor más amenazante para la biodiversidad (Sala et al. 2000, Thuiller 2007). No obstante, los paisajes agrícolas pueden cumplir un papel fundamental en el mantenimiento de la biodiversidad y de servicios ecosistémicos, incluso se ha sugerido que los paisajes rurales son la única alternativa de conservación posible en alrededor del 70% del territorio andino de Colombia (Lozano-Zambrano et al. 2006). En este contexto, consideramos que el éxito de las estrategias de conservación de la biodiversidad y el préstamo de servicios ecosistémicos en el paisaje rural cafetero de Risaralda depende del diseño y manejo de paisajes, que contengan diferentes tipos de vegetación nativa como bosques y matorrales, así como la vegetación ribereña. Esta información es de mucho interés para los propietarios de los predios, manejadores y conservacionistas, al señalar los elementos del paisaje que pueden favorecer las interacciones biológicas y el servicio de dispersión de semillas en áreas rurales.

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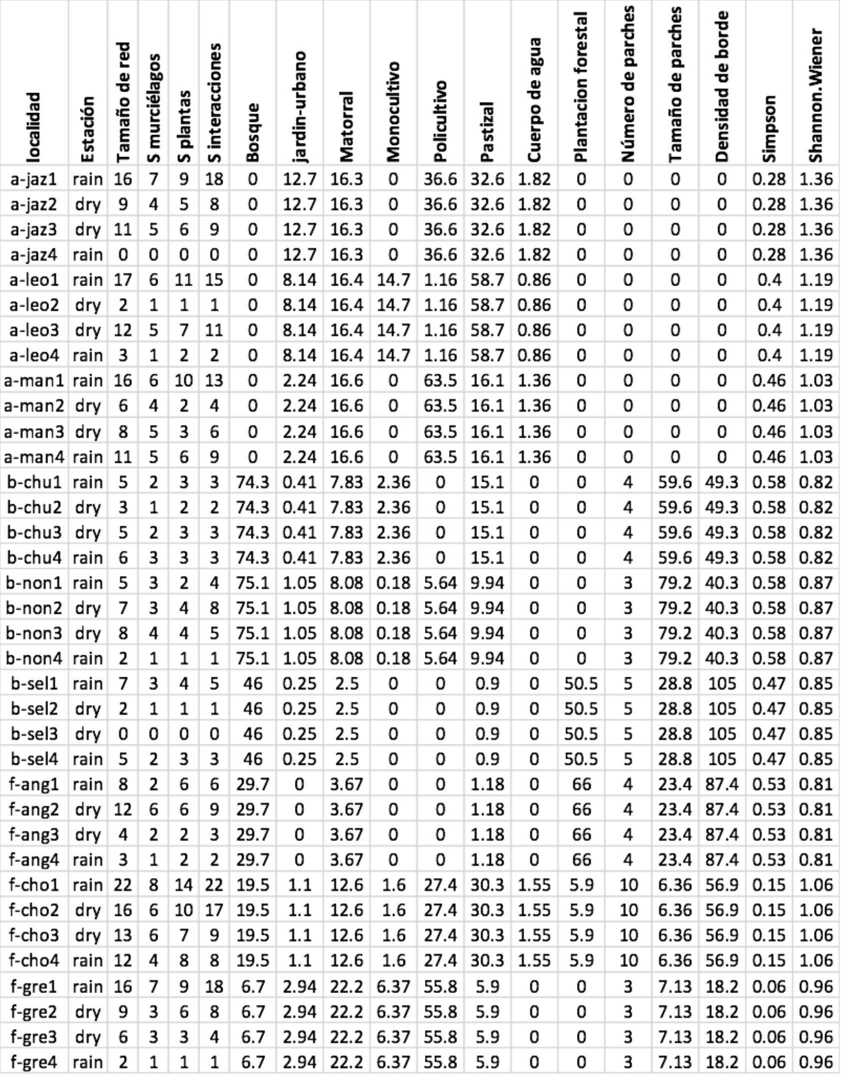
Material Suplementario 1. Matriz de datos de las 32 redes de interacción entre murciélagos frigívoros y plantas quiropterocoras en el paisaje rural cafetero. Variables estructurales de las redes (Tamaño de red, riqueza de murciélagos, de plantas y de interacciones), valores de las diferentes coberturas (Monocultivo, Policultivo, Jardín-Urbano, Pastizal, Plantación forestal, Bosque, Matorral y Cuerpos de agua) y variables de configuración del paisaje (Número de parches de bosque, Tamaño promedio de los parches de bosque, Densidad de bordes de bosque, índices de estructura de Simpson y Shannon-Wiener).



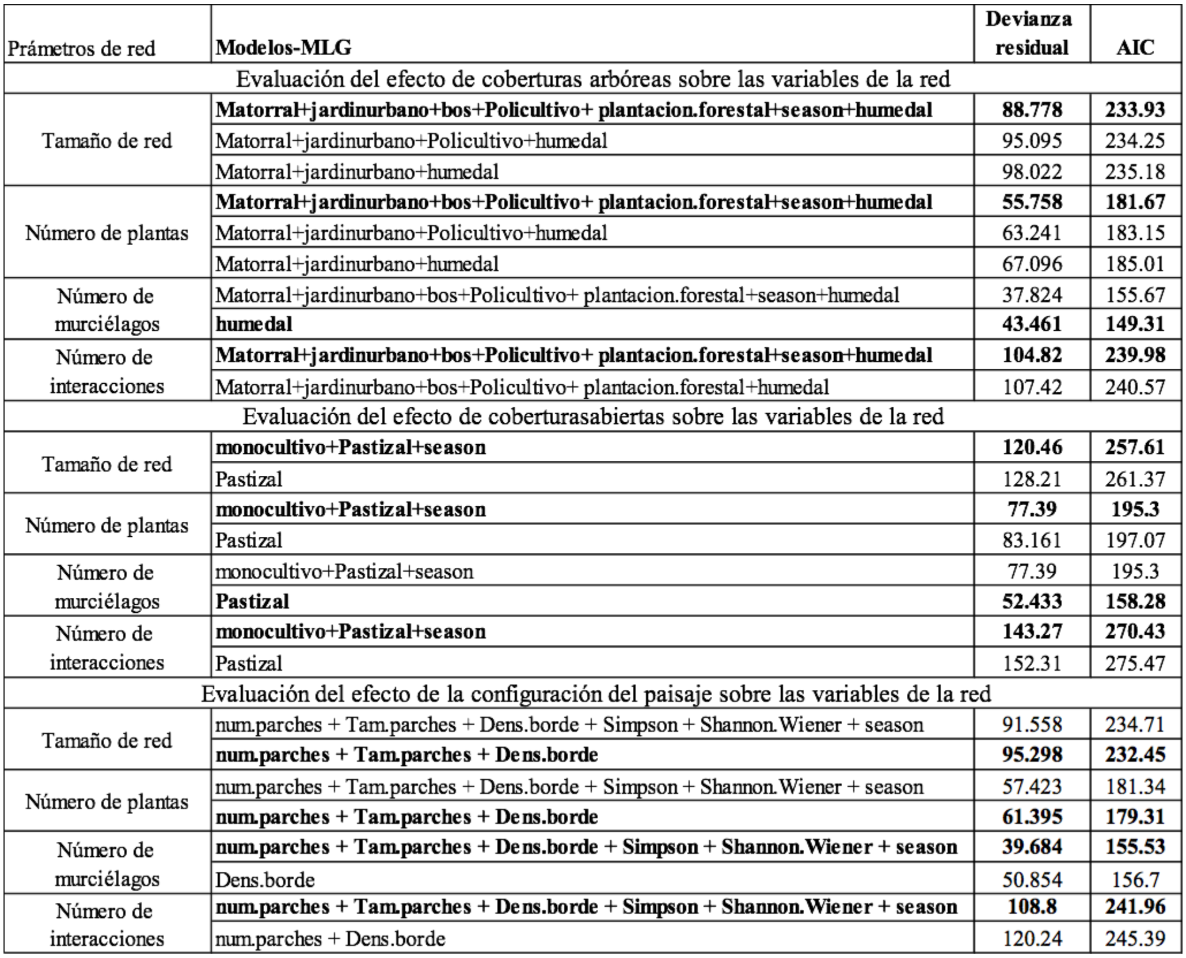
localidad	Estación	Tamaño de red	S murciélagos	S plantas	S interacciones	Bosque	jardin-urbano	Matorral	Monocultivo	Policultivo	Pastizal	Cuerpo de agua	Plantacion forestal	Número de parches	Tamaño de parches	Densidad de borde	Simpson	Shannon.Wiener
a-jaz1	rain	16	7	9	18	0	12.7	16.3	0	36.6	32.6	1.82	0	0	0	0	0.28	1.36
a-jaz2	dry	9	4	5	8	0	12.7	16.3	0	36.6	32.6	1.82	0	0	0	0	0.28	1.36
a-jaz3	dry	11	5	6	9	0	12.7	16.3	0	36.6	32.6	1.82	0	0	0	0	0.28	1.36
a-jaz4	rain	0	0	0	0	0	12.7	16.3	0	36.6	32.6	1.82	0	0	0	0	0.28	1.36
a-leo1	rain	17	6	11	15	0	8.14	16.4	14.7	1.16	58.7	0.86	0	0	0	0	0.4	1.19
a-leo2	dry	2	1	1	1	0	8.14	16.4	14.7	1.16	58.7	0.86	0	0	0	0	0.4	1.19
a-leo3	dry	12	5	7	11	0	8.14	16.4	14.7	1.16	58.7	0.86	0	0	0	0	0.4	1.19
a-leo4	rain	3	1	2	2	0	8.14	16.4	14.7	1.16	58.7	0.86	0	0	0	0	0.4	1.19
a-man1	rain	16	6	10	13	0	2.24	16.6	0	63.5	16.1	1.36	0	0	0	0	0.46	1.03
a-man2	dry	6	4	2	4	0	2.24	16.6	0	63.5	16.1	1.36	0	0	0	0	0.46	1.03
a-man3	dry	8	5	3	6	0	2.24	16.6	0	63.5	16.1	1.36	0	0	0	0	0.46	1.03
a-man4	rain	11	5	6	9	0	2.24	16.6	0	63.5	16.1	1.36	0	0	0	0	0.46	1.03
b-chu1	rain	5	2	3	3	74.3	0.41	7.83	2.36	0	15.1	0	0	4	59.6	49.3	0.58	0.82
b-chu2	dry	3	1	2	2	74.3	0.41	7.83	2.36	0	15.1	0	0	4	59.6	49.3	0.58	0.82
b-chu3	dry	5	2	3	3	74.3	0.41	7.83	2.36	0	15.1	0	0	4	59.6	49.3	0.58	0.82
b-chu4	rain	6	3	3	3	74.3	0.41	7.83	2.36	0	15.1	0	0	4	59.6	49.3	0.58	0.82
b-non1	rain	5	3	2	4	75.1	1.05	8.08	0.18	5.64	9.94	0	0	3	79.2	40.3	0.58	0.87
b-non2	dry	7	3	4	8	75.1	1.05	8.08	0.18	5.64	9.94	0	0	3	79.2	40.3	0.58	0.87
b-non3	dry	8	4	4	5	75.1	1.05	8.08	0.18	5.64	9.94	0	0	3	79.2	40.3	0.58	0.87
b-non4	rain	2	1	1	1	75.1	1.05	8.08	0.18	5.64	9.94	0	0	3	79.2	40.3	0.58	0.87
b-sel1	rain	7	3	4	5	46	0.25	2.5	0	0	0.9	0	50.5	5	28.8	105	0.47	0.85
b-sel2	dry	2	1	1	1	46	0.25	2.5	0	0	0.9	0	50.5	5	28.8	105	0.47	0.85
b-sel3	dry	0	0	0	0	46	0.25	2.5	0	0	0.9	0	50.5	5	28.8	105	0.47	0.85
b-sel4	rain	5	2	3	3	46	0.25	2.5	0	0	0.9	0	50.5	5	28.8	105	0.47	0.85
f-ang1	rain	8	2	6	6	29.7	0	3.67	0	0	1.18	0	66	4	23.4	87.4	0.53	0.81
f-ang2	dry	12	6	6	9	29.7	0	3.67	0	0	1.18	0	66	4	23.4	87.4	0.53	0.81
f-ang3	dry	4	2	2	3	29.7	0	3.67	0	0	1.18	0	66	4	23.4	87.4	0.53	0.81
f-ang4	rain	3	1	2	2	29.7	0	3.67	0	0	1.18	0	66	4	23.4	87.4	0.53	0.81
f-cho1	rain	22	8	14	22	19.5	1.1	12.6	1.6	27.4	30.3	1.55	5.9	10	6.36	56.9	0.15	1.06
f-cho2	dry	16	6	10	17	19.5	1.1	12.6	1.6	27.4	30.3	1.55	5.9	10	6.36	56.9	0.15	1.06
f-cho3	dry	13	6	7	9	19.5	1.1	12.6	1.6	27.4	30.3	1.55	5.9	10	6.36	56.9	0.15	1.06
f-cho4	rain	12	4	8	8	19.5	1.1	12.6	1.6	27.4	30.3	1.55	5.9	10	6.36	56.9	0.15	1.06
f-gre1	rain	16	7	9	18	6.7	2.94	22.2	6.37	55.8	5.9	0	0	3	7.13	18.2	0.06	0.96
f-gre2	dry	9	3	6	8	6.7	2.94	22.2	6.37	55.8	5.9	0	0	3	7.13	18.2	0.06	0.96
f-gre3	dry	6	3	3	4	6.7	2.94	22.2	6.37	55.8	5.9	0	0	3	7.13	18.2	0.06	0.96
f-gre4	rain	2	1	1	1	6.7	2.94	22.2	6.37	55.8	5.9	0	0	3	7.13	18.2	0.06	0.96

]

Material suplementario 2 Matriz general de interacciones entre murciélagos frugívoros (columnas) y plantas quiropterocoras (filas) registradas en el presente estudio

		Carolliinae		Stenodermatinae										
Fam pla	**Plantas**	**Carollia brevicauda**	**Carollia perspicillata**	**Artibeus jamaicensis**	**Artibeus lituratus**	**Dermanura bogotensis**	**Dermanura phaeotis**	**Mesophylla macconnelli**	**Platyrrhinus albericoi**	**Platyrrhinus dorsalis**	**Sturnira bogotensis**	**Sturnira ludovici**	**Sturnira parvidens**	**Vampyressa thyone**
Araceae	Ant. Sp1	1	0	0	0	1	0	0	0	0	0	0	0	0
	Anthurium glaucospadix	6	3	0	3	0	0	0	0	0	1	1	2	0
	Anthurium popayanense	0	0	0	0	0	0	0	0	0	0	1	0	0
	Anthurium versicolor	1	2	0	0	0	0	0	0	0	0	0	0	0
	Phylodendron	2	0	0	0	1	0	0	0	0	0	0	0	0
	Xanthosoma	1	0	0	0	0	0	0	0	0	0	0	0	0
Campanulaceae	Centropogon	3	0	0	0	0	0	0	0	0	0	0	0	0
Cyclanthaceae	Cyclanthus bipartitus	6	1	0	2	1	2	1	0	0	1	0	0	0
	Spharadenia garciae	0	0	0	0	0	0	0	0	0	0	0	1	0
Ericaceae	Cavendishia nitida	0	0	0	0	2	0	0	0	0	0	0	0	0
	Psamisia	0	0	0	0	1	0	0	0	0	0	0	0	0
Gesneriaceae	Columnea	4	0	0	0	0	0	0	0	0	0	0	0	0
Hypericaceae	Vismia guianensis	7	0	0	0	0	0	0	0	0	0	0	0	0
indet	negra pequeña	0	0	0	1	0	0	0	0	0	0	0	0	0
	rojiza diminuta	1	0	0	0	0	0	0	0	0	0	0	0	0
Moraceae	Ficus americana	1	0	0	6	0	0	0	1	0	0	1	0	0
	Ficus brevibracteata	0	1	0	1	0	0	1	0	1	0	0	0	0
	Ficus brill	0	0	0	2	0	0	0	0	0	0	0	0	0
	Ficus insipida	0	0	1	4	0	0	0	1	0	0	0	0	0
	Ficus sp1	0	0	2	5	0	0	0	2	0	0	0	0	0
	Ficus sp3	1	0	0	2	0	0	0	24	0	0	0	0	1
	Ficus tonduzi	0	1	2	16	0	0	0	2	0	0	0	0	0
Myrtaceae	Psidium guajava	0	0	1	8	0	0	0	0	0	0	1	0	0
Piperaceae	Piper aduncum	8	1	0	2	0	0	0	0	0	7	0	11	0
	Piper carpunya	4	2	0	1	0	0	0	0	0	0	0	0	0
	Piper crassinervium	19	1	0	2	0	1	0	1	0	0	0	0	1
	Piper sp1	1	0	0	0	0	0	0	0	0	1	0	0	0
	Piper umbellatum	3	0	0	0	0	0	0	0	0	0	0	0	0
Solanaceae	Solamun sp5	0	0	0	0	0	0	0	0	1	0	0	0	0
	Solanum acerifolium	1	0	0	0	0	0	0	0	0	0	0	0	0
	Solanum aphyodendron	9	8	1	17	8	8	1	0	0	6	5	10	0
	Solanum sp1	1	2	0	1	0	0	0	0	0	0	0	7	0
	Solanum sp2	0	1	0	0	1	0	0	0	0	0	1	0	0
	Solanum sp3	2	0	0	0	0	0	0	0	0	0	0	0	0
	Solanum sp4	4	1	0	0	0	0	0	0	0	1	5	2	0
Urticaceae	Cecropia angustifolia	1	0	0	4	0	0	0	0	4	0	0	0	0
	Cecropia telealba	5	0	12	58	2	1	0	6	6	0	2	0	0

Material Suplementario 3 Modelos evaluados para explicar las 4 variables estructurales (Tamaño de red, riqueza de plantas, de murciélagos y de interacciones) de las redes de interacción entre murciélagos frigívoros y plantas quiropterocoras en el paisaje rural cafetero de Risaralda, Colombia. Se resaltan aquellos con menor devianza residual y criterios de información de Akaike (AIC) < 2.



Prámetros de red	**Modelos-MLG**	**Devianza residual**	**AIC**
Evaluación del efecto de coberturas arbóreas sobre las variables de la red			
Tamaño de red	**Matorral+jardinurbano+bos+Policultivo+ plantacion.forestal+season+humedal**	**88.778**	**233.93**
	Matorral+jardinurbano+Policultivo+humedal	95.095	234.25
	Matorral+jardinurbano+humedal	98.022	235.18
Número de plantas	**Matorral+jardinurbano+bos+Policultivo+ plantacion.forestal+season+humedal**	**55.758**	**181.67**
	Matorral+jardinurbano+Policultivo+humedal	63.241	183.15
	Matorral+jardinurbano+humedal	67.096	185.01
Número de murciélagos	Matorral+jardinurbano+bos+Policultivo+ plantacion.forestal+season+humedal	37.824	155.67
	humedal	**43.461**	**149.31**
Número de interacciones	**Matorral+jardinurbano+bos+Policultivo+ plantacion.forestal+season+humedal**	**104.82**	**239.98**
	Matorral+jardinurbano+bos+Policultivo+ plantacion.forestal+humedal	107.42	240.57
Evaluación del efecto de coberturasabiertas sobre las variables de la red			
Tamaño de red	**monocultivo+Pastizal+season**	**120.46**	**257.61**
	Pastizal	128.21	261.37
Número de plantas	**monocultivo+Pastizal+season**	**77.39**	**195.3**
	Pastizal	83.161	197.07
Número de murciélagos	monocultivo+Pastizal+season	77.39	195.3
	Pastizal	**52.433**	**158.28**
Número de interacciones	**monocultivo+Pastizal+season**	**143.27**	**270.43**
	Pastizal	152.31	275.47
Evaluación del efecto de la configuración del paisaje sobre las variables de la red			
Tamaño de red	num.parches + Tam.parches + Dens.borde + Simpson + Shannon.Wiener + season	91.558	234.71
	num.parches + Tam.parches + Dens.borde	**95.298**	**232.45**
Número de plantas	num.parches + Tam.parches + Dens.borde + Simpson + Shannon.Wiener + season	57.423	181.34
	num.parches + Tam.parches + Dens.borde	**61.395**	**179.31**
Número de murciélagos	**num.parches + Tam.parches + Dens.borde + Simpson + Shannon.Wiener + season**	**39.684**	**155.53**
	Dens.borde	50.854	156.7
Número de interacciones	**num.parches + Tam.parches + Dens.borde + Simpson + Shannon.Wiener + season**	**108.8**	**241.96**
	num.parches + Dens.borde	120.24	245.39

SUMARIO

En las últimas décadas el desarrollo de la teoría de grafos y la teoría de sistemas han sido incorporadas a la ecología para ayudar a entender las consecuencias de la estructura de comunidades en las interacciones ecológicas y las propiedades emergentes de éstos sistemas (Moreira et al. 2018). Las redes de interacción entre especies pueden ser más informativas que los análisis clásicos de diversidad de especies para evaluar los efectos de la transformación del hábitat. Considerando que las redes de interacción varían de acuerdo a la transformación de los ecosistemas, lo cambios en éstas, podrían predecir las consecuencias de los impactos antrópicos, no solo sobre la biodiversidad, sino también sobre los procesos ecológicos (Soares et al. 2017). Sin embargo, aún hay mucha controversia teórica y poca evidencia empírica que evalúe el efecto de la pérdida de hábitat naturales sobre la estructura de las redes de interacción (Hagen et al. 2012, Moreira et al. 2018).

Este es el primer estudio que evalúa la respuesta de redes de interacción mutualista planta-frugívoro ante diferentes escenarios de transformación. contribuyendo a llenar los vacíos de información, donde las redes de dispersión de semillas más conocidas son acerca de aves-plantas (Escribano-Avila et al. 2018) y los pocos estudios empíricos que investiguan los cambios en las redes de interacción ante transformaciones medioambientales se han enfocado en redes planta-polinizador (Soares et al. 2017).

Nuestros resultados muestran que a medida que se reduce el porcentaje de bosque, las redes tienden a reorganizarse manteniendo atributos asociados con su estabilidad (Modularidad y anidamiento) manteniendo su funcionalidad, incluso aumentando la riqueza de interacciones y el tamaño de la red. Indicando que en este escenario la red de interacciones MF-PQ son robustas ante la transformación del hábitat manteniéndose modulares y anidadas en los diferentes escenarios de transformación. Sin embargo, el papel de las especies cambió. En el escenario más transformado las interacciones fueron menos especializadas indicando que métricas a nivel de especies son más sensibles que las métricas a nivel de red.

Es importante aclarar que estos resultados están relacionados con la alta heterogeneidad presente en el paisaje rural cafetero de Risaralda. Nosotros evidenciamos que la estructura y composición del paisaje tiene incidencia sobre la estructura de interacciones entre MF-PQ. Los paisajes con mayor cobertura de matorrales, cuerpos de agua, mayor número de parches de bosque afectaron positivamente el número de interacciones y la riqueza de especies tanto de plantas como de murciélagos. Identificar esta relación tiene importantes implicaciones en manejo y conservación de la biodiversidad ya que permite explicar los mecanismos potenciales que afectan las redes de interaccione entre murciélagos y plantas y los servicios ecosistémicos que prestan.

En este contexto, consideramos que el éxito de las estrategias de conservación de la biodiversidad y el préstamo de servicios ecosistémicos en paisajes rurales depende del diseño y manejo de paisajes, que contengan diferentes tipos de vegetación nativa como bosques y matorrales, así como la vegetación ribereña. Esta información es de mucho interés para los propietarios de los predios, manejadores y conservacionistas, al señalar los elementos del paisaje que pueden favorecer las interacciones biológicas y el servicio de dispersión de semillas en áreas rurales.

Anexos

Anexo 1: Responses of bats to landscape transformation in an Andean agricultural landscape

Anexo 2: Diet and trophic structure in assemblages of montane frugivorous phyllostomid bats

Anexo 3: Does seed ingestion by bats increase germination?: a new meta-analysis 15 years later

Anexo 4: Mamíferos del departamento de Risaralda, Colombia

Anexo 1

Responses of bats to landscape transformation in an Andean agricultural landscape

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Mammal Research

Responses of bats to landscape transformation in an Andean agricultural landscape

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Abstract:	The current debate on the future of biodiversity gives rise to the need to integrate agricultural landscapes into conservation strategies. Bats are an important component of vertebrate diversity in many terrestrial landscapes where they provide invaluable and important ecosystem services to human societies such as insect pest control, pollination and seed dispersal. Here we study bat diversity and abundance in three landscapes representing a transformational gradient (continuous forests, forest fragments and crops) in an Andean agricultural scenario known as Colombia's "Coffee Cultural Landscape". We captured 1146 bats from 32 species and 4 families. The bat diversity and abundance in this landscape were high, especially for frugivorous bats, but there were no differences among the three transformational landscapes. However, some species were captured differentially between landscapes, suggesting that these landscapes have characteristics that influence the relative abundance of bats. Additionally, body weight and sex affect the abundance of some species in forest fragments and crops.
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Responses of bats to landscape transformation in an Andean agricultural landscape

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Abstract

The current debate on the future of biodiversity gives rise to the need to integrate agricultural landscapes into conservation strategies. Bats are an important component of vertebrate diversity in many terrestrial landscapes where they provide invaluable and important ecosystem services to human societies such as insect pest control, pollination and seed dispersal. Here we study bat diversity and abundance in three landscapes representing a transformational gradient (continuous forests, forest fragments and crops) in an Andean agricultural scenario known as Colombia's "Coffee Cultural Landscape". We captured 1146 bats from 32 species and 4 families. The bat diversity and abundance in this landscape were high, especially for frugivorous bats, but there were no differences among the three transformational landscapes. However, some species were captured differentially between landscapes, suggesting that these landscapes have characteristics that influence the relative abundance of bats. Additionally, body weight and sex affect the abundance of some species in forest fragments and crops.

Key Words: Andes; Chiroptera; coffee landscape; Colombia.

Introduction

The current debate on the future of biodiversity in a context of accelerated species extinction rates (Ceballos et al. 2017) and ecosystem deterioration (Hansen et al. 2013), exacerbated by the insufficiency of protected areas for conservation (Chazdon et al. 2009), gives rise to the need to integrate agricultural landscapes into conservation strategies. These agricultural landscapes have generated a particular interest as reservoirs of biodiversity, since some of them may resemble natural ecosystems in terms of species diversity (Harvey et al. 2006) and in their capacity to generate ecosystem services (Landis 2017).

The structural and compositional heterogeneity of agricultural landscapes influences their capacity to maintain biodiversity (Fahrig et al. 2011). Simple landscapes, for instance, show a lower diversity of arthropods and vertebrates than more complex landscapes (Schmidt et al. 2005; Harvey et al. 2006; Frishkoff et al. 2014). Therefore, heterogeneous agricultural landscapes, in addition to maintaining productive activities, also favor the permanence of biodiversity and the supply of ecosystem services.

Bats are an important component of vertebrate diversity in many terrestrial landscapes. They provide important ecosystem services for human societies, such as insect pest control, pollination and seed dispersal (Kunz et al. 2011). The accelerated ecosystems transformations throughout the world, particularly because of deforestation, threaten many bat populations (Meyer et al. 2016) and the ecosystem services that they provide (García-Morales et al. 2016).

In the Andean region of Colombia, the country with the highest neotropical bat diversity known (Solari et al. 2013), more than 70% of the forest cover has been transformed to urban, agriculture or pasture (Etter and van Wyngaarden 2000). However, factors such as environmental variability and cultural diversity in the management of productive systems have generated a heterogeneous spatial mosaic where forest areas are mixed with cultivated areas, probably favoring the persistence of bat populations (Cardona et al. 2016).

The objective of this work was to study the bat diversity in a heterogeneous agricultural landscape in the Colombian Andes. Specifically we asked (1) if bat diversity is favored in this landscape and (2) how bats respond to three different transformational scenarios (continuous forests, forest fragments and crops). As bats are highly mobile, we expected no differences in overall bat diversity among transformational scenarios; however, since individual bats differ in functional traits (e.g. body weight, trophic guild and sex), we also expected species-specific responses to these transformative scenarios.

Materials and methods

Study area

The study area is located on the western slope of the Central Andes (Colombian Cordillera Central) of Colombia. UNESCO recognizes this region (including the departments of Riseralda, Quindío and Caldas) as a World Heritage site known as the “Colombian

Coffee Cultural Landscape", due to a particular combination of coffee-growing cultural practices and sustainability, example of outstanding human adaptation to difficult geographic conditions over which a homogenous mountainous coffee agriculture in a mixture of natural, economic and cultural elements have become highly and successfully blended in a sustainable manner. In this region, coffee has been produced for more than 100 years and is one of the most important crops in the area. Other important crops are pastures, bananas, vegetables, forest plantations and other fruits. The annual mean temperature oscillates between 16 - 24 °C, the mean relative humidity is 79% and the mean precipitation is 3358.4 mm.

We selected three landscapes representing a transformational gradient: (1) continuous forests, (2) forest fragments, which are immersed in a matrix of crops, and (3) crops without forests but with bamboo (*Guadua angustifolia*). Three sampling points were located in the center of a 1 km buffer of each landscape scenario totaling nine sampling localities. Each sampling point was separated by at least 4 km from other sampling points. All sampling points were located between an elevation of 1600 - 2000 meters.

Bat sampling

Bats were captured between August 2016 and August 2017 using mist nets (12 meters long) located at 1 - 5 m above the ground. In total we accumulated 47012 net hours of sampling effort (forests: 9297; fragments: 19116; crops: 18599). Each captured bat was weighed, measured, sexed and marked with a consecutive number using tattoo pliers. Each bat was identified to species and a series of 41 individuals were collected as voucher specimens to be deposited in the mammalogy collection of the University of Santa Rosa de Cabal (Appendix I). Regional environmental authorities approved animal's capture (CARDER- Corporación Autónoma Regional de Risaralda, license number 2004 -Sep 2016) and the Animal Use and Care Committee of the University of Santa Rosa de Cabal approved all of the procedures.

Data analyses

We used capture rate as an indication of bat abundance. Abundance was calculated as *CR=(i.n/m.h)*, where *i*=captured bats, *n*=sampling nights, *m*=number of nets, and *h*=sampling hours (Pérez-Torres and Ahumada 2004). To assess inventory completeness we divided the observed species richness between the species richness estimated by the index Jackknife 1, which was calculated with the software Estimates based on a matrix of species presence or absence and randomized 100 times (Colwell and Elsensohn 2014).

Capture rate was calculated for the three most abundant feeding guilds (nectarivorous, frugivorous and insectivorous) for species and for body weight intervals. We used a Chi-square to test differences in the capture of adult male or females using total abundances. Shannon-Wiener and Simpson indices were used to quantify the diversity between forests, fragments and crops. A Kruskal-Wallis test was used to find differences in capture rate and diversity among landscapes. Finally, the Jaccard index was used to explore the similarity between forests, fragments and crops. ANOVAs were run with the statistical software GraphPad Prism. The significance level was set at 5% ($P<0.05$). Data was expressed as mean ± standard deviation.

Results

We captured 1146 bats from 32 species and 4 families (Table 1). Bats from five feeding guilds (frugivorous, nectarivorous, aerial insectivorous, gleaning animalivorous and hematophagous) were present; however, frugivorous bats were the richest and most abundant guild. The species richness estimator Jack 1 (Fig. 1A) suggested a greater richness than that observed, reaching a sampling completeness of 84%. The three landscapes showed a medium degree of similarity with forests and fragments being more similar to each other (66%) than to crops (60%) (Fig. 1B).

Neither the indices of diversity nor capture rates were different among the three landscapes (Fig. 2); however, there were differences when analyzed by species (Fig. 3A). *Anoura caudifera* was significantly more abundant in forests ($H = 5.6$; $P = 0.04$), *C. brevicauda* in fragments ($H = 7.2$; $P = 0.003$) and *S. parvidens* in crops ($H = 5.96$, $P = 0.02$). When pooled by feeding guilds, the capture rate of nectarivorous (Fig. 3B), frugivorous (Fig. 3C) and insectivorous bats (Fig. 3D) were the same among the three landscapes.

In four species the abundance of adult bats by sex varied between landscapes (Table 1). In fragments *C. brevicauda* and *D. bogotensis* females were more abundant than males and *P. albericoi* and *D. rotundus* males were more abundant than females. In crops *D. bogotensis* females and *A. caudifera* males were more abundant . In forests, differences in sex proportions were not detected. Finally, larger bats were captured more frequently in crops than in forests or fragments (H = 27.6, P = 0.0001) (Fig. 4A), particularly those with a body weight between 60 and 80 grams (H = 10.8, P = 0.02) (Fig. 4B).

Discussion

The Colombian Coffee Cultural Landscape showed a high diversity of bats. As we predicted, there was no difference between continuous forests, forest fragments, and crops. This could be explained by the dispersal abilities of bats. However, some bat species were captured differentially between landscapes

The bat diversity found in this rural landscape is highly dominated by frugivorous bats. Bats were not only the most diverse in terms of species, but they were also the most abundant, which is the common pattern in tropical Andean forests (Soriano 2000) and coffee agricultural landscapes (Numa et al. 2005; Cardona et al. 2016). Furthermore, two frugivorous bats, *C. brevicauda* and *A. lituratus,* account for almost half of the captures. Aerial insectivorous bat diversity was probably underestimated because of the use of mist nets. We captured only six of the 16 aerial insectivorous bat species recorded for this area of the Colombian Andes (Castaño et al. 2018b), so relative abundances of this feeding guild between landscapes must be interpreted with caution.

Commuting flights of bats can reach several kilometers (Bernard and Fenton 2003), so it was early recognized that bats experience the landscape in a different way than other animals with less mobility (Moreno and Halffter 2000). For instance, individual bats might roost in forests, fly to crops and fragments to eat and return to the forests to roost (Bernard and Fenton 2003; Aguiar et al. 2014). This dispersal capacity could explain why no differences were found in diversity indices between scenarios of the landscapes studied.

Artibeus lituratus, with a body weight of 62.91±7.57 g (n=363) was the most captured species in crops. Two other large frugivorous bats, *P. albericoi* (62±7.35 g; n=61) and *A. jamaicensis* (65±8.64 g; n=41), were also frequently captured in this landscape. The presence of these three species explains why in crops the capture rate of bats having a body weight interval of 60-79.9 g was significantly high. The abundance of large bats in transformed ecosystems (e.g. urban areas) has been explained because of the availability of nutrients and by the abilities that larger bodies confer (Jara-Servín et al. 2017): for example stronger bites (Freeman and Lemen 2010) allow access to more food items. In our study landscape, for instance, *Cecropia angustifolia* is abundant in crops and other transformed areas. These trees fruit year-round (Zalamea et al. 2011) and are eagerly consumed by *Artibeus spp.* and *Platyrrhinus alberico* (Castaño et al. 2018a). Also, cultivated species such as guava (*Psidium guajava*) are abundant in crop areas, providing bats with many fruits.

Processes such as forest fragmentation or forest replacement by crops modify the vegetation composition and dynamics, favoring the recruitment and establishment of pioneer plants at the border of fragments (Zhu et al. 2004) and open areas such as *Solanum*, *Piper* and *Cecropia*. *Carollia brevicauda* and *S. parvidens* feed preferentially on the fruits of these plant species (Andrade et al. 2013; Castaño et al. 2018a), which might explain why these two species were captured more frequently in fragments and in crops. A similar relation to the composition of the vegetation might be drawn for the bat *A. caudifera*, captured mainly in forests. This is a nectarivorous species highly dependent on flowering plants that grow inside or at the border of forests (Muchhala and Jarrín-V 2002).

Differences in relative abundance of the sexes were detected in five species. This phenomenon has been found in many species of bats (Stoner 2001) and is generally attributed to foraging segregation and differences in habitat preferences; however, more data are needed to explore the causes of these patterns in our studied landscape.

Despite the establishment of fragmentation and crops, bat diversity in this Andean landscape remains high. Since not all bat species are favored by the same landscape scenarios, it is important to maintain diverse landscapes such as fragments, continuous forests, crops, gardens, pastures and forest plantations to favor the conservation of bats of different feeding guilds and the ecosystem services that they provide.

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Conflict of interests

The authors declare that they have no conflict of interest.

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Table 1. Species list, trophic guilds and sex ratios of captured bats in the Andean agricultural landscape. Sex ratio is based only in adult captures.

			Sex Ratios											
			Forests				Fragments				Crops			
Species	**Abundance**	**Trophic guild**	♂	♀	**Chi2**	**p**	♂	♀	**Chi2**	**p**	♂	♀	**Chi2**	**p**
Molossus molossus	3	Aerial insectivore	0	0			0	0			2	0	2.00	0.16
Anoura caudifera	64	Nectarivore	19	25	0.82	0.366	4	3	0.14	0.705	4	0	4.00	**0.046**
Anoura peruana	4	Nectarivore	0	0			1	0	1.00	0.317	0	2	2.00	0.16
Artibeus jamaicensis	58	Frugivore	9	8	0.06	0.808	3	2	0.20	0.655	14	18	0.50	0.48
Artibeus lituratus	385	Frugivore	26	37	1.92	0.166	36	47	1.46	0.227	101	107	0.17	0.68
Carollia brevicauda	179	Frugivore	13	17	0.53	0.465	41	67	6.26	**0.012**	5	6	0.09	0.76
Carollia perspicillata	43	Frugivore	3	3	0.00	1.000	9	9	0.00	1.000	7	7	0.00	1.00
Chiroderma salvini	1	Frugivore	0	0			0	0			0	1	1.00	0.32
Dermanura bogotensis	40	Frugivore	0	1	1.00	0.317	0	5	5.00	**0.025**	0	4	4.00	**0.046**
Dermanura phaeotis	30	Frugivore	3	5	0.50	0.480	3	7	1.60	0.206	3	5	0.50	0.48
Desmodus rotundus	11	Sanguinivore	0	0			6	0	6.00	**0.014**	1	0	1.00	0.32
Enchisthenes hartii	2	Frugivore	0	0			1	0	1.00	0.317	1	0	1.00	0.32
Glossophaga soricina	37	Nectarivore	0	1	1.00	0.317	0	2	2.00	0.157	8	12	0.80	0.37
Lonchophylla sp.	1	Nectarivore	0	0			0	0			0	0		
Mesophylla macconnelli	10	Frugivore	0	0			4	3	0.14	0.705	1	1	0.00	1.00
Micronycteris megalotis	2	Gleaning insectivore	1	1	0.00	1.000	0	0			0	0		
Phyllostomus discolor	11	Gleaning insectivore	0	0			0	0			2	7	2.78	0.10
Platyrrhinus albericoi	78	Frugivore	4	1	1.80	0.180	27	5	15.13	**0.000**	13	24	3.27	0.071
Platyrrhinus angustirostris	6	Frugivore	1	4	1.80	0.180	0	1	1.00	0.317	0	0		

Platyrrhinus dorsalis	21	Frugivore	1	1	0.00	1.000	7	5	0.33	0.564	1	0	1.00	0.32
Sturnira bidens	1	Frugivore	0	1	1.00	0.317	0	0			0	0		
Sturnira bogotensis	29	Frugivore	1	1	0.00	1.000	2	1	0.33	0.564	8	11	0.47	0.49
Sturnira ludovici	38	Frugivore	3	5	0.50	0.480	10	10	0.00	1.000	4	2	0.67	0.41
Sturnira parvidens	56	Frugivore	2	0	2.00	0.157	3	4	0.14	0.705	25	15	2.50	0.11
Uroderma convexum	1	Frugivore	0	0			0	0			1	0	1.00	0.32
Vampyressa thyone	9	Frugivore	1	1	0.00	1.000	1	4	1.80	0.180	0	0		
Thyroptera tricolor	1	Aerial insectivore	0	0			0	0			1	0	1.00	0.32
Eptesicus chirriquinus	4	Aerial insectivore	0	0			0	0			3	1	1.00	0.32
Lasiurus blossevilli	1	Aerial insectivore	0	0			0	0			1	0	1.00	0.32
Myotis causencis	12	Aerial insectivore	0	3	3.00	0.083	2	1	0.33	0.564	2	2	0.00	1.00
Myotis keaysi	4	Aerial insectivore	0	0			0	0			1	3	1.00	0.32
Myotis riparius	4	Aerial insectivore	0	2	2.00	0.157	0	0			1	1	0.00	1.00
Total	**1146**													

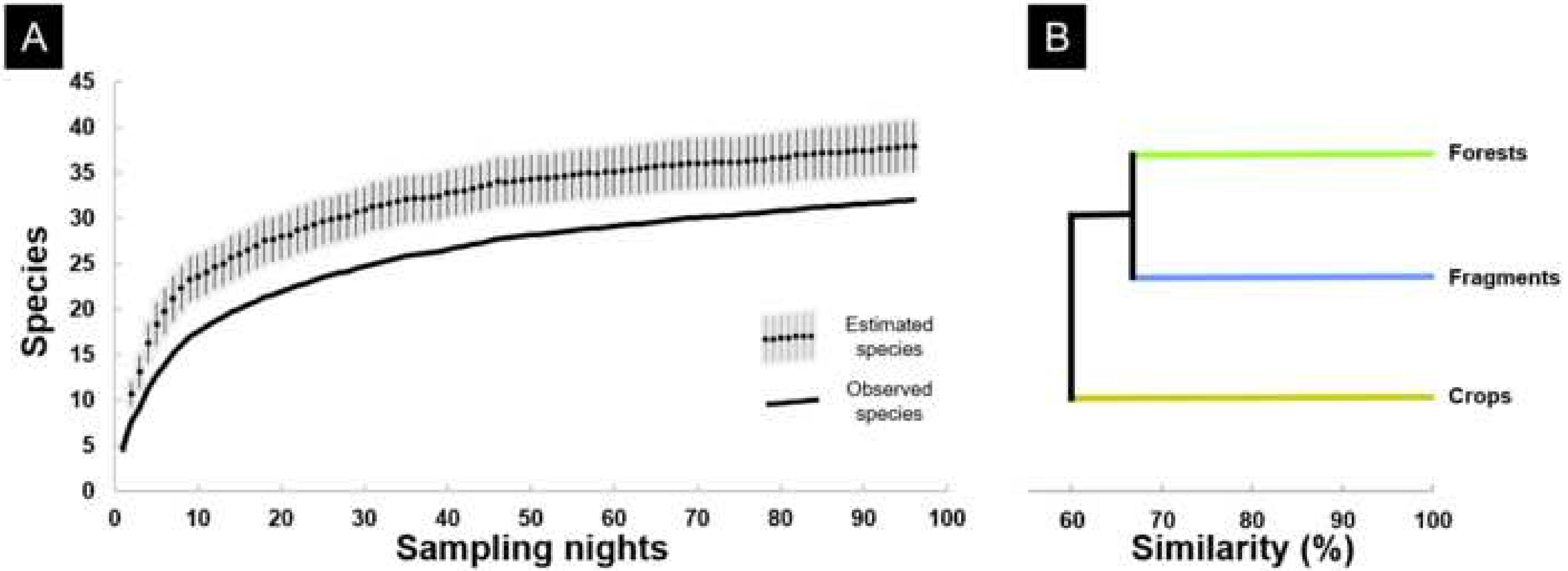
Fig 1 Curves of estimated (Jacknife 1 ± SD) and observed species richness (A). Dendrogram obtained with Jaccard similarity coefficient and average linkage method for the three landscape scenarios.

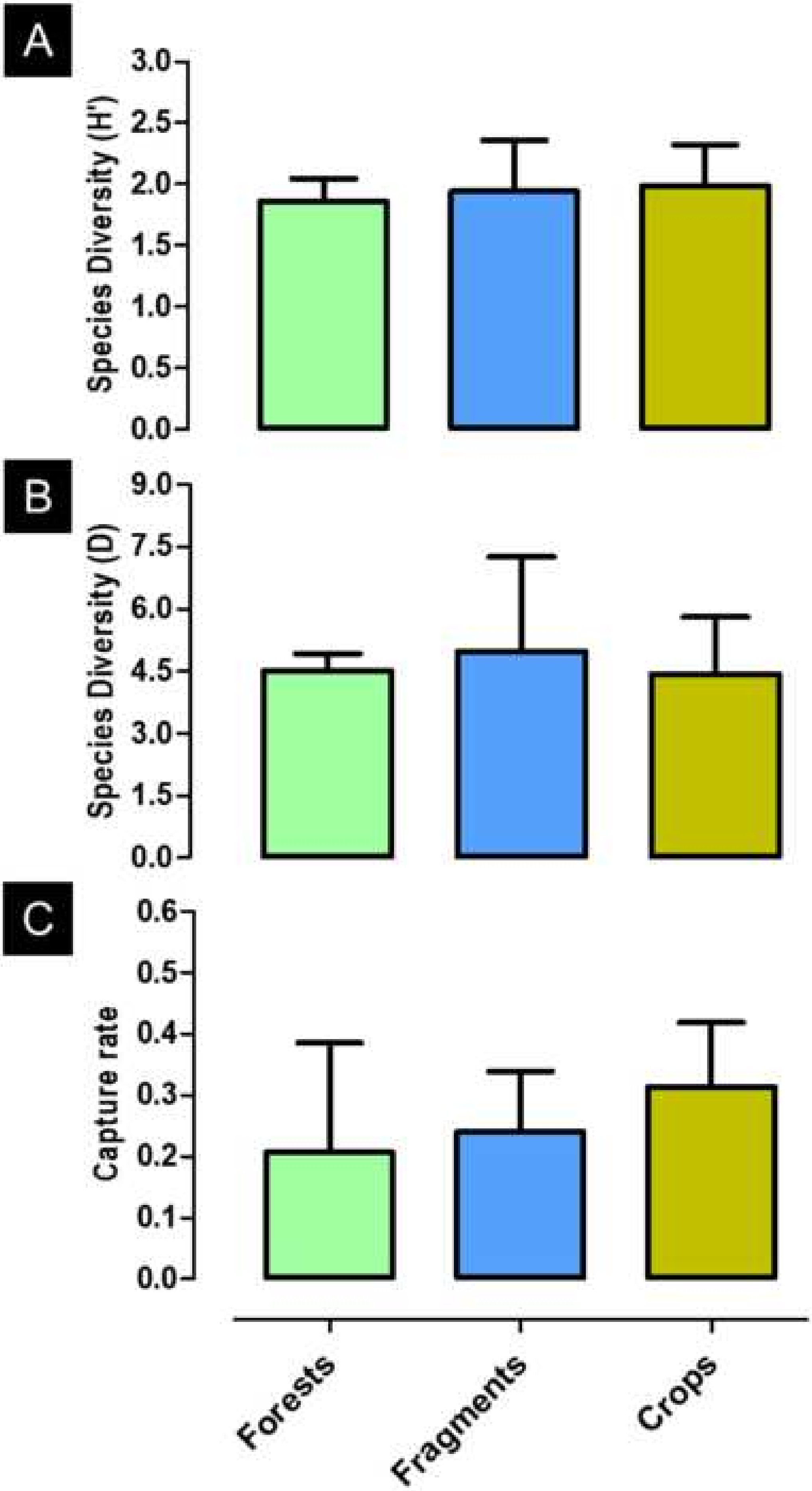
Fig 2 Shannon-Wiener (A) and Simpson (B) indices of diversity, and the relative abundance (capture rate) of all bat species (C) in the three landscape scenarios. Data are expressed as mean ± SD.

Fig 3 Relative abundance of species (captured rate) in each of the three landscape scenarios (A) and relative abundance pooled by the three most common trophic guilds: nectarivorous (B), frugivorous (C) and aerial insectivorous (D). Red asterisks indicate species with capture rates significantly different among the three landscape scenarios. Data are expressed as mean ± SD.

Fig 4 Body weight of all captured bats (A), excluding young and pregnant females, and the relative abundance (capture rate) of body weight intervals in each of the three landscapes (B). Red asterisks indicate species with capture rates significantly different among the three landscape scenarios. Data are expressed as mean ± SD.

Figure1


A
45
40
35
30
25
20
15
10
5
0
Species
0
10
20
30
40
50
60
70
80
90
100
Sampling nights
Estimated species
Observed species
B
Forests
Fragments
Crops
60
70
80
90
100
Similarity (%)


A
Species Diversity (H')
3.0
2.5
2.0
1.5
1.0
0.5
0.0
B
Species Diversity (D)
9.0
7.5
6.0
4.5
3.0
1.5
0.0
C
Capture rate
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Forests
Fragments
Crops

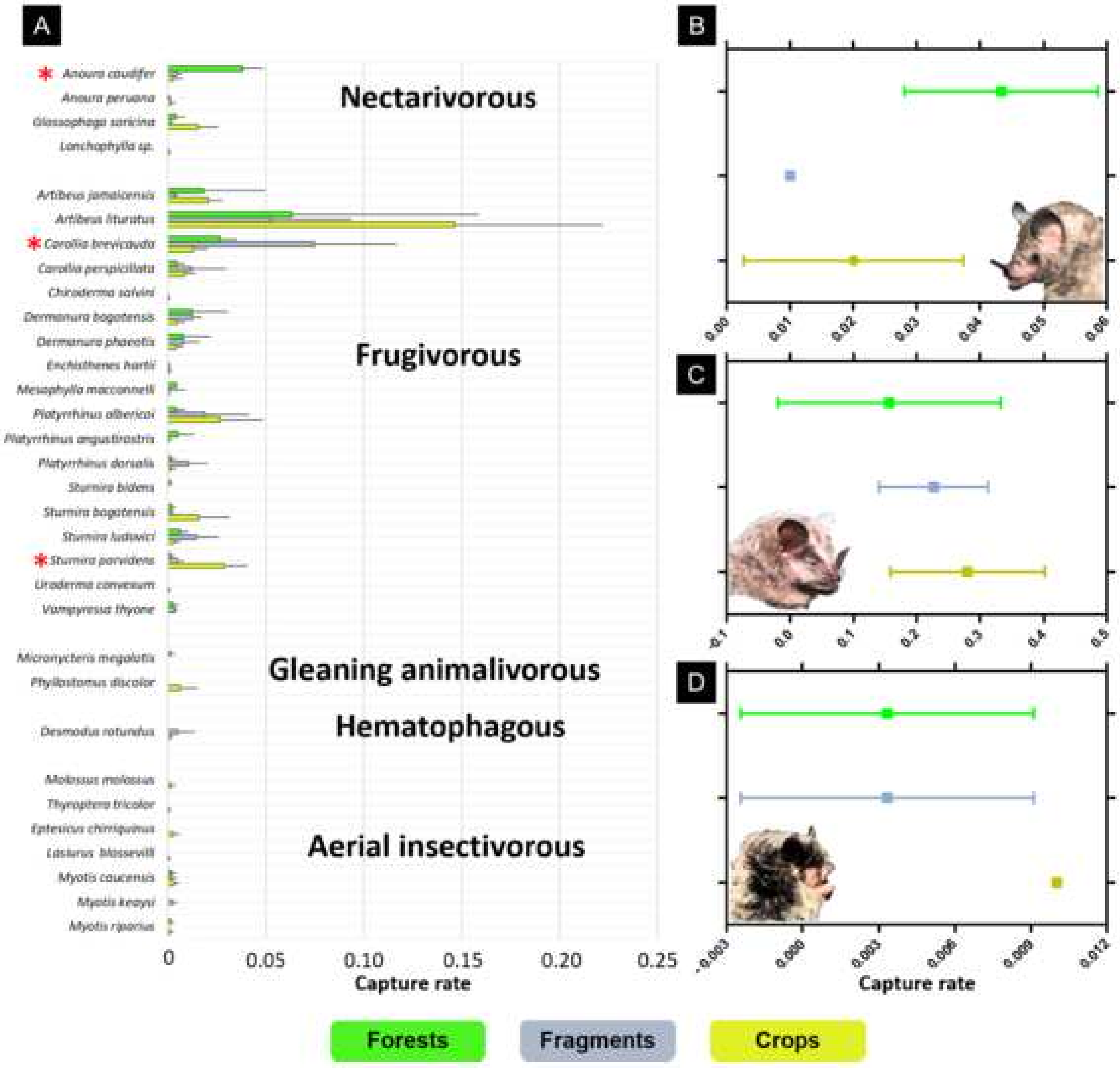
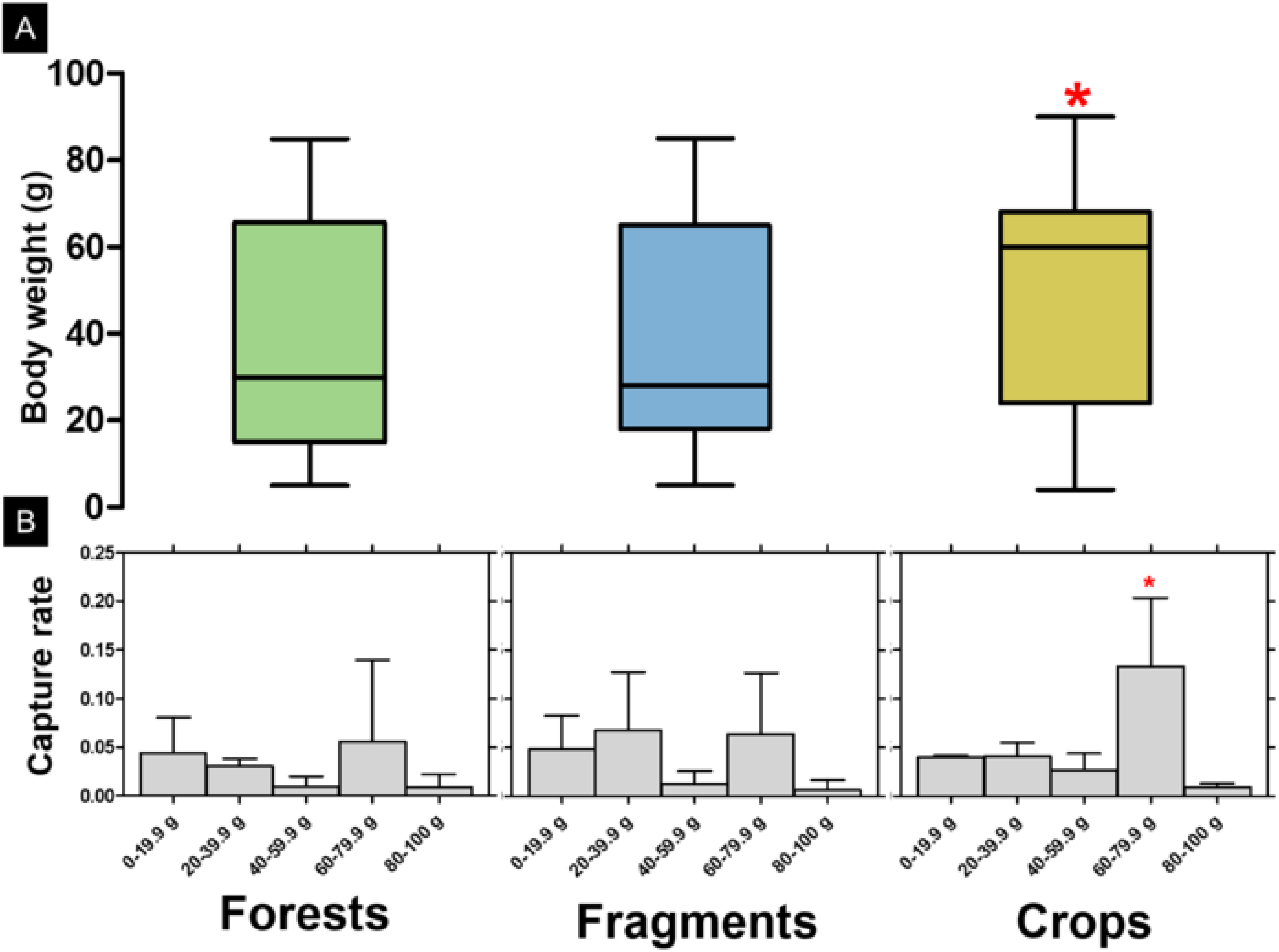

A
B
C
D
Nectarivorous
Frugivorous
Gleaning animalivorous
Hematophagous
Aerial insectivorous
* Anoura caudifer
Anoura peruana
Glossophaga soricina
Lonchophylla sp.
Artibeus jamaicensis
Artibeus lituratus
* Carollia brevicauda
Carollia perspicillata
Chiroderma salvini
Dermanura bogotensis
Dermanura phaeotis
Enchisthenes hartii
Mesophylla macconnelli
Platyrrhinus albericoi
Platyrrhinus angustirostris
Platyrrhinus dorsalis
Sturnira bidens
Sturnira bogotensis
Sturnira ludovici
* Sturnira parvidens
Uroderma convexum
Vampyressa thyone
Micronycteris megalotis
Phyllostomus discolor
Desmodus rotundus
Molossus molossus
Thyroptera tricolor
Eptesicus chiriquinus
Lasiurus blossevillii
Myotis caucensis
Myotis keaysi
Myotis riparius
0
0.05
0.10
0.15
0.20
0.25
Capture rate
0.00
0.01
0.02
0.03
0.04
0.05
0.06
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
-0.003
0.000
0.003
0.006
0.009
0.012
Capture rate
Forests
Fragments
Crops

Figure4


A
Body weight (g)
100
80
60
40
20
0
*
B
Capture rate
0.25
0.20
0.15
0.10
0.05
0.00
0-19.9 g
20-39.9 g
40-59.9 g
60-79.9 g
80-100 g
*
Forests
Fragments
Crops

Anexo 2

Diet and trophic structure in assemblages of montane frugivorous phyllostomid bats

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Diet and trophic structure in assemblages of montane frugivorous phyllostomid bats

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ABSTRACT

Neotropical frugivorous bats display a trophic structure composed of bat species with dietary preferences of core plant taxa (*Artibeus-Ficus* + *Cecropia*, *Carollia-Piper, Sturnira- Solanum* + *Piper*). This structure is hypothesized to be an ancestral trait, suggesting that similar diets would be observed throughout a species' range. However, most evidence comes from lowlands where data from montane habitats are scarce. In high mountain environments both diversity of bats and plants decreases with altitude; such decline in plant diversity produces less plants to feed from, which should ultimately affect the trophic structure of frugivorous bats in mountain environments. Here, we present a comprehensive review of the diet of frugivorous bats in Neotropical montane environments and evaluate their trophic structure in middle and higher elevations by combining a literature database with field data. We use the concept of modularity to test whether frugivorous montane bats have dietary preferences on core plant taxa. Our database revealed 47 species of montane bats feeding on 211 plant species. We find that the networks are modular, reflecting the trophic structure previously reported. We also found that in highlands the tribe Ectophyllini are *Cecropia* + *Cavendishia*-specialists rather than *Ficus*-specialists, and we describe new interactions reflecting 14 species of plants, including three botanical families previously not reported to be consumed by bats.

1. Introduction

Frugivory has been considered the essential condition for the morphological and ecological diversification of the family Phyllostomidae (Rojas et al., 2012). Compared to other families within Chiroptera, the Phyllostomidae is the most taxonomically diverse both in terms of number of genera and number of feeding strategies (Baker et al., 2003; Rojas et al., 2012). Phyllostomid species that feed on fruits, either as their main or complementary resources, represent almost half of the family. All species in the subfamilies Carolliinae, Rhinophyllinae and Stenodermatinae (at least 25 genera) are considered obligate frugivores, and 25 genera in the subfamilies Macrotinae, Micronycterinae, Lonchorininae, Phyllostominae, Glossphaginae, Lonchophyllinae, Glyphonycterinae are opportunistic frugivores (Rojas et al., 2011). These bats feed on at least 550 species of plants (62 plant families) in the Neotropics (Lobova et al., 2009).

Despite the great diversity of bats within the Phyllostomidae and the high number of fruits that they consume, assemblages of neotropical frugivorous bats display a trophic structure composed of bat species with dietary preferences of core plant taxa (*sensu* Fleming, 1986). The three main preferences are: *Artibeus* (feed primarily on fruits of Moraceae *sensu lato Ficus* and *Cecropia*), *Carollia* (feed primarily on *Piper,* Piperaceae), and *Sturnira* (feed primarily on *Solanum,* Solanaceae and *Piper*). Various authors (e.g., Giannini and Kalko, 2004; da Silva et al., 2008; Sánchez et al., 2012; Andrade et al., 2013; Parolin et al., 2016) have explored the predictive power of these preferences and have also extended them beyond *Artibeus, Carollia* and *Sturnira* to include the clades that contain these bat genera (*Ectophyllini, Carollinae,* and *Sturnirini*, respectively). These dietary associations are hypothesized to be an ancestral trait, suggesting that very similar diets should be observed throughout a species' range (Sánchez et al., 2012). Despite the central role that dietary preferences have played in the study of Phyllostomidae, most of the evidence for phyllostomid bats has been collected in lowland habitats ($<$ 1000 m a.s.l.), The evidence for dietary preference from montane habitats is quite scarce. For example, less than 15 studies have been published from highlands compared to approximately 350 papers from lowland habitats (Geiselman et al., 2015; Lobova et al., 2009).

By virtue of their lower temperatures, high mountain environments demand higher energetic expenditures for endotherms to maintain a

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constant body temperature (Soriano et al., 2002). Therefore, low temperatures of montane environments may impose important constraints on bat physiology that in turn should affect the composition of frugivorous bat assemblages in the highlands (Castaño and Corrales, 2010; Soriano, 2000). In fact, the differences between high mountain bat assemblages in terms of composition and diversity with respect to their lowland counterparts (Patterson et al., 1996) may be due to changes in physiological constraints and dietary preferences triggered by changes in temperature (i.e. elevation). Likewise, the relative importance of plant families and the structure and composition of plant communities changes with elevation (Vázquez and Givnish, 1998). There is a linear decline of plant diversity in Andean forests above 1500 m (Gentry, 1988). Such a decline produces a less diverse flora to feed from, which should ultimately affect the trophic structure of frugivorous bats in mountain environments.

The trophic structure formed by groups of animals that have dietary preferences from core plant taxa is equivalent to the concept of modularity in network theory; a network is considered modular if it is formed by cohesive subgroups of closely connected animals and plants (Dormann and Strauss, 2014; Mello et al., 2011). Traditionally, the way to find and delimit link-rich clusters of species in the assemblages of neotropical frugivorous bats (i.e. modules) has been through group species (or genera) using ordination techniques (i.e. Giannini and Kalko, 2004; da Silva et al., 2008). Despite its benefits, ordinations are not able to identify modules with enough precision, even if modules are perfectly separated into compartments, that is there are no species with interactions that reach beyond their own modules (Dormann and Strauss, 2014). Contrary to ordinations, modularity does a much better job at measuring how well links and interactions can be separated into different modules. In sum, network theory facilitates an understanding of the structure of interactions at the community level and it provides the adequate tools to study dietary preferences in frugivorous bat assemblages.

In this study we first present a comprehensive review of the diet of frugivorous bats in Neotropical montane environments (> 1000 m a.s.l.). Second, we hypothesize that the structure of the interactions between montane bats and fruits at middle elevations (1000–2000 m a.s.l.) are modular (according to the network theory) and whether the species composition of the modules reflects dietary preferences on the core plant taxa observed in the lowlands (e.g *Artibeus* feeding primarily on fruits of *Ficus* and *Cecropia*, *Carollia* on *Piper* and *Sturnira* on *Solanum* and *Piper*; Fleming, 1986; Giannini and Kalko, 2004). Third, we hypothesize that, as a consequence of the reduction of available resources in highlands (> 2000 m a.s.l.), frugivorous bats become generalists without modularity in the network.

2. Material and methods

The dataset comprises a literature review and field data collected by the authors.

2.1. Literature review

We compiled information on the diet of montane phyllostomid bats from the literature. We built our database by using "bats," "Phyllostomidae," "seed dispersal," "diet," and "frugivory" as key words in Google Scholar (search in English and Spanish translation) and ISI Web of Knowledge databases. We also searched for studies in the Bat Eco–Interactions Database (Geiselman et al., 2015) and then complemented with additional literature cited by relevant studies. The search was not limited by year of publication or by journal and we also included the data found in the gray literature (thesis). We selected studies from the literature when 1) it reported a given bat species fed on a given fruit taxa, 2) when the bats were identified to species, 3) when the plants were identified to genus or species and this identification was supported by a reference collection of the study site, 4) when the study site was located over 1000 m a.s.l. Data relating to bats that were unidentified at species level or plants unidentified to genus or species were omitted. Given that elevation was not reported in every study, we obtained an approximate elevation by using the geographic coordinates on GoogleEarth software (Google, Inc., version 7.0.2, Mountain View, California) when necessary. We consider a record every time a given bat species was reported as feeding on a given fruit species. Finally, we decided to include studies with sampling efforts shorter than 1 year because our goal was a comprehensive review of the interactions between frugivorous bats and plants in Neotropical montane environment, and because our analyses was conducted at genus rather than species level.

2.2. Field data

We conducted bat surveys in 10 localities within the municipality of Santa Rosa de Cabal, Risaralda, Colombia (elevation ranges 1600–2300 m a.s.l.) during August 2016 to August 2017. Each locality was surveyed four consecutive nights every three months. We used 5–7 mist nets (12 × 2.5 m; 30 mm mesh) per survey, opened mist nets at 18:00 p.m. and closed them at 06:00 a.m. In the event of ongoing heavy rain, nets were closed. Species were identified using the taxonomic keys in Diaz et al. (2016).

We collected fecal samples from captured frugivores. Bats were held in cloth capture bags for no longer than 2 h to allow them to defecate so we could maximize sample yield. We cleaned the bags thoroughly between captures to prevent cross-contamination of fecal samples. Bats were released after the collection of data and fecal samples. Voucher specimens were collected to represent the species diversity of bats at each sampling locality and were deposited in "Colección de Vertebrados UNISARC (CUS-M)". Each sample from each individual was collected separately and then dried and stored in plastic bags. Seeds were identified to species based on a reference collection of the study area deposited in "Herbario UNISARC (CUS-P)".

We built a mixed database with our field data and 28 studies from literature review (14 journal articles, 14 theses) representing 936 independent records of bat–fruit interactions in montane forests between 1000 and 2850 m a.s.l. from Central America (México, El Salvador, Costa Rica) and South America (Argentina, Bolivia, Colombia, Ecuador, Perú, Venezuela) (Table 1).

The taxonomy and nomenclature of frugivorous bats across all studies was updated according to the following authors. We followed Solari et al. (2009) for *Dermanura*; Larsen et al. (2010) for *Artibeus* (*A. intermedius* synonym of *A. lituratus*); Velazco and Patterson (2013) for *Sturnira* (*S. parvidens* for the little yellow-shouldered bat of Mexico, Central America and Colombia, *S. lilium* for South América, *S. hondurensis* for the big yellow-shouldered bat of Mexico and Central America, and *S. adrianae* for the big yellow-shouldered bat of Venezuela (Molinari et al., 2017)); and Mantilla-Meluk (2014) for *Uroderma* (*U. convexum* for Yucatan, Northern Guatemala, Honduras, Nicaragua, Costa Rica, Panamá, and the Pacific slope of Colombia and Ecuador, *U. davisi* for El Salvador, southern Guatemala, and México, and *U. bilobatum* for cis-Andean populations of South America). Plant taxonomy and nomenclature were updated to follow Tropicos® Database.

2.3. Trophic structure in montane fruit bats

We use the concept of modularity from network theory to test whether frugivorous montane bats have dietary preferences on core plant taxa (*Carollia-Piper, Artibeus-Ficus/Cecropia, Sturnira-Solanum*). A network is considered modular if it is formed by cohesive subgroups of closely connected animals and plants that are linked to each other by species with interactions that reach beyond their own modules (i.e., connectors). Therefore, the concept of modules in network theory is related to the ecological concepts of guilds and functional groups, and may be used as a tool to test predictions derived from ecological theory

Table 1
Localities in montane environments (> 1000 m.a.s.l) where interactions between frugivorous bats and plants have been studied.

Country	Locality	Elevation	Source
Argentina	Las Capillas-Jujuy	1000	(Sánchez et al., 2012)
	Tucuman	600–1850	(Giannini, 1999)
Bolivia	Tunquini-Cotapata	1400–1700	(Loayza et al., 2006)
Colombia	Chinchiná-Caldas	1000	(Lozano-Ríos, 2013)
	Curití-Santander	1553	(Borray-Escalante, 2015)
	Filandia-Quindío	2000–2200	(Aguilar-Garavito et al., 2014)
	Jamundí-Valle del Cauca	990–1000	(Montoya-Bustamante et al., 2016)
	Manizales-Caldas	1900	(Ceron and Orozco, 2013)
	Pereira-Risaralda	1800–2100	(Estrada-Villegas et al., 2010, 2007)
	Santa Rosa de Cabal-Risaralda	1600–2300	This study.
	Bogotá-Cundinamarca	2750–2850	(Bolaños-Silva, 2000; Pérez-Torres, 2004)
	Yotoco-Valle	2300	(Moreno-Mosquera, 2011)
Perú	Chanchamayo-Junín	1370–1900	(Arias-Arone, 2016)
	San Pedro-Cusco	1100–1600	(Maguiña et al., 2012)
Ecuador	Zamora-Chinchipe	950–2080	(Zamora-Delgado, 2008)
Venezuela	Calderas-Barinas	1400–1600	(Castaño, 2009)
	Mérida	2000–2500	(Molinari, 1984; Ruiz, 2006)
	Mérida	1400	(Muñoz-Romo and Herrera, 2010)
El Salvador	Santa Ana-Metapán	1000–2418	(Morales-Rivas, 2016)
	Santa Ana-Metapán	1000–2368	(Quijano-Vásquez, 2017)
Mexico	San Luis Potosí	0–1500	(García-Morales et al., 2012)
	Soconusco-Chiapas	1080–1550	(García-Estrada et al., 2012)
	Xalapa-Veracruz	1300–1500	(Hernández-Montero et al., 2015; Saldaña-Vázquez et al., 2010)
	Sierra Manantlán-Jalisco	1600–2180	(Schöndube Friedewold, 1994)
	Sierra Manantlán-Jalisco	1600–2100	(Hernández-Conrique et al., 1997)
Costa Rica	Monteverde	700–1850	(Dinerstein, 1986; Engriser, 1995).

Table 2
Dietary diversity of frugivorous bats in neotropical mountains and number of families (Fam), Genus (Gen) and Species (spp.) of plants consumed, from Argentina (Ar), Bolivia (Bo), Colombia (Co), Costa Rica (Cr), Ecuador (Ec), El Salvador (Sv), Perú (Pe) and Venezuela (Ve). Elevation refers to where the interaction was registered, middle elevations (m) between 1000 and 2000 m a.s.l., and higher elevations (h) > 2000 m a.s.l.

Bats	Plants			Country	Elevation
	Fam	Gen	Spp		
Phyllostominae					
Phyllostomus hastatus	1	1	3	Co, Pe, Ve	m
Glossophaginae					
Anoura caudifer	1	1	1	Ve	m
Anoura cultrata	2	2	2	Ve	m
Glossophaga commissarisi	2	2	2	Me, Sv	m, h
Glossophaga soricina	3	4	6	Me, Ve	m
Lonchophyllinae					
Lonchophylla robusta	2	2	2	Ve	m
Carolliinae					
Carollia brevicauda	15	27	91	Bo, Co, Cr, Ec, Pe, Ve	m, h
Carollia castanea	2	2	4	Co	m
Carollia perspicillata	12	13	42	Bo, Co,	m
Carollia sowelli	6	7	14	Sv, Me	m
Stenodermatinae					
Tribe Ectophyllini					
Artibeus amplus	4	4	4	Ve	m
Artibeus jamaicensis	17	23	43	Co, Sv, Me, Ve	m, h
Artibeus lituratus	17	21	42	Co, Sv, Me, Ve	m, h
Artibeus planirostris	5	5	7	Ar	m
Chiroderma salvini	3	4	5	Co, Ve	m, h
Chiroderma trinitatum	3	3	3	Bo	m
Dermanura bogotensis	9	10	12	Co	m, h
Dermanura glauca	7	10	13	Ec, Pe, Ve	m, h
Dermanura phaeotis	8	11	20	Co, Me	m
Dermanura tolteca	15	19	43	Cr, Sv, Me	m
Enchisthenes hartii	5	5	9	Co, Pe, Ve	m, h
Mesophylla macconnelli	7	7	10	Co, Pe, Ve	m
Platyrrhinus albericoi	2	2	7	Co, Ve	m
Platyrrhinus angustirostris	3	3	4	Ve	m
Platyrrhinus dorsalis	5	5	5	Co	m, h
Platyrrhinus incarum	1	1	1	Pe	m
Platyrrhinus infuscus	3	4	7	Ec, Pe	m, h
Platyrrhinus lineatus	1	1	1	Ec	h
Platyrrhinus masu	7	7	12	Bo, Pe	m
Platyrrhinus umbratus	4	4	6	Ve	m
Platyrrhinus vittatus	1	1	1	Co	m
Uroderma bakeri	2	2	3	Ve	m
Uroderma bilobatum	2	3	3	Pe	m
Vampyressa melissa	3	3	7	Pe	m
Vampyressa thyone	4	4	5	Co, Ve	m
Tribe Sturnirini					
Sturnira adrianae	7	12	22	Ve	m, h
Sturnira aratathomasi	1	1	1	Co	h
Sturnira bidens	7	10	17	Co, Ec, Ve	h
Sturnira bogotensis	11	12	20	Co, Ve	m, h
Sturnira erythromos	13	21	48	Ar, Co, Ec, Pe, Ve	m, h
Sturnira hondurensis	18	25	69	Cr, Sv, Me	m, h
Sturnira lilium	9	12	30	Ar, Co, Ve	m
Sturnira ludovici	10	12	26	Co, Ec	m, h
Sturnira magna	3	3	4	Pe	m
Sturnira oporaphilum	2	2	3	Ar	m
Sturnira parvidens	10	18	47	Co, Sv	m, h
Sturnira tildae	3	3	5	Bo, Pe	m

(Mello et al., 2011).

We pooled all the datasets into two quantitative matrices of interactions, one for middle elevations between 1000 and 2000 m a.s.l. and the other for higher elevations > 2000 m a.s.l. Given that many studies did not report quantitative data for the interactions, each bat species reported in each study was considered as one observation. So the intensity of the interaction between a bat genus (rows) and a fruit genus (columns) was assigned by the number of localities where the same interaction (bat genus-plant genus) has been recorded.

We estimated the degree of quantitative modularity (Q) using the algorithm QuanBiMo (Dormann and Strauss, 2014). This algorithm uses the hierarchical random graph approach, which organizes interacting species into a graph so that close species are more likely to interact. Then it swaps branches at different levels randomly and reassesses the modularity of the network selecting the more modular organization. We calculated Q (varying from 0 to 1) using the bipartite package for R (Dormann et al., 2008). To test the significance of the modularity, we generated 1000 random networks fixing the probability that two species interact, based on the observed real networks. We used the Patefield null model to estimate the significance of the observed network metrics. We then calculated the modularity of the networks and evaluated whether observed modularity fell within the 95% confidence interval calculated from the randomized matrices. We finally standardized the modularity by calculating the Z-score Q (ZQ). Although there is a new algorithm for maximizing weighted modularity in bipartite networks (Beckett, 2016), we continued using QuanBiMo in our modularity analysis because we employ pairwise comparisons (between QuanBiMo and the new algorithm DIRTLPAwb+) and both algorithms detected the same modularity score and similar community partitions. However, QuanBiMo was the appropriate null model to measure the significance of the observed network metrics.

3. Results

Our interaction database revealed 47 species of montane bats (subfamilies Glossophaginae, Lonchophyllinae, Phyllostominae, Carolliinae and Stenodermatinae Table 2) feeding on 211 plant species

Table 3
Plants consumed by frugivore bats in montane forest of neotropical mountains. The bats are grouped by categories, obligate frugivorous include subfamily Carollinae and the tribes Ectophillini and Sturnirini in the subfamily Stenodermatinae, Facultative frugivorous include subfamilies Phyllostominae (Phy.), Glossophaginae (Glo.) and Lonchophyllinae (Lon.). Names of bats are represented by the first letter of the genus and first two letters of specific epithet. Asterisk (*) indicates new records of plants consumed by bats.

Plants	Obligate			Facultative		
	Carollinae	Ectophillini	Sturnirini	Phy.	Glo.	Lon.
Actinidiaceae						
Saurauia brachybothrys	*Cbr*					
Saurauia bullosa			*Sbi*			
Saurauia excelsa	*Cbr*		*Sbi*			
Saurauia kegeliana			*Spa*			
Saurauia madrensis		*Dph, Dto*	*Sho, Spa*			
Saurauia peruviana			*Ser*			
Saurauia spp.	*Cbr, Cso*		*Sho*		*Gco*	
Saurauia tomentosa	*Cbr*					
Saurauia veraguensis		*Dto*	*Sho*			
Anacardiaceae						
Mangifera indica		*Ali*				
Annonaceae						
Rollinia sp.	*Cbr*					
Araceae						
Anthurium bernardii	*Cbr*		*Sad*			
Anthurium effusispathum			*Sbi*			
Anthurium humboldtianum			*Sad, Sbi*			
Anthurium longistrorsum			*Sbi, Ser*			
Anthurium myosuroides	*Cbr, Cpe*		*Sbo, Spa*			
Anthurium nymphaeifolium	*Cbr*		*Sad, Sbi*			
Anthurium spp.	*Cbr, Cpe*	*Dbo*	*Sad, Sbo, Sho, Slu, Sma, Spa*			
Anthurium triphyllum	*Cbr*					
Anthurium versicolor	*Cbr, Cpe*					
Monstera sp.		*Dgl*				
Philodendron spp.	*Cbr*	*Dph, Pma*	*Sad, Sbi, Ser, Slu*			
Xanthosoma daguense			*Ser*			
Xanthosoma microrhiza			*Sho*			
Xanthosoma spp.	*Cbr*	*Dgl*				
Araliaceae						
**Schefflera* sp.		*Dbo*				
Asteraceae						
Aldama sp.		*Aja*				
Barnadesia spinosa			*Sbo, Slu*			
Tridax sp.		*Aja*				
Vernonia sp.		*Aja*				
Bromeliaceae						
Aechmea tillandsioides	*Cpe*					
Calophyllaceae						
Calophyllum brasiliense		*Aja, Ali*				
Campanulaceae						
Burmeistera cyclostigmata		*Dto*	*Sho*			
Centropogon sp.	*Cbr*					
Cannabaceae						
Celtis iguanaeus		*Apl*	*Ser, Sli*			
Trema micrantha		*Aja, Ali, Dto*	*Sho, Spa*		*Gco*	
Caryophyllaceae						
Drymaria sp.		*Aja*				
Chloranthaceae						
Hedyosmum mexicanum	*Cso*		*Sho, Spa*			
Clusiaceae						
Garcinia intermedia		*Ali*	*Sho*			
Cyclanthaceae						
Asplundia sp.			*Sma*			
Asplundia tetragona	*Cbr*					
Asplundia vagans	*Cbr*	*Pum*	*Sad, Ser, Sho*			
**Cyclanthus* sp.	*Cbr, Cpe*	*Ali, Dbo, Dph, Mma*	*Sbo*			
**Sphaeradenia* sp.	*Cbr*		*Sad*			
***Ericaceae**						
**Cavendishia pubescens*	*Cbr*	*Dbo*				
**Cavendishia* sp.		*Ali, Dbo, Eha, Pdo*	*Sbo, Ser, Slu*			
**Cavendishia zamorensis*			*Ser*			
**Psammisia penduliflora*	*Cbr, Cpe*	*Aam, Aja, Dgl, Mma, Pum*	*Ser, Sli*			
**Psammisia* sp.		*Dbo*				
Euphorbiaceae						
Alchornea latifolia		*Aja, Dto*				
Fabaceae						
Acacia sp.	*Cpe*					
Gesneriaceae						

(*continued on next page*)

Table 3 (*continued*)

Plants	Obligate			Facultative		
	Carollinae	Ectophillini	Sturnirini	Phy.	Glo.	Lon.
**Columnea* sp.	*Cbr*					
Drymonia rubra		*Dto*	*Sho*			
Gesneriaceae indet.	*Cbr*					
Hypericaceae						
Vismia baccifera	*Cbr, Cpe*	*Aam, Aja, Ali, Dgl, Mma, Pan, Vth*	*Sad, Sbi, Sbo, Ser, Sli*		*Acu, Gso*	
Vismia glaziovii	*Cpe*					
Vismia guianensis	*Cbr, Cpe*	*Aja, EhaPdo*	*Slu, Spa*			
Vismia mexicana	*Cso*	*Dto*	*Sho, Spa*			
Vismia spp.	*Cbr, Cpe,*	*Ctr, Pma*	*Sti*			
Vismia tomentosa			*Ser*			
Lamiaceae						
Salvia sp.		*Dph, Dto*	*Spa*			
Malvaceae						
Guazuma ulmifolia		*Aja, Ali*				
Marcgraviaceae						
Marcgravia helverseniana			*Ser*			
Marcgravia spp.	*Cbr*					
Melastomataceae						
Clidemia sp.					*Gso*	
Conostegia icosandra		*Dto*				
Conostegia volcanalis		*Dto*	*Sho*			
Conostegia xalapensis			*Spa*			
Melastomataceae indet	*Cbr*	*Pma*	*Vme*			
Miconia glaberrima			*Sho*			
Miconia mexicana			*Spa*		*Gso*	
Miconia spp.	*Cso*	*Ali, Dbo, Pdo*				
Moraceae						
Ficus americana		*Ali, Eha, Pal, Pdo, Pma*	*Sbi, Spa, Slu*			
Ficus aurea		*Aja, Ali, Dph, Dto*	*Sho*			
Ficus citrifolia		*Dgl*				
Ficus cotinifolia		*Aja, Ali, Dto*	*Sho, Spa*			
Ficus cuatrecasasiana		*Csa, Dbo*				
Ficus insipida		*Aja, Ali, Csa, Dgl, DphEha, Mma, Pal, Pan, Pvi, Uba, Vth*				
Ficus maxima	*Cbr*	*Aam, Aja, Ali, Apl, Dgl, Mma, Pan, Pum, Uba, Vme, Vth*				*Lro*
Ficus obtusifolia		*Ali, Aja, Dto*				
Ficus pertusa		*Ali, Aja, Dph, Dto*	*Sho*			
Ficus spp.	*Cbr, Cpe*	*Aja, Ali, Dph, Dto, Mma, Pal, Pin, Pma, Pum, Ubi, Vme*	*Sad, Sho, Slu*			
Ficus tonduzii		*Aja, Ali, Pal*				
Ficus yoponensis		*Dto*	*Sho,*			
Maclura tinctoria	*Cpe*	*Ali*	*Sho, Spa*			
Poulsenia armata		*Csa*				
Trophis mexicana		*Aja, Ali*	*Spa*			
Muntingiaceae						
Muntingia calabura		*Aja, Ali*				
Myrtaceae						
Eugenia acapulcensis		*Dto*				
Myrcia popayanensis	*Cpe*					
Psidium caudatum	*Cbr*					
Psidium guajava	*Cca*	*Aja, Ali, Dto*	*Slu*			
Psidium sp.	*Cbr*					
Syzygium jambos		*Aja, Ali*				
***Onagraceae**						
**Fuchsia hartwegii*	*Cbr*					
**Fuchsia microphylla*			*Sho*			
**Fuchsia* sp.		*Dbo*				
Passifloraceae						
Passiflora kalbreyeri			*Ser*			
Passiflora sp.	*Cbr*					
Passiflora umbilicata			*Sli*			
Piperaceae						
Peperomia spp.		*Aja, Ali, Dph, Dto*	*Sho, Spa*			
Piper imperiale			*Slu*			
Piper aduncum	*Cbr, Cca, Cpe*	*Aja, Ali, Ctr, Dgl, DphMma, Pma*	*Sad, Sbo, Ser, Sli, Slu, Spa, Sti*			
Piper aequale			*Sho*			
Piper amalago		*Aja, Dto*	*Sho, Spa*			
Piper augustum	*Cpe*		*Sli, Slu*			
Piper auritum	*Cbr, Cso*	*Aja, Ali*	*Sho, Spa*			
Piper barbatum	*Cbr*		*Sad, Ser*			
Piper bisasperatum		*Dto*	*Sho*			
Piper carpunya	*Cbr*					
Piper crassinervium	*Cbr, Cpe*	*Ali, Dph, Vth*	*Slu, Spa*			
Piper diffamatum	*Cbr, Cpe*	*Ali, Dgl, Mma*	*Sad, Sbi, Sbo, Ser*			
Piper dotanum		*Dto*	*Sho*			

(*continued on next page*)

Table 3 (*continued*)

Plants	Obligate			Facultative		
	Carollinae	Ectophillini	Sturnirini	Phy.	Glo.	Lon.
Piper ecuadorense			*Ser, Slu*			
Piper epigynium		*Dto*	*Sho*			
Piper gibbosum			*Sho*			
Piper glabratum	*Cbr, Cca, Cpe*		*Slu*			
Piper glabrescens			*Sho*			
Piper hieronymi			*Ser*			
Piper hispidum	*Cbr, Cpe, Cso*	*Aja, Dph, Dto*	*Sho, Spa*		*Gso*	
Piper lanceifolium		*Dto*	*Sho*			
Piper lapathifolium	*Cso*	*Aja*	*Sho, Spa*			
Piper longispicum	*Cbr, Cpe*		*Sad*			
Piper marginatum	*Cbr, Cpe*					
Piper obliquum			*Sho*			
Piper peltatum	*Cbr, Cpe*					
Piper phytolaccifolium	*Cbr, Cpe*	*Csa*	*Sad, Sho*			
Piper pseudo-lindenii			*Sho, Spa*			
Piper psilophyllum	*Cbr, Cpe*	*Pma*	*Sti*			
Piper schiedeanum	*Cbr, Cca, Cpe*	*Dph*				
Piper septuplinervium	*Cca, Cpe*					
Piper spp.	*Cbr, Cso*	*Aja, Dto*	*Sbi, Sbo, Ser, Sho, Slu, Spa*		*Gso*	
Piper tuberculatum	*Cbr, Cpe*	*Ali*	*Sli*			
Piper tucumanum		*Apl*	*Ser, Sli, Sop*			
Piper umbellatum	*Cbr*		*Sho*			
Piper yzabalanum	*Cso*	*Dto*	*Sho, Spa*			
Rhamnacea						
Frangula hintonii			*Sho*			
Rosaceae						
Eriobotrya japonica		*Aja, Dto*				
**Hesperomeles* sp.			*Sbo*			
Prunus integrifolia		*Ali*				
Rubiaceae						
Randia micracantha			*Sad, Sli*			
Rutaceae						
Casimiroa sapota		*Aja, Ali*				
Zanthoxylum sp.			*Sho*			
Salicaceae						
Neosprucea sp.	*Cpe*					
Sapotaceae						
Sideroxylon capiri		*Aja, Ali*				
Siparunaceae						
Siparuna sp.			*Sbo*			
Solanaceae						
Acnistus arborescens	*Cbr*		*Sho*			
Cestrum sp.	*Cbr*		*Sad, Sli, Uba*			
Cuatresia riparia	*Cbr*		*Sad, Sbi, Sbo, Ser, Slu*			
Juanulloa mexicana		*Dph*	*Sho, Spa*			
Lycianthes geminiflora	*Cso*	*Ali, Dto*	*Sho, Spa*			
Lycianthes radiata			*Sbi, Ser*			
Lycianthes spp.	*Cbr*	*Dgl*	*Sad, Ser, Sli, Spa*			
Lycianthes surotatensis			*Sho*			
Nicandra physalodes	*Cbr*	*Dgl, Ubi*	*Spa*			
Nicotiana sp.	*Cbr*	*Pin*	*Spa*			
Physalis sp.		*Dph*	*Ser, Sli*			
Schultesianthus venosus		*Dto*				
Solanaceae indet.		*Mma*	*Spa*			
Solanum abutiloides		*Apl*	*Ser, Sli, Sop*			
Solanum acerifolium	*Cbr*	*Ali,*	*Sho, Sli, Spa*			
Solanum aligerum			*Ser, Sli*			
Solanum aphyodendron	*Cbr, Cpe, Cca*	*Aja, Ali, Apl, Dbo, Dph, Dto, Eha*	*Sad, Sbi, Sbo, Ser, Sho, Sli, Slu, Sop, Spa*			
Solanum appendiculatum			*Sho, Sli, Spa*			
Solanum appressum			*Sti*			
Solanum argenteum		*Dto*	*Sho*			
Solanum bicolor	*Cbr*	*Ali*	*Sli*			
Solanum cf. *abitaguense*	*Cbr, Cpe*		*Spa, Ubi*			
Solanum cf. *sessile*	*Cbr, Cpe*	*Eha*	*Spa*			
Solanum chrysotrichum		*Aja, Ali, Dph, Dto*	*Sho, Spa*			
Solanum confusum			*Ser*			
Solanum diphyllum		*Aja, Dto*	*Sho, Spa*			
Solanum dissimile	*Cbr*		*Sbo, Ser*			
Solanum erianthum			*Sho, Spa*			
Solanum grandiflora			*Ser, Slu*			
Solanum gratum	*Cbr*					
Solanum hispidum			*Sho*			
Solanum mauritianum	*Cpe*					

(*continued on next page*)

Table 3 (*continued*)

Plants	Obligate			Facultative		
	Carollinae	Ectophillini	Sturnirini	Phy.	Glo.	Lon.
Solanum meridense	*Cbr*					
Solanum muela	*Cbr*					
Solanum nigricans		*Dto*	*Sho*			
Solanum ovalifolium			*Sbi, Spa*			
Solanum pseudocapsicum	*Cso*		*Ser, Sli, Sho, Sli*			
Solanum rovirosanum			*Sho*			
Solanum schlechtendalianum	*Cso*	*Aja*	*Sho, Spa*			
Solanum scuticum			*Slu*			
Solanum spp.	*Cbr, Cpe*	*Dbo, Dgl, Pin*	*Sad, Sbi, Sbo, Ser, Sho, Sli, Slu, Spa*			
Solanum sycophanta			*Sar*			
Solanum tanysepalum	*Cpe*		*Sbo, Ser*			
Solanum tenuispinum			*Ser, Sli*			
Solanum ternatum			*Sbo, Ser*			
Solanum trichoneuron			*Ser, Sli*			
Solanum umbellatum	*Cbr*	*Apl, Ctr, Dto, Pma*	*Ser, Sho, Sli, Sti*			
Solanum undulatum		*Aja, Ali*	*Slu, Spa*			
Trianaea sp.			*Ser*			
Vassobia lorentzii			*Ser*			
Urticaceae						
Cecropia angustifolia	*Cbr*	*Ali, Pal*				
Cecropia gabrielis		*Pin, Pli*	*Slu*			
Cecropia latiloba			*Ser*			
Cecropia membranacea	*Cbr*	*Pinc, Pma, Vme*		*Pha*		
Cecropia obtusifolia		*Aja, Ali*	*Sho, Spa*			
Cecropia peltata		*Aja, Ali, Dto*	*Sho*			
Cecropia polyphlebia			*Sho*			
Cecropia reticulata				*Pha*		
Cecropia sararensis	*Cbr, Cpe*	*Aam, Ali, Dgl, Eha, Mma, Pal, Pan, Pum,*	*Sas, Sli, Vth*	*Pha*	*Aca, Acu*	*Lro*
Cecropia spp.	*Cbr*	*Aja, Pma, Sma,*	*Sho*			
Cecropia telealba	*Cbr, Cpe*	*Aja, Ali, Csa, Dbo, Eha, Pal, Pdo, Pum*	*Sbo, Ser, Slu, Spa*			
Coussapoa villosa		*Dto*				
Urera caracasana		*Apl*	*Ser, Sli*			
Urera sp.			*Sho*			
***Winteraceae**						
**Drimys* sp.			*Sbo, Slu*			

from 79 genera and 39 families (Table 3).

3.1. Bats

Of the 47 frugivorous bat species, 19 were present in both the middle and higher elevations, 28 only in middle elevations and only 3 in the higher elevations (Table 2).

The most important frugivore montane bat was *C. brevicauda,* which ate 91 species of fruit from 27 genera in 15 families of plants across the elevation gradient from both Central and South América. The second most important species was *S. hondurensis,* which ate 69 species of fruit from 25 genera in 18 families of plants across the elevation gradient from Central América only. Finally, the most important order of frugivorous bat genera in terms of richness of plants consumed were *Sturnira* (46 genera), followed by *Carollia* (34 genera), *Artibeus* (32 genera), *Dermanura* (32 genera), and *Platyrrhinus* (12 genera).

3.2. Plants

The genera of plants most commonly consumed by montane bats at middle elevations (1000–2000 m a.s.l.) were *Piper* (23%), *Solanum* (19%), *Ficus* (12%), *Cecropia* (9%) and *Vismia* (5%). At higher elevations (> 2000 m a.s.l.) the five most commonly consumed plant genera were *Solanum* (22%), *Piper* (17%), *Anthurium* (8%), *Cecropia* (7%), *Cavendishia* (6%), and *Vismia* (6%).

3.3. Trophic structure in montane fruit bats

Both middle and high elevation networks were modular. The network for middle elevations was composed of four modules ($Q = 0.27$, $ZQ = 15.6$, p-value < 0.001 Fig. 1 right) the first was composed by *Sturnira* interacting with 20 genera of plants, especially with *Solanum*. The second module was composed by *Carollia* and *Glossophaga* interacting with 18 genera of plants especially with *Piper*, *Vismia* and *Anthurium.* The third module was composed by *Chiroderma* interacting with *Poulsenia,* and the last module was composed of 9 genera, (6 from the tribe Ectophyllini plus the 3 facultative frugivorous *Phyllostomus, Anoura* and *Lonchophylla*) interacting with 31 plant genera, especially with *Cecropia* and *Ficus* (Fig. 1 right).

The network from higher elevations was composed of three modules ($Q = 0.26$, $ZQ = 4.2$, p-value < 0.001; Fig. 1 left). The first was composed by *Sturnira* interacting with 13 genera of plants, especially with *Solanum* and *Anthurium*. The second module was composed by *Carollia* and *Glossophaga,* which interacted with 8 genera of plants, especially with *Piper* and *Saurauia*. The last module made up of 4 genera from the tribe Ectophyllini, which interacted with 7 genera of plants, especially *Cecropia, Vismia,* and *Cavendishia* (Fig. 1 left).

4. Discussion

Based on our extensive literature review and our field observations we add important information to our knowledge of the diet and trophic structure of montane frugivorous phyllostomid bats by describing that the networks are modular, where each module reflects the trophic structure previously reported for frugivorous bat assemblages. We also found that at high altitudes, species of the tribe Ectophyllini are *Cecropia* + *Cavendishia*-specialists rather than *Ficus*-specialists as reported for the lowlands, and finally we describe new interactions reflecting 14 species of plants, including three botanical families, previously not reported to be consumed by bats.

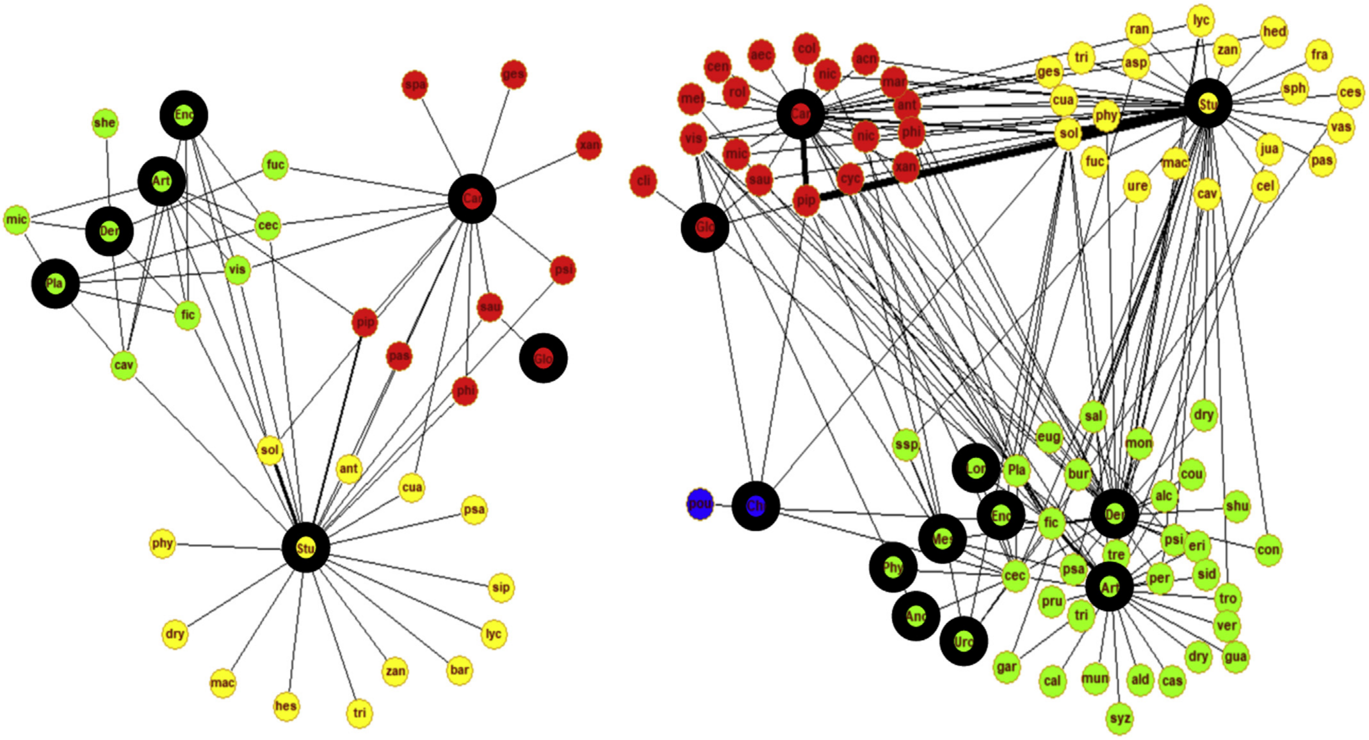

Fig. 1. The modular structure (representing dietary preferences in the interactions between genera of Neotropical frugivorous bats (broad border circles) and fruits (slender border circles) in montane environments. Species in the same module (same color) are more densely connected to each other than to other species in the same network. Right: middle elevations network (between 1000 and 2000 m a.s.l.) Q = 0.27, four modules. Left: higher elevations network (> 2000 m. a.s.l). Q = 0.26, three modules. Line width (edge) represents a frugivory interaction. Genus names are represented by the first three letters.

The modularity analysis was able to separate the three most important clades of frugivores, Ectophyllini, Carollinae, and Sturnirini, into different modules. Even though the structure we found is similar to the tropic structure previously reported employing ordination analysis (i.e. Giannini and Kalko, 2004; da Silva et al., 2008), the network analysis is far more intuitive to understand, easier to visualize, and more amenable to analyze than ordination analysis. Moreover, our modularity analysis showed the modules are not perfectly separated into compartments. Bats consume not only their preferred food items but share resources between modules. This is evidence that the whole assemblage is interconnected.

At middle elevations (1000–2000 m a.s.l.) the trophic structure of the frugivorous montane bat assemblage reflected the dietary preferences of core plant taxa with *Artibeus* feeding primarily on *Ficus* and *Cecropia*, *Carollia* feeding primarily on *Piper,* and *Sturnira* feeding primarily on *Solanum* and *Piper* (da Silva et al., 2008; Fleming, 1986; Giannini and Kalko, 2004). However, the most important difference at higher elevations (> 2000m) is the lack of association between *Artibeus* and *Ficus*. *Ficus* was a rare dietary item for *Artibeus* and was also rare in the diet of other bat genera in the Ectophyllini (*Platyrrhinus, Enchisthenes, Dermanura*). *Artibeus* were initially hypothesized to be *Ficus*-specialists (Fleming, 1986) and this hypothesis was later extended to the whole Ectophyllini tribe (Giannini and Kalko, 2004). However, our findings support what Saldaña-Vázquez et al. (2013) reported that *Artibeus* reduces the intake of *Ficus* and *Cecropia* as elevation increases (between 0 and 2000 m a.s.l.) probably because *Ficus* is less diverse at higher elevations (Franco-Rosselli and Berg, 1997; Gentry, 1995; Shanee and Peck, 2008). *Ficus*-specialists at higher elevations were found to be *Cecropia* + *Cavendishia*-specialists and we found no *Ficus* specialists at high altitudes (> 2000). In fact, *Cecropia* and *Cavendishia* were commonly consumed not only by Ectophyllini but by the majority of the mountain frugivorous bat assemblages.

This result supports previous observations that *Cecropia* is an important dietary item for many frugivores (Charles-Dominique, 1986; da Silva et al., 2008; Horsley et al., 2015), but this is the first report of the consumption of *Cavendishia* and *Psamissia*, both from the family Ericaceae family. Ericaceae was previously unknown to be consumed by bats (Geiselman et al., 2015; Lobova et al., 2009) but it seems to be a common food at higher elevations (> 2000m) in the Andes in Colombia (Bolaños-Silva, 2000; Ceron and Orozco, 2013; Pérez-Torres, 2004), Venezuela (Castaño, 2009) and Ecuador (Zamora-Delgado, 2008). At higher elevations near the timberline Ericaceae is one of the most diverse woody families of woody flora in the Andes (Gentry, 1995). This could explain the importance of *Cavendishia* in the diets observed in the montane bats of the Ectophyllini tribe (*Artibeus*, *Platyrrhinus, Enchisthenes,* and *Dermanura*).

Compared to the lowlands there are very few data on diet from the frugivorous bats of the high mountains, especially above the higher level (> 2500 m a.s.l.). There is just one locality studied in the western part of the savanna of Bogotá, Colombia (Bolaños Silva, 2000; Pérez-Torres, 2004). This information gap in the diet of montane bats is reflected by our findings of 14 species (10 genera) previously unknown that are consumed by bats. This includes three botanical families (Ericaceae, Onagraceae, Winteraceae) not previously reported to be consumed by bats (Table 2).

There is a reduction in the number of frugivorous bats found at higher elevations compared to middle elevations. The decline in species numbers from different fauna groups associated with an altitudinal gradient is a phenomenon widely referred to in the literature (Carvajal-Quintero et al., 2015; Lomolino and Brown, 2009; Soriano, 2000). For bats this has been interpreted as a consequence of the reduction of available resources or physiological limitation in order to face decreases in the ambient temperature (Ruiz, 2006; Soriano, 2000; Soriano et al., 2002). We cannot separate the concomitant effects of the two possible causal factors of this phenomenon (decrease in temperature, and the reduction in abundance of resources). On the one hand, the reduction in the number of species in the genus *Chiroderma, Artibeus, Dermanura* and *Plathyrrhinus,* could be due to a reduction in the abundance of their preferred plant genus *Ficus* at higher elevations (Gentry, 1995). On the other hand, the reduction in number of species in the genus *Carollia* could be due to physiological limitations; the preferred plant genus for *Carollia* (*Piper*) seems to be abundant at higher elevations (Saldaña-Vázquez et al., 2013) and there is only one species from the Carolliinae subfamily at higher elevations. The wide elevational distribution of *C. brevicauda* over 2000 m a.s.l. could be due to adaptations such as very dense fur, reduction of uropatagium, small ears, and densely haired feet and toes allowing them to face lower temperatures. Similarly some species are exclusively associated with the higher elevations (e.g. *S. bidens, S. aratathomasi*), which seems to be an indicator that some bat species at higher elevations must possess certain adaptive features to those environments, which at the same time makes their presence incompatible with the prevalent conditions at the lower elevations (Soriano et al., 2002). It is probable that at least for *Carollia* spp. and *Sturnra* spp. the determining factor that limits their altitudinal distribution are of a physiological nature and linked to their thermoregulatory capacity, since the types of food consumed along their altitudinal range are the same.

5. Conclusions

Our modularity analysis partially confirms that montane frugivorous phyllostomid bats are faithful to core plant taxa, as originally suggested by Fleming (1986), with *Carollia* feeding primarily on fruits of *Piper, Sturnira* on *Solanum* and *Artibeus Ficus* and *Cecropia*. However, our study showed that in montane environments especially above 2000 m, species of the tribe Ectophillini switch to resources different from those they prefer in the lowlands. This new result is particularly important because it shows that a loss in the abundance and diversity of *Ficus* at higher elevation might force species in the Ectophillini to change their dietary preferences. Moreover, this finding supports and extends the idea that *Artibeus* (as proposed by Saldaña-Vázquez et al., 2013), as well as the other genera in the Ectophillini (*Platyrrhynus*, *Enchisthenes,* and *Dermanura*), have the ability to use other plant species as they exploit a wide diversity of habitats from the lowlands to mountain ecosystems.

Author's contributions

JHC and JPT formulated the idea, JHC and JAC conducted the fieldwork, JHC performed network analyses, JHC, JAC, and JPT wrote the manuscript.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2018.06.005.

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Anexo 3

Does seed ingestion by bats increase germination?: a new meta-analysis 15 years later

Manuscrito en proceso de revisión en la revista Mammal Review.
Ya pasó una primera ronda de revisión y actualmente estamos preparando la respuesta a los evaluadores.

Does seed ingestion by bats increase germination?: a new meta-analysis 15 years later.

Abstract

1. The seed dispersal cycle forms the base of vegetation establishment and population dynamics. Evidence shows varied results for the role of frugivorous bats, where ingestion and gut passage increase seed germination for some plant species, but not for others.
2. Using meta-analysis techniques with a novel database spanning 31 years of study, we answered the following questions: 1) Does seed passage through bat digestive tracts increase seed germination compared to seed pulp removal by humans? 2) Does seed ingestion by bats accelerate seeds´ time until germination compared to seed pulp removal by humans? 3) Is there an effect of germination conditions, bat species and plant species on seed germination? and 4) Is there an effect of fruit bat dietary preferences on seed germination?
3. In general, seed passage through bat digestive tracts neither significantly increased nor accelerated seed germination. Seed germination varied mainly with plant species and bat species, as some plant species presented consistently high or low germination rates and less than 25% of plant species responded to bat gut passage. While most bat species had no effect on germination, some had positive and others had negative effects. However, plant species that were preferred by a species of bat showed higher germination success than non-preferred plant species, in line with the core plant taxa hypothesis.
4. These results suggest that the principal role of frugivorous bats in seed dispersal is the transport of seeds away from parent plants, and seed germination of fruits consumed by bats is idiosyncratic to the bat and plant species in question.

Keywords: diet preferences, core plant taxa, frugivory.

Running head: Does seed ingestion by bats increase germination?

Word count: 4525 words.

Introduction

Vertebrates offer three principal services to plants, i.e. the transport of seeds away from parent plants, the enhancement of germination after seeds passed through their guts and finally the increase of seed germination velocity after consumption (Samuels & Levey 2005, Traveset & Verdú 2002, Pires et al. 2018). Seed germination is one of the most important stages of the seed dispersal cycle, because it is related with the first stage of plant establishment (Wang & Smith 2002). However, not all seed dispersers assist seed germination equally well, as the quality of seed dispersal is dually influenced by the seed and fruit handling by vertebrates and the ecophysiological traits of seeds (Schupp et al. 2010).

Bats are one of the principal vertebrate taxa that provide seed dispersal (Traveset 1998, Traveset & Verdú 2002). Many frugivorous bats are dietary specialists and have evolved to obtain their primary nutrients from fruits and their handling facilitates seed germination (Fleming 1986, Dumont 1999, Rojas et al. 2011). The first quantitative review about the effect of seed passage through vertebrate guts found that bat gut passage enhances seed germination, compared to control seeds, suggesting that bats have a physical and chemical effect on seed germination success, due the alteration of the seed coat or endocarp (Traveset & Verdú 2002).

However, there are plenty of factors that could affect the seed germination of fruits consumed by frugivorous bats. For example, the germination conditions which vary among experimental setups, or the bat dietary preferences, which are related to fruit selection and handling, could both account for variation in seed germination (Dumont 1999).

In addition, since the Traveset & Verdú (2002) review, more than 18 studies about seed germination of fruits consumed by bats has been published, with negative and positive effects of fruit bat seed consumption on germination. As the quantity of data available has nearly doubled in the last 15 years, it is worth making a new quantitative review about the effect of frugivorous bats in seed germination, including some questions not previously evaluated.

Thus we asked the following additional questions: Is there an effect of seed origin and germination conditions used in the experiments? In seed germination experiments, the authors had two ways to control the origin of seeds: homogenized or unhomogenized. When the authors used the same fruits for the treatment and control, the seeds were homogenized. If the authors used different fruits for the treatment and control, the seeds were unhomogenized. This experimental design could have an effect on seed germination success, because the viability of seeds could change between plant populations and individuals (Baloch et al. 2001, Cruz et al. 2003). On the other hand, researchers used different germination conditions, such as placing seeds in petri dishes, cylindrical field exclusions, or petri dishes with soil, etc. These methods could result in different ambient conditions and have an effect on germination success (Traveset & Verdu 2002). Therefore, these factors need to be evaluated.

Is there an effect of bat and plant species on germination success? Previous studies of the effect of bat fruit consumption on seed germination success have found that seed germination success varies with bat and plant species, partly because seed plant species consumed by bats had different abilities to germinate and grow independently of the seed disperser (i.e. Naranjo et al. 2003, Rojas-Martinez et al. 2015). On the other hand, frugivorous bats show different fruit handling and digestion times, especially in the Neotropics, and thus may not all have equal effects on seed germination (see Laska 1990, Dumont 1999). Therefore, we would expect significant effects of bat and plant species on seed germination.

Was seed germination of plant species that are preferred by bats higher than seed germination of non-preferred fruits? The evolution of bat diet preferences appeared in the Miocene, more than 20 millions of years ago, and could result in higher germination success of plants preferred by bats (Sánchez & Giannini 2018). These preferences involve associated genera of bats and plants: *Artibeus* species feeds primarily on fruits of *Ficus* and *Cecropia* species, *Carollia* species feeds primarily on *Piper* species, and *Sturnira* species feeds primarily on *Solanum* species (Fleming 1986, Sánchez & Giannini 2018). Therefore, we would expect increased germination success for preferred plant species preferences (core-plant taxa hypothesis).

For all aforementioned questions, germination enhancement is defined as observing a higher proportion of seeds that passed through a vertebrate gut compared to control seeds. As we used meta-analysis techniques to answer our questions, we had to employ a definition of control seeds that accommodated the numerous conditions encountered in the literature. Controls could be seeds that germinate in the intact fruit (which occurs when fruits fall to the ground without fruit removal by the disperser) or control seeds may be manually extracted from fruit pulp, depending on experimental setup. Control seeds that have been manually extracted (depulped by humans) allow researchers to evaluate the physical/chemical consequence of the vertebrate gut on germination via alteration of the seed coat or endocarp, but fail to isolate the effect of pulp removal. Control seeds that remain in intact fruits are ecologically more realistic controls, as they allow researchers to consider the fruit removal and handling effect provided by the disperser (Samuels & Levey 2005). However, few studies employ natural control seeds (but see Heer et al. 2010; Izhaki et al. 1995 and Naranjo et al. 2003), so we combined both natural and human depulped control seeds to define the control seeds for our study. One assumption we must make is that all researchers in our meta-analysis database depulped seeds in a similar manner. While this is certainly questionable, the minutiae of seed handling protocols are not generally shared in sufficient detail to feature in a meta-analysis as moderator variables.

Finally we asked, Does seed consumption by bats increase the speed of germination? By depulping seeds in their guts, bats may influence the speed of germination, due the chemical action of the gut on germination inhibitors and osmotic conditions as lipids, glycoalkaloids, etc. (Samuel & Levey 2005). Accordingly, we predict that germination success of ingested seeds by bats should have similar germination success compared to control seeds depulped by humans. We based this prediction on 1) previous results that reported an enhancement of seed germination by seeds consumed by bats using depulped seeds as a controls (Traveset & Verdú 2002), 2) there are few bat species reported that act as seed predators (Wagner et al. 2015) and 3) the observation that bats handle fruits benignly, exhibit fast transit times and clean seeds during fruit pulp ingestion (Bonaccorso & Gush 1987, Laska 1990, Dumont 1999, Hernández-Montero et al. 2011). Therefore germination velocity should be similar between seeds depulped by humans and bats.

Seed germination rate (velocity) can be measured in two forms: 1) the day in the experiment when the first seed germinated and 2) the total number of days required until all the seeds germinated. For our meta-analysis approach, we decided to use the day of first germination for our definition of the germination velocity. This is because there is considerable variation in the duration of germination experiments in the literature (x-x days), and it is difficult to ascertain whether or not each experiment monitored seed germination until final completion.

Methods

Literature search

We conducted an extensive review of the literature available through Google Scholar and Web of Science. The literature obtained was supplemented with studies cited in the reference lists of the articles surveyed (secondary search). The keywords used were "bats", "murciélagos", "seed germination", "germinación de semillas", and "gut passage". We did not include the words in Portuguese, because the majority of the studies published in Portuguese regularly include a title, abstract and keywords in English. We restricted these terms to appear only in the title of the article when we used Google Scholar. While when we used Web of Science "bats" only appeared in the title and "seed germination" and "gut passage" in the topic of the paper. We did not limit the search by year of publication. We selected studies that contain detailed data about seed germination experiments, such as the number of seeds used in the experiments, number of germinated seeds, bat species that consumed the seeds and the plants' species. When studies did not report the germination data in a table, they were extracted from the figures using the software DATA THIEF III version 1.7 (Tummers 2006).

Database

We obtained a total of 33 studies that presenting useful data (Appendix S1). The 33 studies selected summarized 106 experiments, conducted in 13 countries, from 23 bat species of 14 genera from the families Phyllostomidae and Pteropodidae, and 61 plant species of 16 genera and 12 families (Appendix S1). We included 10 unpublished experiments of our own.

Meta-analysis

We did six analyses, corresponding to our six hypotheses and predictions. In the first, we examined the effect of bat seed ingestion on germination success, without evaluating moderators variables such as bat or plant species. Therefore, we calculated the log odds ratio (logOR) of the control (human depulped seeds) and treatment (seeds consumed by bats) and their associated variance. Because more than one seed germination experiment came from the same author, these data are not independent observations in the analysis (Nakagawa et al. 2017). Therefore, we fitted a random effect model, using the “author” of the studies as a random effect and no fixed effect. In addition, we used the Cochran's *Q* index as a measure of heterogeneity of each analysis. Heterogeneity in meta-analyses is an important characteristic, because it allows us to evaluate if the variation in the effect sizes collected is explained with the population variation or by chance (Harrison 2011, Nakagawa et al. 2017). In addition, if the heterogeneity is significant, this means that variation in effect sizes could be explained by moderator variables (i.e. species, experimental design, etc.). In order to examine the publication bias in our data set, we performed a regression test (Egger et al. 1997). The regression test evaluated if we have balanced effect sizes. If effect sizes are balanced, we should find a similar number of positive and negative effect sizes of germination success among treatments, and the test will be not significant.

In the following analysis, we investigated the effects of germination conditions, bat species, plant species, and seed origin on the logOR of germination success. The germination conditions had five levels (cylindrical exclusions, germination box, petri dishes, soil in petri dishes and sterilized sand in containers), bat species had 23 levels. Plant species had 61 levels, and seed origin had two levels (homogenized and unhomogenized). When the authors use the same fruits for the treatment and control, we categorized the experiment as homogenized. If the authors used different fruits for the treatment and control, we categorized as it unhomogenized. We fitted four mixed effects models, where the fixed variables were germination conditions, bat species, plant species, and seed origin, while the study author was a random variable. Similarly to the first meta-analysis we used the Cochran's Q_{between} index as a measure of heterogeneity (Viechtbauer, 2010). We did not perform a publication bias test in this meta-analysis, because it was done with the data set of the first meta-analysis.

In the last meta-analysis, we probed the effect of bat diet preferences (core-plant taxa hypothesis) on the germination success of ingested seeds. We used the raw proportions of germinated seeds consumed by bats and their associated variances as effect sizes. We included studies that did not report the seed germination success of the control seeds, because we only compared the germination success among the bat and plant genera. We fitted a nested mixed effects model and used the Cochran's Q_{between} index as a measure of heterogeneity of the meta-analysis. Our nested fixed effects were the bat-plant genera and our random effect was the author. The publication bias of this data set was evaluated by a regression test as above (Egger et al. 1997).

Finally, to answer if the ingestion of seeds by bats accelerated the first day of germination, we used a generalized linear model (GLM) with a post hoc χ2 analysis for standardized coefficients and a Poisson distribution of error. The GLM model formulation was: first germination day~treatment (human depulped and bat gut depulped), error=poisson. This model was adjusted with we had 60 observations, 30 for control and 30 for treatment. All analyses were performed using the "escalc", “regtest” and "rma.mv" functions of the “metafor” package and “glm” function of the “stats” package for R language version 3.2.0 (Viechtbauer, 2010, R Core Team 2015) .

Results

In the global meta-analysis, which did not take into account any moderator variable, we did not find a significant effect of bat seed ingestion on germination success (logOR=0.03, C.I.=-0.34–0.41). However, the heterogeneity of our data set was significant (*Q*=1834.87, df=104, *P*<0.0001), suggesting that some variables related with the germination experiments may be important. On the other hand, we did not find a publication bias in our data set (*t*= 0.59, df= 103, *P*= 0.55).

We found that only bat species and plant species had significant effects on germination success (Table 1). When we analyzed which plant and bat species had logOR values different from zero, we found only 10 plant species that increased their germination success after their seeds passed through bats' guts, two species showed decreased germination success (Table 2) and 49 species that showed no effect. While for bats two species increased the germination success of their consumed seeds, three decreased germination success and 18 showed no effect (Table 2).

Table 1. Significance table of the moderator variables evaluated. Only plant and bat species explain the heterogeneity of the logOR of seed germination.

Moderator	d.f.	$Q_{between}$	*P* value
Plant species	52	1231494.05	0.0001
Bat species	22	60.27	0.0001
Germination condition	5	1.83	0.87
Seed origin	3	1.04	0.79

Table 2. List of plant species that increased (positive logOR values) or decreased (negative logOR values) the germination success after their seeds' passage through bat guts. In the second section of the table is the list of bat species that increase or decreased the germination success of plants, after the seed consumption. logOR is the point estimate of the log odds ratio of the difference between seeds ingested by bats and control

seeds. C.I. is the 95% confidence interval, and *P* represents the p-value of a test of logOR against 0, while *k* is the number of germination experiments for each plant and bat species.

Plant species	**logOR**	***P***	**C.I.**	***k***	**life form**
Cecropia peltata	2.37	0.0005	1.03-3.71	1	tree
Ficus grevei	3.90	<0.0001	2.71-5.1	1	tree
Ficus guaranitica	1.2	0.005	0.35-2.06	2	tree
Ficus lutea	4.04	<0.0001	2.82-5.26	1	tree
Morus macroura	-4.35	<0.0001	-5.69-[-3.02]	2	small tree
Piper aduncum	0.81	0.024	0.11-1.53	6	shrub
Piper amalago	1.46	0.004	0.44-2.47	4	shrub
Piper hispidinervum	1.58	<0.0001	0.78-2.37	4	shrub
Solanum aphydendron	1.87	0.008	0.47-3.27	3	shrub
Solanum hazenii	1.79	0.01	0.30-3.29	1	shrub
Solanum mauritianum	0.92	0.02	0.14-1.71	4	shrub
Stenocereus dumortieri	-2.05	0.0002	-3.14-[-0.95]	1	cacti
Bat species	**logOR**	***P***	**C.I.**	***k***	**Family**
Cynopterus sphinx	-4.33	0.0001	-6.37-[-2.28]	1	Pteropodidae
Leptonycteris yerbabuenae	-1.31	0.032	-2.55-[-0.11]	2	Phyllostomidae
Pteropus rufus	1.81	0.036	0.11-3.52	3	Pteropodidae
Rousettus leschenaulti	-4.38	0.0001	-6.43-[-2.34]	1	Pteropodidae
Sturnira lilium	0.80	0.029	0.08-1.52	9	Phyllostomidae

We found significant heterogeneity of raw percentages of seed germination ($Q_{between}$=429.96, df=9, *P*<0.0001), and we found an effect of bat dietary preference (core plant taxa hypothesis) on seed germination success (Fig. 1). Specifically, we found that *Artibeus* bat species increased the germination of *Cecropia* seeds, compared with *Carollia* bat species. Moreover, *Carollia* bat species increased the germination of *Piper* seeds, compared with *Cecropia* seeds and *Sturnira* bat species presented a similar germination success of *Piper* seeds compared with *Carollia* bats (Fig. 1). We did not find a publication bias in our data set (*t*= -1.57, df= 73, *P*= 0.12). Finally, we did not find an effect of bat seed consumption on the first germination day of plants (X^2= 1.0117, df=58, *P*= 0.3145; Fig. 2).

Discussion

We did not find support for the hypothesis that frugivorous bat passage homogeneously increases the germination success of consumed seeds compared to seeds depulped by hand, as proposed by Traveset and Verdú (2002). In contrast to our first prediction, we found no effects of germination conditions and seed origin on seed germination success. According to our second prediction, we found that germination varies among plant species and that bat passage has heterogeneous effects on germination, depending on the species of bat. The core plant taxa hypothesis was also supported as bat dietary preferences explained variation in seed germination as well. Finally, according to our predictions, we found no significant effect of bat seed ingestion on germination speed. In the following sections, we discuss the implication of these results for the seed dispersal processes mediated by frugivorous bats.

Does the consumption of fruit by bats enhance seed germination?

The hypothesis that seed passage through bats' guts should increase germination success homogeneously was not verified. These results do not support the pattern observed in the previous meta-analysis (Traveset & Verdú, 2002). This opposite result, compared with our study, could be due to the increase of observations in our study. Our data set was composed of 33 studies that represented 107 germination experiments, with 23 bat and 61 plant species, while the meta-analysis of Traveset & Verdú (2002) contain 19 experiments and 5 bat and 21 plant species.

The increase of observations among meta-analyses can change the results (Comita et al. 2014, Hyatt et al. 2003); therefore, the inclusion of more bat and plant species had an important effect in the overall effect of seed germination success of fruit consumed by bats. This result implies that, in general, the principal service frugivorous bats may offer to plants is the seed dispersal. This is corroborated by the way bats exhibit good seed handling (Dumont 1999).

Moderator variables that enhance seed germination

The variables of experimental design that had no effect were germination conditions and seed origin. The absence of the effect of seed germination condition could be related to the observation that the majority of plants consumed by bats are present in tropical forests (Muscarella & Fleming 2007, Lobova 2009). These plants had a high germination capacity, compared with plants of temperate forests (Traveset 1998). This may result in high germination success independent of germination condition and seed origin. This result differs from previous reports that showed that seed origin and seed germination condition have an effect on seed germination (Baloch et al. 2001, Traveset & Verdú 2002, Cruz et al. 2003). Specifically, the seed experiments performed in greenhouses are buffered against climatic conditions, compared to field conditions, resulting in different gemination successes in these places (Traveset & Verdú 2002).

Germination success varied between bat species. Curiously, the reduction of seed germination seemed unrelated with the size or taxonomic position of bats (see Table 2). Fruit handling and food transit times of bats species is positively related with their body mass (Bonaccorso & Gush 1987, Laska 1990, Dumont 1999). Therefore, the pattern of negative and positive effects of germination success from bat taxa with different sizes suggests that plant traits could be more important than bat traits in explaining germination of seeds consumed by bats.

The plant species involved in the study (between which seed germination success varied significantly) had wildly different life forms (shrubs, trees, and cacti). The life form of plant species could influence germination success: seeds of trees have higher germination success when passed through vertebrate guts, compared with herbs and shrubs (Traveset & Verdú, 2002), as some tree species need more the abrasive effect of gut passage to activate seed germination (Traveset 1998). Therefore, the life form of plants could be the main factor related to the significance of plant species in germination success. However, this result should be treated cautiously, because only 12 species of 61 plant species had effect sizes different from zero. Finally, this result confirms that the effect of bat fruit consumption on seed germination is idiosyncratic (Lieberman & Lieberman 1986).

Is seed germination dependent on bat dietary preferences?

Our prediction that seed germination success should be related to dietary preferences of frugivorous bats was verified. This result suggests that plant germination success evolved as bat diet preferences did (Sánchez & Giannini 2018). The main idea of the core-plant taxa hypothesis is that *Carollia*, *Sturnira*, and *Artibeus* bat species select their fruit due their size, vertical position in the forest and nutrient availability (Fleming 1986). This hypothesis has been evaluated from an ecomorphological and ecophysiological perspective. *Carollia* and *Sturnira* bat species have been found to be limited and deal with diets of low sugar content and bigger fruit size and hardness compared with *Artibeus* species (Dumont 2003, Saldaña-Vázquez 2014).

Therefore, we hypothesize that ecomorphological and ecophysiological traits of *Artibeus*, *Carollia* and *Sturnira* frugivorous bat species had an effect on the germination success of their preferred consumed plants. This is especially applicable for *Cecropia* seeds, where small bats such as *Carollia* reduce the germination success compared with big bats like *Artibeus*. This could be due to the differences in fruit handling and food transit times between these bats species and the *Cecropia* morphology (Bonaccorso & Gush 1987, Laska 1990, Dumont 1999). *Cecropia* fruits have a mucilaginous pericarp, and if the pericarp is not removed, the seed survival and subsequent germination is reduced (Lobova et al. 2003). Therefore, the higher *Cecropia* germination success of seed consumed by *Artibeus* species could be related with their long transit time and gut of *Artibeus* compared to *Carollia* bats.

Another interesting result is that both *Sturnira* and *Carollia* bat species had similar seed germination success of *Piper* species. Dietary studies about *Sturnira* in montane forests have shown that *Sturnira* consume *Piper* fruits in the same magnitude as their supposedly preferred *Solanum* fruits (Hernández-Montero et al. 2015, Castaño et al. 2018). These results suggest that in montane forests where *Carollia* species abundance decreases, *Sturnira* species provide compensatory seed dispersal services to *Piper* plants.

Seed germination velocity is independent of bat seed consumption

Our last prediction was that seed consumption by bats does not increase germination velocity. This prediction was fulfilled because there was no significant decrease in the day of first germination day of seed consumed by bats. This result is due to plant seeds experiencing similar seed depulpation in bat guts, compared with depulpation by human hands (controls). In addition, this result shows the value of frugivorous bats for plant seed dispersal, as they do not kill the seeds by consuming them

Conclusion and future research avenues

From the most recent evidence we can conclude that, in general, frugivorous bats do not homogeneously improve the seed germination of plants, compared to seeds depulped by hand (control). Seed germination success is idiosyncratic with respect to bat and plant species. New research on the effect of bat ingestion on seed germination should explore the effect of the chemical consequence of the vertebrate gut on germination via alteration of the seed coat or endocarp. Just three of the 33 studies revised had seed with pulp as a control treatment (Izhaki et al. 1995, Heer et al. 2010, Naranjo et al. 2003). Considering fruit pulp with undigested seeds opens considerable possibilities for multifaceted interactions between fruits, fungi, seed predators and seed dispersers (Tewksbury 2002, Levey et al. 2007). We have observed rapid fungal attacks on ripe *Piper* fruits that fall to the ground instead of being dispersed by bats. Morphologically similar fungal attacks were present even in seeds that had been washed from fruit pulp (Baldwin and Whitehead, unpublished data). It is unknown if the presence of fruit pulp facilitates fungal attack. Another possible investigation topic is the effect of bat fruit consumption on the viability of seeds. Finally, the majority of the studies we reviewed come from the Neotropics, and have not evaluated the viability of seeds that failed to germinate.

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Figure legends

Figure 1. Germination percentage (mean and 95% confidence intervals) of seeds from plants consumed by the common Neotropical bat genera. Plant genera in bold are the core plant taxa in bat diet (sensu Fleming 1986). Letters a and b remark germination percentage significantly different among bat and plant genera. This meta-analysis was performed only with data of seeds ingested by bats (raw proportion), because we only compared the germination success among the bat and plant genera.

Figure 2. Density plot of the first germination day of seeds from the control and treatment.

Anexo 4

Mamíferos del departamento de Risaralda, Colombia

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Mamíferos del departamento de Risaralda, Colombia

Mammals of Risaralda State, Colombia

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Resumen

Decenas de investigadores han documentado los mamíferos del departamento de Risaralda. Sin embargo, esta información no ha sido compilada ni actualizada, en razón de los cambios en la nomenclatura. Para la construcción de esta lista, se recopiló información existente en colecciones biológicas, literatura científica y se adicionaron nuevos registros. La lista de mamíferos consolidada confirma 134 especies para Risaralda, que constituyen el 25 % de las especies de mamíferos del país. De estas, 12 son endémicas para Colombia y ocho están en las categorías Peligro Crítico, En Peligro y Vulnerable. Los murciélagos son el grupo con mayor riqueza (59 spp.) seguido de los roedores (33 spp.); estos últimos tienen el mayor número de especies endémicas (8 spp.). La mayor riqueza se localiza en los municipios de Pereira, Santa Rosa de Cabal y Pueblo Rico, donde se concentra la mayor parte de la exploración y registros. En los municipios de Quinchía y Guática no se pudieron localizar registros con respaldo en colecciones científicas. Es posible que la riqueza aumente cuando se incremente el esfuerzo de muestreo hacia otras localidades del departamento. Se espera que esta lista contribuya a direccionar futuros estudios, así como planes de manejo y conservación tanto de especies como de áreas.

Palabras clave. Andes. Chocó biogeográfico. Diversidad. Eje cafetero. Taxonomía.

Abstract

Many researchers have documented mammalian diversity in the state of Risaralda; however, the information has not been consolidated nor updated due to changes in nomenclature. To construct the list presented here, a compilation of information from biological collections, scientific literature, and new records was made. The list contains 134 species of mammals from Risaralda, a number which is equivalent to 25 % of the mammal species of Colombia. Of these species, 12 species are endemic for Colombia and eight are in the categories of Critical, Endangered and Vulnerable. Bats are the richest group (59 spp.), and are followed by rodents (33 spp.), which are the group with the highest number of endemic species (8 spp.). Pereira, Santa Rosa de Cabal and Pueblo Rico are the richest municipalities, and are also those where most of the exploration and records are concentrated. In the municipalities Quinchía and Guática no records with support in scientific collections were found. Possibly, species richness will increase if the sampling effort in other locations are increased. This list will hopefully be useful in guiding future studies as well as management and conservation plans for species and areas.

Key words. Andes. Coffee-growing region. Biogeographic Chocó. Diversity. Taxonomy.

Introducción

Colombia es considerado el sexto país con mayor diversidad de mamíferos (518 especies) (Ramírez-Chaves *et al.* 2016). La alta biodiversidad del país se relaciona con su compleja geografía producto de la historia geológica y su ubicación en el Neotrópico (Hernández-Camacho *et al.* 1992, Morrone 2014). Risaralda con 14 municipios, es uno de los departamentos más pequeños de Colombia (cerca de 4000 km^2); sin embargo, incluye ecosistemas tan diversos como las selvas del Pacífico, en el flanco occidental de la cordillera Occidental, páramos sobre las cordilleras Central y Occidental o el valle interandino del río Cauca, otrora cubierto por bosques secos (Figura 1). Esta variedad de ecosistemas, distribuidos en un gradiente altitudinal que va desde los 300 hasta los 5300 m., alberga una amplia diversidad de mamíferos la cual empezó a ser documentada a inicios del siglo XX.

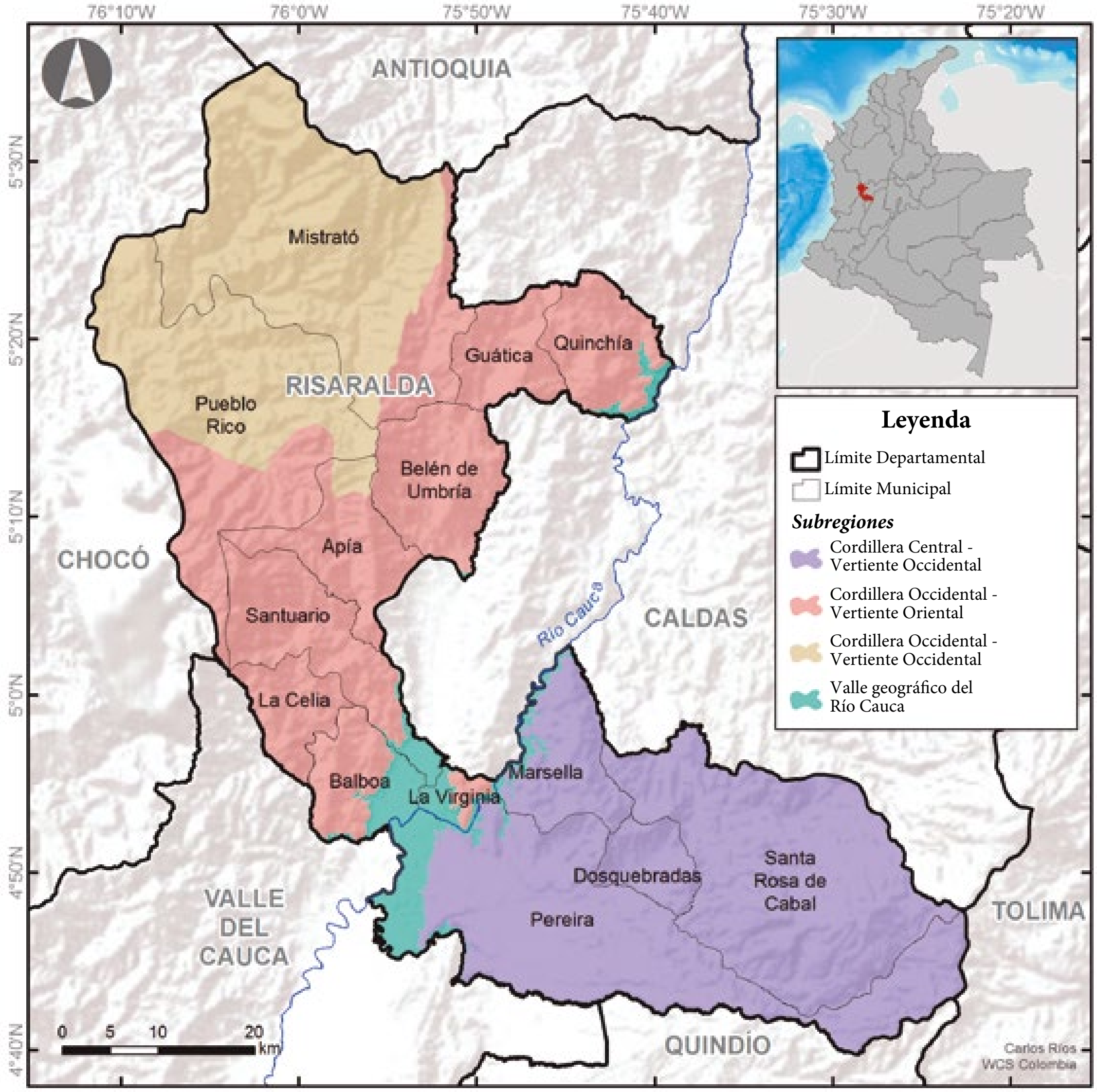

Figura 1. Área de estudio. Ubicación del departamento de Risaralda en Colombia y municipios del departamento.

Los primeros registros científicos de mamíferos de Risaralda datan de 1909 cuando M. G. Palmer recolectó dos especímenes de ardillas (*Notoscirus granatensis*, *Microsciurus similis*) y una comadreja (*Mustela frenata*) en el río San Juan en el municipio de Pueblo Rico; en 1945 el naturalista sueco Kjell E. von Sneidern recolectó dos marsupiales, en el corregimiento Santa Cecilia del municipio Pueblo Rico. Posteriormente en 1951, Philip Hershkovitz trabajando para el FMNH, pasó por territorio risaraldense y recolectó en la cordillera Central siete especímenes del ratoncito de páramo (*Microryzomys altissimus*). Durante las décadas de 1980 y 1990, la recolección de mamíferos fue encabezada por investigadores del Instituto de Ciencias Naturales de la Universidad Nacional de Colombia y el Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

En el siglo XXI la investigación mastozoológica en el departamento ha sido realizada por investigadores provenientes de diversas instituciones nacionales, entre las que destacan: el Centro Nacional de Investigaciones de Café, la Universidad de Caldas, la Pontificia Universidad Javeriana, la Universidad de Santa Rosa de Cabal, la Universidad del Valle, la Fundación EcoAndina, Wildlife Conservation Society y la Corporación Autónoma Regional de Risaralda. En lista de mamíferos de Colombia más reciente Solari *et al.* (2013), registraron 95 especies de mamíferos para Risaralda, un número menor al actualmente conocido. En este trabajo se presenta la lista actualizada de los mamíferos del departamento de Risaralda.

Material y métodos

La presente lista se construyó con base en registros históricos, respaldados por especímenes depositados en las colecciones de historia natural de la Universidad de Caldas (MHN-UCa, Colombia), el Instituto de Ciencias Naturales de la Universidad Nacional (ICN, Colombia), la Universidad de Santa Rosa de Cabal (CUSM, Colombia), la Pontificia Universidad Javeriana (MPUJ-MAMM, Colombia), la Universidad del Valle (UV, Colombia), la Universidad del Cauca (MHNUC, Colombia), el Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH, Colombia), el Field Museum of Natural History (FMNH, Estados Unidos) , el United States National Museum (USNM, Estados Unidos; ahora National Museum of Natural History) y el Royal Ontario Museum (ROM, Canadá). Además, se incluyeron registros verificables de la literatura científica (Morales-Jiménez 2002, Castaño *et al.* 2004, Lizcano y Cavelier 2004, Orjuela y Jiménez 2004, Castaño y Cardona 2005, Navarro 2005, Mantilla-Meluk y Baker 2006, Estrada-Villegas *et al.* 2007, Rivas-Pava *et al.* 2007, Berrío-Martínez 2009, Mantilla-Meluk *et al.* 2009, Velazco y Gardner 2009, Estrada-Villegas *et al.* 2010, Londoño y Gómez-Posada 2010, Lozano 2010, Mantilla-Meluk y Baker 2010, Vélez-García y Pérez-Torres 2010, Saavedra-Rodríguez *et al.* 2012, Arias-Alzate *et al.* 2014, De la Peña-Báez 2014, Saavedra-Rodríguez *et al.* 2014, Torres *et al.* 2014, Castaño y Torres 2015, Cepeda 2016), así como nuevos registros obtenidos durante estudios realizados por los autores en las últimas dos décadas.

Se presenta la lista de especies organizada en los órdenes propuestos por la hipótesis filogenética de O'Leary *et al.* (2016), dejando de lado el uso del orden Soricomorpha por considerarse parafilético y usando Eulipotyphla. También se acepta el uso del orden Cetartiodactyla (Gatesy *et al.* 2013). A nivel de familias se sigue el arreglo de Wilson y Reeder (2005). Para los roedores de la familia Sciuridae se usan los géneros propuestos por De Vivo y Carmignotto (2015); para los roedores oryzominos los géneros propuestos por Weksler *et al.* (2006), el género *Hydrochoerus* se trata como monoespecífico de acuerdo a los hallazgos de Ruíz-García *et al.* (2016). Se separan *Akodon affinis* y *A. tolimae* con base en diferencias morfológicas y cariotípicas (Quiceno 1993). Dentro de Chiroptera se adopta la propuesta de Solari *et al.* (2009) para el uso genérico de *Dermanura*. Siguiendo a Parlos *et al.* (2014) y a Hurtado-Miranda y Pacheco-Torres (2014), se reconoce a los géneros *Lonchophylla* como parafilético y *Mimon* como polifilético, adoptando así el uso de los nuevos géneros *Hsunycteris* y *Gardnerycteris*. Se reconoce el nivel específico de *Sylvilagus andinus* (Ruedas *et al.* 2017).

En esta lista se presentan los mamíferos a nivel de especie, excepto para el género *Nephelomys* que presenta dos especies de distribución probable en el departamento, *N. childi* y *N. pectoralis*, los ejemplares colectados en Risaralda necesitan precisar su identidad, razón por la cual se presentan preliminarmente en la lista como *Nephelomys* sp.

Resultados y discusión

La lista de mamíferos de Risaralda está compuesta por 134 especies, agrupadas en 88 géneros, 32 familias y 12 órdenes (Anexo 1), representando el 25 % de los mamíferos de Colombia (Ramírez-Chaves *et al.* 2016). Los dos grupos más diversos son los murciélagos (59 spp.) y los roedores (33 spp.), concordando con el patrón nacional (Tabla 1).

En Risaralda habitan por lo menos 12 especies endémicas de Colombia, ocho roedores (*Akodon tolimae, A. affinis*, *Handleyomys fuscatus*, *H. intectus, Nephelomys* sp., *Thomasomys bombycinus, T. cinereiventer* y *T. nicefori*), dos musarañas (*Cryptotis medellinius* y *C. colombianus*), un marsupial (*Marmosops caucae*) y temporalmente el murciélago (*Sturnira mistratensis*).

Asimismo habitan 11 especies en alguna categoría de amenaza, de las cuales nueve están amenazadas a nivel mundial (UICN 2016). La especie en Peligro Crítico es el mono araña (*Ateles fusciceps*). La danta de páramo (*Tapirus pinchaque*) se encuentra En Peligro, y siete especies están en categoría de Vulnerable (*Platyrrhinus chocoensis*, *Aotus lemurinus*, *Leopardus tigrinus*, *Tremarctos ornatus*, *Mazama rufina*, *Pudu mephistophiles*, *Dinomys branickii*). Adicionalmente dos especies son catalogadas como Vulnerables en Colombia (*Lontra longicaudis* y *Alouatta palliata*) (Rodríguez-Mahecha *et al.* 2006, Ministerio de Ambiente y Desarrollo Sostenible 2017).

Tabla 1. Mamíferos del departamento de Risaralda. Número de familias, géneros y especies endémicas de Colombia dentro de cada orden.

Orden	Familias	Géneros	Especies	Especies endémicas
Didelphimorphia	1	8	9	1
Paucituberculata	1	1	2	0
Cingulata	1	2	2	0
Pilosa	3	3	3	0
Eulipotyphla	1	1	2	2
Chiroptera	4	28	59	1
Carnivora	5	12	14	0
Perissodactyla	1	1	1	0
Cetartiodactyla	2	3	3	0
Primates	3	4	5	0
Rodentia	9	25	33	8
Lagomorpha	1	1	1	0
Total	**32**	**89**	**134**	**12**

La cantidad de especies de mamíferos de Risaralda de acuerdo a la propuesta nacional vigente (Solari *et al.* 2013) es inferior al registrado para departamentos vecinos como Caldas y Valle del Cauca (Castaño 2012, Rojas-Díaz *et al.* 2012). Probablemente debido a que aún persisten vacíos de información a pesar de los esfuerzos de muestreo en Risaralda, ya que la mayoría de los registros se concentran en tres de los 14 municipios que a su vez presentan la mayor riqueza de especies (Pereira 90 spp., Santa Rosa de Cabal 86 spp. y Pueblo Rico 54 spp.) por encima de los 1500 m. En los demás municipios del departamento y en las zonas bajas, han sido pocos los esfuerzos de muestreo. En dos municipios (Guática y Quinchía) no se pudieron rastrear registros locales de mamíferos; asimismo, la calidad de la información evidenció la poca relación existente entre el área de los municipios con el número de especies y registros en cada uno de ellos (Tabla 2).

Tabla 2. Número de especies de mamíferos registradas, de registros y área de cada municipio del departamento de Risaralda.

Municipio	Especies registradas	N° registros	Área (Km²)
Pereira	85	457	702
Santa Rosa de Cabal	79	259	486
Pueblo Rico	54	281	1020
Mistrató	32	198	483
Santuario	31	234	226
Marsella	27	44	57
Belén de umbría	22	21	178
Dosquebradas	10	12	70,8
La Celia	8	11	87
Apía	7	7	214
Balboa	6	16	119
La Virginia	2	2	33
Guática	0	0	97
Quinchía	0	0	150

Se recomienda revisar la validez de la especie *Sturnira mistratensis* (ICN 11779) dado que las medidas morfométricas y aspecto general del ejemplar son muy similares a las de *S. parvidens*, y es probable que presente una variación atípica de la dentición, lo cual también ha sido similarmente mencionado por Martínez-Arias (com. pers.) citado por Solari *et al.* (2013). También se recomienda una revisión profunda de los ejemplares del género *Nephelomys* necesario para aclarar la distribución real de las especies *N. childi* y *N. pectoralis* en el departamento; otros roedores tales como *Thomasomys nicefori*, *Akodon affinis* y *A. tolimae* también ameritan revisiones en aras de aclarar los debates sobre su identidad taxonómica y distribución en las cordilleras Central y Occidental del norte de los Andes.

Es recomendable ampliar el esfuerzo en los municipios pobremente estudiados, estos vacíos de información en los inventarios de especies dificultan definir con respaldo científico las áreas de alta diversidad y de concentración de especies de interés; por ende, el manejo para la conservación de los mamíferos en el departamento. Se espera que este documento sea un insumo que contribuya a direccionar acciones para cerrar las brechas en el conocimiento de la biodiversidad del departamento y, de esta manera, mejorar la gestión para el manejo y conservación de la biodiversidad y sus hábitats en el departamento de Risaralda.

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Anexo 1. Lista de especies de mamíferos confirmadas para el departamento de Risaralda. Abreviaturas municipios. Ap: Apía. Ba: Balboa. BU: Belén de Umbría. Do: Dosquebradas. LC: La Celia. LV: La Virginia. Ma: Marsella. Mi: Mistrató. Pe: Pereira. PR: Pueblo Rico. SR: Santa Rosa de Cabal. Sa: Santuario. Abreviaturas distribución.

CO: Cordillera Occidental. CC: Cordillera Central. –O: flanco occidental. –E: flanco oriental. RC: Valle Geográfico del río Cauca. *: Especie endémica de Colombia.

Taxón	Intervalo altitudinal (m s.n.m.)	Municipios	Distribución	Referencia
DIDELPHIMORPHIA				
Didelphidae				
Caluromys derbianus (Waterhouse, 1841)	300-2600	Pe	Risaralda	Registro fotográfico
Chironectes minimus (Zimmermann, 1780)	300-2600	Ma, Pe	Risaralda	CUSM 253; registro fotográfico
Didelphis marsupialis Linnaeus, 1758	300-2500	Ap, Pe, LV, SR	Risaralda	CUSM 57, 194; IAvH 5395; MHNUCa 1073
Didelphis pernigra J. A. Allen, 1900	2000-3900	Sa, SR	CO, CC	CUSM 32, 155
Marmosa isthmica Goldman, 1912	300-1200	Mi	Risaralda	ICN 11943
**Marmosops caucae* (Thomas, 1900)	1000-2700	Pe, SR	Risaralda	CUSM 46, 85, 154; ICN 12102
Metachirus nudicaudatus (É. Geoffroy Saint-Hilaire, 1803)	300-1500	PR	Risaralda	CUSM 220; MHNUC M00009
Micoureus demerarae (Thomas, 1905)	300-2200	SR	Risaralda	CUSM 134, 147
Monodelphis adusta (Thomas, 1897)	300-1700	Ma, Pe	Risaralda	CUSM 92, 269
PAUCITUBERCULATA				
Caenolestidae				
Caenolestes convelatus Anthony, 1924	1800-3800	Sa	CO	ICN 11966-11971
Caenolestes fuliginosus (Tomes, 1863)	2000-3800	Pe	CC	ICN 16531-16532, 16534, 16536-16537
CINGULATA				
Dasypodidae				
Cabassous centralis (Miller, 1899)	300-3000	LC, Ma, Pe, SR	Risaralda	Registro fotográfico
Dasypus novemcinctus Linnaeus, 1758	300-3000	Ba, BU, LC, Ma, Pe, PR, SR	Risaralda	CUSM 31, 153, 192, 257; registro fotográfico
PILOSA				
Cyclopedidae				
Cyclopes didactylus (Linnaeus 1758)	300-1000	PR	CO-O	Registro fotográfico
Megalonychidae				
Choloepus hoffmanni Peters, 1858	300-2500	Ap, Pe, Ma, Do, SR	Risaralda	CUSM 272; MHNUCa 422; registro fotográfico
Myrmecophagidae				
Tamandua mexicana (Saussure 1860)	300-1500	Ma, Pe, PR, SR	Risaralda	Registro fotográfico

Cont. **Anexo 1.** Lista de especies de mamíferos confirmadas para el departamento de Risaralda. Abreviaturas municipios. Ap: Apía. Ba: Balboa. BU: Belén de Umbría. Do: Dosquebradas. LC: La Celia. LV: La Virginia. Ma: Marsella. Mi: Mistrató. Pe: Pereira. PR: Pueblo Rico. SR: Santa Rosa de Cabal. Sa: Santuario. Abreviaturas distribución.

CO: Cordillera Occidental. CC: Cordillera Central. –O: flanco occidental. –E: flanco oriental. RC: Valle Geográfico del río Cauca. *: Especie endémica de Colombia.

Taxón	Intervalo altitudinal (m s.n.m.)	Municipios	Distribución	Referencia
EULIPOTYPHLA				
Soricidae				
**Cryptotis colombianus* Woodman & Timm 1993	1800-2200	Pe, SR	CC	IAvH 7386, 7387
**Cryptotis medellinius* Thomas, 1921	1800-3600	PR	CC-CO	IAvH 8025-8032; ICN 16538-16540
CHIROPTERA				
Emballonuridae				
Peropteryx kappleri Peters, 1867	300-1750	Pe	Risaralda	CUSM 180
Saccopteryx bilineata (Temminck, 1838)	300-1100	Pe	Risaralda	MUJ; Solari et al. 2013; registro fotográfico
Saccopteryx leptura (Schreber, 1774)	300-1500	Pe	Risaralda	MUJ; Solari et al. 2013
Phyllostomidae				
Anoura caudifera (É. Geoffroy Saint-Hilaire, 1818)	300-3000	Ma, Mi, Pe, PR, SR, Sa	Risaralda	CUSM 158, 160, 162-164; ICN 11170, 11194, 11460, 11462, 11747, 11832, 11867, 11868, 12295, 12296, 12534-12538, 12583; MHNUCa 281, 282; MPUJ 1109,1129
Anoura cultrata Handley, 1960	1000-2500	SR	Risaralda	CUSM 4, 81-83, 161
Anoura fistulata Muchhala, Mena & Albuja, 2005	1000-1800	PR	CO	ICN 11461
Anoura geoffroyi Gray, 1838	300-3600	BU, Ma, Pe, PR, SR, Sa	Risaralda	CUSM 26, 58, 76, 77, 86, 165; ICN 11171, 11197, 11198, 11200, 11206, 11208, 11209, 11211, 11195, 11203, 11201, 11833, 11834, 11791
Anoura peruana (Tschudi, 1844)	1000-3400	Sa	CO, CC	ICN 11458-11459
Artibeus lituratus (Olfers, 1818)	300-2600	BU, Do, Ma, Mi, Pe, PR, SR	Risaralda	CUSM 21, 87, 102, 174-176, 187, 188; ICN 11188, 11189, 11261-11263, 11265, 11433-11435, 11437, 11438, 11441, 11893, 11894, 11890, 11891, 12210, 12260-12262, 12359; MHNUCa 315-316; 528-529
Artibeus jamaicensis Leach, 1821	0-2200	Pe, Mi, SR	CO-E, RC, CC	CUSM 17, 18; ICN 11260, 11762
Carollia brevicauda (Schinz, 1821)	300-3000	BU, Mi, Pe, PR, SR, Sa	Risaralda	CUSM 6, 75, 108, 156, 157; ICN 11173, 11463, 11467, 11468, 11470, 11471, 11473, 11475-11480, 11482-11485, 11487, 11836, 11837, 11839, 11841, 11869, 12298, 12299, 12301-12303, 12539, 12541, 12542; MHNUCa 299, MPUJ 1101, 1120, 1126, 1135
Carollia castanea H. Allen, 1890	300-2500	Ba, BU, Mi, PR, SR, Pe	Risaralda	CUSM 15, 16 19; ICN 11749, 11751-11753, 11871, 11872, 12211-12215, 12304, 12305, 12307, 12308, 12310-12312, 12313, 12314, 12316; MHNUCa 488
Carollia perspicillata (Linnaeus, 1758)	300-2500	Ba, BU, Mi, Pe, PR, SR	Risaralda	CUSM 12, 109; ICN 11174, 11175, 11417, 11418-11425, 11754, 11873-11878, 12219-12241, 12317-12326, 16751; MHNUCa 499, 500
Chiroderma salvini Dobson, 1878	300-2000	BU, Do, Pe, PR, SR	Risaralda	ICN 11908; MHNUCa 563; MPUJ 1124, 1131; Berrío-Martínez 2009

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Taxón	Intervalo altitudinal (m s.n.m.)	Municipios	Distribución	Referencia
CHIROPTERA				
Phyllostomidae				
Chiroderma villosum Peters, 1860	300-1500	BU	Risaralda	Berrío-Martínez 2009
Choeroniscus godmani (Thomas, 1903)	300-1600	BU, Pe, SR	Risaralda	CUSM 299; MHNUCa 276, 277; Berrío-Martínez 2009
Dermanura bogotensis Thomas, 1893	300-2500	Do, Ma, Mi, Pe, PR, SR, Sa	Risaralda	CUSM 144, 166, 167; ICN 11186, 11187, 11258, 11259, 11510-11513, 11755, 11756, 11758, 11767, 11842-11844, 12258, 12357, 12565; MHNUCa 511-515
Dermanura phaeotis Miller, 1902	300-2000	Ba, BU, Do, Ma, Pe, SR, Sa	Risaralda	CUSM 207, 209; MHNUCa 317, 388, 552-562; ICN 11514-11516, 11895-11907, 12263
Dermanura rava Miller, 1902	300-1600	Mi	CO-O, RC	CUSM 11, 63
Dermanura rosenbergi Thomas, 1897	300-1600	PR	CO-O, RC	CUSM 231
Desmodus rotundus (É. Geoffroy Saint-Hilaire, 1810)	300-3000	Do, Mi, Ma, Pe, SR	Risaralda	CUSM 8, 9, 10; ICN 11192, 11268, 12570; MHNUCa 619
Enchisthenes hartii (Thomas, 1892)	300-2500	BU, Do, Ma, Mi, PR, SR	Risaralda	CUSM 22, 145; ICN 11759-11761; 11879-11889; 12568; MHNUCa 516-517
Glossophaga soricina (Pallas, 1766)	300-2000	Ba, BU, Pe, SR, LC	Risaralda	CUSM 28, 47, 68, 74, 84, 96-100, 106, 107, 142; ICN 16750; MHNUCa 285; 296-297; 454-455; 684-686
Hsunycteris cadenai (Woodman y Timm 2006)	300-1500	PR	CO-O	ICN 12210
Lonchophylla concava Goldman, 1914	300-2000	PR, Sa, SR	CO, CC	CUSM 159; MHNUCa 462
Lonchorhina aurita Tomes, 1863	300-1500	PR	Risaralda	ICN 11458, 11459
Mesophylla macconnelli Thomas, 1901	300-2000	BU, Pe, SR, Sa	Risaralda	CUSM 288, 306; MHNUCa 569, 570, 574; MPUJ 1116
Micronycteris megalotis (Gray, 1842)	300-2500	Mi SR	Risaralda	CUSM 295, ICN 12294
Phyllostomus discolor (Wagner, 1843)	0-1700	Mi, SR	Risaralda	CUSM 303, 305; ICN 12209
Platyrrhinus albericoi Velazco, 2005	500-2000	Mi, Pe, PR, SR	Risaralda	CUSM 90, 103; ICN 11190, 11191, 11267, 11788, 11789, 11940-11942
Platyrrhinus angustirostris Velazco, Gardner & Patterson, 2010	900-1200	BU, Pe, Ma, Sa	RC	CUSM 67, 312, 321, 327; Berrío-Martínez 2009
Platyrrhinus chocoensis Alberico y Velasco, 1991	1100	PR	CO	CUSM 236
Platyrrhinus dorsalis (Thomas, 1900)	300-2500	BU, Mi, Pe, Pr, Sa, SR	Risaralda	CUSM 143; ICN 11266, 11517, 11518, 11784-11786, 11864, 11931-11933, 12268-12269, 12360-12364
Platyrrhinus ismaeli Velazco, 2005	1200-3000	Pe, SR	CC	UV 12694 UV 13042

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Phyllostomidae				
Platyrrhinus nigellus (Gardner & Carter,1972)	300-2800	PR	CO	ICN 11934, 11937
Platyrrhinus umbratus (Lyon, 1902)	300-2500	Pe, PR	CO, CC	UV 2517, 2518, 2520
Sturnira aratathomasi (Peterson & Tamsitt, 1968)	2000-3000	Pe	CO, CC	ICN 11176, 11177, 11214-11216, MPUJ 1111, 1117, 1128
Sturnira bidens (Thomas, 1915)	1000-3100	Pe, SR, Sa	CO, CC	CUSM 23, 24; ICN 11178, 11179, 11217-11219, 11845-11847; MPUJ 1130, 1140
Sturnira bogotensis (Shamel, 1927)	1800-3100	Pe, PR, SR, Sa	CO, CC	CUSM 25; ICN 11220, 11222-11224, 11251, 11493, 11792, 11793
Sturnira erythromos (Tschudi, 1844)	1000-2600	Mi, Pe, PR, Sa, SR	Risaralda	ICN 11182, 11225-11228, 11230-11234, 11236, 11244, 11248-11250, 11253, 11254, 11488-11492, 11494-11496, 11794-11804, 11806-11827, 11848-11860, 11909-11915, 12101, 12327-12333, 12544-12553, 16109, 16110
Sturnira ludovici (Anthony, 1924)	1500-2800	BU, Mi, Pe, PR, Sa, SR	CO, CC	CUSM 48, 139, 169, 170; MPUJ 1104, 1108, 1141, 1143; Berrío-Martínez 2009
**Sturnira mistratensis* Contreras-Vega & Cadena, 2000	980	Mi	CO-O	ICN 11779
Sturnira parvidens Goldman, 1917	300-2300	BU, Mi, Pe, PR	Risaralda	CUSM 13, 14, 64, 140; ICN 11235, 11426-11431, 11497, 11768-11774, 11916-11922, 12242-12250, 12252, 12253, 12334-12350
Uroderma convexum Lyon 1902	300-1500	BU, Pe, PR	Risaralda	CUSM 215; Berrío-Martínez 2009
Vampyressa thyone (Thomas, 1909)	300-2000	BU, Mi, Ma, Pe, PR	Risaralda	CUSM 308, 311, 315, 320; ICN 11443, 11780-11783, 11928-11930, 12266-12267; MPUJ 1151
Vampyrodes major (Thomas, 1889)	300-2000	SR	Risaralda	Colectado por V. Rojas-Díaz, pendiente ingreso a colección biológica
Vespertilionidae				
Eptesicus andinus A. Allen, 1914	2400-3300	Pe, SR	CO, CC	CUSM 171, 181, 306; MPUJ 105
Eptesicus chiriquinus Thomas, 1920	300-2200	BU, SR	Risaralda	CUSM 189; Berrío-Martínez 2009; Solari et al. 2013
Histiotus humboldti (Philippi & Landbeck, 1861)	1800-3500	SR	CO, CC	CUSM 172
Histiotus montanus (Philippi & Landbeck, 1861)	1800-3500	SR, Sa	CO, CC	ICN 11865; Solari et al. 2013
Lasiurus blossevillii (Lesson & Garnot, 1826)	300-3600	SR	Risaralda	CUSM 313
Myotis albescens (É. Geoffroy Saint-Hilaire, 1806)	300-1700	PR	Risaralda	ICN 11444

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CHIROPTERA				
Vespertilionidae				
Myotis caucensis Allen, 1914	300-2800	Ma, Pe, PR, SR, Sa	CO-E, RC, CC	MHNUCa 663; ICN 11445-11447, 11520, 11866, 12270, 12271
Myotis keaysi J. A. Allen, 1914	1000-2500	Pe, SR	Risaralda	CUSM 1-3, 5, 7, 50, 59, 61, 62, 94, 95, 110-116
Myotis oxyotus (Peters, 1867)	1000-2000	Ma, Pe	Risaralda	MHNUCa 633-635; ICN 11193, 11271
Myotis riparius Handley, 1960	300-1600	BU, Ma, Pe, SR, Sa	Risaralda	CUSM 177; MHNUCa 650-653; Berrío-Martínez 2009
Molossidae				
Molossus bondae J.A. Allen, 1904	300-2000	Pe	Risaralda	ICN 9111
Molossus molossus (Pallas, 1766)	300-2200	Pe, PR, SR	Risaralda	CUSM 178; ICN 9110, 11269, 11448-11454, 11790, MPUJ 1114
Tadarida brasiliensis (I. Geoffroy, 1824)	300-2600	Pe	Risaralda	Solari et al. 2013
CARNIVORA				
Canidae				
Cerdocyon thous (Linnaeus, 1766)	300-3200	Ma, Mi, Pe, SR	Risaralda	CUSM 29, 148, 195,198, 202, 205; IAvH 5401; ICN 12367
Felidae				
Leopardus pardalis (Linnaeus, 1758)	300-2500	Pe, PR, Mi	Risaralda	CUSM 259, 271; registro fotográfico
Leopardus tigrinus (Schreber, 1775)	1600-4800	Pe, PR	CO, CC	MHNUCa 952; registro fotográfico
Puma concolor (Linnaeus, 1771)	300-4100	Pe, Sa, SR	CO, CC	registro fotográfico
Puma yagouaroundi (É. Geoffroy Sant-Hilaire, 1803)	300-3200	LV	Risaralda	registro fotográfico
Mustelidae				
Eira barbara (Linnaeus, 1758)	300-3200	Pe, PR, Sa, SR	Risaralda	CUSM 260; registro fotográfico
Lontra longicaudis (Olfers, 1818)	300-2800	Pe	Risaralda	CUSM 274; MPUJ 620; registro fotográfico
Mustela frenata Lichtenstein 1831	300-3600	Pe, SR	Risaralda	CUSM 173; IAvH 5749; USNM 172958
Procyonidae				
Bassaricyon neblina J. A. Allen, 1876	300-2500	Ma, SR	CO, CC	registro fotográfico
Nasua nasua (Linnaeus, 1766)	300-3600	Ma, Pe, PR, SR	Risaralda	CUSM 30, 132,133; registro fotográfico

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CARNIVORA				
Procyonidae				
Nasuella olivacea (Gray, 1865)	1700-4100	Ma, Pe, SR	CC	CUSM 262, 266; IAvH 5402, 5724
Potos flavus (Schreber, 1774)	300-3000	SR	Risaralda	CUSM 270
Procyon cancrivorus (G. Cuvier, 1798)	300-2400	SR	Risaralda	CUSM 201, 204; Cepeda 2016
Ursidae				
Tremarctos ornatus (F. G. Cuvier, 1825)	2000-4000	Pe, PR	CO, CC	Registro fotográfico
PERISSODACTYLA				
Tapiridae				
Tapirus pinchaque (Roulin, 1829)	2000-4000	Do, Pe, SR	CC	IAvH 5881, 6180; ICN 17198, 17199, CUSM 134, 252
CETARTIODACTYLA				
Cervidae				
Mazama rufina (Pucheran, 1851)	2000-4000	Pe, SR	CO-CC	CUSM-91; registro fotográfico
Pudu mephistophiles (de Winton, 1896)	3000-4000	Pe, SR	CC	IAvH 7382; MHNUCa 822
ETARTIODACTYLA				
Tayassuidae				
Pecari tajacu (Linnaeus, 1758)	300-2800	PR	CO	Registro fotográfico
PRIMATES				
Atelidae				
Alouatta palliata (Gray, 1849)	300-2300	PR	CO-O	Registro fotográfico
Alouatta seniculus (Linnaeus, 1766)	900-2000	Pe, SR	Risaralda	Orjuela y Jiménez 2004; registro fotográfico
Ateles fusciceps Gray 1866	300-1000	PR	CO-O	Registro fotográfico
Aotidae				
Aotus lemurinus (I. Geoffroy, 1843)	300-2200	Ap, Do, Ma, Pe, SR, Sa	Risaralda	Castaño y Cardona 2005; registro fotográfico
Cebidae				
Cebus capucinus (Linnaeus, 1758)	300-2100	Pe, PR	CO, RC	Orjuela y Jiménez 2004; registro fotográfico
RODENTIA				
Sciuridae				
Microsciurus similis (E. W. Nelson, 1899)	300-2200	PR	CO-O	FMNH 18877

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RODENTIA				
Sciuridae				
Notosciurus granatensis Humboldt, 1811	300-2500	Ap, BU, LC, Mi, Ma, Pe, SR	Risaralda	CUSM 53-56; FMNH 18160; ICN 12366
Notosciurus pucheranii (Fitzinger, 1867)	1500-2500	Ma, SR	CO, CC	Registro fotográfico
Heteromyidae				
Heteromys australis Thomas, 1901	300-2500	Ma, Mi, Pe, SR	Risaralda	CUSM 51, 135; ICN 11944, 12103, 12712, 12713, 16541, 16542
Cricetidae				
**Akodon tolimae* J. A. Allen 1913	1900-2600	Pe	CC	ICN 12105-12116, 12893, 12939-12941, 16543-16555
**Akodon affinis* (J. A. Allen, 1912)	1500-2600	Mi, PR, Sa	CO	ICN 12597-12615, 12762-12767
Chilomys instans (Thomas 1895)	1500-2600	Pe	CC	ICN 12117, 16556
Handleyomys alfaroi (J. A. Allen, 1891)	300-2000	Pe, Mi, SR	CO, CC	CUSM 137; ICN 12032, 12188
**Handleyomys fuscatus* (J. A. Allen, 1912)	1500-2500	Sa, Mi, PR	CO	ICN 12208, 12700-12710, 12725-12727, 12783-12793, 12795-12799, 12801-12827, 15277
**Handleyomys intectus* (Thomas, 1921)	1500-2500	SR, Pe	CC	ICN 12104, 12158-12179, 12891
Melanomys caliginosus (Tomes 1860)	300-2000	Mi, Pe, PR, SR	Risaralda	CUSM 149, 190; MHNUCa 338; ICN 11456, 11457, 11950-11962, 12272-12275, 12717, 16593-16599
Microryzomys altissimus (Osgood, 1933)	1800-4000	SR	CC	FMNH 71904-71906, 71912-71915
Microryzomys minutus (Tomes, 1860)	1000-3600	Mi, Sa, Pe	CO, CC	ICN 12711, 12720-12722, 16564, 16565
Neacomys tenuipes Thomas 1900	300-1500	Mi, PR	CO, CC	ICN 11455, 11945, 11946
Nephelomys sp. [posiblemente incluye **N. childi* (Thomas, 1895) y **N. pectoralis* (J. A. Allen, 1912)].	300-3400	Ma, Mi, Pe, PR, Sa	CO, CC	CUSM 40-42; 5621; IAvH 7337, 7339; ICN 11521, 11947, 11948, 11949, 11972, 11973, 11975-11997, 12000-12023, 12119-12156, 12180-12187, 12207, 12362-12365, 12616-12618, 12714-12716, 12719, 12892, 12942, 16566-16575, 16603
Neusticomys monticolus Anthony 1921	1800-3800	Pe	CC	ICN 12118
Oecomys trinitatis (J. A. Allen y Chapman 1893)	300-1300	Mi	CO	ICN 11963-11965
Oligoryzomys aff. *delicatus* (J. A. Allen y Chapman, 1897)	300-2500	PR	CO	ICN 12718
Reithrodontomys mexicanus (Saussure, 1860)	300-3000	Pe, Sa, SR	Risaralda	CUSM 138; ICN 11998, 11999, 12195, 12723, 12895, 16578, 16580
Rhipidomys latimanus Thomas 1900	900-3000	Ma, SR	CO, CC	CUSM 211; Colectado por V. Rojas-Díaz, pendiente ingreso a colección biológica

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RODENTIA				
Cricetidae				
Sigmodontomys alfari J. A. Allen 1897	300-2000	Pe	Risaralda	ICN 12157
Thomasomys aureus (Tomes, 1860)	1500-3800	Pe, SR, Sa	CC-CO	CUSM 65; FMNH 71264; ICN 12724, 16581-16584, 17017
**Thomasomys bombycinus* Anthony, 1925	2400-3900	Sa	CO	IAvH 5625
**Thomasomys cinereiventer* J. A. Allen, 1912	2000-3500	Sa	CO	IAvH 5622; ICN 12619-12623
**Thomasomys nicefori* Thomas, 1921	2000-3800	Pe	CO, CC	ICN 12196
Transandinomys bolivaris (J. A. Allen, 1901)	300-1000	Mi	CO	ICN 12034-12040
Erethizontidae				
Coendou rufescens (Gray, 1865)	900-3500	LC, Ma, Sa, SR	CO-O, RC, CC	CUSM 39; 268; IAvH 8023, registro fotográfico
Caviidae				
Hydrochoerus hydrochaeris (Linnaeus, 1766)	900-1200	Pe	RC	CUSM 119, 120, 278-280
Cuniculidae				
Cuniculus paca (Linnaeus, 1766)	300-2500	Ap, BU, LC, Pe, PR	Risaralda	CUSM 241, 242; registro fotográfico
Cuniculus taczanowskii (Stolzmann, 1865)	2000-3700	SR	CO, CC	Registro fotográfico
Dasyproctidae				
Dasyprocta punctata Gray, 1842	300-2000	Ap, BU, LC, Pe, PR, SR	Risaralda	CUSM 182,183, 186,191, 192; registro fotográfico
Dinomyidae				
Dinomys branickii Peters, 1873	1500-3600	Ap, BU, LC, Mi, Pe, PR, Sa, SR	CO, CC	Saavedra-Rodríguez et al. 2012, Saavedra-Rodríguez et al. 2014; registro fotográfico
Echimyidae				
Hoplomys gymnurus (Thomas 1897)	1100	PR	CO-O	CUSM 282
LAGOMORPHA				
Leporidae				
Sylvilagus andinus (Thomas, 1897)	2800-4000	Pe, SR	Risaralda	IAvH 1811, 5418, 5396, 1445, 1909-1911, CUSM 277

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